# PLANT INDICATORS

## THE RELATION OF PLANT COMMUNITIES TO PROCESS AND PRACTICE

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BY

FREDERIC E. CLEMENTS

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## PREFACE.

The present book is intended to be a companion volume to "Plant Succession." The latter was planned to contain several chapters on the applications of ecology, but these were omitted on account of the lack of space. Chief among these was the consideration of succession as the primary basis for a system of indicator plants, and this has been made the theme of the present treatise. For the sake of clearness, it has been necessary to give a concise account of the climax communities of the region concerned. The original plan included a brief summary of the priseres and subseres of the various climaxes, but the limitations of space have precluded this. The same reason has made it desirable to deal with principles and examples in the three fields of practice, rather than to attempt a complete account of the host of climax and seral communities which serve as indicators. The general principles and specific indicators have been tested repeatedly during the field work of the past five years, and the treatment has profited from the fact that a special inquiry into indicator relations throughout the West was made during the season of 1918.

It is believed that succession and indicators constitute the most essential and useful form into which the results of research can be put for practical use. They are the fundamental responses of plant and community to the conditions in control, and hence contain their judgment as to the fitness of the environment in which they grow or are to be grown. Such responses require translation into familiar terms, and for this purpose the quantitative analysis of habitats and responses by means of instruments and phytometers is indispensable. Moreover, habitat and response vary not only with the development of the community, but also in accordance with the phases of the climatic cycle. The importance of the latter can hardly be overestimated, and it seems certain that the climatic cycle must be accorded a unique position in all future research and practice.

The indicator method will naturally have its greatest usefulness in new or partly settled regions. While the results given apply only to western North America, and to the western United States particularly, the principles and methods are of universal application. They should be of especial value on other continents where there is still a distinct frontier. Australia, South Africa, and South America should furnish fertile soil for indicator investigations and applications, while large portions of Asia and northern Africa should possess almost equal promise for this work. Even in Europe and in other thickly settled regions, indicator studies will have much value, and this will be true everywhere that natural or semi-natural vegetation is found. Indeed, it is probable that indicator methods in some form will come to be applied to all cultural vegetation with the advance of quantitative ecology and the disappearance of the artificial barrier between science and practice.

The author is under especial obligation to Dr. H. L. Shantz for many helpful suggestions arising from the reading of the manuscript. Grateful acknowledgment is made of the indispensable help given by Dr. Edith Clements, who has assisted throughout the field work, made the larger number of the photographs, and read the manuscript. The latter has also been read by Dr. H. M. Hall and Dr. J. E. Weaver, to whom acknowledgment is given. The author is indebted to Dr. Frances Long and Miss Rena Huber, who have aided in many ways in the preparation of the manuscript and the illustrations. Prints for several of the forest illustrations have been furnished by Dr. G. E. Nichols and Mr. C. G. Bates, and the graphs have been drawn by Professor F. C. Kelton, to whom due acknowledgment is made.

FREDERIC E. CLEMENTS.

TUCSON, ARIZONA, *April 1919.*

## CONTENTS.

## LIST OF ILLUSTRATIONS.

### PLATES.

## TEXT-FIGURES.

# PLANT INDICATORS

## THE RELATION OF PLANT COMMUNITIES TO PROCESS AND PRACTICE

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# I. CONCEPT AND HISTORY.

**The practical aspect.**—Every plant is a measure of the conditions under which it grows. To this extent it is an index of soil and climate, and consequently an indicator of the behavior of other plants and of animals in the same spot. A vague recognition of the relation between plants and soil must have marked the very beginnings of agriculture. In a general way it has played its part in the colonization of new countries and the spread of cultivation into new areas, but the use of indicator plants in actual practice has remained slight. It is obviously of greatest importance in newly settled regions. However, it is in just these regions that experience is lacking and correlation correspondingly difficult. In fact the pioneer is often misled by his endeavor to transfer the experience gained in his former home to a new and different region. Differences of vegetation and climate, and often of soil as well, make a wholly new complex of relations. As a consequence, the settler is very apt to go astray in reaching conclusions as to the significance of a particular plant. As the country becomes more settled, experience accumulates and makes it increasingly possible to recognize helpful correlations. But this period usually passes too quickly to establish a procedure before the native plants have disappeared, except from roadsides, meadows, and pastures. The manner and degree of utilization of natural meadows and pastures are clearly indicated by the plants in them. Yet it is exceptional that these indicators are recognized and made use of by the farmer.

**The scientific aspect.**—On the scientific side, the concept of indicators could hardly be expected to emerge until plant physiology had made a beginning. Looking backward, one discerns something of this idea in the studies of vegetational changes by King (1685:950), Degner (1729), Buffon (1742:234, 237), and Biberg (1749:6, 27).[1] It is likewise suggested in the description of stations by Linné (1751:265) and especially by Hedenberg (1754:73). The basic correlations were made definite by De Luc (1806: Plant Succession, 10) in his studies of succession in peat-bogs and by Schouw (1823: 157, 166) in the classification of plants by habitats. The idea is more or less in evidence in the long series of observations and discussions relating to the chemical theory of the influence of soils. The chief proponents of the chemical theory were Unger (1836), Sendtner (1854), Naegeli (1865), Fliche and Grandeau (1873), Bonnier (1879), Contejean (1881), Hilgard (1888, 1906), and Schimper (1898, 1903). The founder of the physical theory was Thurmann (1849), though his views necessarily placed his results in more or less harmony with the water-content classification of Schouw. The century-old controversy over the chemical theory has centered around the question of the importance of lime in the soil. While the broadening of ecological research has thrown this question more and more into the background, there is still anything but unanimity of opinion concerning it. While it is felt that the problem can be solved only by more comprehensive and thoroughgoing experimentation than it has yet received,

[1]Cf. Plant Succession, 1916:8–10; Development and Structure of Vegetation, 1904:12.

the several divergent views are later considered briefly for the sake of a clearer appreciation of existing opinion. Finally, the many studies of foresters upon the tolerance of trees to shade had large elements of indicator value, but these were never brought together into a system.

Studies of the relation of plants to soil were based upon the response of the individual or species. The first serious attempt to organize these into a system of indicator plants was made by Hilgard (1860, 1906). In a similarly virgin region, Bessey (1891, 1901) also recognized the indicator value of native plants, and especially vegetation for the proper development of agriculture. His ideas of the practical value of vegetational studies stimulated the development of ecology as recorded in the "Phytogeography of Nebraska" (Pound and Clements, 1898, 1900) and the "Development and Structure of Vegetation" (Clements 1904:1). In the latter the need of quantitative studies of habitat and community and the importance of succession were first emphasized, and these were made the basis of a definite quantitative system in "Research Methods in Ecology" (Clements, 1905). As a consequence, the way was prepared for the use by Shantz (1911) of the plant community as an indicator with particular reference to succession. In another direction, E. S. Clements (1905) made a searching investigation of the relation of leaf structure to different factors and habitats and laid the foundation for the use of habitat-forms and ecads as indicators.

The development of the idea that plants are indicators of climate is more difficult to trace. Tournefort (1717) probably furnished the first recorded instance of the idea, when he pointed out that the slopes of Mount Ararat showed many species of southern Europe, while still higher appeared a flora similar to that of Sweden, and on the summit grew arctic plants such as those of Lapland. Perhaps the most important studies of climatic zones of vegetation were those of Humboldt and Bonpland (1805:37), Kabsch (1855:303), Köppen (1884:215), Drude (1887:3), and Schimper (1898, 1903:209). In none of these is there a distinct recognition of the indicator concept. This is likewise true of the formulation of life zones and crop zones on the North American continent by Merriam (1898). His applications of the indicator idea are so numerous and definite, however, that he must be given the credit for organizing the first system of climatic indicators. As to the soil, Hilgard is to be regarded as the pioneer in recognizing the great possibilities of systems of indicators and applying this on an adequate scale, and Shantz as the investigator who has placed the whole matter upon an adequate scientific basis.

## HISTORICAL.

In a general account of the important steps in the spread of the indicator concept, it appears best to deal only with those studies in which the concept is either evident or actually stated. Even with these the details are reserved for discussion under the various climaxes or applications. There are numerous books and papers on plant-geography, forestry, and agriculture, which have some general relation to the idea. Most of these have contributed nothing tangible or important and for the most part are ignored. A few are considered or mentioned in the proper special sections. Entire justice might demand consideration of the work of Bonnier, Fliche and Grandeau, and Contejean at this point, but for many reasons it has proved undesirable to treat these in detail. The following accounts are of these researches in which the term indicator is actually employed or in which the use of instrument, quadrat, or sucessional methods gives them distinct indicator objectives.

## AGRICULTURAL INDICATORS.

Hilgard, 1860.—The following excerpt will serve to show that Hilgard was the first investigator to recognize clearly the importance of indicators in soil studies and to make actual use of them in determining the agricultural possibilities of new lands. A further account of his views and results is given on a later page.

"Judging of land by its natural vegetation. The distinction just mentioned, so far from being of merely theoretical value, is one of the highest practical importance. Agriculturists are accustomed to judge of the quality of lands by the natural vegetation which they find upon it; and they rarely direct their attention to anything but the forest trees. Yet these are, for the most part, indicative rather of what, in the *agricultural* sense is termed the *subsoil*, than that of the surface stratum usually turned by the plow, in the shallow tillage prevailing at present, which may be of a totally different character.

"As a general thing, the forest growth when considered not only with regard to the *kind* (species), but also to the *form* and *size* of the trees, is a very safe guide in judging of the quality of land, and the systematic study of the subject in connection with analyses of soils, promises results of a highly practical importance, which it is intended to communicate more fully in a future report. But this criterion may not infrequently lead to grave mistakes unless a proper examination of the soil and subsoil be made at the same time.

"These examples may suffice to show that while in the forest trees we possess trustworthy guides to a knowledge of the character of the material in which their roots are buried, it is quite essential to determine at the same time, by inspection, that it is the arable soil itself, and not merely the subsoil, which is thus characterized; and we should especially make sure that the smaller plants, viz, the shrubs and perennials, corroborate the evidence of the trees. Annuals are less reliable in their indications because their development is to a greater extent influenced by the accidental circumstances of the seasons."

Chamberlin, 1877.—Chamberlin shares with Hilgard the honor of being a pioneer in the use of native plants to indicate the agricultural possibilities of a region (1877 : 176). He deserves especial credit for being the first to recognize that the community was a better indicator than the species, and for classifying the vegetation of Wisconsin into communities with more or less definite indicator value. Several of Chamberlin's associates on the Geological Survey of Wisconsin made more or less use of his system of indicators (Wooster, 1882: 146; King, 1882: 614; Irving, 1880: 89), though it unfortunately appears to have remained unknown to botanists, and consequently led to no further work in this field.

"The most reliable natural indications of the agricultural capabilities of a district are to be found in its native vegetation. The natural flora may be regarded as the result of nature's experiments in crop raising through the thousands of years that have elapsed since the region became covered with vegetation. If we set aside the inherent nature of the several plants, the native vegetation may be regarded as a natural correlation of the combined agricultural influences of soil, climate, topography, drainage and underlying formations and their effect upon it. To determine the exact character of each of these agencies independently is a work of no little difficulty; and then to compare and combine their respective influences upon vegetation presents very great additional difficulty. But the experiments of nature furnish us in the native flora a practical correlation of them. The native vegetation therefore merits careful consideration, none the less so because it is rapidly disappearing, and a record of it will be valuable historically.

"It is rare in nature that a single plant occupies exclusively any considerable territory, and in this respect there is an important difference between nature's methods and those of man. The former raises mixed crops, the latter chiefly simple ones. But in nature, the mingling of plants is not miscellaneous or fortuitous. They are not indiscriminately intermixed with each other without regard to their fitness to be companions, but occur in groups or communities, the members of which are adapted to each other and their common surroundings. It becomes then a question of much interest and of high practical importance to ascertain, within the region under consideration, what are the *natural groupings* of plants, and then what areas are occupied by the several groups, after which a comparison with the soils, geological formations, surface configuration, drainage and climatic influences, can not fail to be productive of valuable results.

"The following natural groups are usually well marked, though of course they merge into each other where there is a gradual transition from the conditions favorable for one group to those advantageous to another. In some instances it is unquestionably true that other circumstances than natural adaptability control the association of these plants, and an effort has been made in the study of the region, to discern these cases and eliminate them from the results, so that the groups that are given here are believed to be natural associations of plants. Their distribution is held to show in what localities conditions peculiarly advantageous to them occur, and hence advantageous to those cultivated plants that require similar conditions."

The author has used both class and group as synonyms of community, but the latter term is substituted in the following list for the sake of clearness:

A. Upland vegetation.
- (1) Herbaceous.
- 1. Prairie community.
- (2) Arboreous.
- 2. Oak community.
- 3. Oak and maple community.
- 4. Maple community.
- 5. Maple and beech community.
- 6. Hardwood and conifer community.
- 7. Pine community.
- 8. Limestone ledge community.
- 9. Comprehensive community.

B. Marsh vegetation.
- 10. Grass and sedge community.
- 11. Heath community.
- 12. Tamarac community.
- 13. Arbor vitae community.
- 14. Spruce community.

C. Communities intermediate between upland and marsh.
- 15. Black ash community.
- 16. Yellow birch community.

Merriam, 1898.—In "Life Zones and Crop Zones," Merriam summarized the experiential evidence as to the climatic indications for crop plants. This was arranged in relation to seven life zones based theoretically upon temperature, but determined for the most part by the distribution of native plants and animals. As a pioneer attempt to organize a vast field, it deserves great credit, even though later studies have rendered his zonal classification of secondary value. The author's understanding of the nature and scope of climatic indicators is best shown by the following excerpts:

"For ten years the Biological Survey has had small parties in the field traversing the public domain for the purpose of studying the geographic distribution of our native land animals and plants, and mapping the boundaries of the areas they inhabit. The present report is intended to explain the relations of this work to practical agriculture and to show the results thus far attained.

"It was early learned that North America is divisible into seven transcontinental belts or *life zones* and a much larger number of minor areas or *faunas*, each characterized by particular associations of animals and plants. It was then suspected that these same zones and areas, up to the northern limit of profitable agriculture, are adapted to the needs of particular kinds or varieties of cultivated crops, and this has since been fully established. When, therefore, the natural life zones and areas, seemingly of interest only to the naturalist, were found to be natural crop belts and areas, they became at once of the highest importance to the agriculturist. A map showing their position and boundaries accompanies this report, and lists of the more important crops of each belt and its principal subdivisions are here for the first time published. The matter relating to the native animals and plants has been reduced to a fragmentary outline for the reason that this branch of the subject is of comparatively little interest to the farmer and fruit-grower." (p. 7.)

"The Biological Survey aims to define and map the natural agricultural belts of the United States, to ascertain what products of the soil can and what can not be grown successfully in each, to guide the farmer in the intelligent introduction of foreign crops, and to point out his friends and enemies among the native birds and mammals, thereby helping him to utilize the beneficial and ward off the harmful kinds." (p. 9.)

"The farmers of the United States spend vast sums of money each year in trying to find out whether a particular fruit, vegetable, or cereal will or will not thrive in localities where it has not been tested. Most of these experiments result in disappointment and pecuniary loss. It makes little difference whether the crop experimented with comes from the remotest parts of the earth or from a neighboring State, the result is essentially the same, for the main cost is the labor of cultivation and the use of the land. If the crop happens to be one that requires a period of years for the test, the loss from its failure is proportionately great.

"The cause of failure in the great majority of cases is climatic unfitness. The quantity, distribution or interrelation of heat and moisture may be at fault. Thus, while the total quantity of heat may be adequate, the moisture may be inadequate, or the moisture may be adequate and the heat inadequate, or the quantities of heat and moisture may be too great or too small with respect to one another or to the time of year, and so on. What the farmer wants to know is *how to tell in advance* whether the climatic conditions on his own farm are fit or unfit for the particular crop he has in view, and what crops he can raise with reasonable certainty. It requires no argument to show that the answers to these questions would be worth in the aggregate hundreds of thousands of dollars yearly to the American farmer. The Biological Survey aims to furnish these answers."

Life-zone surveys upon the basis laid down by Merriam have been made by Bailey for Texas (1905) and New Mexico (1913), and by Cary for Colorado (1911) and Wyoming (1917). Robbins (1917) has made a somewhat similar study of the zonal relations in Colorado with reference to plants alone. Hall and Grinnell (1919:37) have recently published comprehensive lists of plants and animals which are regarded as "life-zone indicators" for California. As with Merriam's life zones, these are floristic and faunistic in character and hence do not necessarily correspond with community indicators.

Hilgard, 1906.—In summarizing his soil studies of more than 50 years, Hilgard formulated more fully and definitely his ideas of the indicator value of native vegetation. This account makes it clear that to Hilgard must be given the great credit of being the first to adequately realize the significance of indicators and to urge their inclusion in a basic agricultural method.

"The importance of the natural relations of each soil to vegetation is obvious, both from the theoretical and from the practical viewpoint. From the former, it is clear that the native vegetation represents, within the climatic limits of the regional flora, the result of a secular process of adaptation of plants to climates and soils, by natural selection and the survival of the fittest. The natural floras and silvas are thus the expression of secular, or rather millenial experience, which if rightly interpreted must convey to the cultivator of the soil the same information that otherwise he must acquire by long and costly personal experience.

"The general correctness of this axiom is almost self-evident; it is explicitly recognized in the universal practice of settlers in new regions of selecting lands in accordance with the forest growth thereon; it is even legally recognized by the valuation of lands upon the same basis for purposes of assessment, as is practiced in a number of States.

"The accuracy with which experienced farmers judge of the quality of timbered lands by their forest growth has justly excited the wonder and envy of agricultural investigators, whose researches, based upon incomplete theoretical assumptions, failed to convey to them any such practical insight. It was doubtless this state of the case that led a distinguished writer on agriculture to remark, nearly half a century ago, that he 'would rather trust an old farmer for his judgment of land than the best chemist alive.'

"It is certainly true that mere physico-chemical analyses, unassisted by other data, will frequently lead to a wholly erroneous estimate of a soil's agricultural value, when applied to cultivated lands. But the matter assumes a very different aspect when, with the natural vegetation and the corresponding cultural experience as guides, we seek for the factors upon which the observed natural selection of plants depends, by the physical and chemical examination of the respective soils. It is further obvious that these factors being once known, we shall be justified in applying them to those cases in which the guiding mark of vegetation is absent, as the result of causes that have not materially altered the natural condition of the soil. (p. XIX.)

"It was from this standpoint that the writer originally undertook, in 1857, the detailed study of the physical and chemical composition of soils. It seemed to him 'incredible' that the well-defined and practically so important distinctions based on natural vegetation, everywhere recognized and continually acted upon by farmers and settlers, should not be traceable to definite physical and chemical differences in the respective lands, by competent, comprehensively trained scientific observers, whose field of vision should be broad enough to embrace concurrently the several points of view—geological, physical, chemical, and botanical—that must be conjointly considered in forming one's judgment of land. Such trained observers should not merely do as well as the 'untutored farmer,' but a great deal better." (p. 315.)

This attitude toward plants and vegetation as indicators prevails throughout the book, and the subject is treated in considerable detail for the first time in Chapters XXIV to XXVI. These deal respectively with the recognition of the character of soils from their native vegetation, in Mississippi, and in the United States and Europe generally, and with the vegetation of saline and alkali lands. While the author ascribes primary importance to the presence of lime, he does not fail to assign great value to water, especially in the West. He not only recognizes the indicator value of the presence of a particular species or group of species, but also takes into account the size, form, and development of the indicators. Significant tables and lists of indicators are given on pages 490, 497, 514–516, 518–519, and 536. In so far as these concern the West, they are considered in Chapters V, VI, and VII.

Clements, 1910.—In 1908, the work of the Botanical Survey of Minnesota was reorganized upon an ecological basis, for the purpose of making a classification and use survey of the lands of the State. The objectives of the survey were defined as follows (Clements, 1910:52):

"The first step in determining the final possibilities of Minnesota in plant production is to ascertain just what the conditions of soil and climate are from the standpoint of the plant. This must be determined separately for the two great groups of lands, those still unoccupied and those now in use. For the former, a knowledge of soil and climate and of the plant's relation to them is necessary to determine what primary crop, grain, forage, or forest is best. For the farms of the State, the best use is a matter of knowing the soil and climate differences of regions and fields, and of taking advantage of these in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of different areas, to prevent the waste of human effort and happiness involved in trying to secure from the land what it can not give and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it.

"The chief object of a classification survey is to group the unoccupied lands of the State as accurately as possible into three great divisions: (1) agricultural land, for crop production; (2) pasture land, for dairying and stock raising; (3) forest land, for lumbering, water regulation, and recreation parks. Such a division would be determined primarily by studies of soil and climate, necessarily supplemented by the evidence of native vegetation itself and of such cultivation as has been tried. The value of classification depends upon its accuracy, but the study of an area from these three standpoints neglects no source of evidence, and discloses practically all that can be learned of the possibilities."

The survey method was based upon the instrumental and quadrat study of habitats and communities, cultural as well as natural. The main divisions were vegetation mapping, the determination of indicators, and the study of succession. Vegetation and physiography were recorded on maps in which each division of 40 acres was represented by a square decimeter. Quadrat and transect charts were made of typical communities in each section of the township, and determinations of physical factors in all charted quadrats. The indicator work was devoted to the recognition of indicator species and communities so closely dependent upon water-content, soil, acidity, or light that they could always be used as indicating a certain set of conditions. Especial attention was given to the correlation of indicators with crop plants and with the secondary successions in burns, cutovers, fallow fields, pastures, roadsides, etc. Four townships were mapped upon this basis in 1912, and a large number of successional areas from 1913 to 1916. Some of the general results have already been published (Bergman and Stallard, 1916; Stallard, 1916; Bergman, 1919; Stallard, 1919), while a part of the indicator findings are discussed later (Chapter III).

Shantz, 1911.—The study of the natural vegetation of the Great Plains by Shantz is the classic work on indicator plants. It was the first avowed investigation of indicators to be based upon the three cardinal points, namely, instrumentation, succession, and quadrats, and will long serve as the model for all thorough research in this field. Because of its great importance, the original should be consulted for the details. Here it must suffice to quote the author's general principles. (p. 9.)

"Farmers and other persons who have occasion to examine new land in order to form a judgment of its agricultural value depend largely upon the natural vegetation, or plant covering, as an indicator of its crop-producing qualities. But there are many possibilities of error in judging land upon this basis. Species that are closely related botanically and very similar in appearance may indicate quite different conditions of soil and climate. The popular names of plants are likely to cause confusion. Thus, the farmer who has learned in the Great Basin region that 'greasewood' is an indicator of alkali land and that 'sage-brush' usually grows on land free from alkali, will find if he moves to southern Arizona or southeastern California that the scrub there known as 'greasewood' indicates absence of alkali, while the so-called 'sage bushes' of that region grow on strongly alkali land. Furthermore, there is a general tendency to depend upon a single plant species as an indicator, while the investigations set forth in this bulletin show that the composition of the plant covering as a whole is a much more reliable basis for judging the crop-producing capabilities of land.

"The chief object of the present paper is to show how these sources of error may be avoided and how new land may be classified readily and with reasonable accuracy on the basis of its natural vegetation. This paper is not a report of a land survey, but rather a discussion of methods which it is believed could be utilized to advantage in making such a survey, the methods being illustrated by application to a limited territory in the Great Plains area.

"Too much emphasis can not be laid upon certain facts that have been clearly brought out in the course of these investigations: (1) Correlations between the natural plant cover and the crop-producing capabilities of land in a given area can be satisfactorily determined only after careful study of the different types of vegetation of the area in relation to their physical environments; (2) such correlations, determined for some particular region, will need to be modified to a greater or less extent before they can be applied in another region where the physical conditions are different. When, as a result of sufficient investigation, correlations of this nature are determined for a given area, it is believed that they will afford a basis for classifying the land of that area more readily and at least as accurately as by any other known method.

"In order to test and perfect the methods here described, it was necessary to make a detailed study of the vegetation of some particular area in relation to the physical conditions, checking the observations by the study of such examples of actual crop production as exist on the different types of land. It was decided to begin work in the Great Plains area, for this region contains the largest body of land in the United States having possible agricultural value on which the native plant covering is still undisturbed. A further advantage is the comparative uniformity of the climate throughout the area from the Canadian boundary on the north to the 'Panhandle' of Texas on the south. The investigations thus far have been made chiefly in a portion of eastern

A. Short-grass (*Bouteloua gracilis*) on hard land, Colorado Springs, Colorado.
B. Wire-grass (*Aristida purpurea*) on short-grass land, Walsenburg, Colorado.

Colorado, a region which is considered representative because of its central position and because its climatic conditions are almost as severe as anywhere in the Great Plains. But enough data have been gathered in other portions of the Great Plains to make it fairly certain that with comparatively little modification the correlations shown will hold throughout the area.

"The work so far accomplished has brought out clearly that in this area the general conditions, whether favorable or unfavorable to crop production, are indicated by the character of the native plant cover." (plate 1.)

Kearney, Briggs, Shantz, McLane, and Piemeisel, 1914.—The first quantitative study of plant communities as indicators of alkaline soils was made by Kearney and his associates in the Tooele Valley of Utah. This was essentially an application of Shantz's methods to a saline basin and met with similarly important results, as the following indicates:

"In the arid portion of the United States the different types of native vegetation are often very sharply delimited, the transitions being so abrupt that they can not be attributed to climatic factors; this has suggested the possibility of correlating the distribution of the vegetation with the physical and chemical properties of the soil. If such correlations can be made, they may be utilized in the classification of land with respect to its agricultural capabilities.

"One of the writers has described the correlations which exist in the Great Plains between the different types of vegetation and the physical characteristics of the corresponding types of land, and has pointed out how the native growth may be used in that region to determine the suitability of the land for dry-farming.

"The results obtained in the Great Plains made it desirable to undertake similar investigations in the Great Basin region. The problems to be solved were: First, what types of vegetation indicate conditions of soil moisture favorable or unfavorable to dry farming, and second, what types indicate the presence or absence of alkali salts in quantities likely to injure cultivated crops. For the purpose of this investigation it was necessary to find a locality where both dry farming and irrigation farming are practiced, where much of the soil is still covered with the original native growth, and where some of the soils contain an excess of alkali salts.

"After a reconnoissance trip through portions of Wyoming, Utah, Idaho, and Oregon in August, 1911, the Tooele Valley in central Utah was selected for the following reasons: (1) Several very distinct types of vegetation are found in a small area, (2) the soils show a great diversity in their moisture conditions and salt content, (3) the greater part of the area retains its original plant cover, while examples of crop production, both with and without irrigation, exist on different types of land.

"Detailed studies of the vegetation of Tooele Valley in relation to the moisture conditions and salt content of the soil were carried on in 1912. The work was begun near the close of the rainy season (end of May) and was terminated during the first week of August, when the summer drought had reached its height. Additional data were obtained during a third visit to the valley in the latter part of August 1913.

"The distribution of the native vegetation was found to depend in a marked degree upon the physical and chemical properties of the soils, factors which also influence crop production. So far as this particular area is concerned, the vegetation unquestionably can be used with advantage in classifying land with respect to its agricultural value. To what extent the correlations established in the Tooele Valley hold good in other parts of the Great Basin region remains to be determined by future investigation." (p. 365.)

The successional relations of the dominants have been discussed as well as graphically illustrated by Shantz (1916 : 234). The primary succession exhibits two adseres, one from *Salicornia* and *Allenrolfea* to *Artemisia*, and the other from *Allenrolfea* through *Distichlis* and *Sporobolus* to *Chrysothamnus*. These seral facts give much additional value to the indicator studies of the Great Basin, especially in establishing the indicator sequence and in imparting a distinct significance to the various mixed communities. (plate 2.)

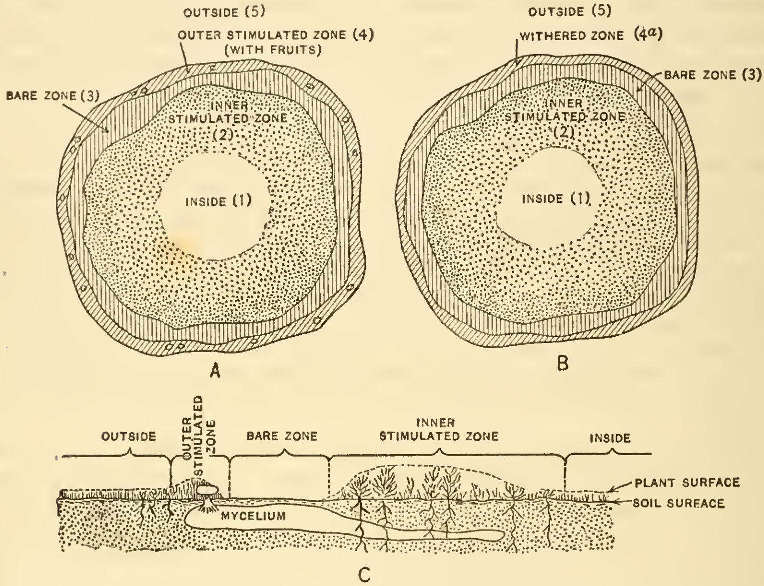
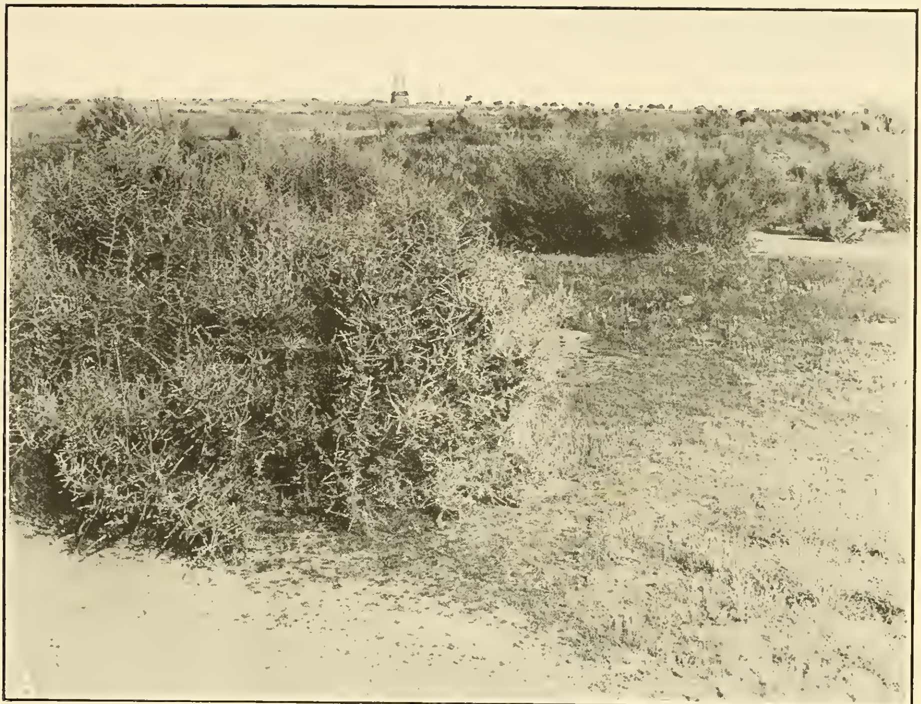
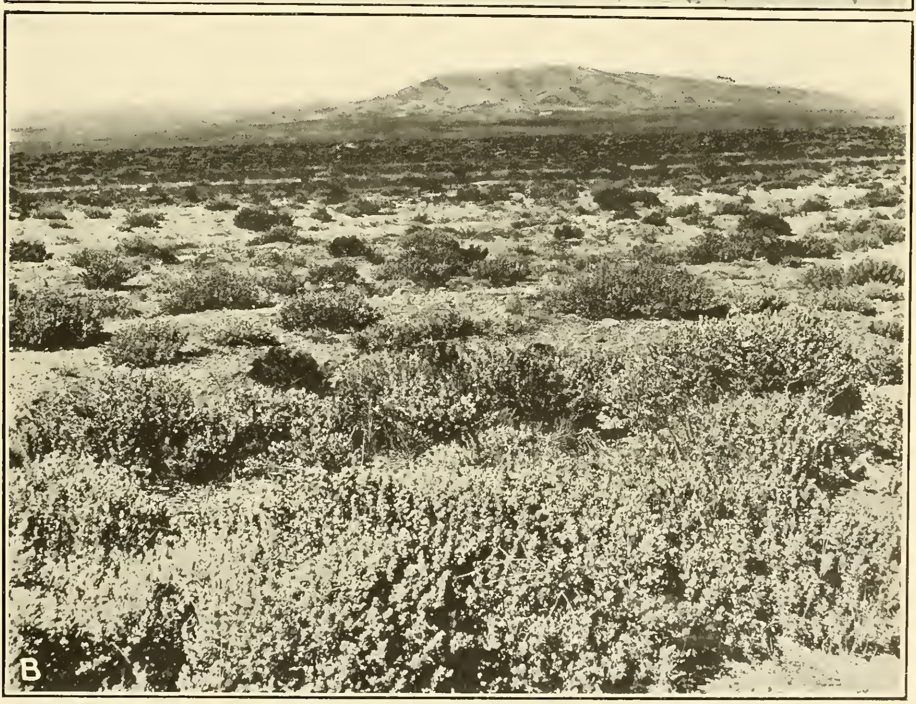



FIG. 1.—Zones of a fairy ring due to *Agaricus tabularis: A* and *C*, during a moist period; *B*, during a dry period. After Shantz and Piemeisel.

Shantz and Piemeisel, 1917.—In their exhaustive study of fairy rings in the Great Plains, Shantz and Piemeisel (1917:191) have shown the causal relation between the rings of mushrooms and grasses, as well as the indicator significance of the latter. They distinguish three types of fairy rings, based upon the effect shown by the vegetation: (1) those in which the vegetation is killed or badly damaged, caused by *Agaricus tabularis* (fig. 1); (2) those in which the vegetation is only stimulated, produced usually by species of *Calvatia*, *Catastoma*, *Lycoperdon*, *Marasmius*, etc.; (3) those in which no effect can be noted in the native vegetation, due to species of *Lepiota*. In the *Agaricus* rings, the vegetation shows three zones concentric to the central area of normal short-grass sod (1): the inner stimulated zone (2) is a broad one, differing in botanical composition, the more luxuriant growth, and the deeper green color from the center. The bare zone (3) is narrower and somewhat more irregular, while the vegetation is either dead or consists of a few very poor perennials or short-lived annuals. The inner zone is the most prominent feature of the ring in spring or wet seasons, the bare one in late summer or fall or in dry seasons. The outer stimulated zone (4) is rather narrow and is made up for most part of species peculiar to the short-grass sod, though resembling the inner zone somewhat. The mushrooms occur in the outer zone near the outside edge.





A. *Spirostachys occidentalis* in salt marsh, Bakersfield, California.
B. Shadscale (*Atriplex confertifolia*) indicating saline land, Rock Springs, Wyoming.

In the case of most fairy rings, the fungus produces a temporary stimulating effect only, and the ring is indicated merely by the increased size, vigor, and chlorophyll-content of the annuals and the perennial grasses.

The stimulation of the grasses and other plants which produced the inner and outer zones is probably due to the presence in the soil of nitrates and ammonia salts derived from (1) the reduction of the organic matter of the soil, (2) the decay of the mushrooms, and (3) the decay of the mycelium. The bare zone results from the death of the vegetation as a consequence of a lack of available soil moisture. Water penetrates very slowly into the sod filled with mycelium when it is once dry. The increased growth in the outer zone hastens the drying-out of the soil and, once dry, the latter is not wetted by heavy and continued rain. The vegetation is not noticeably damaged during growing seasons uniformly wet, but it quickly shows the effect of dry years or periods of drought. The secondary sere initiated by the fairy rings is essentially like that caused by any other disturbance in the short-grass association.

Shantz and Aldous, 1917.—In the field instructions for classifying public lands under the terms of the Stock Raising Homestead Act of 1916, Shantz and Aldous have made the most comprehensive use of indicators for the purpose of land classification. Ninety different types are recognized as indicator communities and are described briefly, though usually without a statement of the correlated conditions. Of these, 32 belong to the prairie-plains grassland climax, 20 to the sagebrush climax, 16 to the desert-scrub climax, and 9 to the chaparral. The types are designated by the names of dominants and subdominants and represent both seral and climax communities. Density, percentage of grasses and grass-like plants, and height of shrubs are also made use of for minor indications, while overgrazed areas are given especial attention. A key to correlation conditions and crop-producing capabilities was filed with the Geological Survey and is used by it in the interpretation of the types.

Weaver, 1919.—While the work of Shantz (1911), Weaver (1915), Sampson (1914, 1917), and of Cannon (1911, 1913, 1917), Markle (1917), and others had laid the basis for the consideration of root systems in connection with indicator values, the first special and comprehensive study of the indicator significance of roots was made by Weaver in 1918. This investigation derives its importance not only from the thoroughness of the methods, but especially also from the large number of species concerned, the wide range of the communities, and the consistency of the instrumental results. Approximately 160 species were investigated, involving the examination of about 1,150 individual plants. These were largely grasses and grassland herbs, but they included shrubs, undershrubs, weeds, and forest herbs as well. The communities represented were the prairies of Nebraska and the Palouse region of the Northwest, the short-grass plains and the sandhills subclimax of Colorado, the gravel-slide and half-gravel-slide associes, and the forest climax of the Pike's Peak region. In practically all these, readings were made cf water-content, humidity, temperature, and light, and in critical ones of transpiration as well. In showing the community relations of competing root systems use was made of the quadrat-bisect (plate A; cf. Weaver, 1919, for plate 26A). Many of the detailed results have been utilized in the discussion of particular indicators in Chapters IV and VI.

## FOREST INDICATORS.

A general idea of indicator plants has existed in forestry for nearly a century, and it is strange that the forester was not the first to formulate a system of indicators. His nearest approach to this is found in the tables of tolerance (Graves and Zon, 1911 : 20). The fact that the forester's attention was fixed primarily upon reproduction and little or not at all upon the shrubs and herbs of the forest floor probably explains the long absence of any definite recognition of indicators. In forestry as elsewhere, but even to a greater degree, a system of indicator plants and communities was impossible before the use of instruments and quadrats and the application of successional principles. As is shown later, however, forestry already possesses a large amount of indicator material which only needs to be organized upon a systematic basis. Practically all site studies have much and some of them great indicator value. However, the researches directed primarily toward this have been few, and it is necessary here to consider only the following:

Cajander, 1909.—Cajander (1909; Zon, 1914 : 119) has made an interesting endeavor to recognize forest types on the basis of the living ground-cover as indicators of the soil conditions. He classified the forests of Germany, composed largely of spruce, fir, beech, and oak, into three types:

1. *Oxalis* type (forests with a layer society of *Oxalis acetosella*).
2. *Myrtillus* type (forests with a layer society of *Myrtillus nigra*).
3. *Calluna* heath type (forests with a layer society of *Calluna vulgaris*).

The *Oxalis* type characterizes the best soils and comprises nearly all the dominant trees. It is further divided into four subtypes, marked by *Impatiens-Asperula*, *Asperula*, *Oxalis*, and *Oxalis-Myrtillus* respectively. As Zon points out, the dominant species of trees are assumed to play no part in determining the type. The author also dismisses the effect of light as of no importance. This appears to be quite unwarranted, as no measurements seem to have been made of light, as is apparently true of the other factors as well, and consequently the correlation between communities and conditions is superlatively general. Little or no attention is paid to the successional sequence of dominants or subdominants, and here again the real indicator values are overlooked or lost. Zon further points out that the author's own statements are contradictory, in that he states in one place that the layer societies indicate the physical conditions independent of the tree species, while in another the trees are said to determine the character of the herbaceous vegetation beneath them. While Cajander has erred in assigning greater importance to the subdominant herbs and low shrubs than to the dominant trees, his use of the forest societies as indicators is sound, and will serve to correct the usual practice of foresters who have neglected the undergrowth.

Clements, 1910.—The investigation of the lodgepole-burn forests of northern Colorado in 1907–1908 was essentially a study of fire indicators, herbaceous as well as woody. Its real importance in this connection lay in the fact that it was the first study of forests made on the complete basis of instruments, quadrats, and succession. It was pointed out that lodgepole pine and aspen are practically universal indicators of fire and not of mineral soil or other conditions, at least for the Rocky Mountains. *Agrostis hiemalis*, *Chamaenerium angustifolium* and *Vaccinium oreophilum* were recognized as the chief

A. Lodgepole forest (*Pinus contorta*) indicating fire, Long's Peak, Colorado.

B. Aspen woodland (*Populus tremuloides*) arising from root-sprouting due to fire, Long's Peak.

pioneers of the burn subsere, together with the mosses *Bryum argenteum* and *Funaria hygrometrica*. Several other species are almost equally good indicators of burns, especially when abundant. These are *Rubus strigosus, Carex rossii, Arnica cordifolia, Achillea lanulosa,* and *Anaphalis margaritacea*. The water and light factors for the six dominant trees were measured and the successional sequence thus obtained exhibits the indicator value of each species. (plate 3.)

A successional study was made of the so-called natural parks of Colorado in 1910 for the purpose of determining their indicator significance as to reforestation, both natural and artificial. The conclusion was reached that all such grassland areas in forested regions are but seral stages leading to a forest climax. The majority of them are due to repeated burns or the slow filling of lakes, with the result that they persist as apparent climaxes for several hundred years. Their origin is readily disclosed by the indicators in them, as is also true of the rate of development.

Pearson, 1913–1914.—In discussing the proper basis for the classification of forest lands into types, Pearson (1913 : 79) has reached the following conclusions:

"The only scientific basis for such a classification is that of potential productiveness, considering both agricultural and forest crops. The productive value may be ascertained in two ways: The first measures directly, as far as possible, all physical factors on the site and gauges the productive capacity by the measure in which the sum of these factors meets the requirements of various crops. The second method uses characteristic forms of vegetation on the ground as an indicator of the physical conditions present, and upon this basis ascertains the adaptability of the site for different crops. The obvious objection to the first method is the need of climatological data and soil analyses on each site to be classified; and owing to the diversity of sites in our forest regions, together with the almost complete absence of climatological records in many sections, the collection of the needed data would involve an expense which, at this stage of our advancement in forestry, would be almost prohibitive. The second method requires a thorough preliminary investigation in each region to be covered, in order to secure a working knowledge for the actual land classification, and obviously reliable results can only be obtained by the employment of trained men. This method is the simpler and probably the more reliable of the two, and it is considered entirely applicable to the needs of the forester."

A general indicator relation is established between the five forest types and the agricultural possibilities of the Coconino National Forest in northern Arizona. The same author (1914 : 249) has employed seedlings of Douglas fir as indicators of the conditions for planting in aspen and in open situations at 8,700 feet on the south slope of the San Francisco Mountains. The seedlings were planted in two plots in the aspen and two in the opening each spring of the 3-year period, and instrumental readings were made of water-content, evaporation, wind, and temperature. The aspen uniformly gave a larger survival of seedlings than the opening, the percentage varying from 7 to 13. The critical factor in this was evaporation, which was 50 to 90 per cent higher in the open than under the aspen. The author further points out that the results indicate that yellow pine, because of its lower moisture requirements and greater demands for light, will probably prove more suitable than Douglas fir for openings within the natural range of the former. A later study has dealt with the correlation of height-growth with precipitation, but this is considered under growth-forms in Chapter II.

Zon, 1915.—At the suggestion of the writer, a conference was held at the Utah Forest Experiment Station in 1915 to discuss the feasibility of a system of indicators for silvics and grazing, and especially the indicator value of shrubby and herbaceous species and communities, with particular reference to succession. The conference consisted of Mr. Zon, chief of silvics, Mr. Jardine, inspector of grazing, Dr. Sampson, director of the station, Dr. E. S. Clements, and the writer. There was general agreement upon the value of indicators as a basis for the experimental regeneration of forest and grassland. As an outcome, Mr. Zon drew up a preliminary outline of the indicator significance of the important dominants of the various zones and represented this graphically in a schematic transect (fig. 25). This appears to have been the first definite organization of the indicator experience of the Forest Service in silvical work. Its proposals as to indicators are considered in Chapter VII.

A similar conference on indicators and succession was held at the station in 1917. It was attended by Professor Toumey, Professor Pool, Dr. E. S. Clements, Dr. Sampson, Mr. Korstian, Mr. Baker, Mr. Weil, and other members of the staff, together with the writer. Particular attention was given to seral indicators of grazing burns, erosion and slides, as well as to climatic indicators in the chaparral belt. Some of the conclusions are to be found in the discussion of indicator papers in Chapter VII, as well as in the body of the text itself.

Hole and Singh, 1916.—In studying the reproduction of sal (*Shorea robusta*) in the forests of India, Hole and Singh have made a quantitative study of the water and light factors which control germination and ecesis. Their work is especially noteworthy in that experimental quadrats have been employed for the analysis of different sites (p. 48), and that a detailed study was made of soil aeration as a critical factor. The general indicator results are given in the following excerpts:

"Broadly speaking three principal soil types may be distinguished in these areas, and these are characterized by different types of vegetation, as follows:

A. Containing a large percentage of sand and a relatively small percentage of the finer particles of silt. The soil is also frequently shallow, with gravel and boulders below, and is therefore essentially dry.
   Dry miscellaneous forest with *Acacia catechu* and *Dalbergia sissoo* prominent, or grassland with *Saccharum munja* dominant.

B. Sal forest or grassland, well aerated deep loam with *Saccharum narenga* (often mixed with *Anthistiria gigantea arundinacea*) dominant.

C. Badly aerated deep loam. This differs from (B) either in containing more clay and silt, in being actually denser with less pore space per cubic foot, or in having the water-table nearer the surface.
   Moist miscellaneous forest with *Butea frondosa, Stereospermum suaveolens, Terminalia, Cedrela toona* and others, or grassland with *Erianthus ravennae* (often mixed with *Anthistiria gigantea villosa*) dominant.

"One of these types is unsuitable for the growth of sal, inasmuch as the water-content of the soil falls rapidly to the death-limit after the close of the rainy season, while another type is unsuitable on account of bad soil-aeration which leads to a low percentage of germination, a high percentage of deaths during the rains, and a superficial root system. The latter point is of great importance, inasmuch as it leads to the roots being situated in those layers of soil the water-content of which is reduced to the death-limit in the dry season. It will thus be seen that the results obtained go far to explain the natural distribution of sal, and also indicate those grasslands and forestless areas in which afforestation with sal offers the greatest chance of success. Finally, it has been shown that, owing chiefly to the heavy shade, the aeration of the superficial soil layers in dense sal forest is commonly below the death-limit for several weeks during the rains and that this factor is responsible (1) for the holocaust of sal seedlings which takes place during the rains in shady forests in years of heavy rainfall and (2) for the development of a superficial root system which, in the hot season when the sal sheds its leaves and the forest canopy thins out, leads to widespread damage from drought among those plants which survive the rains. Opening of the cover and temporary removal of the humus are obvious expedients by means of which the soil-aeration can be improved. Firing would also in some cases probably be beneficial in this respect." (p. 38.)

"It will be seen that the management of any particular sal forest to a great extent depends on the fact whether the seedlings in it suffer chiefly from drought or from bad soil-aeration and therefore the determination of this point is of primary importance. Observations regarding the season when the seedlings chiefly die and the dryness of the soil at the time naturally indicate to a great extent which factor is primarily concerned. In addition to this, however, the work which has been carried out at Dehra during the last few years has shown that the dominant grasses on an area are, as a rule, excellent indicators of the soil conditions. Thus in northern India, where *Saccharum narenga* and *Anthistiria gigantea arundinacea* tend to be dominant, the soil moisture and aeration are as a rule suitable for the best development of sal and sal forests of the moist type prevail. In shady forest in such localities, the seedlings suffer chiefly from bad soil-aeration and the most efficient remedy consists in opening the cover and exposing the soil. On the other hand, such grasses as *Saccharum munja*, *S. spontaneum*, *Eragrostis cynosuroides*, *Imperata arundinacea*, *Vetiveria zizanoides*, *Andropogon contortus*, and *Ischæmum angustifolium* usually indicate a soil too dry or too dense for the best sal development, and such forests as occur are of the dry sal type. The recognition of the dominant grasses in the sal tracts therefore is a matter of considerable practical importance, and a subsequent paper will deal in more detail with the grasses of the sal tracts, in their capacity as soil indicators." (p. 83.)

Korstian, 1917.—In a study of permanent quadrats on the Datil National Forest of New Mexico, Korstian (1917: 267) gives the increment data for *Pinus ponderosa* on sites I and II, and points out that the growth of a dominant tree is the best indication of the quality of forest sites. The differences in the native vegetation on the two sites were so great as to suggest its correlation with tree-growth and its use as an indicator of forest sites. A large number of list quadrats were employed, but the lack of previous successional studies makes their accurate interpretation difficult and probably explains in part the conclusion that

"In studying the indicator significance of the native vegetation it is necessary to go directly to the individual species instead of attempting to stop at the association, society, or community.

"The writer believes that the native vegetation found on deforested areas may be considered as a criterion of the latent potentialities of the site for forest production provided the vegetation has not been too seriously or too recently disturbed and that the more important phases of the successional series are properly understood.

"The fundamental study of forest planting sites logically resolves itself into three categories: (1) The empirical establishment of plantations and the observation and study of their survival and subsequent development; (2) the measurement and study of the most important physical factors of the site, such as the available soil moisture or growth water and evaporation; and (3) the indicator significance of the native vegetation occurring on the sites, implying a very careful correlation of all three phases.

"It is readily conceivable that site studies of this character will be of the utmost value in explaining the presence or absence of tree growth on certain areas, in the judicious selection of the proper species and sites in the reforestation of much of the denuded forest land of the United States, and in establishing a working basis for the classification of forest lands. Only after considering the relative agricultural and forest productivity of the land on a combined scientific and economic basis, can a positive conclusion be reached that its greatest utility lies in its use for forestry or for agricultural purposes."

## GRAZING INDICATORS.

Grazing has been recognized as a distinct field for investigation for scarcely more than a decade. Complete recognition of grazing as a subject for experiment should perhaps be dated from the establishment of the Utah Forest Experiment Station for grazing in 1912. Three more or less marked steps in advance had preceded this and had made it inevitable. The first was a general study of the West with reference to the species, distribution, and value of the native grasses and forage plants. The stimulus for this seems to have been the work of Bessey in Nebraska, as indicated by the publication of many reports dealing with grasses and forage plants from 1886 to 1907. Webber (1890), Smith (1890), and Williams were associated with Bessey in some of this work and the last two later carried on extensive grassland studies over the Great Plains and the Rocky Mountain region (Smith, 1898; Williams, 1897, 1898). Similar studies were made by Shear and Clements in 1896, by Rydberg and Shear in 1897, by Pammel in 1897, Nelson in 1898, and others (cf. Shear, 1901). The second step was perhaps the most significant, inasmuch as it introduced the quantitative study of grazing areas by means of the quadrat, and provided an exact method of measuring carrying capacity and determining the degree of overgrazing or the amount of regeneration. This work was begun by Griffiths and Thornber in 1901 and enlarged in 1903 on what is now the Santa Rita Grazing Reserve of the Forest Service. It has been carried on continuously since that time by Griffiths, Wooton, Thornber, Hurtt, and Hensel in turn, and now constitutes the classic field for grazing study anywhere in the world. It has yielded publications of primary importance by Griffiths (1901, 1904, 1907, 1910), Thornber (1910), and Wooton (1916). Somewhat similar lines of experiment were begun by Coville and Sampson in 1907 in the Wallowa National Forest in northeastern Oregon. The results are recorded in a series of reports of unusual significance, namely, Sampson (1908, 1909, 1913, 1917) and Jardine (1908).

The third period of rapid development in grazing studies began with the organization of grazing reconnaissance in the six districts of the Forest Service in 1911. During the past seven years reconnoissances have been made on practically all of the National Forests, and the grazing upon these has been administered upon the basis of a definite carrying capacity. The result has been to favor regeneration to such an extent that most of the ranges have recovered their normal carrying capacity to a large degree. With the extensive work in reconnoissance went the establishment of permanent quadrats. especially in the Coconino, Targhee and Deerlodge National Forests. Those on the Coconino especially have been actively studied (plate 89, B), and have already yielded results of much value (Hill, 1917).

The most signal advance has been marked by the organization of a grazing experiment station of the Forest Service at Ephraim, Utah, in 1912. This has been followed by the establishment of experimental pastures for grazing at Mandan (North Dakota), and Ardmore (South Dakota), by the Office of Dry Land Agriculture of the U. S. Department of Agriculture. Somewhat earlier than this, in 1908, Marsh had begun experimental work in Colorado on poisonous plants, and this is now carried on at a special experiment station at Salina, Utah, on the Fishlake National Forest. In 1914, the Jornada Grazing Reserve was established near Las Cruces, and this, like the Santa Rita Reserve, is essentially a grazing experiment station in the open range country. It seems inevitable that the organization of grazing reserves and experiment stations will proceed rapidly until they are found in all the important grazing types of the country, as well as in each State, including the South. An account is given in Chapter VI of the inauguration of a comprehensive system of grazing investigations throughout the West during 1917–1919.

Practically none of the grazing studies abstracted in the following pages was intended to deal with indicator plants. In spite of this fact, however, they all contribute more or less definitely to the understanding of grazing indicators, because of the simple and direct relation grassland dominants and subdominants have to grazing. In addition, the abstracts furnish a fairly complete outline of the progress of grazing investigations during the past twenty years.

Smith, 1899.—The first clear recognition of grazing as a fundamental field for investigation was accorded by Smith in his study of grazing problems in the Southwest. His paper is a mine of valuable suggestions, and foreshadows a large number of the later experiments. The author has a distinct idea of grazing indicators and of succession, as the following excerpts show:

"Before the ranges were overgrazed the grasses of the red prairies were largely bluestems or sage grasses (*Andropogon*), often as high as a horse's back. After pasturing and subsequent to the trampling and hardening of the soil, the dog grasses or needle grasses (*Aristida*) took the whole country. After further overstocking and trampling, the needle grasses were driven out and the mesquite grasses (*Hilaria* and *Bulbilis*) became the most prominent species. The occurrence of any one of these as the dominant or most conspicuous grass is to some extent an index of the state of the land and of what stage in overstocking and deterioration has been reached.

"There is often a succession of dominant grasses in nature through natural causes, but never to so marked an extent as on the cattle ranges during the process of deterioration from overgrazing. Thus, the grasses in any given valley are liable to change in a long series of years through destruction by wood lice, prairie dogs, by fires, unusually early or late frosts, or by failure on the part of the plant to ripen seed. This latter contingency frequently occurs in the case of the big bluestems and the feather sedge, and probably with some others of the *Andropogon* species. The curly mesquite will stand almost any amount of drought, trampling, and hard usage, but is easily killed and rotted out during a wet cold winter. The drought-resistant needle grass is frequently destroyed by wood lice over considerable areas. This usually happens in the spring on burned areas after light local showers. Finally, the entire seed crop may be destroyed by early autumn fires. Thus it is seen that through some one of many natural causes a species of grass may be all but exterminated and its place taken by others, often of less value.

"On overstocked land there is uniformly an alternation of needle grass and mesquite at short intervals, unless the overstocking is carried too far, when these perennials give way to annuals and worthless weeds. The carrying capacity then depends almost absolutely on the proper distribution of rainfall through the growing season in order to bring this transient vegetation to its fullest maturity." (p. 28.)

The text is divided into the following heads: (1) investigation of carrying capacity, (2) destruction of grasses by animal pests, (3) deterioration through increase of weeds, (4) renewing the cattle ranges, (5) rest versus alternation of pastures, (6) additional aids to range improvement, (7) grazing regions in Texas and New Mexico, (8) relation of land laws to range improvement, and (9) benefits of improving the ranges. The most significant part of the report is that which has to do with the regeneration of the range by means of rotation pastures. Experimental sections were selected at Abilene and Channing, Texas, representing prairie and plains respectively.[1] On these the following experimental pastures and areas were established (p. 20; Bentley, 1902 : 15).

Pasture No. 1 (80 acres): No treatment except to keep all stock off until June 1 of each year, pasturing the balance of the season.

Pasture No. 2 (80 acres): To be cut with a disk harrow, and stock to be kept off until June 1 of each year, pasturing the balance of the season.

Pastures Nos. 3 and 4 (40 acres each): To be grazed alternately, the stock to be changed from one pasture to the other every two weeks, thus allowing the grasses a short period for recovery after each grazing.

Pasture No. 5 (80 acres): No treatment except pasturing until June 1 and keeping stock off the balance of the season.

Pasture No. 6 (80 acres): No treatment except to keep stock off during the first season.

Pasture No. 7 (80 acres): To be harrowed with an ordinary straight-toothed harrow and stock kept off during the first season.

Pasture No. 8 (80 acres): To be disked and stock kept off during the first season.

Pasture No. 9 (70 acres): Reserved for special experiments, viz, to determine (1) whether or not seeds of a number of wild and cultivated varieties of grasses and forage plants, exclusive of the grasses, could be sown directly in the sod with satisfactory results. (2) Whether the roots of certain sod and pasture grasses could be transplanted to the bare spots and a good stand secured in that way. (3) Whether the stand of grass could be improved by opening furrows across the pasture, in which the grass seeds blown over the ground by the winds could be arrested and the stand of grass be improved.

Bentley, 1902.—The preceding experiments, though initiated by Smith, were carried out by Bentley from 1898 to 1901. His results are of great value as the first outcome of actual and successful experimentation in improving the range. At the beginning the maximum carrying capacity of the area was determined to be 16 acres per head, or 1 : 16. During the first year, the carrying capacity was estimated to have increased to 1 : 8, or 100 per cent.

[1]No record seems to have been made of the experiments at Channing, and it is assumed these were early discontinued.

Unfortunately, no detailed report was made on the different pastures, and it was impossible to tell whether rotation or disking and harrowing was of the greater value in securing these results. At the end of the second year, a further improvement of 30 to 50 per cent was noted in the disked pastures. By the close of the three-year period, while the whole area had improved more than 100 per cent, the greatest improvement was noted in the pastures which had been disked and harrowed. Two minor experiments of much practical interest were also carried out successfully. The one consisted of plowing furrows 12 feet apart over 10 acres of pasture 9. The many fruits caught in the furrows germinated readily and grew vigorously because of the increased water-content. The latter also benefited the grasses between the furrows. The other test involved the transplanting of grass mats and bunches for the purpose of covering bare areas in prairie-dog towns and other denuded areas. The results are of especial significance and are further discussed in Chapter VI.

Griffiths, 1901, 1904, 1907, 1910, 1915.—Griffiths's work upon the grazing ranges of southern Arizona from 1903 to 1910 is entitled to great credit as the earliest consistent study of range production. The quadrat method was employed more or less, and some attention was paid to physical factors and incidentally to changes of population. The objects of the investigation were (1) to demonstrate that run-down and overstocked ranges will recover under proper treatment, (2) to ascertain how long a time is necessary to get appreciable and complete recovery, and what methods of management will produce such results, (3) to carry on reseeding and introduction experiments in the hope of increasing the total quantity of feed, (4) to measure as accurately as possible the carrying capacity of a known representative area. The report of 1915 on the native pasture grasses of the United States contains a large amount of valuable material with direct bearing upon grazing indicators (plate 4, A).

The general results of the investigations are shown by the following summary (1910:24):

"The lands under consideration appear to regain their original productivity in approximately three years of complete protection.

"Evidence thus far secured seems to indicate that the best lands in the vicinity will improve under stocking at the rate of one bovine animal to 20 acres. The poorer lands take a correspondingly larger acreage for each animal. The areas that will carry one head to 20 acres are very limited.

"Brush and timber are encroaching upon the grasslands, due, it is believed, to protection from fires.

"A ground cover is not a factor below an altitude of about 3,500 feet.

"Although the maximum yield of forage may be reached in about three years of protection, improvements in quality of forage will probably go on longer through the continued supplanting of annual plants by perennials of greater value.

"Thus far alfilerilla is the only introduced plant which has succeeded and this only in the most favored situations. It does not appear to thrive in competition with the native perennial grasses at those altitudes where the latter are not grazed.

"None of the other 200 lots of seed sown has given any promise of success except those of three or four native species. These give beneficial results, but the cost is high.

"Results seem to be secured much more rapidly through proper protection from overgrazing than by any other method."

Sampson, 1908, 1909, 1913, 1914.—The series of reports by Sampson on revegetation in the Wallowa National Forest constitute a contribution of the first importance to the science of grazing. They likewise furnish a large amount of experimental data as to grazing indicators in the montane and subalpine zones. The general results (1914: 146) are applicable to a wide range of grasslands and are summarized below. They not only take into account the need of thoroughgoing and extensive studies of quadrats, factors, and succession, but they also consider in detail the ecological requirements of the various species.

"(1) Normally the spring growth of forage plants begins in the Hudsonian zone about June 25. For each 1,000 feet decrease in elevation this period comes approximately 7 days earlier.

"(2) In the Wallowa Mountains the flower stalks are produced approximately between July 15 and August 10, while the seed matures between August 15 and September 1.

"(3) Even under the most favorable conditions the viability of the seed on summer ranges is relatively low.

"(4) Removal of the herbage year after year during the early part of the growing season weakens the plants, delays the resumption of growth, advances the time of maturity, and decreases the seed production and the fertility of the seed.

"(5) Grazing after seed-maturity in no way interferes with flower-stalk production. As much fertile seed is produced as where the vegetation is protected from grazing during the whole of the year.

"(6) Germination of the seed and establishment of seedlings depend largely upon the thoroughness with which the seed is planted. In the case of practically all perennial forage species, the soil must be stirred after the seed is dropped if there is to be permanent reproduction.

"(7) Even after a fertile seed crop has been planted there is a relatively heavy loss of seedlings as a result of soil heaving. After the first season, however, the loss due to climatic conditions is negligible.

"(8) When 3 years old, perennial plants usually produce flower-stalks and mature fertile seed.

"(9) Under the practice of year-long or season-long grazing, both the growth of the plants and seed production are seriously interfered with. A range so used, when stocked to its full capacity, finally becomes denuded.

"(10) Year-long protection of the range favors plant growth and seed production, but does not insure the planting of the seed. Moreover, it is impracticable because of the entire loss of the forage crop and the fire danger resulting from the accumulation of inflammable material.

"(11) Deferred grazing insures the planting of the seed crop and the permanent establishment of seedling plants without sacrificing the season's forage or establishing a fire hazard.

"(12) Deferred grazing can be applied wherever the vegetation remains palatable after seed maturity and produces a seed crop, provided ample water facilities for stock exist or may be developed.

"(13) The proportion of the ranges which should be set aside for deferred grazing is determined by the time of the year the seed matures. In the Wallowa Mountains, one-fifth of the summer grazing season remains after the seed has ripened, and hence one-fifth of each range allotment may be grazed after that date.

"(14) The distribution of water and the extent of overgrazing will chiefly determine the area upon which grazing should first be deferred.

A. Protected pasture in *Aristida-Bouteloua* association, Santa Rita Range Reserve, Tucson, Arizona.

B. Fenced quadrat in rotation pasture, *Bouteloua eriopoda* consociation, Jornada Range Reserve, Las Cruces, New Mexico.

"(15) After the first area selected has been revegetated, it may be grazed at the usual time and another area set aside for deferred grazing.

"This plan of rotation from one area to another should be continued, even after the entire range has been revegetated, in order to maintain the vigor of the forage plants and to allow the production of an occasional seed crop."

Jardine, 1908, 1909, 1910, 1913.—Jardine has made a careful study of the relation of coyote-proof pastures to carrying capacity, and finds that the latter is nearly 100 per cent greater than under the usual method of herding in large bands. This is due to the fact that the sheep graze much more openly and do much less trailing, with the result that the vegetation is trampled very much less (1908:31, 1909:38).

The establishment of grazing reconnoissances on the six forest districts and the organization of a method by Jardine in 1911 marked the beginning of an adequate system of grazing on the National Forests. This work has yielded a large number of facts of importance in connection with grazing indicators. Although it has never been published, its value is such as to warrant a brief abstract of it here. The main object of the reconnoissance was to secure a map classifying all the land of each National Forest into grazing types, and the location of each type, its carrying capacity and nature, whether winter, summer, or year-long range. The field notes dealt with the dominant species of each type, the density of ground cover expressed in tenths, the degree of utilization, and the presence of poisonous plants and range-destroying animals. Of most interest to the student of indicator plants is the system of types and subtypes which is outlined below. As quadrats gradually came into use in connection with reconnoissance, the latter is now intensive to some degree in its methods.

Type 1. Open grassland other than meadow and secondary meadow.
Subtypes: bunch-grass, grama grass.
Type 2. Meadows.
Subtypes: wet meadow, dry or secondary meadow.
Type 3. Weed.
Type 4. Browse.
Type 5. Sagebrush.
Type 6. Timber, with a cover of grasses, weeds, and browse.
Subtypes: pine-grass, weeds, browse.
Type 7. Waste range.
Subtypes: waste timber, waste brush.
Type 8. Barren land.
Type 9. Woodland.
Type 10. Aspen.

Wooton, 1915, 1916.—In his discussion of the factors affecting range management in New Mexico, Wooton (1915:20, 23) has touched incidentally upon grazing indicators. The bulletin on the carrying capacity of ranges in southern Arizona (1916) continues the studies carried on by Griffiths from 1903 to 1910. Five associations are recognized, and an interesting account is given of the secondary succession following plowing in the crowfoot-grama and the six-weeks grass communities. Of especial interest is the account of carrying capacity as determined by cut-quadrats, and by actual grazing tests in the various pastures. The conclusions are grouped under the following heads:

*Recovery.*—The revegetation above 3,200 feet had become marked in about three years after fencing. This improvement has continued, but more and more slowly each year, indicating that the normal condition is being reached. Below 3,200 feet, the rate of recovery has been slower and hence it should continue for a longer period. Three years of complete protection gave about three-fourths of complete recovery for the crowfoot-grama consociation with an annual rainfall of 15 to 18 inches. After 11 years the grazed areas are but partially recovered, though their carrying capacity has increased about 30 per cent.

*Reseeding.*—Practically all attempts to introduce new species of forage plants or to increase the abundance of endemic species beyond the normal have failed. Alfilaria and some aggressive annuals have given promise, but in the course of a few years the native perennials have crowded them out.

*Carrying capacity.*—This has been determined by means of cut-quadrats, hay-cutting, mapping the communities, and by grazing tests of the best part of the reserve. For the latter, the carrying capacity is 14 acres per head, while it is 20 acres for the whole reserve. One of the pastures stocked on the basis of 58 acres per head was not noticeably different in condition from adjacent land protected for 11 years, thus indicating a utilization below 50 per cent.

Jardine and Hurtt, 1917.—In the account of the results obtained on the Jornada Grazing Reserve from 1912 to 1917, Jardine and Hurtt have embodied the essentials of the first complete grazing system based upon actual experimental study of the herd as well as of the range. As a consequence, it serves as an excellent model for all ranches large enough to permit the rotation system of pastures and to warrant the segregation of herds by ages and classes. Taken in conjunction with the more intensive grazing experiments such as have been carried on by Sarvis (1919) at Mandan, it furnishes a complete experimental method of range studies. It is especially important in demonstrating how much experimental work and resulting improvement of range and herd can be carried on even under existing economic conditions on well-managed ranches (plate 4, B).

The authors' most important conclusions are as follows:

The grama-grass range has improved at least 50 per cent in three years, compared with adjoining unfenced range grazed yearlong. This has been secured by reducing the number of stock during the main growing season from July to October to about half the average number the area will carry for the year, by refraining from overstocking during the other eight months and by better distribution of watering places. The range thus lightly grazed during the growing season has apparently improved as much as similar range protected during the whole year. Where the whole of a range unit is grama, about one-third should be reserved in rotation for light grazing during the growing season for two successive years.

Fairly efficient utilization of the range is secured by watering places with a 2.5 mile grazing radius. When the distance is greater than this, serious overgrazing or actual denudation occurs around the well or tank, while the remote areas are but partially utilized. The carrying capacity of the grama grass is 20 to 30 acres, of the tobosa grass 38 to 45 acres, and of the mountain range 60 acres. This is based upon carrying stock through the average year in good condition, and feeding the poorer stock concentrates to eliminate loss from starvation at critical periods.

Jardine and Anderson, 1919.—In an account of range management on the National Forests, Jardine and Anderson (1919: 17) have discussed briefly the general indicators of overgrazing:

"Overgrazing for an extended period will leave 'earmarks,' which usually will be recognized. To recognize current overgrazing at the time of examination on a range previously not overgrazed is difficult and yet important in order to make timely adjustment. The following obvious earmarks are the most reliable indicators of overgrazing prior to the year of examination:

"*The predominance of weeds and grasses* such as knotweed (*Polygonum* spp.), tarweed (*Madia* spp.), mustard (*Sophia incisa*), annual brome grasses (*Bromus hordeaceus, brizaeformis, tectorum*), and fescues (*Festuca megalura, microstachys, confusa*), with a dense stand of such species and lack of variety in species. This condition is a severe stage of overgrazing such as occurs around sheep bedding grounds which have been used for long periods each year for several years in succession.

"*The predominance of plants which have little or no value for any class* of stock, such as sneezeweed (*Dugaldia hoopesii*), niggerhead (*Rudbeckia occidentalis*), yellowweed (*Senecio eremophilus*), snakeweed (*Gutierrezia sarothrae*) and gumweed (*Grindelia squarrosa*). These and similar plants frequently occur in abundance over large areas of range and indicate that the range needs careful management to give better forage plants a chance to grow.

"*The presence of dead and partly dead stumps of shrubs*, such as snowberry (*Symphoricarpos oreophilus*), currant (*Ribes* spp.), willow (*Salix* spp.), service berry (*Amelanchier* spp.), birch-leaf mahogany (*Cercocarpus montanus*), and Gambel oak (*Quercus gambellii*). This condition usually indicates that the most palatable grasses and weeds have been overgrazed. There may be some exceptions to this, as in the case of drawfed willows on ranges where grasses predominate above timber line. Sheep sometimes kill the willows before the grasses are overgrazed.

"*Noticeable damage to tree reproduction*, especially to western yellow-pine (*Pinus ponderosa*) reproduction on sheep range and aspen (*Populus tremuloides*) reproduction on cattle range. Lack of aspen reproduction on a weed sheep range indicates overgrazing, provided the natural conditions are favorable to aspen reproduction. On a sheep range where grass predominates severe injury to western yellow-pine or aspen reproduction may indicate that the range is not well suited to sheep.

"The earmarks described are, perhaps, more typical of overgrazed sheep range than of overgrazed cattle range, but the general appearance of the two does not differ greatly when overgrazing reaches a stage to be recognized by one or more of these earmarks. The main differences are in the species of plants indicating the overgrazing. Weeds eaten by sheep are often found in abundance on overgrazed cattle range; coarse grasses palatable to cattle are often abundant on overgrazed sheep range. This fact has given rise to the use of the term 'class overgrazing.'"

Sarvis, 1919.—The first adequate intensive experiments in grazing have been carried on by Sarvis (1919) at Mandan, North Dakota, since 1916, and at Ardmore, South Dakota, since 1918. These have dealt primarily with carrying capacity and rotation grazing, though a number of related problems have been taken into account, such as rate of growth, effect of mowing, etc. The experiments are based upon actual grazing tests to determine the present carrying capacity of a particular type and the optimum utilization resulting from rotation At Mandan, for example, the carrying capacity tests comprise four fields of 30, 50, 70 and 100 acres respectively, each grazed by 10 animals of the same age and class. These are weighed at frequent intervals and the carrying capacity expressed in terms of pounds gained in weight. There are three rotation pastures to permit grazing during one-third of the growing season—spring, summer, and fall respectively. The behavior of the community under the different degrees and kinds of grazing is measured by means of an unusually complete system of chart- and cut-quadrats. The details of the method are discussed in Chapter VI.

## CHRESARD AND WATER REQUIREMENT STUDIES.

Significance.—While practically all studies of the chresard or available water in soils have been made without definite reference to indicator plants, it is clear that they have a direct bearing upon the latter. This is likewise true of researches upon water requirements, especially those that relate to controlling physical factors. Since the value of an indicator depends upon the exactness of its correlation with direct factors, and especially water, it is often totally misleading to relate it to obvious or superficial facts. For this reason a scientific system of indicators has but recently become possible. It was a distinct step in advance to connect species with the total water-content or holard. But this gives trustworthy results only for the same soil. To obtain exact results it has become necessary to determine the water-withholding power of different soils and the water-using capacity of different plants. It has likewise proved imperative to take into account the salt-content and air-content of the soil solution. In the further analysis of indicators, it proves desirable to utilize their form, growth, and abundance for more minute and exact values. Hence a knowledge of the growth requirements, which are largely water requirements, has come to be highly significant.

Much work has been done upon the chresard of different soils and plants, and a still larger amount upon water requirements. Most of the former is American, and has been done in the West. As a result, it has a direct bearing upon the problem under consideration here. Of the great mass of water requirement data only a few deal with native or non-cultivated species, and are pertinent to the present discussion. For these reasons a concise account is given of the progress of the chresard concept.

The chresard.—The earliest studies of the water-content non-available to plants were incidental and failed to recognize the fundamental importance of the distinction.

Sachs (1859, 1865 : 173) found that a young tobacco plant began to wilt in a mixture of sand and beech mold at 12.3 per cent and that the chresard for this soil was 33.7 per cent. A second plant in clay wilted at 8 per cent, with a chresard of 44.1 per cent, while for a third the echard in sand was 1.5 per cent and the chresard 19.3 per cent. Heinrich (1874) determined the echard of barley in peat as 47.7 per cent and of rye as 53.4 per cent. In calcareous soil corn wilted at 8.6 per cent and broad beans at 12.7 per cent. Mayer (1875) observed that pea plants wilted at 33.3 per cent in sawdust, 4.7 per cent in marl, and 1.3 per cent in sand, while Liebenberg found that beans wilted in loam at 10 per cent, in marl at 6.9 per cent, and in coarse sand at 1.2 per cent.

Gain, 1895.—Gain (1895 : 73) has studied the behavior of three mesophytes in six different soils, with the results indicated in the table below. The echard varies less than 50 per cent for these species in any one of the first three soils, but the variation rises as high as 60 to 130 per cent in the last three. Part of this may be due to a larger error in determining the low echard. The author concludes that species not only wilt at different points, but also that this varies for different stages of the development of the same species.

| Soils. | Erigeron canadensis. | | Phaseolus vulgaris. | | Lupinus albus. | |
|---|---|---|---|---|---|---|
| | Echard. | | Echard. | | Echard. | |
| | I. | II. | I. | II. | I. | II. |
| | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* |
| Heath soil.. | 9.26 | 9.40 | 10.73 | 10.60 | 10.90 | 11.10 |
| Clay....... | 7.73 | 7.78 | 9.73 | 9.58 | 11.50 | 11.35 |
| Humus..... | 6.80 | 6.83 | 6.10 | 5.92 | 6.86 | 6.95 |
| Lime soil... | 4.19 | 4.25 | 2.94 | 2.90 | 5.15 | 5.23 |
| Garden soil. | 2.30 | 2.40 | 1.79 | 1.88 | 2.82 | 2.91 |
| Sand....... | 0.45 | 0.48 | 0.33 | 0.35 | 0.76 | 0.75 |

Kihlmann (1890 : 105) was probably the first to perceive the ecological significance of the echard, in connection with his studies of water relations in the frozen bogs of Lapland. However, Schimper first recognized the universal application of the concept and formulated it definitely as follows (1898 : 3; 1903:2):

"It is necessary to distinguish between physical and physiological dryness and wetness; the physiological water-content alone is important for plant-life and hence for plant-geography."

Neither Kihlmann nor Schimper appears to have made actual determinations of the physiological water-content. Clements (Pound and Clements, 1900: 167; Clements, 1904: 23; 1905: 30; 1907: 13; 1916) developed methods for determining the echard and chresard in the field as well as under control. These were applied to various habitats in the prairie and woodland regions of Nebraska, and on Pike's Peak in Colorado. The general results were in accord with those of the earlier investigators, Sachs, Gain, and others, with respect to the variation of the echard with different species as well as with different soils. This led to a comprehensive investigation by Hedgcock (1902) of the echard and chresard of some 130 species under control, and 25 in the field. These were largely native and ruderal species, though a number of cultivated ones were included also. The great majority were mesophytes, though they ranged from xerophytic grasses, such as *Bouteloua gracilis,* to such hydrophytes as *Sagittaria* and *Potamogeton.* The author reaches the general conclusion that "the ability of plants to take water from the soil varies in an ascending scale from hydrophytes through mesophytes to xerophytes."

Briggs and Shantz, 1912.—The most complete and thoroughgoing investigation of the echard has been made by Briggs and Shantz in connection with crop-plants for the Great Plains. Their methods and results are perhaps too well known to require comment, but it seems desirable to touch the latter briefly for the sake of comparison. The term wilting coefficient is employed for non-available water or echard, but it is an exact synonym of these. The determinations of the echard for various soils are in essential accord with those of all other investigators, the values ranging from 1 per cent to 16 per cent, or in the heaviest clays to 30 per cent. But a striking departure from all previous results occurs with respect to echard for different species. While Heinrich, Gain, Clements, and Hedgcock found differences between species in the same soil represented by a ratio of 1 to 1.5 or 1 to 2, or even more in the case of hydrophytes, the greatest ratio found by Briggs and Shantz was 1 to 1.1. The thoroughness of their work seems to leave little question of the soundness of the conclusion "that the differences exhibited by crop plants in their ability to reduce the mositure content of the soil before wilting occurs are so slight as to be without practical significance in the selection of crops for semi-arid regions." The issue must still be regarded as open with reference to material differences in the echard of native species, and this can only be settled by further research. Recent studies by Dosdall (1919) have shown that *Equisetum* differs greatly from *Helianthus* and *Phaseolus* in its ability to draw water from the soil, as was likewise demonstrated by growing them side by side in the same spots. In seeking to harmonize the discordant results of qualified investigators, it has become more and more probable that types of echard must be recognized.

Water requirement.—In summing up the results of their own researches, as well as those obtained by many earlier observers, Briggs and Shantz (1913 : 1:46; 2:88) reach the following conclusions:

Experiments upon the effect of water-content on the water requirement show that the latter increases as a rule when the water-content approaches either extreme.

A reduction in water requirement generally accompanies an increase in the nutrient-content, while a higher water requirement may result from a deficiency in the amount of a particular nutrient.

The type of soil affects the water requirement only though the water or the solutes it contains.

The water requirement increases with the dryness of the air, and is profoundly affected by climatic conditions.

The water requirement varies greatly for different species and varieties. In Colorado, it was found to be approximately 1,000 for alfalfa, 700 for sweet clover, and 300 for millet and sorghum. The grains ranged from 369 for corn to 507 for wheat and 724 for rye.

The greatest value of water requirement work for indicator studies is in connection with the phytometric analysis of climates and habitats. So far as the water relation is concerned, the values obtained by means of phytometers can be expressed in terms of water-loss per unit area or rate of growth, or in the water requirement in terms of dry weight or seed production. For crop plants, the latter are the most important, but for native species all four values must be taken into account, in addition to photosynthetic efficiency.

## CONCEPT.

General.—Every plant is an indicator. This is an inevitable conclusion from the fact that each plant is the product of the conditions under which it grows, and is thereby a measure of these conditions. As a consequence, any response made by a plant furnishes a clue to the factors at work upon it. While this general principle seems to be of universal significance, its application is far from simple. This is because the most direct responses are physiological and for the most part can be determined only by experiment. Such complex physiological processes as growth and reproduction are exceptions inasmuch as they are subject to direct observation. Consequently they are among the most valuable of indicator evidences. Structural responses are the most visible of all, but their exact use is the most difficult since they stand at the end of the process initiated by the causative factors. Structure also possesses a well-known inertia, as a result of which it may register the impact of factors but partially or slightly. Moreover, the adaptation to the habitat may be made in the tissues of the leaf without affecting the gross features to an appreciable degree. A plant may show the most exact response to changing conditions by the behavior of chlorenchyma or stomata, and yet reveal no sign of this in its outward appearance (E. S. Clements, 1905).

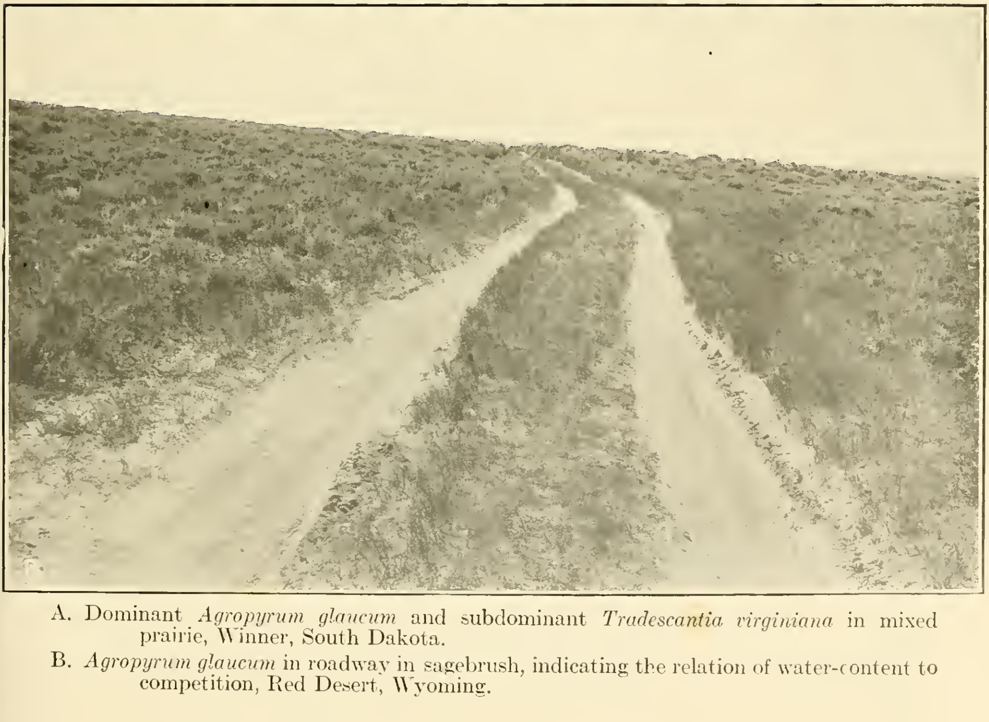
The interpretation of indicators is profoundly affected also by the double complex of factors and plants. The species of a community do not always register the same response, nor do they respond to any one factor in the same degree. The habitat itself is still largely a puzzle, and it is often difficult to assign well-marked effects to definite causes. The behavior of individuals, though manifestly of less importance, is not without its difficulties. It is impossible to tell at present whether the varying behavior of individuals of the same species is due to individuality or to minute differences in the habitat. Hence, the problem of indicator values is chiefly one of analyzing the factor-complex, the habitat, and of relating the functional and structural responses of both the plant and community to it. This then makes possible the accurate employment of indicators in practical operations.

Animals as indicators.—Since their response is direct, plants are the best indicators of physical processes and factors. They are by no means unique in this respect. Animals likewise show direct responses to physical conditions and to this extent serve as indicators of them. For a number of reasons they are inferior to plants, however. The chief reason is that their significance is subordinate to that of plants because the latter as food-supply usually constitute the controlling factor. In other words, animals are as a rule indicators of plants more directly than of physical conditions. Their mobility makes the control of a particular habitat or set of conditions less absolute, especially with land animals. With the exception of insects, land animals are much less abundant than plants, and the indications of an animal community are much less complete and definite. Finally, our knowledge of the ecology of animals is much less than that of plants, especially with reference to factor control and succession. In spite of all this, however, animals do have great indicator value, second only to that of plants. While the time has not yet come for an adequate treatment of them in this connection, they are taken into account at various points in the text. Indeed, any other course would be illogical in view of the conviction that the complete response to habitat is the biome, or community of both plants and animals.

Plant and community.—It has already been suggested that the individual, the species, and the community are all involved in the indicator concept. Each of these has its own value, while all of them must be taken into account sooner or later. Up to the present, the species has almost monopolized the rôle, though the work of Shantz (1911) in particular has emphasized the importance of the community as an indicator. In constructing a complete scale of indicator values, the individual will play a necessary part. Its indications are more minute and subject to greater error. While further quantitative work will increase the accuracy and usefulness of individual indicators, at present they are distinctly secondary. In fact this will probably always be their relative position, inasmuch as they will serve to refine the major indications of species and communities. The question of species and community values is much simpler than appears at first. It is not a matter of employing one to the exclusion of the other, but of taking advantage of their complementary relation. There can be no doubt that the community is a more reliable indicator than any single species of it. This is a necessary consequence of the essential harmony of the important species as to physiological response and factor control. The community not only affords a better norm for the major indications, but it is likewise, so to speak, more finely graduated and hence more sensitive, owing to the fact that no two of its dominants or subdominants are exactly equivalent. It is also a better indicator of the whole habitat, since it levels the variations from one point to another.

The indicator value of a species depends primarily upon its rôle in the community. A secondary or subordinate species may be of little or no practical value, in spite of the general rule. It merely accompanies the major species, or as a subordinate accepts the conditions made by them, thus indicating minor differences. It assumes practical value only in case of the destruction of the dominants, as often happens in overgrazing and in deforestation. Even here the real meaning of a secondary species is due to the fact of its association with more important indicators. The significant species are the dominants and subdominants which give character to definite communities. With these the species and community values approach closely or merge completely. In fact such species give their typical indication only where dominant. Their incidental or scattered occurences may have meaning, but it is not the normal one. In the present stage of our problem, then, attention should be focussed upon the dominants and subdominants of the climaxes and their various seres. When these have been correlated on the one hand with their efficient factors and on the other with practical processes in agriculture, grazing, and forestry, it will become evident whether an analysis of secondary species is profitable. The dominant may well be regarded as the real basis of indicator study, so commanding is its rôle in the processes of vegetation (plate 5, A).

Sequences.—Every indicator owes its value to its position in a cause-and-effect sequence. With this, however, must always be associated correspondence with another cause-and-effect sequence. The value of the compass-plant, *Silphium laciniatum*, as an indicator of corn production rests not merely upon its preference for relatively moist rich soils, but also upon an experiential knowledge at least of the production capacity of such soils. Up to the present, our knowledge of indicators rests chiefly upon the basis of experience. In emphasizing the point that this alone is usually inaccurate and insufficient, there is no intention of failing to give it proper recognition. It is an essential and often the critical part of indicator research, but its true value can be obtained only by correlation with the other steps of the process. As a consequence, it makes little difference whether the approach has been through experience or investigation. Both must be taken into account before the



A. Dominant *Agropyrum glaucum* and subdominant *Tradescantia virginiana* in mixed prairie, Winner, South Dakota.

B. *Agropyrum glaucum* in roadway in sagebrush, indicating the relation of water-content to competition, Red Desert, Wyoming.

exact meaning of any indicator is secured. For the future it is clear that much time will be saved by a method of investigation which replaces more or less vague experience by actual investigation.

Direct and indirect sequences.—As is shown later, plants may indicate conditions, processes, or uses. The simplest of these is the first, the most practical is the last. The plant may indicate a particular soil or climate, or some limiting or controlling factor in either. This would seem to be axiomatic, but it is well known that grassland, which is typically a climatic indicator, often occupies extensive areas in forest climates. Thus, the presence of a plant, even when dominant, is only suggestive of its meaning. It is necessary to correlate it with the existing factors and, better still, to check this correlation by experimental planting, or an actual tracing of the successional development.

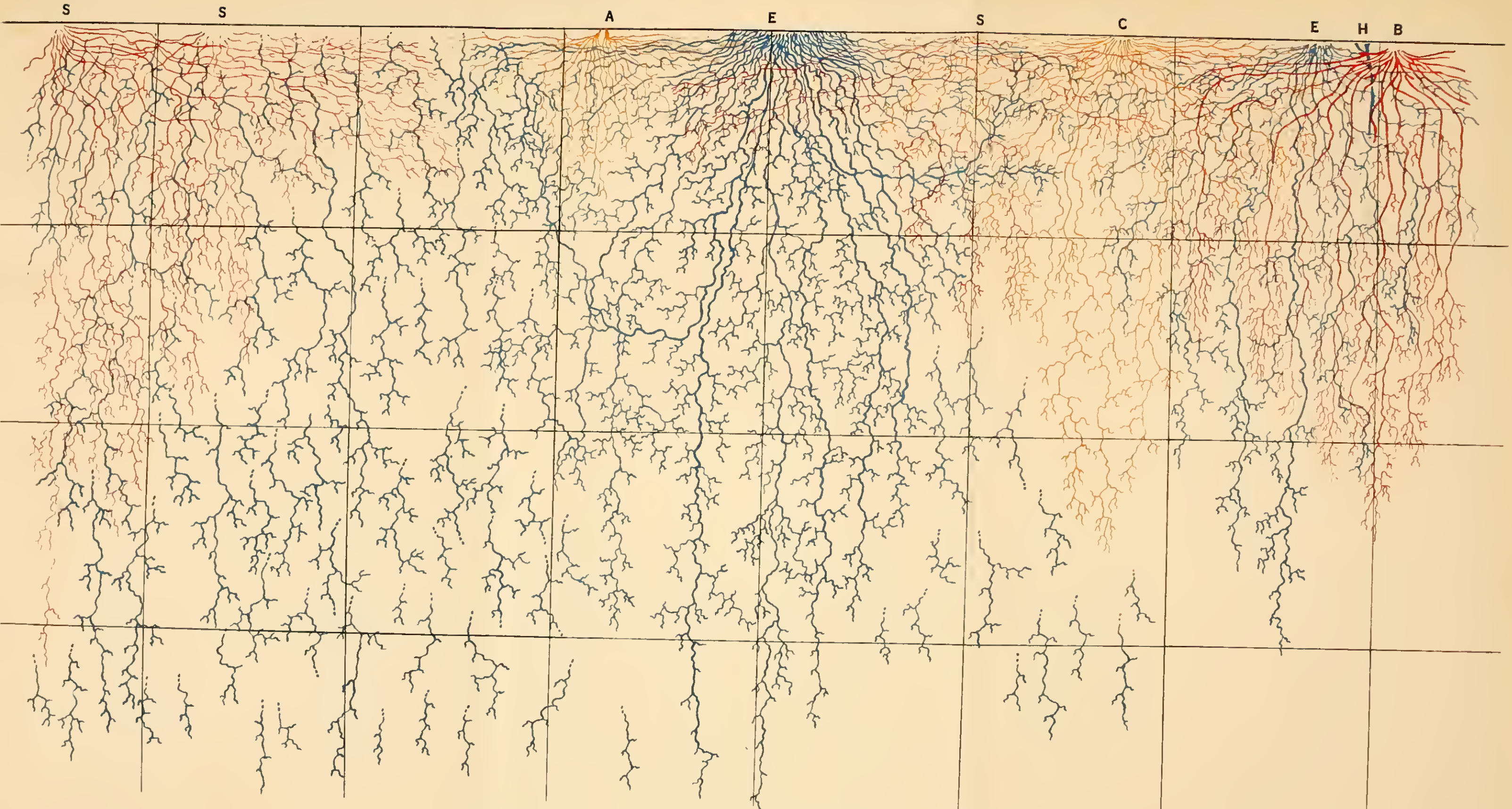
Indicators of processes usually require a double correlation, namely, that of the plant with the controlling factor, and that of the factor with the causal process, such as erosion, disturbance, fire, etc. Thus, in the Red Desert of Wyoming, roads through the sagebrush are marked by vigorous growths of *Agropyrum*. The latter is here a clear indicator of disturbance. From its usual position in adjacent lowlands, it is presumably an indicator of increased water-content as well. Actual instrumental study alone can determine the exact relation between the disturbance and the water-content, and between the water-content and the presence of *Agropyrum*. The indicator sequence is further complicated by the question whether the increased water-content is due to disturbance directly, to the elimination of competition, or to both. As a matter of fact, however, the field study of *Agropyrum* and *Artemisia* under a wide variety of conditions and in different successional relations indicates that disturbance acts through competition upon water-content (plate 5, B; plate A; cf. Weaver, 1919, for plate 26 A).

In the case of use or practice indicators, the sequence differs in accordance with the nature of the crop. When the crop is a natural one as in grazing, the sequence is simple and direct. This is especially true of grazing in which the value of the range is determined directly by actual experiential or experimental grazing tests, which establish the indicator value of each species. With overgrazing, the sequence is similar to that found in process indicators. Trampling disturbs the soil and destroys the less resistant plants. Both effects tend to increase the water-content of the soil and to give the advantage to such plants as *Gutierrezia* and *Artemisia frigida* (Clements, 1897 : 968; Shantz, 1911 : 65). This relation is clearly recognizable in the field from the fact that *Gutierrezia*, for example, is characteristic of depressions, alluvial fans, roadways and other disturbed areas. In the case of forests, plants may serve directly as indicators of water or light values, or indirectly of disturbance such as lumbering or fire, and of such practices as reforestation and afforestation. In these processes the crop is partly or wholly artificial, and the indicator sequence is essentially the same as for crop plants. This involves the correlation of indicator and crop plants with their respective habitats, and the close correspondence of the controlling factors in the latter. With forage and grain crops, the sequence is more complex, partly because the species concerned ar not native, but largely because the physical conditions are unnatural as well as controlled. As a consequence, while factor correlation and indicator correspondence are still important, the chief part must be taken by experiment and experience extending over a period of years. It is desirable if not essential that this period be 12 to 15 years, in order to cover the range of conditions from the wet phase to the dry phase of a climatic cycle. This is particularly true in the use of indicators for land classification, in which grazing, forestation, and crop production must all be taken into account.

Direction of indication.—The increasing attention paid to plants as indicators during the past decade has largely arisen from practical considerations. While this is highly desirable, it must be recognized that indicators have also a wide range of scientific application. Moreover, the more important and certain practical values are made possible only through the ecological study of indicators. It is in the ecological sense that every plant is an indicator. The indicators of actual practice will be obtained by the selection of those which are the most distinctive and dependable. Thus, while the indicators for grazing, forestry, agriculture, and land classification will be established by more and more exact study, many indicators will find their chief use in ecology and related fields, which must lay the foundation for the scientific agriculture and forestry of the future.

For these reasons, it is necessary to recognize that every dominant can be used as an indicator of past and future as well as of present conditions. This is due, of course, to the fact that every dominant or subdominant has a definite position in succession. As a consequence, it is an indicator not only of the plants which precede and follow it, but also of the soil conditions in which they grow. At the same time the definite existence of a climatic cycle makes it possible to relate growth and successional movements to climatic changes, both past and future, and to extend the application of indicators correspondingly. On the one hand, this enables us to greatly broaden and definitize the use of plants as indicators of soil, climate, and vegetational movements in the geological past; on the other, it permits us to look ahead and anticipate the changes due to climatic cycles and the development and movements of vegetation and habitat.

Scope.—A complete understanding of the broad significance of indicator studies must rest upon a recognition of the aims and methods of modern ecology. In the early characterization of this field (Clements, 1905 : 1) it was emphasized that ecology is the central and vital part of botany and that all the questions of botanical science lead sooner or later to the two ultimate facts, plant and habitat. These statements appear even truer to-day in the light of the progress made during the past twelve years. The one essential amplification is the inclusion of zoology, due to the growing conviction that the real unit of response to the habitat is the biological community. Furthermore, it is desirable to place all possible emphasis upon the fact that ecology must fix its attention upon habitat and community in their natural relation. Finally, there must be the clearest recognition of the fact that the plant or animal must be the final arbiter in ecology, except of course in the vast field of human ecology. Fascinating and valuable as they are, instruments and quadrats are useful only in so far as they tell us what the plant, animal, or community is doing. The most complete records of climate, for example, have no merit in themselves. They acquire value only as the plant or animal discloses by its responses the factors or quantities which are effective or controlling.




Quadrat-bisect in the half-gravel slide. The face of the trench was cut along the front of the quadrat shown in Plate 26 A: S, *Solidago oreophila;* A, *Allium cernuum;* E, *Elymus triticoides,* fragments of which are represented in blue; C, *Calamagrostis purpurascens;* H, *Heuchera parvifolia;* B, *Besseya plantaginea.*

The threefold basis of ecology is factor, function, and form (Clements, 1907: 1). As a consequence, every ecological fact has its indicator significance, and it becomes possible to determine these just as rapidly as factor correlations are made. The chief objective for the student of indicators is the cause-and-effect relation, and his chief task to show how effects may be used as signs of their causes. In a sense, the use of indicators reverses ecological procedure inasmuch as it leads from effects to causes. Sooner or later it involves a more or less complete system of reading all the evidence afforded by the responses of plants and animals, whether as individuals or communities.

With respect to its application, the scope of indicator work is far-reaching. It not only furnishes a basic method in ecology, and especially in succession, but it is also equally applicable in paleo-ecology. Because it gives us the judgment of the plant upon the physical factors of the habitat, it is indispensable to studies of soil and climate in so far as they have to do with vegetation. For the same reason, it is invaluable in land classification, and to the great plant industries, agriculture, grazing, and forestry. While this is truest of new regions, it holds to some degree for older agricultural communities as well. It applies with especial force to the great unoccupied or poorly utilized interiors of other continents, such as South America, Africa, Asia, and Australia, and is not without meaning for large stretches in Europe. In short, wherever plants grow, in field, forest, grassland, or desert, indicator results are always of some, and usually of paramount, importance.

In their relations to succession and to climatic cycles, plants exhibit some of the most important indicator values. These involve quantitative relations of abundance and growth which in conjunction with factor determinations will give to ecology an accuracy and certainty more and more approaching those of the physical sciences. As a consequence, it will become increasingly possible to definitize ecological processes and principles, and to use them as a basis for accurately forecasting the behavior of plants under changed conditions. Such prophecy is possible at present in any region where an adequate study of succession has been made. Its scope will be extended and its probability increased in just the proportion that instrumental, quadrat, and developmental studies of vegetation become the rule.

Materials.—As has been suggested earlier, while every study of the actual relation between habitat and plant is a possible source of indicator materials, only those are of real value which are based upon instrumental, quadrat, or successional investigations. The permanent foundation of indicator research must be laid by those studies which employ all three methods. For these reasons the published sources of indicator material are relatively few and recent. They are largely American and are confined almost wholly to the period since 1900. In fact, adequate ecological studies having indicator values as their avowed objective are all subsequent to 1910, and are largely due to the appearance of Shantz's paper on the indicator value of natural vegetation in 1911. As a consequence, the present treatise is of necessity based primarily upon the investigations of the author during the past 20 years and of Shantz for the last decade or more. While these have had indicator plants as a definite objective only since 1908, the preceding 10 years of instrument, quadrat, and succession work were an intrinsic part of the investigation.

Basing studies.—Initial studies of grassland were made in Nebraska from 1893 to 1898. These included a journey along the Missouri and Niobrara Rivers during the summer of 1893, one to the plains and foothills in 1897, and to the Black Hills in 1898. The first ecological expedition to Colorado was made in 1896, at which time a provisional outline of the plant communities was drawn up. Beginning with 1899, all the summers were devoted to investigations in Colorado until 1913, with the exception of that of 1911, which was spent abroad. During the spring and fall from 1899 to 1907, studies in prairies and woodland in eastern Nebraska were carried on with the aid of advanced classes. The six summers from 1913 to 1918, inclusive, have been devoted to vegetation studies throughout the West, with especial emphasis upon succession, indicator plants, and climatic cycles. From 1912 to 1917, the work of the Botanical Survey of Minnesota was directed along similar lines.

The use of quadrats was begun in 1897 and the instrumental analysis of habitats in 1898. The principles of succession were formulated into a working system for the field in 1898 (Clements, 1904: 5), while studies of the echard and chresard were first made in 1900. The fundamental importance of the distinction between climax and seral communities was recognized in 1913, and the significance of climatic cycles in 1914. The two most recent advances which extend the use of indicators are the organization of the field of paleo-ecology in connection with the study of Badlands in 1915–16 and the formulation in 1916 of the concept of the biome as the basic biotic unit.

Shantz (1906) began the ecological study of Colorado vegetation in 1903 on the basis of instrumental, quadrat, and successional methods. This led to the direct study of indicator plants on the Great Plains (1911) and in the Great Basin (1914). Out of this grew the extensive series of water requirement studies, as well as of transpiration, made by Briggs and Shantz between 1912 and 1916. During the same period much attention was paid to western vegetation, and this was crystallized in the list of indicator types for land-classification (Shantz and Aldous, 1917) and a map of the climax communities of the United States (Zon and Shantz, 1919). The text accompanying the map contains much information relating to the indicator value of the different vegetation types.

# II. BASES AND CRITERIA.

## BASES AND METHODS OF DETERMINATION.

Fundamental relations.—Plants serve as indicators by virtue of their response to conditions about them. Every plant response has some significance, the kind and degree of which must be subjects of exact determination in each case. Some responses are obvious, others less evident, while still others are invisible though demonstrable. All these, however, must be referred to the habitat for the decision as to their meaning and their possible use as indicators. It is clear that the causal relation of the habitat to the plant is the primary basis of plant indicators. Each response is the effect of some factor or factor-complex acting as a cause, and is consequently the indication of this factor. The chief task of the investigator is the measurement of responses, and their correlation with measured factors.

In deciding upon possible bases for an indicator method, physiological responses and physical causes must be given the place of first importance. As further consequences of these must be considered the responses shown in the development and structure of communities, *i. e.*, the basic facts of association and succession. The method of obtaining the facts in these four great fields will continue to be both empirical and experimental. Experiment will steadily increase in amount and value, but the result will be to refine and direct observation and not wholly to displace it. In fact, the more completely experiment is taken into the field, the more readily will observation reveal the meaning of the innumerable natural experiments brought about by changes of habitat and of climate. In this there is no intention of minimizing the crucial value of experimentation, but rather to widen its scope so that all experiments can be taken into account. This is especially important when one recalls the slow advance in experimentation under natural conditions and the insignificant area covered by it. The possibilities of this method have been strikingly shown for many years at the Alpine Laboratory, where numerous examples of natural transplanting in fragmented habitats verify and extend the results of a relatively small number of artificial transplantings. Similar results are to be obtained from natural experiments on a wider scale. The value of *Bouteloua gracilis* as an indicator of climate was graphically shown in the bad-land levels at Glendive, Montana, in 1917. The drying culms of the current year were just half as tall as those of 1916 which still persisted in the same mat. The rainfall for the two years was 26 and 12 inches, respectively. Thus the inevitable adjustment of the short-grass cover to decreased rainfall and water-content furnished results hardly to be surpassed by the most carefully checked experiment.

In indicator work, as in all adequate investigation, by far the best method is that which uses all sources of information and does not emphasize one to the neglect of others. While the very nature of indicators insures proper consideration of habitat and plant, the study of each species must be accompanied by that of its associational and successional relations, and all four of these objectives must be reached by the combined use of observation and experiment, in which each must be utilized to the fullest capacity consistent with accurate results.

## THE PHYSICAL BASIS.

**Direct and indirect factors.**—An adequate understanding of the habitat as the cause of plant responses which serve as indicators must rest upon two facts. The first of these is that the habitat is a complex, in which each factor acts upon other factors and is in turn acted upon by them. The second is that some of these factors are direct causes of plant response, while others can affect the plant only through them. Water, light, solutes, and soil-air are direct factors of the first importance because of their variation from habitat to habitat. Other direct factors, such as carbon dioxid, oxygen, and gravity, are negligible because of their constancy. Temperature is both direct and indirect, but its indirect action through the water relation is usually the most tangible. Wind, pressure, slope, exposure, soil texture, etc., are all indirect, acting for the most part through water-content or humidity, or through temperature upon these.

Too much importance can not be given this distinction between direct and indirect factors. The indicator value of every plant depends upon it absolutely. A plant can only indicate a direct factor. But by the correlation of the latter with factors which are modifying it, the indicator response of the plant may be related to these. Thus, dwarfed herbs usually indicate a lack of water. In alpine regions this lack is largely caused by excessive transpiration and evaporation due to low pressure. As a consequence, dwarfs are typical indicators of high altitudes and hence of alpine climates. By other correlations of direct factors with causative processes, such as disturbance, erosion, cultivation, etc., plants come likewise to be used as process or practice indicators. The true basis of all plant indicators is to be found in the responses made to direct factors, especially water, light, solutes, and soil-air. These once established, it becomes a simple matter to connect indicators with any correlated factor or process.

**Controlling and limiting factors.**—It is evident that the factor in immediate control of the behavior of plant or community must be a direct one. But the latter may be profoundly affected by another factor in which the actual control may be said to reside. For example, montane timber-lines are often determined by water, but the availability of the water-content is decided by frost and its sufficiency by the wind. As indicated above, the immediate control and hence the immediate indication must be sought among the few direct factors, while the final control and indication will be found among the indirect factors which exert a critical effect.

All the direct factors of the habitat play a part in the responses of the plant, but only those which vary widely in quantity leave a distinct impress upon it. This is necessarily true, since such constant factors as carbon dioxid, oxygen, and gravity produce fairly uniform responses, and consequently do not differentiate species or communities. In the case of each individual plant or species, its distinctive features are due to one of the variable direct factors. In practically all cases at least one of these will be deficient, with the result that it becomes the limiting factor in the plant's development. This term is used in an ecological sense and not in the physiological one employed by Blackman (1905) and others. As a result the search for indicator correlations among the four direct factors narrows itself to the one or two which are deficient. Some of these factors regularly bear an inverse relation to each other and all of them often show such a relation. Thus an abundance of water means a lack of oxygen, and a deficit of water a strong soil solution. Habitats deficient in light rarely show a lack of water or nutrients, though the oxygen-content of the soil may be low also. In practically all herbaceous communities, light is usually at the maximum, and the limiting factor must be sought in the soil. Hence, a careful scrutiny of many habitats narrows the search for limiting factors to a single one, and it is then possible to proceed at once with the quantitative correlation of factor and indicator.

It must also be recognized that some factors limit plant response in consequence of an excess. This is true to some extent of solutes and water, but not of light or oxygen in nature. Even with the former, while the excess definitely limits or at least characterizes the plant's activity, the corresponding deficit of water in saline soils and of oxygen in wet ones or in ponds also plays a significant rôle. For water and solutes, it is probably more accurate to say that the extremes, either excess or deficiency, act as limits. While there are statements to the effect that full sunlight is directly injurious to many species, there is little or no conclusive evidence. This feeling has been based largely upon Bonnier's work with alpine dwarfing, which has not been confirmed by similar studies in the Rocky Mountains.

After eliminating the large groups of species which owe their indicator character to the limiting action of water, solutes, oxygen, or shade, there remains a much larger group of sun mesophytes which bear no such distinctive impress. In a mesophytic habitat the four factors are present in a more or less balanced optimum. No one exists in marked deficiency or excess. Yet it has been demonstrated experimentally that a moderate increase in any one of the factors will be reflected in an increase of growth. Each factor in reality exerts a circumscribed limiting action as an outcome of competition between the plants. The various effects, however, are so moderate and so well-balanced that it is practically impossible to separate them. While water is usually paramount and light often the least important factor in the competition between sun mesophytes, all four factors show a limiting action in at least a small degree. In spite of its apparent lack of a distinctive impress, a mesophyte is as much the product of its habitat as the well-marked hydrophyte or halophyte, and serves equally well as an indicator.

Climatic and edaphic factors.—The factors of climate and soil are so intricately interwoven in the habitat as to discourage analysis. For many reasons it is better to ignore such a distinction as of little or no significance to the plant and to fix the attention upon the cause-and-effect relation of one factor to another, quite independently of its location. This will reveal clearly two basic facts, namely, that the habitat is a unit and that the action of this unit is focussed upon plant and community by one or two limiting factors. The relation of the plant to water makes it evident that the distinction is merely one of classification which has no real significance to the plant. Water-content as a direct factor resident in the soil is directly or indirectly the result of precipitation, a climatic factor, and is profoundly affected by humidity, a climatic factor which it also influences. Its availability is determined by soil-texture, solutes, and oxygen, all soil factors, and by temperature, which belongs to both soil and air, though in origin it is climatic. The baffling nature of the distinction has been well shown by Raunkiaer (Plant Succession, 1916:6).

In one sense, however, the distinction may possess some value. This is with reference to the factors which give character to the great areas marked by climaxes, in contrast to localized ones occupied by successional stages. It is more or less convenient to refer to such areas as climatic or edaphic, if it is recognized that the one denotes a permanent condition over a wide region and the other a relatively transitory stage in a restricted area.

Moreover, the grouping of factors as physical and biotic appears to have little value beyond that of mere classification. Furthermore, it does not conduce to clear thinking to use the same causal terms for the physical conditions which control plants and animals, and for the plants and animals themselves. With the growing recognition of the community as consisting of both plants and animals, the true nature of biotic factors will become evident, and they will be recognized as reactions.

Climates and habitats.—If one accepts the developmental basis for the study of vegetation, he must also admit the same process in habitats. Habitat and community develop reciprocally from extreme conditions to the final climax controlled by the climate. At this point climate and habitat become merged and are coextensive with the major community, the climax formation. In this connection, however, it is necessary to discard our ordinary ideas of climate and to accept the plant's view of what constitutes a climate. The fact has been appreciated by Wojeikov especially, in his work on the climate of beech (1910). The great grassland climax of North America lends particular emphasis to the difference between climates as determined by plants and by man. In the human sense the climate of southern Saskatchewan is very different from that of northern Arizona, chiefly because of temperature, yet *Bouteloua gracilis* is an important grass in both places and the grassland formation is characteristic of both regions. Likewise the Palouse district of Washington and Idaho with its winter rainfall seems wholly different from the bunch-grass hills of Utah and the prairies of Nebraska; but if the vegetation be taken as the indicator of climate, all three are essentially the same, since they are characterized by prairie associations (Weaver, 1914, 1917).

The acceptance of the climax climate as the major or climax habitat enables us to establish a perfect correlation between habitat and vegetation. The climax habitat will show divisions corresponding to the association, and each association habitat will exhibit subdivisions in agreement with the consociations. This is practically axiomatic, since each community is the product of the factor complex of its habitat. The habitat of one association must necessarily differ from that of another to the degree that one association does from the other. The subordinate communities of a formation, viz, societies and clans, also have their minor habitats, though these are less clearly marked, as would be expected. The structure of the climax climate or habitat corresponds closely if not exactly with that of the climax formation. It may be best illustrated by the grassland climax with its five associations, namely, the true prairie, mixed prairie, bunch-grass prairie, the short-grass plains, and desert plains. While all of these fall in the same climax climate, each one marks a corresponding division of it, or a subclimate. In the case of the true prairie, there are five dominants or consociations, *Stipa spartea*, *S. comata*, *Agropyrum glaucum*, *Koeleria cristata*, and *Andropogon scoparius*, no two of them exactly equivalent as to habitat. Their requirements approach each other so closely, however, that they occupy the same sublicmate, in which they mix or separate in accordance with local variations. An interesting regional separation occurs with the two species of *Stipa*, as well as in the case of *Agropyrum*. *Stipa spartea* marks the eastern portions of the true prairies and *S. comata* the western; *Agropyrum glaucum* is typically associated with *Stipa comata*, while *A. spicatum* is best developed in the Northwest, especially in the Palouse. The essential point is that each consociation or mixture of two or more marks a subdivision of the association habitat, and is the indicator of it. Similar though minor habitat divisions are indicated by such characteristic societies as those of *Glycyrhiza lepidota*, *Amorpha canescens*, *Psoralea argophylla*, *P. tenuiflora*, *Petalostemon candidus*, and *P. purpureus*, the water relations of which are essentially in the order given here. In the eastern prairies, where water is abundant, several of these may occur together more or less constantly, but farther west each tends to form a distinct society, and to indicate a corresponding water-content. The differences are slighter than in the case of consociations, and hence society habitats do not necessarily fall in the habitat of a particular consociation. This is probably to be explained partly also by the action of climatic cycles. For example, the wet phase would favor the local extension of *Psoralea argophylla* and *Petalostemon candidus* for a few years, while during the dry phase the less mesophytic *Psoralea tenuiflora* and *Petalostemon purpureus* would have the advantage.

Since the habitat, like the formation, shows development in the course of succession, it exhibits developmental divisions and subdivisions. Each of these necessarily has its own indicator community, namely, the associes, consocies, and socies. The habitats which correspond to these have a time as well as a space relation. If the best-known succession, the hydrosere, be taken as an example, these two relations are shown in the familiar zones of lakes and ponds. Each plant zone or associes from the center of submerged plants to the surrounding climax of forest or prairie indicates a major developmental habitat, *e.g.*, the habitat of the floating aquatics, of the reed-swamp the sedge-swamp, etc.[1] Each of these associal habitats is subdivided into the habitats of consocies indicated in the reed-swamp, for example, by *Scirpus*, *Typha*, and *Phragmites*, respectively. Within the latter may be minor habitats characterized by such socies as *Sagittaria*, *Alisma*, *Heleocharis*, etc. As a result every region is a complex of climax and developmental habitats of varying rank and extent, each controlling a plant community which serves as the indicator of it.

**Variation of climate and habitat.**—While many reasons make it desirable if not necessary to regard each habitat as a unit, it should be clearly recognized that it varies from place to place and from year to year. The seasonal variations are more or less of the same character and they are marked by their own indicators in the form of the seasonal societies. A grassland climate is characteristically different from a forest climate by virtue of its product, the grassland climax. This has its explanation in the average difference between

[1]Pearsall (1917 : 78) has recently recognized three associes of submerged plants, namely, (1) linear-leaved associes of *Naias*, etc.; (2) *Potamogeton* associes; (3) *Nitella* associes. This is in full accord with our growing knowledge of vegetational development, which must result in the general acceptance of more rather than fewer units (Clements, 1916 : 132). However, the latter must be based upon quantitative studies and checked by extensive scrutiny of other vegetations if the results are not to be mere personal judgments, leading to the condition in which taxonomy finds itself to-day.

the controlling factors of the two during a term of years, but this difference is often less than that shown by the grassland climate in the dry and wet phases of the same climatic cycle. The rainfall of the wet phase if continued for a century or two under natural conditions would turn the prairie into forest, that of the driest period would under the same conditions convert it into desert. Similarly the distribution of rainfall is so erratic that two contiguous localities may show striking differences amounting to the success or failure of a particular crop. Progressive changes of rainfall, temperature, and evaporation occur with increasing altitude, latitude, and longitude. Further, each climate shades imperceptibly into the next, often through wide stretches. These are all elementary facts and the climatologist might well say that they are taken account of in the ordinary way of determining means or normals. As a matter of climatology this is true, but from the standpoint of indicator vegetation it is not. It is a simple matter to trace the line of 20 inches of rainfall, or of the 60 per cent ratio of rainfall to evaporation and to assume that it marks the line between prairies and plains. Such an assumption reverses the proper procedure, in which the associations themselves must be permitted to indicate their respective climates. When this has been done and the limits of the various communities established, it will be possible to determine the correlated factors.

The real importance of climatic variations within a climax habitat lies in the fact that the correlations of vegetation and climate must be studied on the spot year by year. No single station can be typical of the whole habitat, and no year of the whole cycle. Yet for each station and for each year the indicator evidences of the vegetation should correspond closely if not exactly with the controlling factors. As a result, the study of representative localities for each year throughout a climatic cycle should disclose the range of fluctuation in both climax habitat and vegetation, and establish all the indicator values of the latter upon a secure basis.

The minute study of habitats reveals differences which are reflected in the behavior of plant and community, and hence cause the latter to serve as indicators. It is probable that every square foot of a habitat differs in some degree from every other one. Moreover, when the reactions of competing plants are taken into account, the differences are often more minute. In natural studies of competition made in Colorado and in California, as well as in competition cultures, differences of height and flowering have been found for each inch or two. Corresponding differences of density are of even more frequent occurence in herbaceous communities. These indications have been checked by factor determinations only in a few cases as yet, but there can be little question that many more habitats show the most minute differences, each with the corresponding indication in terms of density, height, reproduction, etc. In short, the indicator correlation of plants and habitats exemplifies a universal principle which applies from the relation between climax formation and habitat through units of diminishing rank to the relation between the individual plant and its miniature habitat.

Inversion of factors.—One of the early puzzles encountered in indicator studies, especially in connection with succession, was the occurrence of the same dominant in adjacent but diverse areas. This was first noted for *Andropogon scoparius* and *Calamovilfa longifolia* in sandhill and badland regions. These were found in rough areas and in blowouts on the one hand and in

A. Lowland mesquite (*Prosopis juliflora*) at 2,500 feet in the San Pedro Valley, Arizona.
B. Foothill mesquite meeting oak at 4,500 feet, Patagonia Mountains, Arizona.

meadows on the other. While the seral relations were very different, the relation to water was much the same. On the broken or sandy ridges the soil was porous and the competition relatively small, due largely to the bunch habit, while in the moist meadows the grasses grew in a sod, the competition for water was keen, and the amount for each plant correspondingly limited. A similar inversion in hilly and mountainous regions has since been found for the majority of grass dominants, as well as for an increasing number of shrubs. The breaking-down of the Miocene rim of the Bad Lands of Nebraska and South Dakota yields a talus in which *Rhus*, *Ribes*, *Symphoricarpus*, *Rosa*, and other shrubs occur, all of which form dense thickets in the valley several hundred feet below. *Chrysothamnus*, *Artemisia*, and *Atriplex* grow far up the walls and buttes of bad lands, and are found again as dominants in the ravines and draws. In the Southwest the desert scrub consists of two major dominants, *Prosopis* and *Larrea*. While they are often mixed in the vast stretch over which they occur, *Prosopis* is typical of the valley and washes. The valley plains and bajadas are characterized by a zone of *Larrea*, above which lie *Aristida-Bouteloua* grasslands wherever broad sloping plains occur. In these *Prosopis* again occurs as a consequence of increasing rainfall, at an elevation of 1,000 to 2,000 feet above its position in the desert (plate 6).

Similar inversions occur in mountain regions, either as a consequence of air-drainage or of exposure, or often indeed of both. In the case of exposure, the general relations are obvious, though the relative importance of water and temperature is usually uncertain. It seems probable that both are directly concerned, and that water plays the primary rôle, except in mountain regions characterized by a very short growing season and minimum night temperatures (cf. Shantz, 1906:25; Shreve, 1915:64; Weaver, 1917:44). The effect of temperature inversions was pointed out by Kerner (1876 : 1) and Beck (1886 : 3) in Europe and has been studied by MacDougal (1900) and Shreve (1912 : 110; 1914 : 197; 1915 : 82). The latter's conclusions are as follows (1914 : 115):

"The influence of cold-air drainage might be expected to affect both the upward limitation of lowland species and the downward occurrence of montane species. As a matter of fact the downward limitation of the forest and chaparral vegetation of the desert mountain ranges is due to the operation of the factors of soil and atmospheric aridity, and not to the chimenal factors. The limitation of the upward distribution of desert species appears to be attributable to chimenal factors, as the writer has shown for *Carnegiea gigantea*. The writer has observed that a number of the most conspicuous desert species range to much higher altitudes on ridges and the higher slopes of canyons than they do in the bottoms and lower slopes of canyons. Samples indicate that there is no essential difference between the soil moisture of ridges and the bottoms of canyons during the driest portions of the year. Neither is there any evidence that desert species would fail to survive in the canyon bottoms if they were somewhat higher in soil-moisture content. An explanation of the absence of desert species from canyon bottoms and their occurrence at higher elevations on ridges must be sought in some operation of the chimenal factors rather than in the factors of soil and atmospheric moisture. An analysis of the operation of the chimenal factors will be sure to discover that cold-air drainage plays an important rôle in determining not only the lowness of the minimum, but also the still more important features of the duration of low temperature conditions."

**Measurement of habitats**—The importance of correlating indicator plant or community with the controlling factors of the habitat has already been emphasized. While the standard method of doing this has been by means of physical instruments, a number of attempts have been made to utilize plants themselves for this purpose. While the work of Bonnier (1890 : 514), in which he made reciprocal plantings of alpine and lowland plants, was essentially of this nature, he seems to have had no thought of using plants as instruments. The first conscious endeavor to do this was perhaps in 1906, when potometers of several different species were used with recording instruments to determine the effect of pressure on transpiration at different altitudes on Pike's Peak (Clements, 1907 : 287; 1916 : 439). Sampson and Allen (1909: 45) employed sun and shade forms in different habitats at the Alpine Laboratory to determine transpiration in various light intensities, while standardized plants of *Helianthus annuus* were utilized in habitat measurements conducted by the Botanical Survey in Minnesota in 1909. During 1912–1913, Pearson (1914 : 249) grew seedlings of *Pseudotsuga* beneath aspen and in openings to determine the better habitat for planting operations, and the method has since had a limited application by foresters. The most comprehensive use of the planting method has been made by Hole and Singh (1916 : 48; cf. Chapter III), who established experimental quadrats in the sal forests of India to measure the rôle of shade and aeration in reproduction.

McLean (1917 : 129; cf. Livingston and McLean, 1916) employed soy beans to measure general climatic conditions by means of growth at two stations in Maryland. The three main criteria used in determining growth were leaf area, stem height, and dry weight of tops, all of which showed the Easton region to be nearly 2.5 times as efficient as the Oakland one. A definite correlation was established for temperature, but not for water, owing to auto-irrigation of the plants. Weaver and Thiel (1917 : 46) measured the transpiration relation by means of bur-oak seedlings in three habitats, prairie, hazel-scrub, and oak forest, near Minneapolis. Similar measurements were made with maple and elm seedlings in scrub and prairie at Lincoln. Further experiments were made with sun and shade forms of the same species, and with sun and shade branches of the same plant. The species employed were *Acer saccharinum, Ulmus americana, Fraxinus lanceolata, Rosa arkansana, Prunus serotina,* and *Acer negundo.* The general results showed a transpiration 2 to 3 times greater in prairie than in scrub and 6 to 10 times greater than in the *Typha* swamp. Evaporation was regularly greater than transpiration, and no constant relation was found between the two, as would be expected. Sampson (1919 : 4) has recently made a comprehensive use of *Pisum arvense, Triticum durum,* and *Bromus marginatus* as standard plants in measuring the differences of the climax zones of the Wasatch Mountains in central Utah (cf. Chapter VII).

The use of plants to measure light intensities has as yet received almost no attention in spite of its great promise. This correlation has been made from the standpoint of adaptation by E. S. Clements (1908 : 83); when combined with growth and gross form, as in later studies, this method is simple and of great value. Even more significant is the use of standard plants for measuring light intensity and quality by means of the photosynthate produced in unit areas. Preliminary work of this nature has been carried out by Clements and Long (Clements, 1918:29; 1919; cf. Long, 1919) in the habitats at the Alpine Laboratory, and the chemical procedure has been refined to furnish a basic method of universal application. The use of plants as instruments for habitat analysis is further discussed on a later page.

## THE PHYSIOLOGICAL BASIS.

Kinds of response.—With rare exceptions a physical factor produces a functional response. Such responses are the most direct and the most accurate measures of the habitat, and hence would serve as nearly perfect indicators were it not for their being invisible. Fortunately, functional responses when marked regularly bring about structural changes which are visible. This is especially true of growth which, as the middleman between function and form, has the advantage of being direct as well as visible. Growth, like structure, has the further merit of showing qualitative as well as quantitative differences and thus serves as an obvious record of abnormal response. From the standpoint of indicators, it is desirable to take all three kinds of response—function, growth, and structure—into account and to assign to each its proper value. The relative value is indicated by the sequence of the three as successive effects of controlling factors as causes. The rapidity and accuracy of the response decreases with the distance from the impinging factors, while the readiness of its recognition correspondingly increases. As a consequence, indicator values have so far been based largely upon species and form. The importance of growth has later been recognized and it is but recently that function has been taken into account. In the further investigation of plants as habitat measures and indicators, it is essential to determine the functional responses first, as the most direct and quantitative. These should then be correlated with growth measures and the latter with structural adaptations. When this has once been done, either structure or growth can be used as ready and accurate measures, without resorting each time to the experimental analysis involved in functional measurements. As a matter of practical application, however, it is probable that growth and reproduction will serve as the best indicators of conditions for crop plants since the habitat is more or less controlled. In the case of forest and grassland, where the factors are essentially natural, a further analysis by means of functional determinations seems desirable if not imperative.

Effect of habit—There are three reasons for the superiority of function over form for indicator correlations. The first is that considerable adjustments to factors can occur without affecting structure at all, the demands being fully met by functional responses. Another is that there is almost always a lag between function and structure, by which the effects of a factor appear in the latter only after a time or in diminished degree. These reasons are relatively unimportant compared with the rôle of habit, however, and the second is perhaps only a consequence of the latter. While there has been little experimental study of habit as such, there are many suggestions of its importance in modifying or reducing response, especially in structure. This influence of habit is well known to foresters and agriculturists in connection with the germination of seeds from different regions and the behavior of their seedlings. It has also been shown in the case of alpine species transplanted to lower levels in that some retain the dwarf habit and others do not (Bonnier, 1890), and for subalpine trees, some of which change their form and not their seasonal phenomena, while others reverse this behavior (Engler, 1912 : 3). The response of herbaceous species grown in two or more habitats is equally significant. Some are so responsive or plastic that both form and structure show practically perfect adjustment to each habitat in the first generation. Others modify the form and not the anatomy, and still others the interior of the leaf but not its form. There are all degrees of completeness of response to the stable plant, in which form and structure change little, and all the adjustment must be secured through function (E. S. Clements, 1905: 93).

As a consequence, the indicator value of any species can not be known until its functional response has been measured and correlated with the structural. This does not mean that the constant occurrence of a species in certain conditions can not be turned to practical account, but it does suggest the wisdom of regarding such correlation as tentative until the functional indication has been determined. The latter will also solve the puzzles presented by communities in which very different life-forms, such as evergreen and deciduous trees, appear to flourish on equal terms. The most striking case of the masking of the real response by habit is seen in such leafless rush-forms as *Scirpus lacustris* and *Equisetum*, in which it is now proved that the functional response is that of a hydrophyte (Sampson and Allen, 1909 : 49; Dosdall, 1919).

Individuality in response.—Indicator values center about the species. Uniformity of behavior under uniform conditions and clear-cut adjustment when these are changed are the essentials of a good indicator. For these reasons it is important to deal chiefly with species which are represented by many individuals, such as dominants and subdominants, and hence to use the community as the basis for indicators. This makes it necessary to determine the range of individual response in function and growth as well as in structure. In developing the use of standard plants as instruments, this matter is of the first importance. While the question of standardization will always enter, it will be convenient to use those species in which the individuality or functional response is slight. In the use of indicators, the range of individual behavior is a less important consideration than the knowledge of the range.

Sampson and Allen (1909 : 37) have studied the individual behavior of four montane species as to transpiration and reached the following conclusion:

"Only slight variations occur, not usually exceeding 3 mg. per square centimeter for a period of 12 hours. Therefore, it may be concluded that plants of the same species grown in the same habitat when tested under the same physical conditions show but slight variation in transpiration per unit of surface exposed."

Effect of extreme conditions.—The significance of extreme conditions for response and the relation to indicator values is shown by the case of xerophytes and halophytes. While the latter are now known to be merely xerophytes of a somewhat special type, they were long thought to constitute a distinct class. This is still true in a measure of those species which tolerate salts directly injurious, but it is well known that the majority owe their impress to physiological dryness due to the abundance of salts. But, while halophytes are indicators of arid conditions, it is a special type of aridity, and the indication must not be assumed to mean just what it does in ordinary soils.

A somewhat similar case is afforded by the evergreen shrubs. In spite of the work of Kihlmann (1890 : 88, 105), it has been generally assumed that the evergreen shrubs of bogs, such as *Chamaedaphne*, *Andromeda*, *Vaccinium*, *Ledum*, etc., were xerophytes essentially similar in water relations to evergreen shrubs of arid climates. Recently the experiments of Gates (1914 : 445) have confirmed the conclusions of Kihlmann that while they are xerophytic, it is in response to physiological dryness in winter, and that they do not indicate aridity in such habitats during the summer. In fact, the summer indications are rather those of deficient aeration.

When growth is considered, the response of the same species to different extremes of one factor or another is often very similar. E. S. Clements (1905 : 93) has found in control experiments with *Chamaenerium*, *Aquilegia*, and *Anemone* that extremes of any factor which are not optimum for the species tend to dwarf plants growing in them. The general principle has been formulated as follows by Clements (1905 : 105):

"When a stimulus approaches either the maximum or minimum for the species concerned response becomes abnormal. The resulting modifications approach each other and in some respects at least become similar. Such effects are found chiefly in growth, but they occur to some degree in structure also. It is imperative that they be recognized in nature as well as in field and control experiment, since they directly affect the ratio between response and stimulus."

This applies with especial force to the recognition of indicators, since their value depends primarily upon the close correspondence between response and the causative factor.

Phytometers.—The best indicator of the nature of a habitat and of its practical utilization is the particular plant or community concerned. This is axiomatic, but it needs emphasis in connection with the experimental study of indicators. Such study may be made by means of physical instruments, standard plants, or the plants to be grown as a natural or artificial crop. The former is the simplest of the three, the latter the most effective. The use of standard plants combines the advantages of both to a large degree, and seems destined to undergo extensive development during the next few years. The refinement of method will lead to an increasingly wider range of possible standard plants, until it includes a large number of the species of greatest importance in agriculture, forestry, and grazing. Out of these will emerge a few species of broad powers of adjustment and adaptation which can be used as measures over great areas, such as between the associations of a climax formation or even between climax habitats themselves. A number of species of this sort are already clearly pointed out by their vast ranges and their vigorous growth in different regions. Of the grasses, *Bouteloua gracilis*, *B. racemosa*, *Stipa comata*, and *Andropogon scoparius* are perhaps the most promising, and among shrubs *Rhus trilobata*, *Cercocarpus parvifolius*, *Ceanothus velutinus*, and *Rubus strigosus*. Of the trees, aspen is the best, with *Pinus ponderosa* and *Pseudotsuga mucronata* as the best of the conifers for the western half of the continent. As general standards, such weedy herbs as *Helianthus annuus*, *Melilotus alba*, and *Brassica nigra* are most useful. The most satisfactory cultivated plants are yet to be determined, but wheat, corn, and beans have obvious advantages.

Preliminary results justify the feeling that standard plants or phytometers can be developed with more or less readiness to measure varying amounts of the direct factors, water, light, temperature, soil-air, and solutes. Such functional responses as transpiration and photosynthesis furnish the most accurate measurements, but growth responses are also of the greatest value, especially where factor-complexes are to be measured. Determinations based upon responses in form and structure are also distinctly valuable. Because of the longer time involved, they do not permit of such complete control, and their correlation is less exact. In all of these, the error due to individual behavior must be checked out by careful selection of individuals and by using a number sufficiently large to yield a mode and to permit the elimination of those which depart widely. In addition it has proved increasingly desirable to use a battery of two or more species as phytometers, since this increases the number and accuracy of the results quite out of proportion to the extra labor involved.

The first application of the phytometer method was made by Clements and Weaver (Clements, 1918 :288; 1919) at Pike's Peak in 1918 and 1919. The plants used were sunflower, beans, oats, wheat, sweet clover, and raspberry, *Rubus strigosus.* These were grown in sealed containers, with plants in open pots as checks on the conditions for favorable growth in the former. The normal number of pots for each species was 3 to 5, but this was often reduced by mishaps. Three series were grown during the summer; the period varying from 28 to 45 days. The habitats measured were those of the short-grass association at 6,000 feet, the half-gravel associes, the gravel-slide associes, and the *Pseudotsuga* consociation at 8,500 feet, and the *Picea engelmanni* consociation at 9,000 feet. Stations were visited each week for the purpose of making weighings and of reading the various recording instruments. The responses primarily considered were transpiration and growth, though photosynthesis was measured also. These showed marked differences with reference to altitude, degree of shade, and seasonal factors. The relative values were the same for the native *Rubus* as for the cultivated plants, and the complete results seem to leave no question of the paramount importance of plants for the quantitative study of habitats and communities (plate 7).

The use of several dominants in a phytometer battery amounts almost to employing a plant community as a measure, and suggests the possibility of utilizing portions of actual communities in this way. The simplest way of doing this at present is by means of permanent quadrats which are visited each month or each year and growth actually recorded by height or volume measures or by weight. Since many communities containing both dominants and subdominants, such as *Stipa* with *Amorpha canescens, Psoralea tenuiflora,* and *Brauneria pallida,* occur throughout the area of most climaxes, a series of quadrats containing essentially the same population can be established through a wide range of conditions. Locally, where diverse habitats are found within short distances, as in the case of zones about ponds and of dynamic areas, it is not difficult to transfer soil-blocks of the same community to several different habitats and to follow their behavior in terms of the growth and abundance of the species concerned. Such communities afford the best possible measure of the seral habitats and reactions typical of succession, especially when reciprocal transfers are made between two contiguous or successive stages.


A. Phytometer station in grassland at 6,000 feet, Colorado Springs, Colorado.
B. Battery of oats, gravel-slide station, Minnehaha, Colorado.
C. Battery of oats, brook-bank station, Minnehaha.

## THE ASSOCIATIONAL BASIS.

**Nature of association**—The association of two or more species in a community is due to one or two of the following three reasons: (1) general similarity of functional response to controlling factors; (2) dependence upon the reactions of the dominants modifying these factors; (3) dependence upon the autophytes as hosts or matrices. The last two reasons also explain as a rule the presence of the animals of a community as well. Hence it is obvious why one species of a community should indicate the actual or probable presence of the others regularly associated with it, and likewise the corresponding factors. This principle is susceptible of extended application, but it is nowhere more striking than in the case of relict herbs of a former forest. Though axiomatic, it must be used with some care, since no two species are exactly alike in response and indication, and since successional factors often enter to cause confusion.

The occurrence of a dominant indicates not only the presence or possibility of its associated dominants, but also that of the related subdominants, secondary species, hysterophytes, and animals. This is as axiomatic as it is patent in the case of an actual community in the field. This relation becomes of real indicator significance where the community is partially or largely destroyed, when it is rapidly changing, or is but incompletely known, especially in the case of fossil vegetation. A subordinate species likewise indicates other subordinate species as well as the controlling dominants, except in those plants which occur in two or more associations or formations, as well as in different seral stages. Even hysterophytes have a distinct indicator value when they are restricted to particular hosts. Moreover, it is clear that the associational relation signifies that animals may often be indicators of plants, as well as plants of animals.

**Dominants.**—A dominant is the most important of all indicators. This is due to several reasons. The first of these is that it receives the full impact of the habitat, usually throughout the growing period. The second reason is that it reacts upon the controlling factors, and thus modifies the response of its associates. It also marks the progress of succession and consequently is bound up in a sequence of dominants, with the result that it affords both developmental as well as associational indications. In addition, it shows great abundance over extensive areas and occupies a wide range. In fact, its very dominance is the sign of its success under the conditions where it controls. However, it is necessary to recognize that a dominant species is not always dominant, and that its control may be local and developmental in parts of its range, while it is extensive and climax in the main portion. *Bouteloua gracilis* is one of the most exclusive of climax dominants in its typical area, the short-grass association of the Great Plains, but it becomes a co-dominant or merely a successional one in the related associations of the grassland formation, and on the edge of adjacent climaxes, such as the chaparral and the sagebrush. In the *Stipa-Koeleria* prairies it is subclimax on the ridges and drier slopes, while in the *Aristida-Bouteloua* desert plains it is usually subclimax also, but in the valley plains and swales it is truly climax. In all three associations it possesses indicator value as a dominant, but this value is different in each one, both as to its associates and the relative conditions. Near the edge of its range it loses its dominance and becomes merely a subordinate member of the community with a greatly modified or restricted significance.

The distinction between the dominance and the mere presence of a species is vital, from the standpoint of the structure of vegetation as well as from that of indicators. It is this which makes catalogues, lists of species, and general descriptions of the flora of a region of little value to the ecologist. In fact, such materials are trustworthy only in associations already known, where they are superseded. This is exemplified by a number of grass dominants. *Bouteloua gracilis* is found from Manitoba to Wisconsin and Mississippi, west to Texas, central Mexico, and California, and northward to Alberta and Saskatchewan. It occurs as the characteristic climax dominant of the short-grass association only in eastern Colorado, southwestern Nebraska, western Kansas and Oklahoma, northeastern Arizona, northern and eastern New Mexico, and in the Panhandle and Staked Plains of Texas. Usually with *Bulbilis*, it is more or less regularly associated with *Stipa* and *Agropyrum* from northwestern Nebraska and northern Wyoming through the Dakotas and Montana, into Saskatchewan. Altogether it is a climax dominant over perhaps a quarter of its range and a seral dominant over another quarter. *Stipa comata* is a climax dominant to-day only in Nebraska, northern Colorado, Wyoming, the Dakotas, Montana, and Saskatchewan, though it ranges from the latter to Nebraska, New Mexico, California, and northward to Alaska. As a consequence, the vegetational and indicator importance of any dominant species can be determined only by field studies of its abundance and rôle. Maps and conclusions based upon the distributional area alone are both misleading and erroneous (plate 8.)

Equivalence of dominants.—The dominants of a formation owe their association to the generally similar responses which they make to the climax habitat. This fact is further attested by the identity of life-forms and, to a small degree as yet, by actual measurement of the controlling factor. As the sum of similar responses, the formation is thus the largest and most distinctive of all indicator communities. Within the formation the dominants fall into associations by virtue of still closer similarity in response. Thus *Stipa*, *Agropyrum*, and *Koeleria* constitute the climax prairies. By their height and general turf habit they indicate a rainfall of 20 to 30 inches. *Bouteloua gracilis* and *Bulbilis dactyloides* form the short-grass plains. Their short stature and mat habit are responsive to a smaller rainfall of 12 to 22 inches, which in effect is much reduced by evaporation. The *Aristidas* and *Boutelouas* of the desert plains from Arizona to western Texas are somewhat taller, but their bunch habit is an index of a smaller water efficiency, largely the result of excessive evaporation. This relation is further indicated by the presence of *Bouteloua gracilis* in the moister valleys, and by the fact that *Stipa* and *Agropyrum* regularly mix with the short-grasses as indicated above, but have never yet been found mixed with the species of *Aristida* and *Bouteloua* characteristic of the desert plains. So far as our present knowledge goes, dominants of the same association or of the same associes are never exactly equivalent. Actually, they may seem to be since the annual variations of the climatic cycle are often much greater than the difference in conditions. Even here, however, they tend to maintain their position or abundance, relative to the controlling factor. As a consequence, each consociation has its own indicator value, which, so far as its presence is concerned, necessarily varies somewhat from wet to dry phases of the cycle, but is checked by corresponding variations in growth, reproduction, and abun-


A. *Anogra albicaulis* as a seral dominant in a fallow field, Agate, Nebraska.
B. *Stipa comata* as a climax dominant of the mixed prairie, Chadron, Nebraska.

dance. Thus, *Stipa spartea* and *Agropyrum glaucum* show climatic differences from *S. comata* and *A. spicatum*, while *Stipa comata* and *Agropyrum glaucum* occur together over thousands of square miles, but are differentiated by water relations determined by soil and slope. The actual physical differences in equivalence are slight, and hence the dominants of an association tend to mix or to alternate intimately instead of being pure over wide areas. However, this is necessarily truer of an association with several to many dominants than of one with but a few (cf. Zon, 1914 : 124).

Each dominant will grow in a fairly wide range of conditions, but will thrive only in a much narrower range. The field optimum for each is not a single point but an area. The areas of the dominants of the same association or associes overlap to such an extent that they coincide except at the extremes. If the ranges of normal adjustment of *Stipa comata* and *Agropyrum glaucum* be represented in each case by a rectangle, the two rectangles will coincide for three-fourths of their lengths approximately. This indicates the degree of equivalence, the projections of each rectangle representing the actual difference in water-response for each species. This overlapping has its real counterpart in communities where the dominants are zoned. The mixed area between two zones represents the range of factors for which the two dominants are equivalent, and the pure zone on either side indicates the range peculiar to each. There is no necessary correspondence between the width of the zones and the mixed area, and the range of factor coincidence for the two dominants, owing to the varying rate at which such a factor as depth of water or amount of water-content may change. In the lakes of Nebraska, the two successive dominants, *Scirpus* and *Typha*, occupy the same depths from a few inches to several feet. Over most of this range they are mixed or alternating, but beyond 4 to 5 feet *Typha* drops out, while *Scirpus* may persist to a depth of 6 to 7 feet. Except where shores slope rapidly, the mixed zone is many times wider than the zone of pure *Scirpus*.

In this connection it should be recognized that dominants show a wider margin between the normal range and better conditions than between it and worse conditions. In other words, a species is quickly and definitely limited by unfavorable factors, while those generally favorable to growth exert little limiting effect, the real effect being due to competition. This is the obvious explanation of the number of dominants and the abundance of species in sunny well-watered habitats, such as prairies, open woods, alpine meadows, etc., and their paucity in deserts and saline wastes. In short, abundance is itself an indicator, whether it concerns the individuals of one species or the species of a community.

Absence of dominants.—The absence of a dominant from its particular community is often of indicator significance. A dominant may be lacking as a result of several different causes. Its absence may be due to unfavorable controlling factors, to very uniform conditions, to competition, destruction, or to the failure of invasion for any reason. In all of these cases except the last, absence has a definite indicator value, though it is practically always supplementary to the presence of its associates. This is perhaps its chief value, in that it enables us to check the positive indications obtained from presence. Absence due to unfavorable conditions or to competition is the rule. Uniformity of conditions, however, is a more frequent cause than has generally been recognized. This is well illustrated by shallow lakes in the sandhills of Nebraska, where the depth is so uniform that *Scirpus* is the sole dominant in spite of the fact that neighboring lakes show *Typha*, *Zizania*, and *Phragmites*. Absence as a result of destruction is usually difficult to determine and yet is of the greatest indicator importance. The grassy parks of the Uncompahgre Plateau in Colorado are so extensive and appear so permanent that their real significance, as well as that of the absence of the trees, was finally determined only by the discovery of burned wood deep in the soil. Similarly, much evidence has been found to show that the absence of *Stipa* or *Agropyrum* over wide stretches of the Great Plains reveals overgrazing of a type that has never been suspected. Thus, while absence is necessarily correlated with the presence of the related dominants in order to be usable, it does furnish indications of much value.

Subdominants.—Subdominants are species which exert a minor contro within the area controlled by one or more of the dominants of an association or associes. They are the successful competitors among the species which accept the conditions imposed by the dominants. As a rule they differ from the latter in life-form, and their competition is largely mutual rather than with the dominants. This is obviously the case in forests where the subdominants form layers. In grassland, where light controls in a minor degree alone, the layering is in the soil, but with a somewhat similar result that the dominants use the water before it reaches the deep-rooted herbs. In prairie and meadow, there is often enough water for both, a condition favored by the fact that subdominants reach their maximum at different times during the season, and hence cause the characteristic seasonal aspects. During dry phases of the climatic cycle, however, there is direct competition between dominants and subdominants, but usually at the expense of the latter.

Within the limitations set by the dominants, subdominants follow the same general principles as to indicator values. This applies to their association in a community, either climax or seral, their equivalence, their dominance as compared with mere presence, and to their absence. They diverge, however, in exhibiting a seasonal sequence in many associations, by which they appear to escape too intense competition with each other. Prairies purple with *Astragalus crassicarpus* in April and May are covered with *Amorpha*, *Psoralea*, *Petalostemon* and *Erigeron* in June and July, and these in turn yield to golden rods, asters, and blazing stars in August and September. To a large extent these successive societies occupy the sa ne ground and would seriously compete with each other were it not for the fact that the maximum demands of *Astragalus*, for example, are over before those of *Psoralea* and *Erigeron* begin. Societies thus have a time as well as a space value as indicators. While the subdominants of the same aspect are equivalent to a large degree, those of the three aspects, spring, summer, and autumn, differ in being progressively more xerophytic, owing to the seasonal relations of rainfall and evaporation. Societies are not only most numerous and best-developed during the early summer because of optimum conditions, but they likewise reach a maximum in those communities with optimum conditions, such as prairie and forest. In the short-grass plains they are greatly reduced, and in desert they are relatively few, except in the spring. This exception covers those deserts with two rainy seasons in which the socies of winter and summer annuals are possible only because of a relative excess of moisture near the surface at these times (plate 9).

A. *Pentstemon gracilis* as a climax subdominant in mixed prairie, Gordon, Nebraska.

B. *Pedicularis crenulata* as a seral subdominant in a *Juncus-Carex* swamp, Laramie, Wyoming.

**Secondary species.**—This is here used as an inclusive term to comprise all the autonomous species of a community outside of dominants and subdominants. Their subordinate importance has caused them to receive relatively little attention, but their correlation with habitat factors has gone far enough to show that they all possess indicator value to some degree. In a sense, this is thrice removed from the habitat, since in climax communities in particular the conditions to which secondary species respond have been modified by the dominants and then by the subdominants. Secondary species either make minor communities such as clans, *e. g.*, *Antennaria dioeca*, *Meriolix serrulata*, *Anemone caroliniana*, *Delphinium carolinianum*, etc., or they occur as scattered individuals in society or consociation. When they form more or less extensive clans which recur throughout an association, their indicator value approximates that of a subdominant. In fact, it must be recognized that some of the most important clans might well be regarded as societies. Or to put it more clearly, some subdominants vary sufficiently in abundance and control from place to place and year to year that they may form societies at one place or time, and clans at another. Apart from these, clans and scattered species have their chief importance in revealing minor differences of habitat within the consociation or society. They are often due to small disturbances and to succession in minute areas, and derive their indicator significance from this fact. It is probable that the careful study of secondary species will disclose some indicators of much sensitiveness and usefulness.

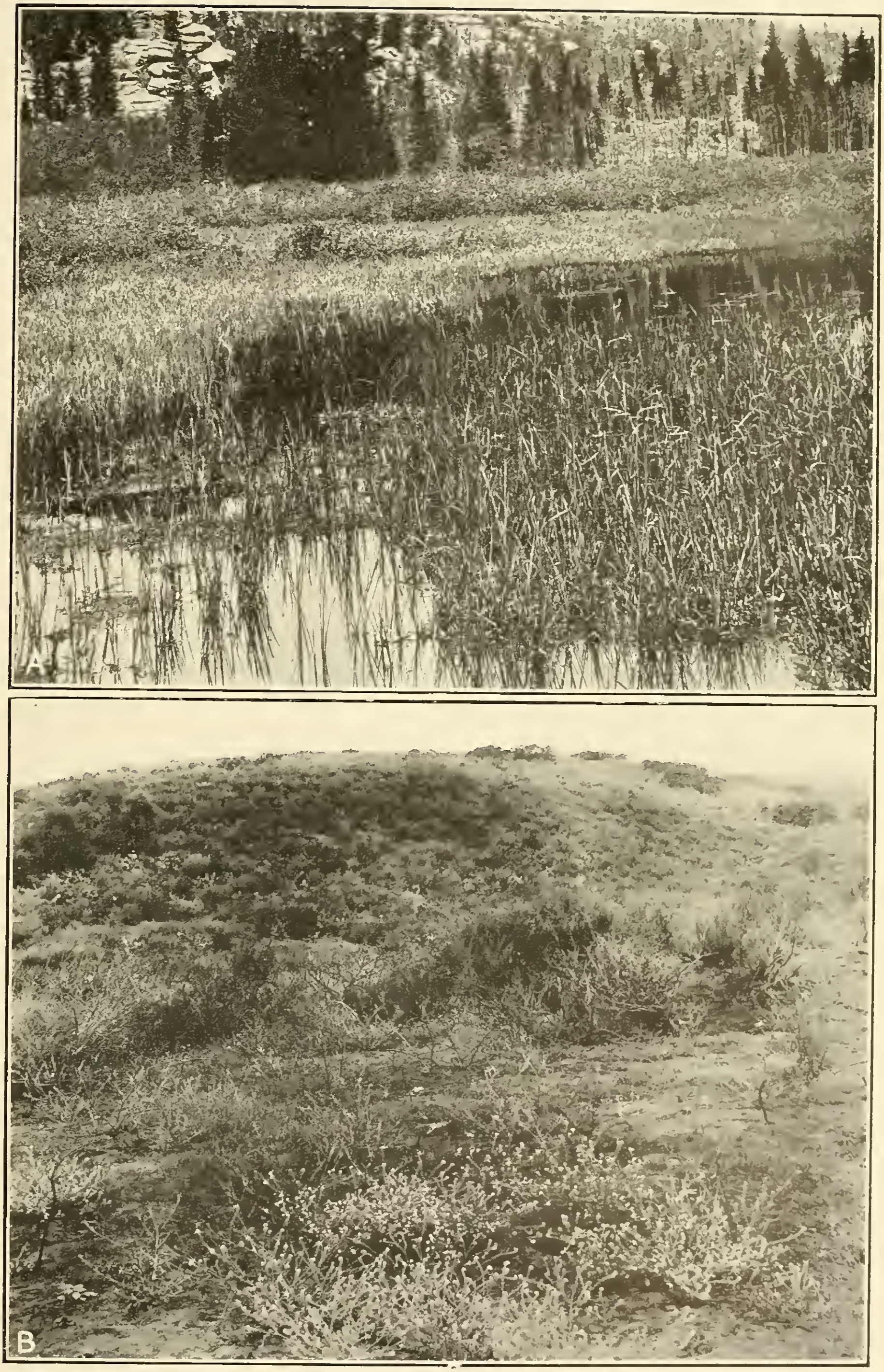
**Plant and animal association.**—It is desirable for many reasons to consider animals an intrinsic part of the community as a biological unit. The great value of this is that it insures an adequate and correlated treatment of both plants and animals. It does not change in the least the basic relations between physical factors, plants, and animals, upon which their mutual indicator significance depends. Just as the plant indicates the factors and processes to which it responds, so does the animal serve as an indicator of the plant or community which furnishes it food, shelter, or building materials. The animal also indicates physical factors in so far as they affect it directly. The plant, however, has a double indicator relation by virtue of its response to factors on the one hand and of its control of animals on the other. Since animals are mobile for the most part, the control and the indications afforded by plants are necessarily less definite and exact. While the study of animal communities has gone far enough to provide a qualitative basis for plants and animals as reciprocal indicators, there has been no conscious endeavor to investigate this relation as yet. This is not true of paleontology, however, in which such causal relations as that between grassland and grazing animals have been much used. Even here an adequate and comprehensive system must await a fuller development of indicator values in present-day communities. A preliminary attempt at such a system in both ecology and paleoecology is made in Chapter III.

## THE SUCCESSIONAL BASIS.

**Scope.**—Since the nature of the habitat and the character of the population are constantly changing in all seral areas, succession is of profound importance in connection with indicators. While the basic rule that plants respond to the controlling factors holds for developmental as well as climax communities, the indicators change as the succession advances. Each stage of the succession is marked by factors which act upon species which react in turn. Hence the indicator relations change more or less slowly but inevitably from one stage to the next. While the developmental areas of a formation are usually less in aggregate extent than those occupied by the climax stage, they are so numerous and various as to demand constant attention. The relative permanence of an indicator relation depends wholly upon whether it is determined by developmental or climax conditions. Since the use of any area for cropping, forestation, or grazing either demands or effects constant changes in it, succession is the basis of all utilization of communities or dominants as indicators. This is especially true in the case of land classification, as Shantz has shown (1911 : 18), and it applies also to all engineering and construction operations in which the soil is disturbed or new habitats produced.

Sequence of indicators.—Succession has been defined and analyzed as the development of a complex organism, the climax community or formation (Clements, 1905 : 199; 1916 : 3). It is a chain of causally related functions or processes. Development begins at certain definite points, pursues a regular course, and ends in the final or mature stage, the climax. As a result, each seral dominant or community has indicator values beyond those arising from the basic relation between plant and habitat. Each stage is the outcome of those that precede and the precursor of those that follow until the climax is reached. It indicates not merely the existing conditions, but it also points backward through successively remote stages to the beginning of the sere, and forward through those which lead up to the climax. Since the development of the habitat proceeds step by step with that of the formation, each stage is an indicator of earlier and later habitats as well as communities. Succession, moreover, is always progressive, and makes it possible to forecast not only the direction of development but something of the rate as well. It depends primarily upon the production of new, denuded, or disturbed habitats, and thus serves as an indicator of the many processes, physiographic, biotic, etc., which initiate new habitats or denude existing ones.

The several indicator values of a seral community depend primarily upon the climax and the sere to which it belongs. The climax determines the dominants and subdominants from which the stages are drawn, indicates the climate in general control of the habitat changes, and constitutes the final stage toward which all the successions are moving. It is in itself an indicator of succession, since it permits the prediction of the general course of development that results from any disturbance in it. The division of seres into primary and secondary rests upon the double basis of habitat and development, and explains why each sere has indicator significance in itself. The primary sere or prisere indicates an extreme condition of origin, such as water or rock, slow reaction on the part of the earlier communities especially, and hence a large number of successive communities. The secondary sere or subsere begins on actual soil in which the conditions are not extreme, requires less reaction, exhibits few stages as a rule and runs its course to the climax with much rapidity. All seres, but primary ones in particular, are distinguished upon the basis of the climax and the water relations of the initial area. The great majority of seres are mesotropic, that is, they progress to a mesophytic climax. In desert regions they are xerotropic and in the tropics may be hydrotropic (Whitford, 1906). Their indicator meaning varies accordingly, but it is even more subject to the water-content of the initial area. Seres are termed hydrarch (Cooper, 1912: 198) when they originate in water or wet areas, and xerarch when the initial




A. Stages of a hydrosere from floating plants to forest, Pike's Peak, Colorado.

B. Stages of a burn subsere from the pioneer annuals to the chaparral climax, San Luis Rey, California.

condition is xerophytic or at least considerably drier than the climax. The nature and indicator value of hydroseres differ in accordance with their origin in lakes and swamps, or in bogs or other poorly aerated wet soils (oxyseres). Similarly, the indicator values of xeroseres vary with their origin upon rock, dune-sand, or in saline areas (plate 10).

**Major successions as indicators.**—The seres or unit successions discussed above are themselves parts or stages of greater successions. The cosere is a series of two or more unit successions in the same spot, and is best illustrated by those peat bogs in which the remains of the various stages and seres are accumulated in sequence and in position. In addition to the indications furnished by each sere, the cosere always indicates one or more striking changes of condition. When it exists over a wide area or recurs in the same relation in several regions, it is an indicator of climatic change. An effective change of climate is denoted by the occurrence of the peat formed by water-plants as the layer above that which records the presence of the climax or subclimax trees. Such coseres have been industriously studied by European investigators, Steenstrup, Blytt, Lewis, and others (Plant Succession, 378), and their climatic correlations established with much certainty. The record of a cosere is well preserved in water and especially in peat-bogs, but the more or less fragmentary records furnished by burns, dunes, moraines, and volcanic deposits are often of great value. This is especially true of the deposits of periods of great volcanic activity, such as the Miocene, as found in Yellowstone Park and the John Day Basin (Plant Succession, 367).

Major changes of climate are accompanied by the shifting of climaxes as well as by the succession of seres in the same spot. The differentiation of climates during the Paleophytic and Mesophytic eras led to corresponding differentiation of vegetation with characteristic zones grouped around centers of deficiency or excess. These zones were clearly marked out by the middle of the Cenophytic era, since which time the major effects of climate have been recorded in their shifting. It seems highly probable that the climatic cycles which produced and characterized the glacial period were accompanied by marked shifting of climax zones and that the close of the period left the primary zones of continents and mountains much as they are to-day. Such zones are the most striking and important of all climatic indicators, and their significance has been appreciated and investigated for more than a century. Perhaps even more important is the fact that such a series of shiftings or zones is a successional process by which it becomes possible to predict the general effect of any climatic cycle. This relation has already been developed to some extent (Plant Succession, 347, 364) and is further discussed in connection with paleo-ecology (Chapter III). The greatest climatic changes of geological times are thought to be indicated by the evolution of the great land-floras and their differentiation into climax vegetations. Thus, the entire course of the development of the earth's vegetation, which is called the geosere, is divided into eoseres corresponding to the three great eras, and each eosere then exhibits clisere shifting in response to lesser cycles. The use of zones as indicator criteria is discussed in the next section.

## THE EXPERIMENTAL BASIS.

**Nature.**—Indicators derive their importance chiefly from their practical applications. For all practical purposes, indicator values must finally be determined by experiment. The degree of their usefulness will depend mostly upon the kind and thoroughness of the experimental test. The planting of a trial crop by a settler will give some idea of the indicator meaning of the native vegetation that has been removed. In such a case the evidence is slight and its value tentative. If the planting is repeated for several years or is extended to other farms or localities, its value increases accordingly. As this is the usual course for a crop in a new region, it is obvious that ordinary agricultural practice must suggest indicator correlations with crop plants. This is well known to be the case, but the actual utilization of indicators by farmers seems always to have been inconsiderable. This is largely due to a lack of knowledge of native plants, especially in a new region, but also to the fact that this knowledge was needed most in selecting land and choosing crops, at a time when it was still to be acquired. Thus, while the aggregate experience of a neighborhood might possess real value, there has rarely been any method of formulating it and making it effective.

The extension of experiment stations and substations throughout the West initiated the period of scientific study of agricultural problems. The investigations were directed chiefly to the selection of the best varieties for different regions and soils and to the improvement of yields. Unfortunately, the botanist was not interested in the problems of field crops and the agronomist was little or not at all concerned with native vegetation. The result was that a great mass of experimental data remained unavailable because it lacked correlation. It was possible to give this only through ecological studies, and then only after quantitative methods had been devised for the analysis of habitat and community. As a consequence, exact and purposeful studies on indicators date from the present decade for each of the three great fields, agriculture (Shantz, 1911), forestry (Clements, 1910), and grazing (Clements, 1916 : 102; 1917 : 303; 1918 : 296; 1919). In spite of this late beginning, the recognition and utilization of indicators are destined to undergo rapid development. This is especially true of forestry and grazing, owing to the fact that the corresponding experiment stations and reserves are organized upon the basis of exact ecology.

Essentials.—It has already been insisted that experiment affords the only decisive test of an indicator. A single experiment may do this if properly checked, but repetition is regularly necessary to cover the range of conditions in space and in time. The experiment itself must be made with the fullest knowledge of the factors concerned as well as the vegetation to be correlated. As already pointed out, this involves quadrat study of the community and its successional relations, and instrumental study of the habitat and its variation through the climatic cycle. The thoroughgoing application of this method makes it possible to take advantage of countless natural happenings to convert them into experiments. The number of such possibilities furnished by denudation, lumbering, fire, cultivation, grazing, etc., is countless. If adequately utilized, they will not only greatly reduce the number of set experiments necessary, but will also make the latter possible on a scale otherwise out of the question. The natural experiment has the advantage in economy of time and effort, and in repetition of examples. The checked experiment permits of a definite choice as to time and place, and allows greater control. It is the essential task of experimental ecology to combine these into a complete method, which will give quantitative results throughout the field of ecology as well as in connection with indicators. This is one of the primary objects of the present treatment, though the indicator relations are necessarily given first place.

## INDICATOR CRITERIA.

**Nature and kinds of criteria.**—Every response of the plant or community furnishes criteria for its use as an indicator. These are most serviceable when they are visible, but demonstrable functional responses may be even more valuable, though invisible. The evidence as to functional responses in natural habitats is still very limited, and will be considered in the next chapter under the factors concerned. Here the discussion is confined chiefly to the criteria afforded by form and structure, with which growth is included. The development of the community is also considered along with its structure for the same obvious reasons

Criteria may first be divided into two kinds in accordance with their relation to the individual plant or to the plant community. Individual criteria are phylogenetic when they have to do with species and genera, and ecological when they relate to life-forms and habitat-forms. It is probable that these are all ecological responses, and that species and genera are more remote in origin and hence their ecologic significance less evident. Life-forms are less remote and their dependence upon the habitat more evident, while habitat-forms are mostly of more recent origin and their relation to the habitat obvious. This view seems to be supported by the fact that it has proved impossible to make a system of life-forms which is not based in part upon taxonomic forms and in part upon habitat-forms. All of these criteria permit still finer analysis, as species into varieties and forms, and habitat-forms into those produced by local or minute habitats. The experimental study of species and life-forms is still too slight for such a procedure, and it is possible as yet with only a small number of habitat-forms. The consideration of indicator criteria is based upon the following divisions: (1) species and genera; (2) life-forms; (3) habitat-forms; (4) growth-forms; (5) communities.

**Species and genera.**—Quite apart from the life-forms and habitat-forms which they exhibit, species and genera, and to some extent families also, have an indicator value dependent upon their systematic position. The latter is determined primarily by the responses recorded in the reproductive structures at a time relatively remote. Their indicator meaning is consequently often obscure, and this obscurity is increased by a complete lack of experimental knowledge as to the factors which originate reproductive characters. Thus, while many species and genera show correlations with habitat or climate, this is chiefly on the side of vegetative responses, such as the relation of the *Nymphaeaceae* to bodies of water. They often exhibit, however, a valuable indirect correlation with climate due to origin and migration. This is the basis of floristic studies such as those of Sendtner (1856), Drude (1890), and others, and of the more exact floristic methods of Jaccard (1901–1914) and Raunkiaer (1905–1916). The value of these must remain statistical and general until they are related to successional movements and to measured physical factors.

Species and genera acquire their chief significance by virtue of the ecological values involved in phylogenetic relationship. This is obviously true of all genera which are largely or wholly consistent as to life-form, and it holds to a considerable degree for all others. Habitat, successional, and indicator values are concerned in this, and the genus thus becomes a sign of a more or less definite ecological complex of responses. This is likewise true of species in the general sense employed by Linné and Gray. A genus consists of several to many species because of the diverging evolution of an original stock under the more or less direct control of changing habitats. A species shows a similar evolution of forms, distinguishable from each other but mutually related to each other by descent, as are the species of a genus. For the ecologist, the relationship of such forms to the parent species is fully as important and even more significant than their recognition. It is imperative for his purposes that this relationship to the species be shown by the name as the latter shows that of species to the genus. This demands the use of trinominals, which is in accord with the general practice of ornithologists and mammalogists, but contrary to that of many systematic botanists. The one disadvantage of the trinomial is length, but this is readily obviated by using merely the initials of the specific name, *e. g.*, *Achillea m. lanulosa*, *Ranunculus f. reptans*, *Galium b. scias* (Clements, 1908 : 263; Clements and Clements, 1913). This has long been the well-known practice of mammalogy and ornithology, *e. g.*, *Citellus t. parvus*, *Lepus c. melanotis*, *Cyanocitta s. frontalis*, *Buteo b. calurus*, etc. This or a similar method is inevitable if systematic biology is to aid and not hinder the development of ecology and the closely related practical sciences of agriculture, horticulture, forestry, plant pathology, economic zoology, etc. Three reasons would appear to lead irresistibly to this result. The field worker must deal with units which are recognizable in the field with a fair exercise of patience and keenness. He must carry in mind the names and characteristics of a large number of species, and he can do this only by relating them to each other. There is a very definite limit to the capacity of the average memory, and this limit is greatly overstepped by a system which trebles the total number of species in a region and substitutes for a clearly marked genus like *Astragalus* 17 genera recognizable with difficulty by the systematist and practically impossible for others. Finally, while the ecologist is willing to go even farther than the systematist in recognizing minor differences, providing these are based upon statistical field studies and experiment and not upon herbarium specimens, the practical scientist is concerned primarily with real species rather than the many varieties and forms into which some of them fall. At least, when the need for a closer knowledge arises in a particular case, it is infinitely easier and more helpful to deal with the variations of a well-recognized species than with a dozen binomials, none of which to him have the slightest relation to each other.

If taxonomy is to be helpful to anyone but taxonomers, it must clearly do several things. It must recognize the field as the only adequate place for determining new forms, and must commit itself unreservedly to the methods of statistical and experimental study. It must restrict the use of the binomial to species in the Linnean and Grayian sense and employ the abbreviated trinomial for all segregates of such species, except in the rare cases where a coordinate species has been overlooked. It must realize that the splitting of genera only places so many stumbling-blocks in the way of all non-systematists, and makes them still more unsympathetic with such methods. Finally, it must recognize that a manual which can be used with success only by the systematist fails signally in its purpose, and be willing to construct keys and descriptions primarily for foresters, agronomists, grazing ecologists, and others whose knowledge of taxonomy is slight. Upon such a basis, species and genera will not only have vastly greater usefulness, but greater significance also to the ecologist, and he will be encouraged to do his share by handling them with greater accuracy and certainty.

## LIFE-FORMS.

**History.**—The concept of the life-form was first formulated by Humboldt (1805 : 218), who used the term vegetation-form. Under various names, the concept has since been employed by many plant geographers and ecologists, and several have proposed more or less complete systems of classification. Grisebach (1872), like Humboldt, based vegetation-forms upon physiognomy, and both systems have in consequence little more than historical value to-day. Warming (1884) and Reiter (1885) contributed many of the essentials of the modern systems, but these probably owe more to Drude (1890, 1896) than to anyone else. Krause proposed a classification in 1890 and Pound and Clements (1898) modified that of Drude somewhat in applying it to American vegetation. For this reason it is proposed to treat the latter here in detail, as well as the more recent systems of Raunkiaer (1903–1907), Warming (1908–1909) and Drude (1913). It will readily be seen that all of these have much in common, though this is not obvious in Raunkiaer's classification, which is based mainly upon adaptation for overwintering. All of them are founded more or less upon the two principles enunciated by Drude, namely, (1) the rôle played by a particular species in vegetation and (2) its life-history under the conditions prevailing in its habitat, with especial reference to duration, protection, and propagation. In the following discussion life-form is used as the general term to include vegetation-forms, habitat-forms, growth-forms, etc.

**Pound and Clements, 1898-1900.**—As indicated above, the system employed by Pound and Clements in the "Phytogeography of Nebraska" (1898 : 45; 1900 : 95; cf. Clements, 1902 : 616) was essentially the earlier system of Drude (1896) modified to fit the vegetation of a prairie State. It possessed some intrinsic interest in that the entire flora of the State was passed in review from the standpoint of the various groups, and with reference to the general conditions of the different habitats (1900 : 95–312). Vegetation-forms were arranged in 7 main groups, which were divided into 34 minor ones. This system was used by Clements and Clements in "Herbaria Formationum Coloradensium" in 1902 and "Cryptogamae Formationum Coloradensium" in 1906.

I. Woody plants.
- 1. Trees.
- 2. Shrubs.
- 3. Undershrubs.
- 4. Climbers and twiners.

II. Half shrubs.
- 5. Half shrubs.

III. Pleiocyclic herbs (perennials).
- 6. Rosettes.
- 7. Mats.
- 8. Succulents.
- 9. Creepers and climbers.

*Turf-builders*
- 10. Sod-formers.
- 11. Bunch-grasses.

*Rhizomata.*
- 12. Rootstock plants.
- 13. Bulb and tuber plants.
- 14. Ferns.

IV. Hapaxanthous herbs.
- 15. Dicyclic herbs (biennials).
- 16. Monocyclic herbs (annuals).

V. Water plants.
- 17. Floating plants.
- 18. Submerged plants.
- 19. Amphibious plants.

VI. Hysterophytes.
- 20. Saprophytes.
- 21. Parasites.

VII. Thallophytes.
- 22. Mosses.
- 23. Liverworts.
- 24. Foliaceous lichens.
- 25. Fruticulose lichens.
- 26. Crustaceous lichens.

*Fungi.*
- 27. Geophilous fungi.
- 28. Xylophilous fungi.
- 29. Biophilous fungi.
- 30. Sathrophilous fungi.
- 31. Hydrophilous fungi.
- 32. Entomophilous fungi.

*Algae.*
- 33. Filamentous algae.
- 34. Coenobioid algae.

Raunkiaer, 1905.—The system of Raunkiaer (1905 : 347) seems on the surface to differ radically from all others. This is due to the fact that the winter protection of buds is assigned the first rank and the growth-form during the vegetative season is regarded as secondary. The apparent difference is increased by the use of new terms based upon the degree of bud protection. As a matter of fact, Raunkiaer's system, like the others discussed here, takes account of both summer and winter conditions, and its difference is more a matter of arrangement and terminology than of essentials. For example, the group of phanerophytes corresponds essentially to woody plants, cryptophytes constitute the bulk of pleiocyclic herbs, and therophytes are annuals, while the subdivisions practically all have their equivalents in the other systems. The hemicryptophytes are far from satisfactory as a group, because of their similarity to helophytes on the one hand (p. 420) and therophytes on the other (p. 423). By the omission of cryptogams, the classification avoids confusion with systematic types and presents an attractively consistent character, increased by a consistent terminology. While the terms are well-chosen and properly constructed, their length will preclude their common use, except perhaps in the case of the five major groups:

I. Phanerophytes (bud-shoots aerial):
 1. Herbaceous phanerophytes.
 2. Evergreen megaphanerophytes (above 30 m.) without bud-scales.
 3. Evergreen mesophanerophytes (8 to 30 m.) without bud-scales.
 4. Evergreen microphanerophytes (2 to 8 m.) without bud-scales.
 5. Evergreen nanophanerophytes (below 2 m.) without bud-scales.
 6. Epiphytic phanerophytes.
 7. Evergreen megaphanerophytes with bud-scales.
 8. Evergreen mesophanerophytes with bud-scales.
 9. Evergreen microphanerophytes with bud-scales.
 10. Evergreen nanophanerophytes with bud-scales.
 11. Phanerophytes with succulent stem.
 12. Deciduous megaphanerophytes with bud-scales.
 13. Deciduous mesophanerophytes with bud-scales.
 14. Deciduous microphanerophytes with bud-scales.
 15. Deciduous nanophanerophytes with bud-scales.
II. Chamaephytes (bud-shoots protected by snow or fallen leaves):
 16. Suffrutescent chamaephytes: many Labiatae.
 17. Passive decumbent chamaephtyes: species of Sedum, Saxifraga.
 18. Active chamaephytes: Linnaea, Empetrum.
 19. Cushion plants: Azorella, Raoulia.
III. Hemicryptophytes (bud-shoots at the soil level):
 20. Protohemicryptophytes.
  A. Plants without creeping offshoots: Linaria, Verbena, Medicago.
  B. Plants with creeping offshoots, stolons, or rhizomes: Urtica, Saponaria.
 21. Subrosette plants.
  A. Plants without creeping offshoots: Caltha, Geum.
  B. Plants with creeping offshoots: Ranunculus reptans.
 22. Rosette plants.
  A. Plants without offshoots: Primula, Taraxacum, Carex.
  B. Plants with offshoots: Hieracium, Petasites.
   Plants with monopodial rosette.
    I. Monopodium with leaves but no scales.
     A. Aerial leaf and flower shoots: Trifolium pratense.
     B. Aerial shoots flower-bearing only.
      *a.* Without creeping offshoots: Plantago major.
      *b.* With creeping offshoots: Fragaria, Trifolium repens.
    II. Monopodium with both leaves and scales.
     A. Without creeping offshoots: Anemone hepatica.
     B. With creeping offshoots: Convallaria majalis.
    III. Monopodium with scales alone: Sedum rhodiola.

IV. Cryptophytes (bud-shoots buried in the soil):
   Geophytes:
      23. Rhizome geophytes: Polygonatum.
      24. Tuber geophytes: Cyclamen.
      25. Tuberous root geophytes: Orchis.
      26. Bulb geophytes: Allium, Lilium.
      27. Root-bud geophytes: Cirsium arvense, Moneses.
   28. Helophytes: Typha, Scirpus, Equisetum, Sagittaria.
   29. Hydrophytes: Nymphaea, Zostera, Hippuris, Potamogeton.

V. Therophytes (3); annuals: Galium aparine, Thlaspi arvense.

**Warming, 1908.**—Warming (1909 : 5) has based his outline of growth-forms upon the following principles:

"Just as species are the units in systematic botany, so are growth-forms the units in oecological botany. It is therefore of some practical importance to test the possibility of founding and naming a limited number of growth-forms upon true oecological principles. It can not be sufficiently insisted that the greatest advance not only in biology in its wider sense, but also in oecological phytogeography, will be the oecological interpretation of the various growth-forms: From this ultimate goal we are yet far distant.

"It is an intricate task to arrange the growth-forms of plants in a genetic system, because they exhibit an overwhelming diversity of forms and are connected by the most gradual intermediate stages, also because it is difficult to discover guiding principles that are really natural. Nor is it an easy task to find short and appropriate names for the different types. Genetic relationships and purely morphological or anatomical characters such as the venation and shape of leaves, the order of succession of shoots, monopodial and sympodial branching, are of very slight oecological or of no physiognomic significance. Oecological and physiological features, particularly the adaptation of the nutritive organs in form, structure, and biology, to climate and substratum, or medium, are of paramount importance. Cases are not wanting, however, in which oecological grouping runs parallel with systematic classification.

"In the case of the polycarpic plants it is necessary to consider, first, their adaptation to climate, and in particular the season unfavorable to plant life; secondly, the vegetative season; and finally the conditions prevailing in regard to the soil, which Schimper terms *edaphic* conditions. Of greatest importance is—

"1. *Duration of the vegetative shoot:* Lignified axes of trees, shrubs, and undershrubs; perennial herbaceous shoots; herbaceous shoots deciduous after a short period.

"And closely associated with this is—

"2. *Length and direction of the internodes:* Whether the shoots have short internodes (rosette-shoots) or long internodes, and whether the latter are erect (orthotropous) or prostrate and creeping (plagiotropous).

"3. *Position of the renewal buds* during the unfavorable season high up in the air, near the soil, under the surface of the soil, or buried in the soil (geophilous).

"Of less importance is—

"4. *Structure of the renewal-buds or of buds in general.*

"5. *Size of the plant* is of some moment, not only because in the struggle for existence the taller plants are enabled to establish a supremacy more easily, but also because they are more exposed to the inclemency of climate; shrubs reach greater altitudes and latitudes than trees, while dwarf shrubs and herbs extend even further than shrubs.

"7. *The adaptation of the assimilatory shoot to the conditions of transpiration.*

"8. *The capacity for social life* is of great importance in the struggle between species and consequently in the composition and physiognomy of the plant-community. This capacity is due in some cases to the prolific production of seed, but usually to more vigorous vegetative multiplication by means of traveling shoots, or shoots given off from the root. And this latter is to some extent determined by the soil (moist or wet soil, loose sandy soil, etc.)"

Warming divides growth-forms into six classes and subdivides this into subclasses and types as follows:

1. Heterotrophic growth-forms: holoparasites and holosaprophytes.
2. Aquatic growth-forms.
3. Muscoid growth-forms.
4. Lichenoid growth-forms.
5. Lianoid growth-forms.
6. All other autonomous land-plants.
   - I. Monocarpic herbs.
     - (*a*). Aestival annual plants.
     - (*b*). Hibernal annual plants.
     - (*c*). Biennial-perennial herbs.
   - II. Polycarpic plants.
     - (*a*) Renascent herbs.
       - (1) Herbs with multicipital rhizomes: Silene inflata.
       - (2) Mat-geophytes.
         - *a*. With stem-tubers: Crocus.
         - *b*. With root-tubers: Ophrydeae.
         - *c*. With bulbs: Liliaceae.
         - *d*. With perennial tuberous stem: Cyclamen.
       - (3) Rhizome-geophytes.
         - *a*. On loose soil of dunes: Ammophila, Carex.
         - *b*. On loose humus soil in forests: Polygonatum, Anemone nemorosa.
         - *c*. On mud in water or swamp: Phragmites, Hippuris.
     - (*b*) Rosette-plants.
       - (1) Leaves sessile, elongated: Plantago, Taraxacum.
       - (2) Leaves long-stalked, broad: Anemone, Hepatica.
       - (3) Leaves succulent: Crassulaceae.
       - (4) With runners: Fragaria, Potentilla anserina.
       - (5) Flowers on leafy shoots: Alchemilla, Geum.
       - (6) Flowers on leafless shoots: Primula.

6. All other autonomous land-plants—*cont.*
   - II. Polycarpic plants—*continued.*
     - (*b*) Rosette-plants—*continued.*
       - (7) Grass-rosettes: grasses, sedges, Eriocaulaceae.
       - (8) Musa-form: gigantic tropical herbs (banana).
       - (9) Tuft-trees.
         1. Trunks without secondary growth; leaves large and divided: tree-ferns, palms, cycads.
         2. Trunks with secondary growth; leaves undivided, linear; Yucca, Dracaena.
         3. Strelitzia-form.
     - (*c*) Creeping plants.
       - (1) Herbs: Lycopodium clavatum, Menyanthes.
       - (2) Dwarf shrubs: Arctostaphylus uva-ursi, Linnaea.
       - (3) Jungermannia-form.
     - (*d*) Land-plants with long, erect, long-lived shoots.
       - (1) Cushion-plants: Silene acaulis, Azorella.
       - (2) Undershrubs:
         1. Labiate type: Salvia, Thymus, Artemisia.
         2. Acanthus type: Acanthaceae.
         3. Rhizome-undershrubs: Vaccinium myrtillus.
         4. Cane-undershrubs: Rubus idaeus.
         5. Soft-stemmed plants: Araceae.
         6. Cactus-form: Cactaceae, Stapelia.
         7. Woody plants with long-lived lignified stems, canopy-trees, shrubs, dwarf shrubs.

Drude, 1913.—In broadening his earlier classification into a universal system of life-forms, Drude (1913 : 29) has applied the following criteria:

1. The basic form (tree, shrub, annual or perennial herb), by the organization of which for a long period of years, or for a single season of growth, each plant maintains its own place. The method of propagation is an essential part of this basic form.
2. The form and duration of the leaves.
3. The protective devices of leaf- and flower-shoots during the period of rest.
4. Position and structure of the organs of absorption.
5. Flowering and fruiting in relation to reproduction as a single or recurrent process.

On this basis, Drude makes three great divisions in which he recognizes 55 types and many subtypes.

I. Aerophytes (woody plants, perennial and annual herbs).
1. Monocotyl tuft-trees: Sabal, Yucca.
2. Monocotyl palm shrubs and limes: Bactris, Calamus.
3. Dwarf palms: Nipa.
4. Tree-ferns and cycads: Cyathea, Cycas.
5. Needle-leaved woody plants.
6. Dicotyl trees.
7. Dicotyl shrubs and bushes.
8. Dicotyl woody lianes.
9. Mangrove-form.
10. Lobelia-form.
11. Tree-grasses: Bambusa.
12. Smilaceous bushes and lianes: Smilax, Ruscus.
13. Leafless dicotyl rushwood and thorn bushes: Casuarina, Ephedra, Spartium.
14. Few-leaved columnar woody plants: Adenium, Tumboa.
15. Stemmed evergreen rosette succulents: Agave, Sempervivum.
16. Dicotyl stem succulents: Cactaceae.
17. Dicotyl dwarf shrubs: Calluna, Artemisia, Dryas.
18. Woody parasites: Loranthus.
19. Monocotyl giant herbs: Musa, Bromelia.
20. Monocotyl root-climbers: Monstera.
21. Rosette ferns and cycads: Aspidium.
22. Tuber-stemmed epiphytes: Bulbophyllum, Myrmecodia.
23. Perennial and renascent grasses: Andropogon, Poa, Carex.
24. Sedges and rushes with suppressed leaves: Juncus, Scirpus.
25. Erect half-shrubs: Ruta.
26. Half-shrubs with creeping stems or offshoots: Linnaea.
27. Dicotyl cushion-plants: Raoulia, Silene acaulis.
28. Succulent cushion-plants: Aloe, Mesembryanthemum.
29. Biennial and perennial rosettes: Pulsatilla, Verbascum.
30. Renascent and annual climbers: Dioscorea, Ipomoea.
31. Renascent multicipital herbs: Peucedanum, Galium.
32. Geophilous rootstock plants: Iris, Circaea, Equisetum.

I. Aerophytes (woody plants, perennial and annual herbs)—*continued.*
33. Geophilous tuber plants: Orchis, Cyclamen.
34. Geophilous bulb plants: Allium, Oxalis.
35. Monocotyl therophytes: Eragrostis.
36. Dicotyl therophytes: Chenopodium.
37. Dicotyl short-lived herbs: Koenigia.
38. Saprophytic and parasitic herbs: Corallorhiza, Monotropa, Cuscuta.

II. Water plants:
39. Amphibious slime-rooted plants with aerial leaves: Sagittaria, Nelumbo, Marsilea, Equisetum.
40. Amphibious free-swimming plants with aerial leaves: Pistia, Eichhornia.
41. Amphibious plants rooting on stones: Podostemaceae.
42. Hydrophytes with rooting axis and immersed leaves: Isoetes, Zostera, Lobelia.
43. Hydrophytes with rooting axis and floating leaves: Potamogeton, Nymphaea.
44. Free-swimming hydrophytes: Lemna, Utricularia, Azolla.

III. Life forms of mosses and thallophytes:
A. Aerophytes:
45. Terrestrial cushion-mosses: Leucobryum.
46. Terrestrial tall-stemmed mosses: Polytrichum.
47. Terrestrial and epiphytic mat-mosses: Hypnum, Frullania.
48*a*. Petrophilous creeping mosses, chiefly liverworts: Marchantia, Jungermannia.
48*b*. Petrophilous mat- and cushion-mosses: Georgia, Andreaea.

B. Hygrophytes and hydrophytes:
49. Bog mosses: Sphagnum.
50*a*. Streaming mosses: Fontinalis.
50*b*. Forming mats in water: Aneura, Scapania.
51. Epiphytic lichens: Usnea.
52. Fruticose and foliose lichens on rocks and earth: Cetraria, Umbilicaria, Cladonia.
53. Crustose lichens: Lecanora.
54. Forms of marine algae, green algae, bluegreen algae, etc.
55. Forms of saprophytic and parasitic fungi.

**Comparison of the systems.**—The three systems of Raunkiaer, Warming, and Drude differ greatly as to manner of classification, but they are in much greater harmony as to the essential basis. Drude, however, constantly uses taxonomic criteria, though he is very far indeed from consistent, separating monocotyls, dicotyls, and ferns sometimes into distinct types, sometimes into subtypes, and then frequently uniting two of them or all three into the same type or subtype. Raunkiaer ignores taxonomy altogether and Warming practically does the same, with the exception of the thallophytic forms, in which taxonomic form and life-form are more or less identical. The treatment of aquatics, in which the impress of the habitat is marked, is very different in the three cases. Raunkiaer makes helophytes and hydrophytes two types of cryptophytes, coordinate with geophytes. Warming treats aquatic plants as one of his six main divisions, though he considers them under ecological classes or habitat-forms (136), while Drude makes water plants one of his two great divisions of flowering plants and recognizes three amphibious and three aquatic types. Raunkiaer uses bud-position as the primary criterion for his five main groups (all flowering plants and ferns). Warming employs systematic criteria for two of his six divisions, ecologic for three, and physiologic for one. Land-plants are divided upon the nature of the life-period into monocarpic and polycarpic. Drude's first division is ecologic for aerophytes, and water-plants, and systematic for mosses and thallophytes. In all three systems the types and subtypes are frequently the same, except that Drude usually divides the same type or subtype upon the basis of taxonomy.

The systems of Raunkiaer and Drude are the most unlike, while Warming's occupies an intermediate position. Raunkiaer's classification is much the most compact and consistent, probably because he has adhered to one criterion throughout. Because of this, and because he has given definite names to practically every type, it is also much more usable. In fact, its great merit lies in the possibility of using it as a sort of climatic index, while the other two systems merely classify a great mass of plants in the usual static fashion. As Warming points out, Raunkiaer's system has one disadvantage in that it fails to take account of the growing season response (1906 : 6) and hence applies to the flora and not to the vegetation of a region or country.

**Vegetation-forms.**—For our purpose, much the most useful and consistent view of life-forms is obtained from a single point of view, that of vegetation. The development and structure of vegetation are chiefly a matter of dominants and subdominants, and it is the life-forms shown by these which are of paramount importance. Hence it becomes desirable to speak of them as vegetation-forms, as Drude did originally, following Grisebach and Humboldt. For practical purposes, it is undesirable to make a complete classification of vegetation-forms and the latter is carried only so far as the demands of indicator vegetation warrant.

The dominance of a species depends upon the perfection of its methods of increase on the one hand, and upon the success of its vegetative shoots in competition on the other. While the latter is partly a matter of length of shoot and rate of growth, it is chiefly one of carrying the shoots of one season over to the next. A wholly consistent and usable system is possible upon the basis of these three processes. It avoids the complexities and uncertain correlations introduced by taxonomy and permits a consistent treatment of habitat-forms with their more evident factor correlations. It contains the essentials of the systems discussed above, inasmuch as Drude states that the basic life-forms are trees, shrubs, perennial and annual herbs, Warming divides his group of land-plants into monocarpic and polycarpic, while Raunkiaer's largest groups, phanerophytes, cryptophytes, and therophytes, practically correspond to woody plants, perennial and annual herbs. In giving more or less equal value to the life-period, method of over-wintering, and conservation of shoots and success in competition, it appears desirable to recognize four coordinate groups, viz, annuals, biennials, herbaceous perennials, and woody perennials, characterized as follows:

1. *Annuals:* Passing the winter or dry season in seed or spore form alone; no propagation or accumulation of aerial shoots; living one year.
2. *Biennials:* Passing one unfavorable season in the seed or spore form, and the next as a propagule; no accumulation of aerial shoots; living two or parts of two years.
3. *Herbaceous perennials:* Passing each unfavorable season in both seed or spore and propagule form; no accumulation of aerial shoots; living several to many years,
4. *Woody perennials:* Passing each unfavorable season as seeds or spores, and aerial shoots or masses, often with propagule forms also, especially when injured; living many seasons as a rule.

Each of these divisions is thoroughgoing and all forms of annual habit are placed in the first group, whether flowering plants, mosses, or fungi, just as perennials are placed in their respective group regardless of their systematic position or habitat-form. The varying nature of the four groups makes it obviously impossible to employ the same criterion for the division into types. For annuals and biennials, the form of the aerial plant body is probably of first importance and the size next, while for woody plants height is perhaps most decisive, leaf-character next, and form last. While perennial herbs usually show the most marked differences in the propagules, the form of the aerial shoot is often even more distinctive, and both criteria must be employed as occasion warrants. The final result is a simple compact system, closely resembling the earlier one of Drude (1896; Pound and Clements, 1900) and different but little in essence from that of Raunkiaer. For the study of indicators only the major divisions appear to be of value at present, and these alone are given in the outline.

1. Annuals.
2. Biennials.

Herbaceous perennials:

3. Sod-grasses.
4. Bunch-grasses.
5. Bush-herbs.
6. Cushion-herbs.
7. Mat-herbs.
8. Rosette-herbs.
9. Carpet-herbs.
10. Succulents.

Woody perennials.

11. Halfshrubs.
12. Bushes.
13. Succulents.
14. Shrubs.
15. Trees.

**Indicator significance of vegetation-forms.**—It is obvious that the vegetation-forms of climax dominants are indicators of climate. This has long been recognized as the basis for the climatic zones of continents and mountains. The same principle applies to climax formations generally; and these are accordingly taken as indicators of the major climates of the globe (Clements, 1916). This close correlation between the major vegetation-forms and climate as expressed in progressively favorable conditions of temperature and moisture is paralleled by the succession of vegetation-forms in the development of a climax. In the development of a sere, extreme conditions as to water yield to those more and more favorable to growth, and this change is accompanied by a sequence of dominants belonging to successively higher vegetation-forms. In short, the more striking indicator values of succession are afforded by the changes from one vegetation-form to another, just as those next in importance are marked by the change from one associes to another of the same form. Moreover, while the exact significance of any species can be known only by determining its functional response to the factors of its habitat, its general meaning is indicated by the vegetation-form to which it belongs.

Raunkiaer (1905, 1908; Smith, 1913: 16) has employed his system of vegetation-forms to determine the climatic relations of a particular flora. He establishes a hypothetical *normal spectrum* for the whole earth by selecting 1,000 representative species, of which 400 were carefully analyzed. The *biological* or *phyto-climatic* spectrum of a particular region is obtained by finding the percentage of species belonging to each life-form. Raunkiaer's method adds interest and detail to the long-accepted relations between climate and flora. It can not be applied to vegetation and hence it has no real indicator value, as is shown by the author's own statements (1905 : 433):

"If we consider the flora of Denmark, it is characterized from the botano-climatic viewpoint by its hemicryptophytes and not by its phanerophytes, for, however important may be the rôle played by the forests in the vegetation of Denmark, the small number of species of phanerophytes is significant of the conditions offered by this region: The species of phanerophytes represent but 6 to 7 per cent of those living in Denmark, while the hemicryptophytes constitute nearly a half of all the species.

"But from the standpoint of the formation, the phanerophytes, or trees, dominate by their size wherever one finds them. In spite of the inferiority in number of the species of phanerophytes to those of hemicryptophytes or cryptophytes, our forests belong to the phanerophytic formations because the phanerophytes they contain dominate the other components of the forests."

## HABITAT-FORMS.

**Concept and history.**—In addition to the taxonomic form and vegetation-form, species exhibit a form which is much more distinctly related to the habitat. These usually bear the clear impress of the latter and hence are called habitat-forms. The fuller recognition of their basic importance by Warming (1895, 1896 : 116) was largely responsible for the rapid development of ecology during the last two decades. Unlike taxonomic forms and vegetation-forms, their value is primarily ecological and not floristic, and they are of correspondingly greater importance as indicators. Their significance lies in the fact that they bear the primary impress of the controlling or limiting factor, and thus serve as direct indicators of the critical factors of the habitat. They are the essential basis of all indicator values, and must be regarded as the main objective in all such studies.

**Warming's system.**—Warming (1896 : 116) was the first to adequately organize the four universally known groups of habitat-forms, namely, hydrophytes, xerophytes, halophytes, and mesophytes (cf. Clements, 1904 : 20). Pound and Clements (1898: 94; 1900 : 169), feeling the need of recognizing light as well as water, divided mesophytes primarily upon the basis of light and combined halophytes with xerophytes, thus establishing the following six groups: hydrophytes, mesophytes, hylophytes, poophytes, aletophytes, and xerophytes. This division of mesophytes retained some idea of life-forms, and it was later dropped (1902 : 166; 1907 : 183) for the consistent light grouping of mesophytes into *heliophyta*, *sciophyta*, and *scotophyta*, corresponding essentially to Schouw's classification into sun, shade, and darkness plants (1823 : 166). A detailed classification of habitat-forms was made by Clements (1902 : 5–14), in which light, solutes, aeration, and other factors were taken into account, but with water-content as the primary basis. The 64 subdivisions were largely successional and physiographic; and this number can be greatly reduced if factors alone are considered. This is essentially what Warming has done in his most recent grouping of formations (1909 : 136), which also represents much the best classification of habitat-forms up to the present. His system is as follows:

A. The soil (in the widest sense) is very wet, and the abundant water is available to the plant; the formations are therefore more or less hydrophilous:
   Class 1. Hydrophytes (of formations in water).
   Class 2. Helophytes (of formations in marsh).

B. The soil is physiologically dry, *i.e.*, contains water which is available to the plant only to a slight extent; the formations are therefore composed essentially of xerophilous species:
   Class 3. Oxylophytes (of formations on sour (acid) soil).
   Class 4. Psychrophytes (of formations on cold soil).
   Class 5. Halophytes (of formations on saline soil).

C. The soil is physically dry, and its slight power of retaining water determines the vegetation, the climate being of secondary import; the formations are therefore likewise xerophilous:
   Class 6. Lithophytes (of formations on rocks).
   Class 7. Psammophytes (of formations on sand and gravel).
   Class 8. Chersophytes (of formations on waste land).

D. The climate is very dry and decides the character of the vegetation; the properties of the soil are dominated by climate; the formations are also xerophilous:
   Class 9. Eremophytes (of formations on desert and steppe).
   Class 10. Psilophytes (of formations on savannah).
   Class 11. Sclerophyllous formations (bush and forest).

E. The soil is physiologically or physically dry:
   Class 12. Coniferous formations (forest).

F. Soil and climate favor the development of mesophilous formations:
   Class 13. Mesophytes.

Modifications of Warming's system.—In making use of habitat-forms as indicators in North American vegetation, a few modifications of the above groups are desirable. These are perhaps further warranted by some advance in ecological knowledge in the ten years since Warming made the following statement concerning habitat-forms (1909 : 133):

"When endeavoring to arrange all land-plants, omitting marsh-plants, into comprehensive groups, we meet with first some communities that are evidently influenced in the main by the physical and chemical characters of the soil which determine the amount of water therein; secondly, other communities in which extreme climatic conditions and fluctuations, seasonal distribution of rain and the like, decide the amount of water in soil and character of vegetation. In accordance with these facts, land-plants may be ranged into groups, though in a very uncertain manner. The prevailing vagueness in this group ing is due to the fact that *oecology is only in its infancy*, and that very few detailed investigations of plant-communities have been conducted, the published descriptions of vegetation being nearly always one-sided and floristic, as well as very incomplete and unsatisfactory from an oecological standpoint."

The terms employed are those suggested by Clements (1902 : 5) and adopted by Warming for most of his divisions:

I. Hydrophytes: Chresard maximum to very high, the soil being water or covered with water; climate usually moist.
  1. Emophytes: Entire plant submerged; no transpiration or functional stomata.
  2. Plotophytes: Plant floating, at least the leaves; transpiration and functional stomata on upper surface of leaves at least.
  3. Helophytes: Amphibious, rooted in water or mud; transpiration high and stomata on both surfaces, the stem often functioning as a leaf.

II. Mesophytes: Chresard medium, soil moist; climate moist; transpiration high to medium.
  4. Heliophytes: Sun-plants, growing in sunlight or light stronger than 0.10.
  5. Sciophytes: Shade-plants, growing in light less than 0.10.

III. Xerophytes: Chresard low, soil physically or physiologically dry, climate usually dry, or various; transpiration low.
  A. Soil physiologically dry, climate various:
  6. Halophytes: Chresard low, due to an excess of soil salts.
  7. Psychrophytes: Chresard low, due to cold soil or to ice.
  8. Oxyphytes: Chresard low, due to lack of oxygen in the soil.
  B. Soil physically dry, climate various:
  9. Lithophytes: Chresard low, due to a rock matrix.
  10. Psammophytes: Chresard low, due to sandy or gravelly soil.
  11. Chersophytes: Chresard low, due to a rock substratum.
  C. Climate dry and soil physically dry in consequence:
  12. Eremophytes: desert plants, chresard low or lacking much of the year.
  13. Psilophytes: grassland plants (prairie, plains, steppes), chresard low some of the year.
  14. Drymophytes: bushes, shrubs, and small trees, mostly sclerophyll scrub, chaparral, and woodland; chresard low or discontinuous.

The changes from Warming's system lie in the subdivision of hydrophytes and mesophytes, well-recognized distinctions which Warming himself makes use of (18, 165), in the distribution of conifers among helophytes, mesophytes, psammophytes, and drymophytes, in the line drawn between desert and grassland plants, and in treating the bush-shrub form as primary and the division into sclerophyll and deciduous types as secondary.

**Indicator value.**—Habitat-forms are the most satisfactory of all indicator-forms. This is chiefly because of their obvious response to the controlling factors which the forester, grazing expert, and others must deal with. This is partly also because they mark out a definite area in which these factors prevail. For all practical purposes in a particular region, habitat-forms constitute the ground-work of an indicator system. This is evident when it is realized that the fourteen groups comprise all dominants and thus each habitat-form has a community value as well. When reinforced by vegetation-forms in so far as their significance for climate is known, and by ecads and growth-forms for the more recent or the minor effects of physical factors, habitat-forms afford a nearly complete system of indicators for the practical application of biology. It is still necessary to interpret some of them with greater accuracy and certainty. This will come about from the quantitative study of their physiologic response, permitting the closer correlation of form and function, as well as by the increasing use of standard plants as even more accurate indicators.

Habitat-forms can be used to give a general statistical expression to the climatic or physiographic conditions of a region, and thus permit comparisons, much as Raunkiaer has used vegetation-forms. Their paramount value lies in their positive indication of definite local conditions on the basis of known correlation with measured factors. It should be noted that the mesophytes and the last three groups of xerophytes represent climax habitats and communities, while the hydrophytes and the first six groups of xerophytes characterize developmental stages. This is a natural outcome of the fact that the climate is controlling as to soil conditions in the former, while the climatic control is much reduced or is none at all for the latter. The general correlation of climax habitat-forms and their most important representatives with physical factors is given in Chapter IV, in so far as quantitative results are available.

In a recent paper, Raunkiaer (1916 : 225; cf. Fuller and Bakke, 1918 : 25) has sought to express the general relation of plants to climate by a series of leaf classes based upon size. Of the latter, he recognizes six kinds as follows: leptophyll, 25 sq. mm.; nanophyll, $9 \times 25$ sq. mm.; microphyll, $9^2 \times 25$ sq. mm.; mesophyll, $9^3 \times 25$ sq. mm.; macrophyll, $9^4 \times 25$ sq. mm.; megaphyll. While this classification will serve a useful purpose in drawing the attention of ecologists to such relations, it seems quite too subjective for final acceptance. This seems obvious from the author's difficulties as to compound and lobed leaves, and especially from the following statement (l. c., 29):

"Originally I multiplied by 10, but the resulting limits between the 'size-classes' did not seem as natural as when 9 was used. It is easy in the final analyses to separate the single classes into the groups of small, medium, and large."

Thus, while there can be little question that leaf-size often serves as an indicator of climate or habitat in some degree, it must be refined by means of leaf-number, thickness, structure, outline, and texture, and checked by quantitative studies of factors (cf. E. S. Clements, 1905 : 91).

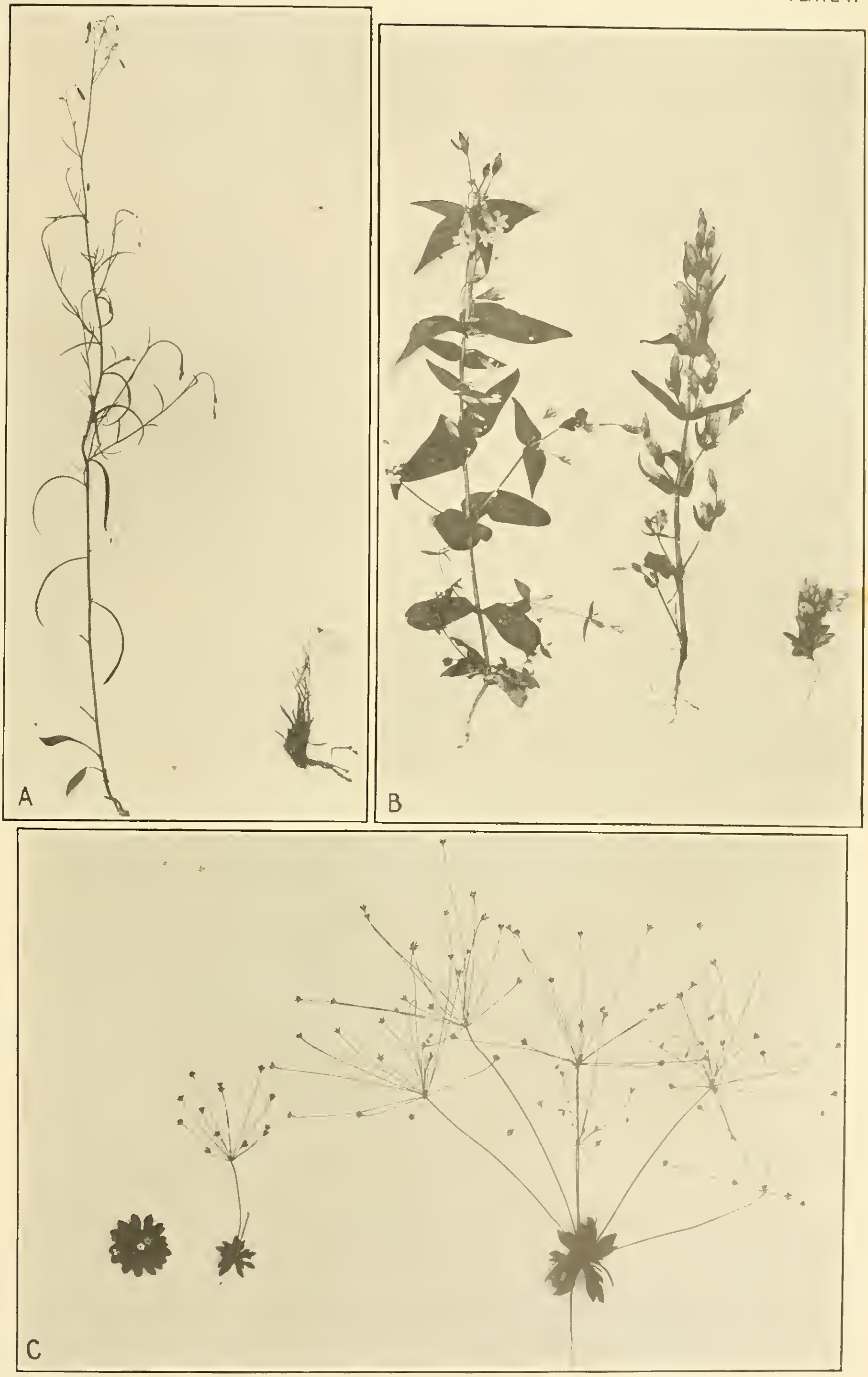
Ecads.—An ecad is produced by direct and demonstrable adaptation to a habitat. It is a habitat-form in the making. The habitat-form, while capable of modification within certain limits, has recorded the impress of a particular habitat for so long that its general character is fixed and transmitted. An ecad, though it may show just as striking adaptation, is a recent product, and its character is not yet fixed and transmissible. The difference between the two is solely one of inheritance, and it seems probable that ecads become fixed and pass over into habitat-forms after a long residence in the same habitat. This is indicated by the behavior of alpine dwarfs, some of which retain their form when moved to lower altitudes or shifted to wetter alpine situations, while others at once change in response to the new conditions. The former have attained the stability of habitat-forms, the latter are ecads.

Because of its plastic nature, the ecad is a more exact and sensitive indicator than the habitat-form. Its structural change corresponds more nearly to the functional response and can be regarded as a measure of the latter to a considerable degree. Its growth as well as its form is often characteristic, and its indicator value can be based upon both. One unique advantage of the ecad is that it is produced in abundance in nature, wherever habitats touch, especially where they recur constantly, as in mountain regions. A plastic species found in two or more habitats regularly shows an ecad corresponding to each. Similar results are readily obtained by transplanting such species to several different habitats. Ecads produced under definite quantities of water and light may be grown under control (Clements, 1905 : 157; 1919) and used for comparison with the natural ones (E. S. Clements, 1905) (plate 11).

Ecads have been classified and named with reference to habitats, as *hylocolus*, *psilocolus*, etc. (Clements, 1902 : 17; 1904 : 329). It seems much better to group and designate them with reference to the controlling factor (Clements, 1908 : 263), as water ecads, light ecads, etc. Thus the general classification of ecads would necessarily correspond closely to that of habitat-forms, except in xerophytes, where the groups would be fewer. Such a classification would be of little value, however, since it is the relationship of the ecad to a particular species which is significant, as well as the number and kind of ecads actually occurring. A floating species, such as *Sparganium angustifolium*, forms both submerged and amphibious ecads, while *Nymphaea polysepala* has been seen to produce only amphibious ones. A plastic helophyte, such as *Ranunculus sceleratus*, or a mesophyte, such as *Achillea millefolium*, may give rise to several ecads. The same species may produce both water and light ecads, though as a rule wide a range of adaptation to the one factor is accompanied by a narrow range for the other. Under control it has been possible to produce ten distinct water ecads of *Ranunculus*, but beyond this point differences have to do chiefly with amount of growth rather than with structure. For the present, it is sufficient to recognize the controlling factor by designating ecads as hydrads, xerads, sciads, heliads, halads, etc., and to leave the question of a more exact terminology for the future. The importance of ecads in indicator work is so great that their recognition can no longer be neglected.

## GROWTH-FORMS.

Nature.—While it is assumed that all plant forms are referable to the immediate or remote action of the habitat, this correlation is least certain for taxonomic forms. Its certainty increases progressively through life-forms and habitat-forms to reach a maximum in growth-forms. While Warming in particular has used this term in place of life-form and vegetation-form, the latter have the preference, both by priority and significance. But growth-form is such a desirable term for the immediate quantitative response made by a plant to different habitats or conditions that its retention in this sense seems well-warranted. As the direct visible response of the plant to physical factors, growth affords a more delicate scale of measurements even than the ecad. In fact, the latter is only a growth-form in which adaptation as shown by a qualitative change of form or structure is more striking than the quantitative difference in amount of growth. In the case of dwarfing, both changes usually occur together, and the growth-form differs from the ecad only in




A. Normal *Campanula rotundifolia* at 8,300 feet, and alpine ecad at 14,100 feet, Pike's Peak, Colorado.

B. Shade ecad and normal *Gentiana amarella* at 8,300 feet and alpine ecad at 13,000 feet, Pike's Peak.

C. Alpine ecad, normal form and shade ecad of *Androsace septentrionalis*, Pike's Peak.

being the product of the conditions presented by a single season. If these continue, the growth-form persists and becomes an ecad characteristic of the particular habitat. Thus, while the two forms may be measures of the same conditions, the one is an indicator of the annual variation, the other of the normal condition of the habitat. From the ecological side, it appears that growth-forms may become ecads, ecads become habitat-forms, and these finally fixed as vegetation-forms.

Kinds.—Every direct factor exerts an influence upon growth and produces corresponding growth-forms. Such factors are water, light, temperature, and aeration, and possibly certain solutes. Since all of these are concerned in the growth of each plant, it is possible to assign a particular one as the cause of any growth-form only when it is the controlling or limiting factor. In the majority of cases, the limiting action is evident, as with water in arid and semi-arid habitats or dry seasons, light in forests and thicket, temperature in high altitudes or latitudes or cold seasons, and aeration in wet areas or seasons. Maximum growth results when all four factors are at the optimum for a particular species. An apparent exception is afforded by the behavior of many species in moderate shade, but their height is usually offset by their slenderness, and the mass growth and dry weight are usually less than in the sun. With the optimum growth as the basis, it becomes possible to distinguish growth-forms due to the extremes of each factor, as well as to correlate different amounts of growth with known quantities of the limiting factor. In the case of water, growth is decreased by both an excess and deficit as a rule, but the former seems to operate through reduced aeration and lowered temperature. Similarly, growth is diminished by both high and low temperatures, but high temperatures act chiefly through the water relation. It is doubtful whether full sunshine as light ever inhibits growth, since photosynthetic activity decreases with any material reduction in light intensity. While many species are taller and more branched in moderate shade, it appears that mass growth is at a minimum and often becomes completely impossible with the increasing density of forest or thicket.

As a consequence of the above, it is most practical to distinguish four types of growth-forms, based upon the lack of the direct limiting factors, namely, those due to insufficient water, to insufficient heat, to shade, and to poor aeration. Since growth is primarily quantitative, each species will exhibit a series of forms from the optimum to the minimum, corresponding to each effective degree of change in the limiting factor. This relation lies at the base of ecological response and can only be determined experimentally. Two factors may act together in producing a growth-form, as in the case of alpine dwarfs due to drouth and low temperature. One factor may serve to emphasize another, as where the drouth of a desert is reinforced by an excess of salts in the soil, or it may decrease or counteract the effect of another, as is true of shade in arid regions. Finally, all four factors may be concerned causally in an effect produced directly by one of them. This is apparently the case in the death of sal seedlings in tropical forests, as shown by Hole and Singh (Chap. III). The immediate cause is poor aeration, due to the accumulation of soil-water as a consequence of lower temperature resulting from shade.

Indicator relations.—The growth of a species varies from one year to the next, and from one habitat to another. It often differs also in different portions of the same habitat. In an area which is uniform physically, individuals frequently show striking variations due to competition. These four relations sum up the indicator values of growth-forms as they occur in nature and hence serve as the basis of all correlations. While they are well-known, little quantitative work has yet been done with them. This has been due to the time necessary to organize quantitative studies and methods out-of-doors and to focus these upon growth as the most basic of visible responses. Pearson (1918) has made measurements of the annual growth in height of yellow-pine seedlings for a period of six years and has found a close correlation with spring rainfall. Sarvis (1919) has clipped and weighed the growth on permanent grass quadrats at intervals of ten days and has made a general correlation with seasonal factors. Since species vary greatly in rate and amount of growth, it is desirable to select those most responsive to the habitat.

It is impossible to say as yet what type of growth is most readily correlated with seasonal variations or habitat differences. Theoretically, it seems that total growth as indicated by the dry weight of mature plants would furnish the best correlation (cf. Pearson, 1918; Frothingham, 1919; Sarvis, 1919). Actually, however, vegetative growth and reproductive growth make different demands, and are often antagonistic to each other. This is true to a large degree of the height-growth and width-growth of woody plants. The determination of dry weight is a practical impossibility for trees except when young, and the indicator correlation must be with growth directly. At present it is only possible to say that for the first 100 to 150 years height-growth offers the better correlation, and after this period growth in diameter reflects conditions more accurately. Mitchell (1918 : 23) has shown in the case of incense cedar (*Libocedrus decurrens*) that the mean height-growth for the first 100 years was 65 feet, for the second century 28 feet, for the third 12 feet, and for the fourth 6 feet. The width-growth was 13 inches, 14 inches, 9 inches, and 5 inches for the same periods. Thus practically 60 per cent of the height-growth was made in the first century, and but 31 per cent of the width-growth, while the height-growth of the fourth century was but 5 per cent in contrast to a width-growth of 12 per cent. The correlation of reproductive growth and especially of seed-production with seasonal or habitat conditions is known only to the extent that it tends to rise with less favorable conditions as to water up to a certain point, as shown by alpine and arid regions. For most woody plants it is little or none in youth, and it increases steadily up to maturity. In the case of crop plants, it seems clear that the correlation with dry weight offers a satisfactory basis for comparison, though even here greater accuracy can be expected from the separate correlation of vegetative and reproductive growth with the controlling factors in the two periods.

**Standard plants for growth correlations.**—Because of the control possible as well as the opportunity for measuring functional responses, standard plants offer much the best method of establishing growth correlations. The value of the method increases as the standard plant approaches the one to be indicated in character, and reaches a maximum when the latter is itself employed as a standard, as in the use of yellow pine, Douglas fir, etc., in forest investigations. The employment of phytometers in this form is the most basic of all quantitative methods and is destined to play the paramount rôle in all exact studies of communities and habitats in the future.

**Competition-forms.**—The amount of a particular factor available for any species or individual is either determined by the habitat alone or by competition. In the great majority of cases, the major limits are fixed by the habitat, and within these competition determines the amounts available for each plant. Indeed, this is probably true of all communities except those initial ones in which the individuals are widely scattered. In nearly all cases, then, a growth-form is due partly to the nature of the habitat and partly to the modification of this by competition. The part played by each can be determined only by actual experiment or by the comparison of individuals growing in the same habitat but in areas with and without competition. Fortunately, such areas are of sufficient frequence in nature to reveal the normal growth-form of the habitat as well as the growth-form due to competition. A study of the chaparral and strand communities of southern California (Clements and Clements, 1916) disclosed an unusually large number of such competition-forms, especially among the annuals, as would be expected. While competition-forms are probably just as frequent among perennials, they are often much less striking.

As competition may occur in all degrees in accordance with the number and density of individuals, so there may be a complete series of forms from the normal to the extreme in which the plant never develops beyond the seedling stage before it dies. Under somewhat less severe competition, plants develop stems and leaves but fail to form flowers and fruit. In the next degree, reproduction occurs, but the flowers are single or few, while beyond this are more and more perfectly developed forms until the optimum for the habitat is reached. Each form is an index to some degree of competition, but its exact indicator value is more difficult to determine. This is due largely to the fact that competition has as yet received but little attention, especially on the experimental side. The view advanced by Clements (1904 : 166; 1905 : 310; 1907 : 251; 1916 : 72) that competition is purely physical seems to be confirmed by recent experiments. While it is perhaps unnecessary to rigidly exclude metaphor in connection with competition, it should be recognized that the experimental results so far obtained show that plants do not compete for "room." Competition has to do only with the direct factors of the habitat. Water and light are the factors universally concerned, though soil-air, nutrients, and heat must also be taken into account in particular habitats. In addition, there is often more or less decisive competition between the flowers of a community for pollination agents. Furthermore, the course of competition may be determined by a deleterious substance, especially a solute, which handicaps one species more than another. Such a handicapping influence is even more frequently represented by biotic agents, parasitic plants, rodents, grazing animals, etc.

The competition-forms commonly met with are due to competition for water or light, or for both together. There has been no experimental study of competition for soil-air or for nutrients, and it is impossible to assert at present that plants do compete for heat. Studies of germination under different densities of seeding suggest such competition for seedlings at least. No adequate study of competition-forms has been made, and hence it is impossible to relate them to definite quantities of water or light. In fact, it seems increasingly probable that the forms resulting from intense competition are due to a lack of both factors, though in different degree. As a consequence, competition-forms can at present be used directly only as indicators of the general degree of competition. In connection with the habitat-forms or ecad, they have an indirect value in making it possible to distinguish in indicators the direct effect of the habitat as contrasted with the added effect of competition.

## COMMUNITIES AS INDICATORS.

**Value.**—The community as an indicator is a complex of all the preceding values. It derives its primary significance from the dominants, chiefly through their life-forms and ecological requirements. It includes the meanings of the less significant subdominants, and those of the much less important secondary species. In short, it is a complete scale upon which all the indications of the habitat are written. These values can be obtained only by analysis, however, and the latter leads at once to the study of dominants and subdominants, both climax and seral. The general principles of the latter have already been outlined under the sections on associational and successional bases. This leaves for consideration the various types of communities and the functions and structures they exhibit.

**Kinds of communities.**—With reference to association alone, three kinds of communities may be distinguished, viz, consocial,[1] associal, and mixed. The first consists of a single dominant, the second of two or more belonging to the same association or seral stage, and the third of dominants from different associations or associes. The basic indicator value of these is determined by whether they are climax or seral. The consocial community affords the most definite indication, while the associal type has the advantage of checking the indications of one dominant by those of the related ones. This is even truer in the case of mictia, but the indications are necessarily somewhat confused here, since one set of dominants is disappearing and the other increasing in number and importance. In this connection it is desirable to emphasize the fact that seral and climax communities furnish not only indications of existing factors and possibilities, but also of past and future ones. Each seral stage indicates the preceding stage and its habitat. The climax forecasts the consequences of any primary or secondary disturbance in it, and foreshadows the effects of climatic changes. As a result, both serve as invaluable indicators of the course and outcome of all possible human practices in them, and lend themselves to methods of scientific prophecy which can hardly be surpassed. A similar relation exists between consocial and associal communities. Wherever a consocies or consociation is found, the related dominants have occurred or can occur, at least with the slightest modification of the habitat. Thus, the indicator analysis of a community involves not only the measurement of existing conditions, but especially also a study of the linkage with the other communities of the sere or the climax. For indicator research, as in all serious ecological studies, any investigation which fails to take full account of successional and climax relations is inadequate, and at best can only lead to half-truths.

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[1]This term is here used to refer to the community marked by a single dominant, whether consocies or consociation, and associal in a similar sense. Both terms are also used to refer definitely to consocies and associes respectively, but the context is usually decisive.

The basic correlations of communities may be illustrated by the following diagram (fig. 2.):

CLIMAX FORMATION.

| (Prisere) | | | (Subsere) |
|---|---|---|---|
| society - consociation - association | - ecotone - | association - consociation - society | |
| | ↑ | ↑ | |
| socies - consocies - associes | - subclimax - | associes - consocies - socies | |
| | ↑ | ↑ | |
| | mictium. | mictium. | |
| | ↑ | ↑ | |
| | associes. | associes. | |
| | ↑ | ↑ | |
| | associes. | associes. | |
| | ↑ | ↑ | |
| | associes. | associes. | |
| | ↑ | ↑ | |
| | associes. | colony. | |
| | ↑ | ↑ | |
| | associes. | family. | |
| | ↑ | | |
| | associes. | | |
| | ↑ | | |
| | colony. | | |
| | ↑ | | |
| | family. | | |

FIG. 2.—Diagram of the climax and seral communities of the formation.

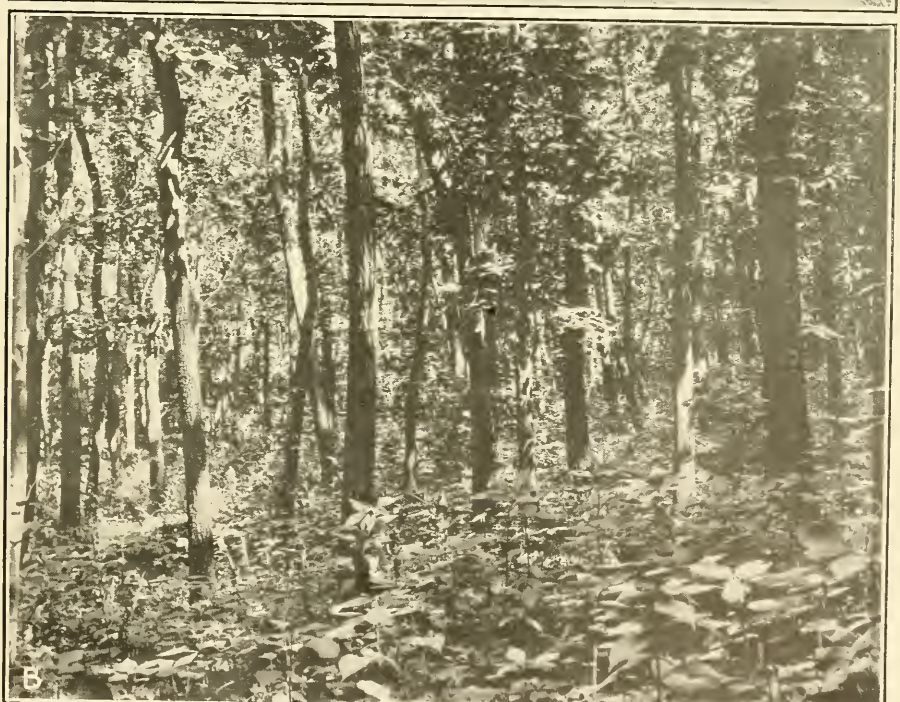
Community structures.—In addition to the units themselves, associal and consocial communities show general structural features, such as zones, alternes, layers, and aspects. These are due primarily to the grouping or appearance of the subordinate communities with reference to a particular factor or factor-complex, and are of the greatest indicator value. The well-known zonation of the hydrosere in and about ponds is the best example of this. Each zone not only marks the general factor limits for its proper community, but also a distinctive step in the decrease of water-content and the increase of soil-air from the extreme conditions in the center. Such a series actually shows on the ground the "before-and-after" correlation of each stage typical of succession. Seral zones may be formed by consocies or associes; in their fullest expression the major zones are marked by associes within which occur minor zones constituted by the consocies in the order of their requirements. The zones of high mountains are essentially similar, though they have to do with climax associations and consociations. The same zonal structure recurs universally, wherever climax or seral communities are grouped about a center of excess or deficiency of some factor or group of factors. Zonation is sometimes obscured, especially in the dense vegetation of prairies (Plant Succession, 133), but it is rarely altogether absent, except in initial communities.

Alternes.—Alternes are due to the interruption of zonation through any cause whatsoever (Clements, 1916 : 115), but they are especially typical where disturbed or other successional areas are found. They are frequent in climax areas wherever inequalities of surface structure and so forth occur. The term alternation is applied to two types of structure, one in which the same dominant or subdominant recurs from place to place, the other in which two or more alternate over the same area. The first kind is usually seral, the second is typical of associes or associations, and also of socies and societies. Recurring alternes are clear-cut indicators of the same set of conditions, and are of the greatest value. Striking examples are found in the burn alternes of aspen or lodgepole in the Rocky Mountains. Alternating dominants or subdominants are likewise indicators of their respective habitats. As indicators, they are naturally less sharply set off from the related dominants, but this is compensated by the evidence afforded of the degree of their equivalence (plate 12, A).

Layers.—Layers are best known in forests and the term has usually been restricted to the subordinate communities in them (Hult, 1881; Clements, 1916 : 15). With the increasing study of root-systems and their competitive relations, it seems desirable to recognize root-layers as well as shoot-layers. Our knowledge of the former is still rudimentary, but it is possible that they are more general and significant than the well-known layers of woody communities. It is almost axiomatic that a layer of either type will have a double indicator value. It indicates the general equivalence with reference to the controlling factor of all the important species in it. Conversely, it denotes the dissimilarity of the adjacent layers and marks a certain stage in the progressive modification of the controlling factor from its point of maximum. Layers also serve to indicate the course of seral development, in that they are generally absent during the initial stages. They appear during the medial stages and usually reach a maximum in the subclimax or climax, often disappearing in woody communities as they become mature. As a consequence, the presence of several layers indicates more or less optimum conditions as to water or light or both (plate 12, B).

Root-layers are regularly determined by water-content, though soil-air and perhaps solutes also must sometimes be taken into account. In saline soils they are due to differences in the salt-content acting through its effect upon water-content, except where the salts are chemically injurious. As to water-content, root layers may be a response to the physical distribution as determined by penetration and evaporation, or to the ecological consequences of competition. In the great majority of soils, both causes play a part (cf. Cannon, 1911; Weaver, 1919). Many communities show a striking correlation between the demands of the shoot and the root-position. This is often expressed in the corresponding development of root and shoot as well. It is best exemplified in the desert scrub, in which the tall shrubs are most deeply rooted, the undershrubs less deeply, the perennial herbs still less deeply, while the low annuals of the rainy season are rooted only in the first few inches.

The obvious relation of shoot-layers is to light, though water-content and humidity must sometimes be taken into account also. The best development of layers is found in well-lighted forests with a light intensity between 0.1 and 0.02. The midsummer values are rarely conclusive, however, as the layers tend to develop in the order of increasing height, with the result that each layer receives the maximum during its period of major activity. Each layer thus has two indicator values, one when it is uppermost and another when it



A. Alternation of sagebrush on southerly slopes, and Douglas fir on northerly ones, King's Ranch, Colorado.

B. Layers of *Impatiens*, *Helianthus*, and *Acalypha* in oak-hickory forest, Weeping Water, Nebraska.

has been overtopped by the later layers. This naturally does not hold for the primary layer of trees or shrubs and for the highest layer of herbs which develops last. The practical value of shoot-layers as indicators is in connection with the natural reproduction of forests and the selection exerted by light upon the tree seedlings of a mixed forest, especially of conifers.

Aspects.—The character of a community changes with the season. This is best shown in prairie where the characteristic subdominants reach their maximum at different times, producing three or even four aspects, viz, prevernal, vernal, estival, and serotinal (Pound and Clements, 1900 : 140). Similar aspects occur in the herbaceous layers of forests. The number decreases with the altitude and latitude, so that arctic and alpine regions usually show but two, spring and summer. The indicator significance of aspects is partly a matter of the societies which characterize them, but they have a seasonal value as well. This lies in recording the advance of the season and in permitting the determination of departures from the normal rate. The correlation of this with the behavior of crop-plants and with all processes which deal with the renewal or rate of growth each year should have considerable practical value. Phenological lists suggest these values, but are too general and unrelated as a rule to be of much service (Lamb, 1915).

## III. KINDS OF INDICATORS.

**Basis of distinction.**—Each plant or community serves as the immediate indicator of a factor or group of factors. As a consequence, it may also be employed to indicate the process or agency which causes or modifies the particular factor, as well as that in which the factor or habitat is involved. When the process is one set up or controlled by man, the plant likewise becomes an indicator of practice, and gives direct service in land classification, agriculture, grazing, and forestry. The relations of the plant or community to process and practice are direct corollaries of the basic principle that each is the best possible measure of the conditions under which it grows. Such measures merely require correlation with a particular process or practice to be of immediate service. This is the inevitable sequence, whether indicator values are the result of actual experience or the outcome of scientific investigation. In the latter case, the correlation is merely more detailed or more definite. Thus, while they all spring from the basic relation of plant or community to habitat, it appears desirable to distinguish indicators with respect to the use made of them. On this basis, they may be recognized as factor indicators, process indicators, or practice indicators. Furthermore, the development of the field of paleo-ecology makes it desirable to extend the application of indicator principles to the geological past. The sequence of indications is essentially identical, but the results must be inferred from present-day investigations, and hence it is desirable to speak of paleic indicators in this connection.

### FACTOR INDICATORS.

**Basis and kinds.**—Every habitat is a complex in which the factors are almost inextricably interwoven. Each factor influences every other factor, and is in turn affected by it. This relation should never be lost sight of, since it is essential to the proper understanding of every factor indicator. Nevertheless, some factors are of such paramount importance in the habitat-complex that it is desirable to relate the plants to them directly. This is particularly true of the direct factors, water, light, temperature, solutes, and soil-oxygen. The indirect factors, soil, slope, exposure, wind, and altitude, can act only through these, but they too may be connected with plants as indicators, whenever they exercise a compelling effect upon a direct factor.

Each factor leaves a distinct impress upon a plant or community in proportion to its intensity and the plant's habitual requirements. The plant becomes an indicator of a particular factor to the more or less complete exclusion of others only when the factor exercises the paramount limiting effect. This is regularly the case when it is present in marked excess or deficiency, and hence a factor indicator usually denotes one extreme or the other, or a tendency toward it. Even in such cases, some at least of the other factors are concerned in producing the particular intensity of the limiting factor or are themselves affected by it. Consequently, each factor indicator not only denotes the controlling or limiting factor, but also a sequence of factors related to it either as causes or effects. A hydrophyte indicates deficient aeration as well as excessive water-content, while a xerophyte as a rule marks high temperatures and low humidity as well as low water-content. In some instances, two or more factors appear to be equally important, and the plant indicates all of them. An excellent example of this is seen in alpine plants, where temperature, water-content, and humidity are of almost equal importance, and wind and pressure of much significance. The situation may be taken to represent the factor-complex, and such plants may be said to indicate high altitudes.

**Quantitative sequences.**—It has already been pointed out that practically every species has an optimum habitat, in which it exhibits its typical indicator value. Outside the optimum or habitual habitat, it has a narrow range in the direction of less favorable conditions for it, and a wider range in that of more favorable conditions. The mere presence of a species or even of a community can not be taken as evidence of its normal indicator value. Its actual value can be determined only by reference to the normal habitat as well as to the plants associated with it. It is this which makes dominance of the first importance in arriving at indicator results. A plant is dominant only within the range of essentially optimum conditions, and its control decreases in both directions, but most rapidly toward less favorable ones. The behavior of the individual plants is in close accord with these changes in abundance. The species has its most typical form where it is dominant, and changes in size and form usually furnish clear indications of departures from the optimum habitat toward either extreme. Subdominance follows the same rules and has similar values, though these are less striking than in the case of the dominants. In the tall-grass prairies, the societies often approximate the value of dominants, but in woodland and forest they are always strictly subordinate, and their indications serve only for a minute analysis of the general conditions of the forest.

In the present condition of quantitative studies, seral and topographic sequences must furnish the chief source of the indicator values of dominants and subdominants. This will probably always be true to a large degree, but the rapid growth of quantitative methods will afford a more detailed basis, and one which can be understood in terms of factors as well as of plants. In this connection, it must be recognized that a floristic census has slight value, and that accurate results can be obtained only by the use of exact methods which have dominance and sequence as their chief objectives. The floristic outlook upon vegetation is a survival of the early days of distributional plant-geography, and it must steadily decrease in importance as ecology becomes truly quantitative in method and result.

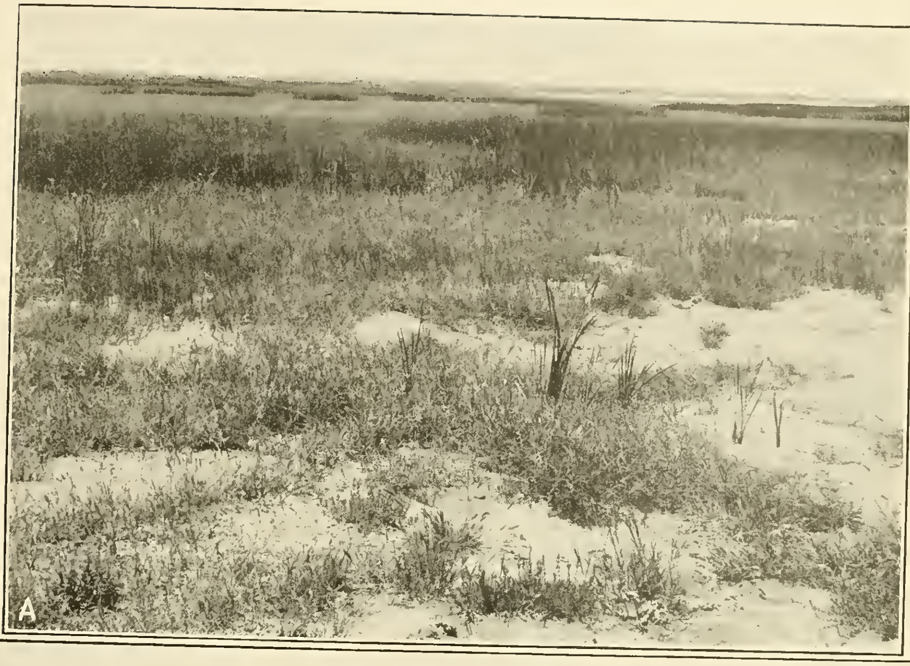
**Climatic and edaphic indicators.**—Every factor plays a part in the development of a community as well as in the control of its final condition. In the developmental habitats the local conditions, especially those of the soil, are paramount, while in climax ones the general climatic factors are controlling. The local or edaphic conditions find their expression in the seral dominants and subdominants, and the communities which they constitute. The widespread climatic conditions are reflected in the climax formation, associations, and societies. As a consequence, it frequently becomes desirable to speak of climatic and edaphic indicators. Certain factors, such as water and temperature, will be represented by both climatic and edaphic indicators. Others, such as light, solutes, soil oxygen, are primarily edaphic, while still others, such as wind and pressure, may be either local or general. In the use of these terms for indicators, it must be clearly understood that the reference is to the nature and size of the area concerned, and not to the position of the factor in the soil or the air. In the sense employed here, climatic and edaphic indicators are synonymous with climax and seral ones, respectively, though the emphasis in the former case is upon the factors rather than the process of development.

Water indicators.—A detailed account of our present knowledge of the indicators of each factor is impossible within the limits of the present treatment. It must suffice to point out here the general relations of each factor to its plant and community indicators and to consider the most important and best understood of the latter in the chapters which have to do with climaxes and with practice indicators. The broader correlations of water and its indicators have already been touched upon in Chapter II, and the following brief statement is intended primarily to emphasize some of the basic points involved and to suggest probable lines of advance in future work.

Water use will undoubtedly become the primary basis for interpreting the water-relations of plants, when the use of phytometric methods becomes general. Expressed in terms of transpiration per unit area and per gram of dry matter produced, this will furnish the first exact basis for the classification of plants on the basis of water. The application of such methods to native species will be a slow matter, however, especially under field conditions. Consequently, the indicator value of native plants for water must still rest largely upon determinations of water-content, humidity, evaporation, and the transpiration of standard plants, supplemented to some degree by studies of the form, structure, and growth of the plants themselves. Thus it becomes particularly important to refine the concept of water-content, since this exerts the basic control in water relations, and to render its expressions more definite and comparable (plate 13).

The general value of the echard for the various kinds of soils is now so well known that determinations of the holard are helpful in refining the values gained from sequences. This is particularly true when a single uniform soil is concerned, though even here account must be taken of differences at the various levels. The importance of the echard at the critical period has obscured the fact that it is the chresard which represents the amount of water available for the work of the plant, and that a very large number, if not the majority of species, probably never reach the echard during their lifetime. The water-response of such plants, and hence their indicator value, is concerned with the chresard. In the case of xerophytes and xeroid plants, including the crop plants of arid regions, the echard may be reached more than once during the growing season, or the plant may remain at that point for a considerable portion of the year. When the latter occurs, the plant bears a distinctive xerophytic impress, the intensity of which is apparently correlated with the length of the period of deficiency. The difficulty of making echard determinations in the field is such that in practice it is much more satisfactory to obtain this indirectly by means of the moisture-equivalent method of Briggs and Shantz (1912 : 56), and to express the seasonal chresard graphically, as has been done by Weaver (1917).

The lack of agreement between the results of the earlier investigators and those of Briggs and Shantz may be due in part to the more exact physical methods of the latter. So far as native plants are concerned, however, there



A. *Typha* alternes indicating pools in a salt-marsh, Goshen, California.
B. *Juniperus* indicating seepage lines in hills of Mancos shale, Cedar, Colorado.

seems to be no question that they vary considerably in their ability to obtain water from the same soil. This is obviously to be explained in part by the fact that the roots are not at the same level, and hence not in the same soil. But there are many cases in which certain species wilt before others, where the roots are interwoven in the same soil. As already mentioned, Dosdall (1919) has found that *Equisetum arvense* regularly wilts before *Helianthus annuus* and *Phaseolus vulgaris* when their roots are at the same depth in uniform soil. This agrees with results obtained in the field at the Alpine Laboratory with uniform gravelly soils, and indicates a considerable difference in the absorbing power of native species. This may be due to striking differences in the rate of transpiration or of the osmotic pressure of the root-hairs, or it may arise from differences in the extent and growth of the roots themselves. As Shull (1916 : 27) has suggested, it would appear less under moderate and uniform conditions, and it seems likewise that it would be less in evidence with crop plants and weeds which grow in fairly uniform root environments. It seems clear that this point must receive further investigation. Meanwhile, it is necessary to recognize that species of the same local group and habitat do wilt at different points, whatever the various causes may be.

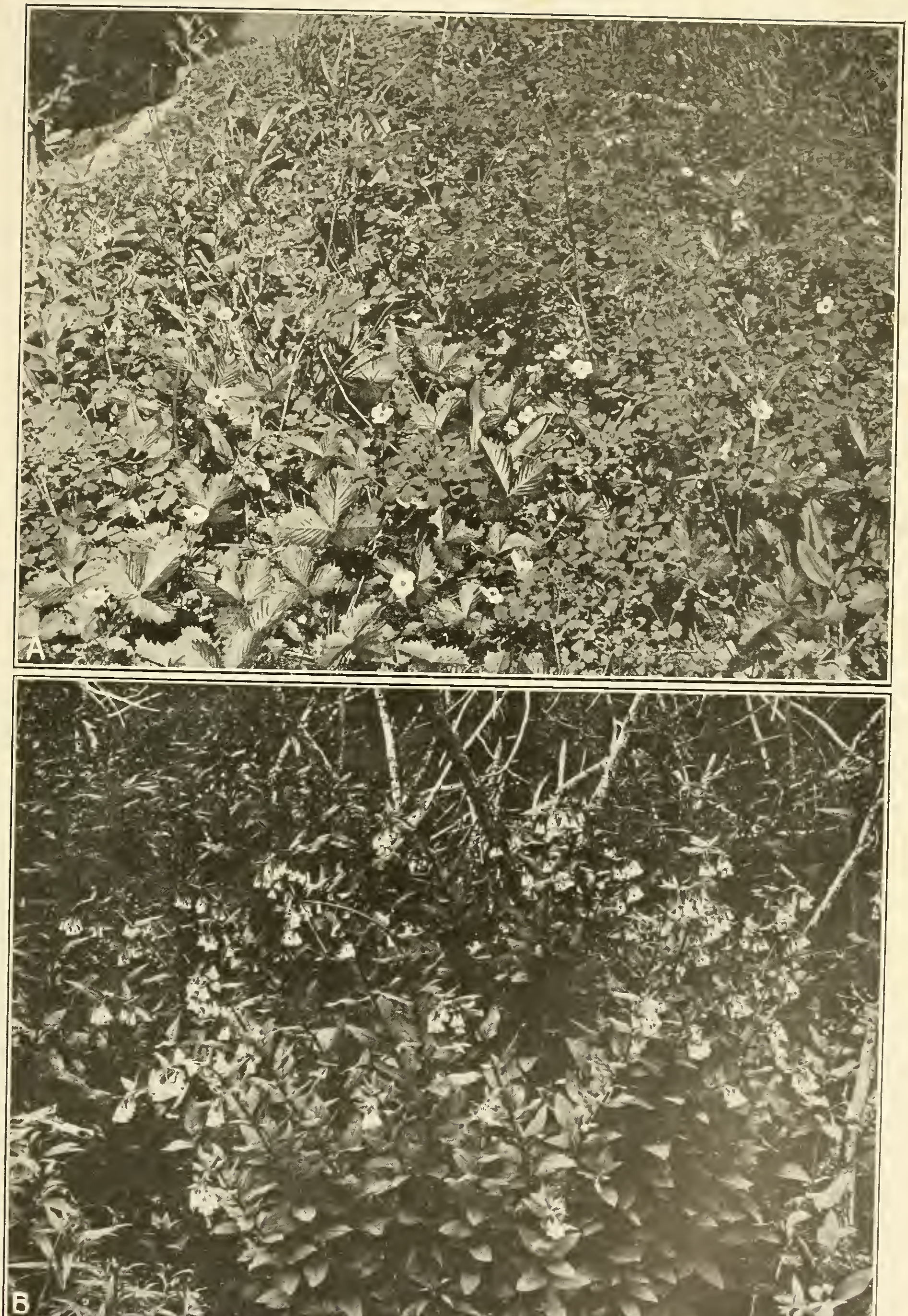
In the endeavor to definitize the significance of water indicators, the primary division into hydrophytes, mesophytes, and xerophytes will still have value. In addition to the subdivision which Warming has already made of them, they will require still further analysis. This will become possible only with more exact study of the controlling factors, and especially of the actual water use. In fact, the precise meaning of any particular indicator will depend wholly upon the latter, and this will involve a readjustment of the relations of the main groups. Meanwhile, a keen appreciation of the need for more exact methods should not be allowed to obscure the fact that indicators of great practical value can still be made available by our present methods of ecological observation and instrumentation.

**Light indicators.**—In spite of the fact that small differences in light values are more readily detected by observation than with water-content, the recognition and use of plants as indicators of different light intensities are matters of recent development. The forester has long understood the general importance of light in the forest, and his tables of tolerance are an indirect recognition of indicator values. As long as he was chiefly interested in silviculture, however, tolerance was a matter of relative growth in the same or similar situations. The development of silvics as a phase of ecology directed attention more to the factors of the habitat, and led to the use of photometers for measuring light intensity. This has made possible the correlation of tables of tolerance with measured intensities and the use of the dominants concerned as direct indicators. Such work has merely been begun, however, and much quantitative study will be required before the general values of tables of tolerance can be made exact. Measurements of light intensity have been largely confined to forests, but it is clear that light values have considerable importance in other communities as well. This is especially true in woodland, scrub, and savannah, but it holds also for grassland, particularly the tall-grass prairies.

Two facts must be taken into account in correlating light indicators with measures of light intensity. One of these is the effect of variations in the composition or quality of the light. There can be no question that white light is modified in passing through the leaves of the forest canopy, the red and blue being absorbed to a larger degree than the green and yellow. In the case of conifers practically no light passes through the needles, and the light beneath them is white light, which has passed through the openings between the needles. In the case of broad-leaved forests, the amount of light entering between the leaves decreases with increasing density of the canopy, and that modified by transmission through the leaves becomes correspondingly more important. In all forests studied by the writer, the light has been essentially normal in composition, but there seems no good reason for questioning the results of Knuchel (1914; 1915: 90) in beech forests especially. Even here, however, his tables and diagram show a somewhat uniform reduction in the different parts of the spectrum. Moreover, several facts indicate that the actual differences in quality in a beech forest are probably of little importance. Photosynthesis takes place almost wholly in the red and blue, which are more or less reduced. Furthermore, this function employs but a small part of the incident light, and a very serious disturbance of the normal composition would be necessary to affect it. Finally, reduction in intensity seems to have much greater influence than the change in quality. Forests of *Picea engelmanni* suppress the undergrowth even more completely than those of beech, in spite of the fact that the composition of the light is practically normal (plate 14).

The significance of light indicators is also complicated by the influence of other factors. As already stated, this is the rule for all factors, but it is more marked in the case of light than of water. This is partly because light affects fewer functions directly, and partly because the modifying influence of water upon tolerance has been too much ignored (Plant Succession, 93). It is perfectly clear that the intimate interaction of water and light in competition, especially in forests, makes it necessary to take them both into account in determining tolerance as well as indicator values. This is true to a much smaller extent of nutrients and temperature, but these would have some influence wherever they tend to become limiting factors. Furthermore, there can be little question that light is usually the controlling factor in tolerance wherever the canopy is closed and that water plays a decisive part only when the light intensity is higher and evaporation and competition consequently greater. However, actual experimental studies of the respective rôles of the two factors, such as those of Fricke (1904), are needed for the various forest communities and the different groupings of dominants within them.

Tolerance has dealt almost wholly with the light relations of forest dominants (Zon and Graves, 1910). The latter are among the simplest and most direct of all light indicators, since they constitute actual experiments in planting, natural or otherwise. As indicators they have the same unique value as crop plants and, so far as practice is concerned, make the use of less direct indicators and of instruments more or less superfluous. In many cases, however, seedlings of a particular dominant or of all the related ones are absent from the forest floor, or the forest itself may be represented only by the undergrowth or certain elements of it. In such cases, the subdominant shrubs and herbs must be employed as indicators. The latter in particular are often more sensitive than the trees themselves and hence furnish a more exact scale



A. *Fragaria* and *Thalictrum*, indicators of medium shade in montane forest, Minnehaha, Colorado.

B. *Mertensia sibirica*, indicator of deep shade in montane forest, Long's Peak, Colorado.

of indications. The widespread occurrence of certain herbaceous societies throughout one or more forest associations, or even formations, affords a striking opportunity for correlating the light relations for dominants associated under varying conditions as to other factors. The perennial herbs are of especial importance in this connection, as the effects of differing light intensities are clearly reflected in a variety of ways, in density, form, height, flowering, etc.

In definitizing the use of light indicators, it will be necessary to resort more and more to quantitative measurements of responses and factors. The most important responses in this connection are photosynthesis and growth. Both of these have certain values, and they will be more and more employed in combination, as complete and accurate results become necessary. At present, however, the determination of photosynthesis and its correlation with light is a much simpler and more exact process. As a consequence, the best determination of indicator values for light will continue to be initiated by close observation of general correspondences, which are first tested by means of measurements of intensity and then by studies of photosynthate production. It is probable, indeed, that this will give the real light indication without recourse to growth responses, but the latter will prove necessary to obtain the full indicator value for practical purposes.

Temperature indicators.—Temperature produces no clear-cut response in structure or grouping, and hence its indicators are not readily recognized by observation alone, as in the case of water and light. The most obvious response to it is growth, but this is affected so profoundly by other factors in nature that a primary correlation with temperature is always difficult and usually impossible. As a consequence of their striking distributional correlation with latitude and altitude, a number of endeavors have been made to classify plants with reference to temperature. The most suggestive are the classifications of A. de Candolle (1874) and Drude (1913 : 154). Both of these are based upon general climatic features, and take some account of water as well as temperature. While they have more or less interest, their ecological value is slight, owing to the almost complete lack of experimental and quantitative bases. Moreover, the usefulness of the groups is further reduced by such terms as "Etesial-Poikilotherme-Psychrochimenen."

The most notable attempt to correlate flora and fauna with temperature is that of Merriam (1890, 1894, 1898). The laws of temperature control of the geographic distribution of plants and animals are stated by him as follows:

"The northward distribution of terrestrial animals and plants is governed by the sum of the positive temperatures for the entire season of growth and reproduction, and the southward distribution is governed by the mean temperature of a brief period during the hottest part of the year."

His well-known system of life-zones was established upon the basis afforded by these hypotheses. As indicated by his discussion of the Arctic, Hudsonian, and Canadian zones (1898 : 54), the life-zones appear to be actually based upon the outstanding vegetation zones of the continent, with temperature control as a more or less correlated principle. While Merriam's system has been of undoubted service in studies of floristics, its ecological value rests upon the extent to which it has followed the natural vegetation zones and climaxes, and upon the correlation of these with crops. It can not be regarded as furnishing adequate proof of the paramount control of temperature in so far as plants are concerned at least. It possesses the disadvantages of every system erected upon a single factor, and emphasizes the basic truth that studies of causes must be grounded upon experiment, and not merely upon field observations and meteorologic data.

While there can be little or no question that every species has a climatic maximum and minimum of temperature, this is known experimentally for none of them. What is ordinarily observed in nature is, broadly speaking, an optimum to which the plant is more or less confined by the action of competition, water, and other factors. Theories of temperature control have generally failed to realize the unique importance of the period of germination and seedling establishment in determining the range and dominance of a particular species. There is sufficient experimental evidence in the case of a few dominants to suggest that many if not all of them can be extended beyond their present northern and southern, as well as their altitudinal limits, by the proper control of local conditions during the period of early ecesis. Moreover, when the part played by water in many of the effects supposed to be caused by temperature is adequately understood, it will be recognized that many of the so-called temperature responses must be ascribed to the combined action of the two.

In accordance with the rule, the impress of temperature should be most pronounced in climates where it is most extreme. These are arctic and alpine regions, and the tropics and subtropics. However, the influence of water is also pronounced in the first two, and over much of the other two. The dwarf shrubs and perennial herbs of alpine and arctic regions have long been regarded as undoubted responses to short seasons and low temperatures. But in the case of some alpine plants at least, it is certain that dwarfing is due as much or more to water than to temperature (Clements, 1907). It appears highly probable that this is true of the dwarfing of trees at timber-line also. In the latter case, the non-availability of the water-content is caused by freezing, and the dwarfing might well be regarded as due to both the direct and indirect action of temperature. A similar relation exists in tropical and subtropical deserts, where the actual impress is largely due to water. The latter is profoundly influenced by temperature, which appears to be in control of distribution to considerable degree, especially in the case of succulents (Shreve, 1911, 1914).

If some weight be assigned to the indirect action of temperature, a considerable number of species may be regarded as temperature indicators. These are primarily alpine and arctic plants, and the succulents of hot desert regions. The trees and shrubs of the boreal tree limit and of timber-line on mountains are similar indicators, and this is true to some degree of those trees which become shrubs as they extend downward into the deserts of the Southwest. The absence of certain life-forms and species as a consequence of frost also constitutes a temperature indication of great importance. As a consequence of the gradual change of temperature with latitude and altitude, climax communities serve as the best of temperature indicators. They combine the responses of both life-form and species on such a large scale that there can be little question of the paramount control of temperature where its extremes are concerned. Between the latter, climax dominants and communities must be regarded as primarily related to water, and hence treated as indicators of it. While these doubtless have relations to temperature which are susceptible of measurement, they are subordinate, and in our present incomplete knowledge can not be regarded as indications of it.

**Indicators of solutes.**—The term solute is used here to indicate any substance dissolved in the holard. It may be solid or gaseous, or even liquid. The best-known solutes are the mineral salts found in the soil, of which some are nutrients, others more or less inactive, and some actually deleterious to the plant. Of the gases dissolved in the holard, oxygen and carbon dioxid are the most important, but oxygen is the only one which bears a clear relation to indicator plants. In addition, there are the debatable toxic exudates and soil toxins, the existence of which is in doubt or the relation to the plant uncertain. Livingston, who has devoted much attention to this subject (1918 : 93), states:

"Evidence that agricultural plants do actually excrete toxic substances into the soil is not very strong in any of this work, however. As to the manner in which these poison substances arise in the soil, no definite statements can yet be made, but they are surely not excreted *as such* from plant roots. There is physiological evidence, however, that such substances are given off by living roots when the latter are practically deprived of oxygen."

In so far as indicator plants are concerned, the effects ascribed to toxins are much better explained on the basis of an inadequate supply of oxygen.

The ordinary nutrient salts of the soil rarely leave a distinctive impress upon plants, owing to lack of concentration. When the concentration reaches a point where absorption is interfered with, the plant makes a definite physiological and structural response to the saline or alkaline conditions. The relation to lime and magnesia is less clear and the indicator impress less marked. In the case of deficient aeration, the response is clear, but its expression is often limited to physiological and histological features. Since all solutes act through water or in conjunction with it, their effects are often obscured by the responses to it. This is particularly true of saline indicators, which are merely xerophytes of a more or less peculiar type.

**Saline indicators.**—The term saline is preferred as the general term for all soil conditions in which soil salts occur in excess or a deleterious alkaline salt is present. In the West it is practically synonymous with the word alkali, and the two are employed interchangeably. Saline indicators are typical of sea-shores the world over, but their most striking development is found in the arid basins of the interior of continents, such as the Great Basin of North America. Practically all the work with them has been done in such regions, where the limits set by alkali to agricultural development are of the greatest importance. The outstanding studies in this field are those of Hilgard (1906) and Kearney (1914), and their respective associates. The work of Hilgard touched a large portion of the West, but dealt especially with California; that of Kearney and his associates was confined to the Tooele Valley in Utah, but it is applicable to the major part of the Great Basin. Both dealt specifically with the tolerance of the important dominants, but the work in Utah was much more intensive, treating the plant communities in detail, and measuring the water-content and salt-content at different depths and in a wide variety of conditions. The indicator values of this classic study were completed by Shantz (Clements, 1916 : 233), who brought out the successional relations of the various communities (plate 15, A).

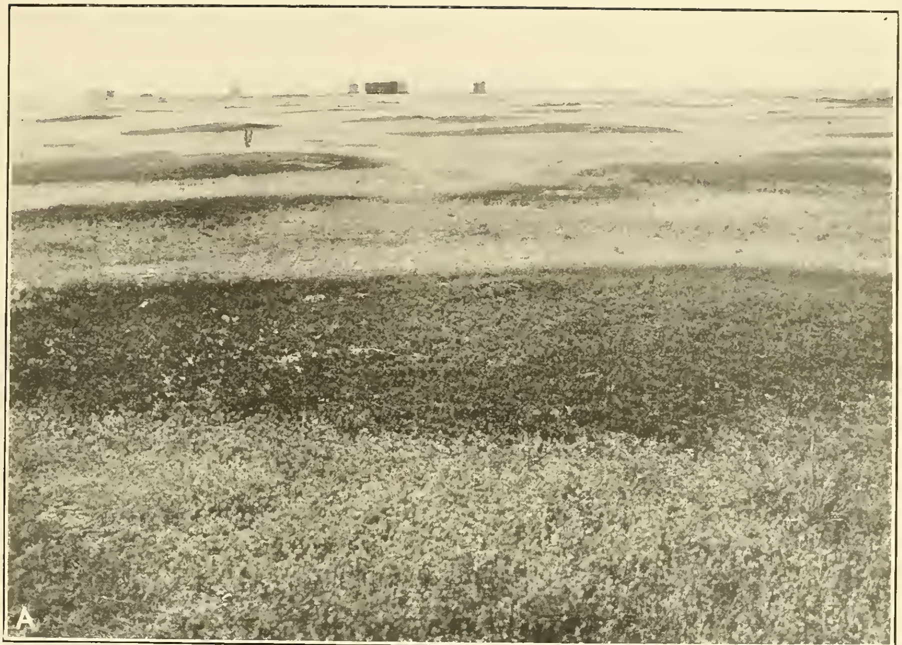
Plants indicate alkali by their presence or absence. The positive indicators are the halophytes, which bear a distinctive xerophytic impress, caused primarily by the decreased chresard in the presence of an excess of salts. When the relation is chiefly one of concentration, the condition is known as "white alkali." This is due to the presence of sodium chloride, sodium sulphate, calcium sulphate, or other salts which possess no directly injurious action. Sodium carbonate produces "black alkali," which is directly deleterious to the plant, probably through corrosion of the tissues. The latter renders the soil useless agriculturally, while the former does not, except when present to an excessive degree. Since the three sodium salts often occur together, the plants of alkali soils serve chiefly as indicators of the total concentration, and the significance of the "black alkali" can be determined only by chemical analysis or crop test. Hilgard (1906 : 535) regards the following species as indicators of irreclaimable land when they occur as dominants, unless the land is underdrained to remove the excess of salts: *Sporobolus airoides*, *Distichlis spicata*, *Spirostachys occidentalis*, *Salicornia* spp., *Dondia torreyana*, *D. suffrutescens*, *Sarcobatus vermiculatus*, *Frankenia grandifolia campestris*, and *Cressa truxillensis*. In the Tooele Valley the crop-producing power of saline lands have been summarized by Kearney *et al.* (1914 : 414) in the following:

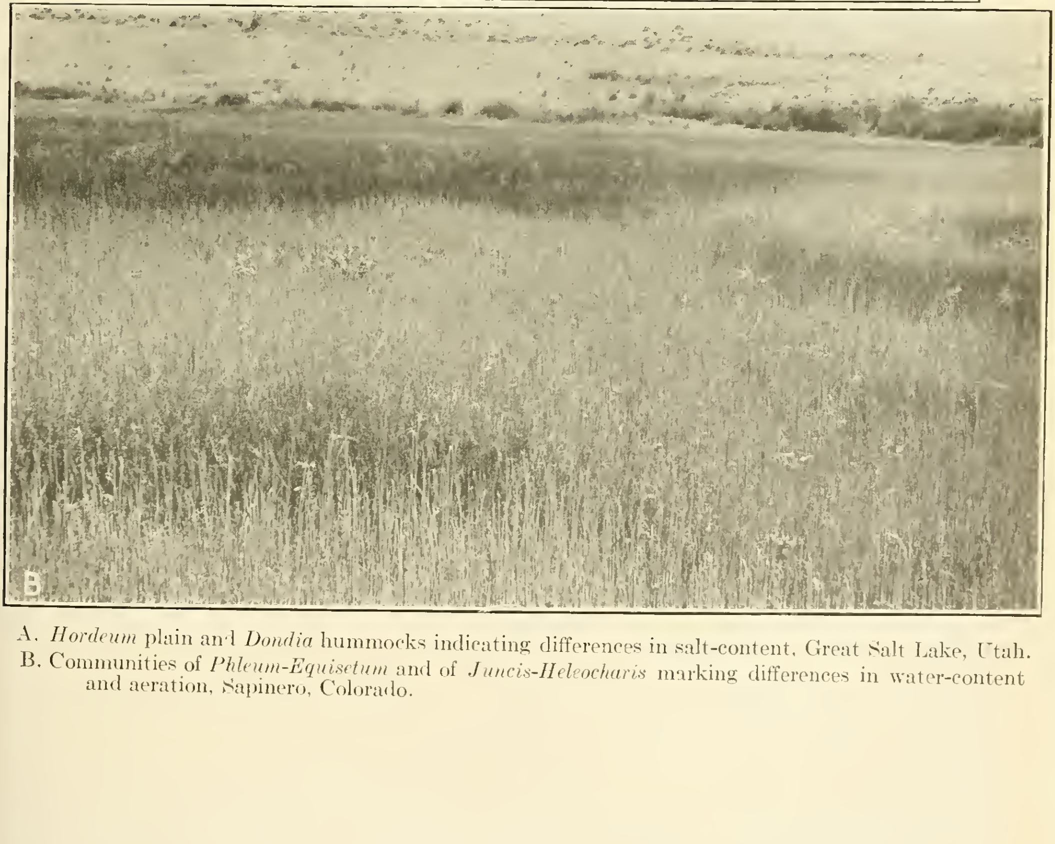
*Community indicators of crop production in saline lands.*

| Type of vegetation. | Is land capable of crop-production— | |
|---|---|---|
| | Without irrigation. | With irrigation. |
| Artemisia tridentata | Yes | Yes. |
| Kochia vestita | Precariously in years of rainfall above the normal | Yes; if alkali can be removed. |
| Atriplex confertifolia | Precariously; conditions rather more favorable than on Kochia land | Yes; after alkali is removed. |
| Sarcobatus-Atriplex | No | Yes; after alkali is removed. |
| Sporobolus-Distichlis | Probably not | Possibly; with drainage. |
| Spirostachys-Salicornia | No | No. |

**Lime indicators.**—The original plan of giving a concise but complete account of the various views as to the effect of lime in native vegetation has necessarily been abandoned by reason of the limitations of space. Consequently, it must suffice to point out that the former views of the calciphily or calciphoby of various species are untenable, and that the effects usually ascribed to lime are either due to a complex of factors or to its indirect action. Schimper (1903 : 94) has presented the best summary of the arguments which support the assumption that lime is a factor of primary importance, but even his account reveals the many weaknesses of the theory. The latter are clearly brought out in the following statement:

"External conditions, however, change with the area. In one area, the silica-form, in another the lime-form, is better adapted to local conditions, whilst in a third area both forms may be able to maintain themselves in the struggle for existence. Accordingly, one and the same species is calciphobous in the first area, calciphilous in the second, and indifferent in the third." (p. 104.)





A. *Hordeum* plain and *Dondia* hummocks indicating differences in salt-content, Great Salt Lake, Utah.
B. Communities of *Phleum-Equisetum* and of *Juncis-Heleocharis* marking differences in water-content and aeration, Sapinero, Colorado.

One by one the "calciphile" and "calciphobe" species have been found or grown in the opposite conditions, until practically no obligate species remain. The present situation is well-expressed by Warming (1909 : 58):

"Recently it has been definitely established that the amount of lime in itself, in so far as it does not operate physically, can not be the cause of differences in the flora, for not only can calcicolous plants be cultivated in soil that is poor in lime, but silicolous plants, and even bog-mosses, which are regarded as pre-eminently calciphobous, can grow vigorously in pure lime-water if the aqueous solution be otherwise poor in dissolved salts. It has been overlooked that nearly all lime soils are rich in soluble mineral substances, and this wealth excludes plants belonging to poorer soils; beyond this the important physical characters of calcareous soil, compared with granite soil, come into play."

The century-old controversy over the significance of lime has been as unscientific as it has been useless. No ecologist questions the influence of both the chemical and physical properties of the soil, though there can still be much opportunity for disagreement as to their respective importance, where observation is the method relied upon. The general employment of quantitative methods and experiments in the fields would long ago have assigned to lime its proper position. Naegeli (1865) was perhaps the first to point out that the response to lime was largely a matter of competition, and the validity of this explanation has been greatly increased by cultures showing the facultative nature of "calciphile" and "calciphobe" plants. His conclusions were based upon observational studies, however, and, like all such work, can only suggest working hypotheses for critical field experiment. The following statement (Clements, 1913 : 76) seems still an adequate summing-up of the lime problem:

"To one skeptical as to the influence of lime, the results of the Excursion were most interesting. One could not fail to be impressed with the abundant evidences of the distributional significance of lime, while he was struck by the fact that scarcely a single 'calciphilous' or 'calciphobous' plant could prove a clear title to the term, physiologically. It is useless to add a single line to the literary solution of this hoary problem, but the British experience serves to emphasize the conviction that nothing but physiological and competition studies in the field can hope to lead to a final solution."

In the western United States lime has nowhere been found to be a direct factor of importance. Neither observation nor experiment has disclosed any definite correlation with it, and hence no plants have been found which can be regarded as lime indicators. The plants of wet soils which have been considered to indicate the absence of lime are dealt with in the next section.

Aeration indicators.—The effects of wet and acid soils upon plant behavior have long constituted a puzzling problem. The leading rôle in such habitats as marshes and bogs has been assigned to various factors, such as acids, bog toxins, toxic exudates, the absence of lime, and the lack of oxygen. Probably all of these are more or less concerned in the problem, with the exception of the supposed exudates, but the view held here is that the lack of oxygen is the cause, and the other conditions, consequences, or concomitants (Clements, 1916 : 90). The presence of acids and bog toxins is regarded as the direct result of the activity of the roots and bog flora under deficient aeration (cf. Stoklasa and Ernest, 1909 : 55; Livingston, 1918 : 95). The absence of lime is apparently a concomitant of acid production, since the addition of lime to an acid soil either neutralizes the acid or affects the colloidal relations in such fashion as to make the soil agriculturally productive. It is significant, however, that lime is not the only substance that has this effect, since it is also produced by other materials which improve aeration. An acid soil is regarded as unfavorable to plant growth primarily because of the deficit in oxygen, and consequently because of the poor development of the micro-organisms that reconvert organic nitrogen into available form (plate 15, B).

The current assumption that bog water contains acids or toxins which are in themselves unfavorable to absorption seems disproved by the experiments of Bergman (1919). This investigator submerged pots containing plants of *Phaseolus* in bog water and tap water respectively until the tops were covered. In both the leaves wilted and turned yellow within 3 days. Both the bog water and tap water were then oxygenated night and morning, and by the following day the leaves had regained their normal turgor, and remained so for several days while oxygen was supplied. Similar results were obtained with *Geranium* and *Impatiens*. With the former, bubbling carbon dioxid through the water containing turgid plants produced wilting on the second day, and led to final chlorosis and fall of the leaves. When pots of *Impatiens* were submerged in water with and without *Philotria*, the ones remained turgid, while the others wilted within 3 days. Plants of *Coleus* and *Fuchsia* were grown in ordinary pots and in submerged ones, and the root pressure was found to be two or three times as great in the former. When the plants in the submerged pots were aerated by bubbling air, or by placing *Philotria* or *Spirogyra* in the water, the root pressure was nearly as great and as well maintained as in the normal conditions. Hydroid species, such as *Salix* sp., *Cyperus alternifolius*, and *Ranunculus sceleratus*, grew about equally well in bog water and tap water, whether aerated or not.

The studies of Hole and Singh (1914 : 10) upon aeration in forest soils indicate that the lack of oxygen is a factor of greater importance and wider extent than has been supposed. The general summary of their results is as follows (101):

"1. The present experiments have confirmed the results previously obtained regarding the very injurious effect of bad aeration on the growth of Sal seedlings in the local forest soil.

"2. When water is long held in contact with this soil, which is the case under conditions of bad aeration, it becomes heavily charged with carbon dioxid and impoverished as regards its supply of oxygen.

"3. The bad growth of Sal seedlings in this soil is correlated with an accumulation of carbon dioxid in the soil-solution and a low oxygen content, and this possibly explains the evil effects of bad aeration. Further work however is required to prove this and also to decide the relative importance of carbon dioxid and oxygen, respectively.

"4. Liming this soil, immediately before sowing, has an injurious effect upon Sal seedlings, and, during the rains, soil which has been thus limed appears to contain more carbon dioxid and less oxygen than the unlimed soil. It seems possible that this may be due to accelerated bacterial activity.

"5. As carbon dioxid is rapidly dissipated and a deficiency of oxygen made good under the ordinary conditions of water cultures, it is not easy to prove the effect of varying quantities of these gases on plants grown in cultures. For the same reason, artificial aeration of such cultures may not show any beneficial result.

"6. As Sal seedlings can be successfully grown in water cultures, the injurious effect of bad aeration is not due to water as such. This probably explains the fact that Sal can grow on the banks of the rivers or even of stagnant lakes, in which the water is kept well aerated by exposure to the air or by the presence of green aquatic plants."

The significance of aeration in field soils has been emphasized by Howard (1913 : 7, 10):

"Important results have been obtained relating to water-logging and drainage, and it is suggested that these matters are of far greater importance than is generally supposed. Even partial water-logging has been shown to reduce the wheat crop 50 per cent. It is possible that the so-called indigo disease is the consequence of water-logging and a want of cultivation in a wet season, and that the best way of dealing with the situation is by improved drainage and by a more thorough aeration of the soil. I believe the damage done to land in Bihar by water-logging during the monsoon is not even dimly realized. Land can be harmed by water-logging when water does not lie on the surface for long periods and when water-logging would not even be suspected."

Plants may indicate good or bad aeration. The former are naturally of little importance as aeration indicators, since their impress is due to some other factor or factor-complex. Aeration indicators proper are correlated with a deficiency of soil-oxygen, and are naturally confined to wet soils and water, owing to the inverse relation existing between the amount of water and of oxygen. They may be conveniently arranged in four groups, based upon the kind of response to deficient aeration. In the first two, the species have developed adaptations which enable them to live so successfully in swamps and bogs that the habit is now obligate for the majority of them. The species of swamps regularly possess a special aerating system of air-passages and diaphragms, often supplemented by superficial roots and a marked movement of the transpiration stream. Such indicators are found typically in *Equisetum, Juncus, Heleocharis, Scirpus, Alisma, Sagittaria, Sparganium,* etc. Air-passages also occur in some bog-plants, but they are little or not at all developed in the shrubby species, such as *Vaccinium, Ledum, Andromeda, Kalmia, Empetrum,* etc. In most of these, the aeration devices are subordinate to those designed to conserve the water-supply during drought, especially in winter (Gates, 1914). Coville (1911, 1913) has emphasized the importance of good aeration for the successful culture of the blueberry, pointing out that this is secured in nature by the superficial roots as well as by their position in hummocks. It is probable also that mycorhiza plays an important rôle, partly in increasing the available nitrogen, and partly also perhaps in directly compensating for the deficit in oxygen.

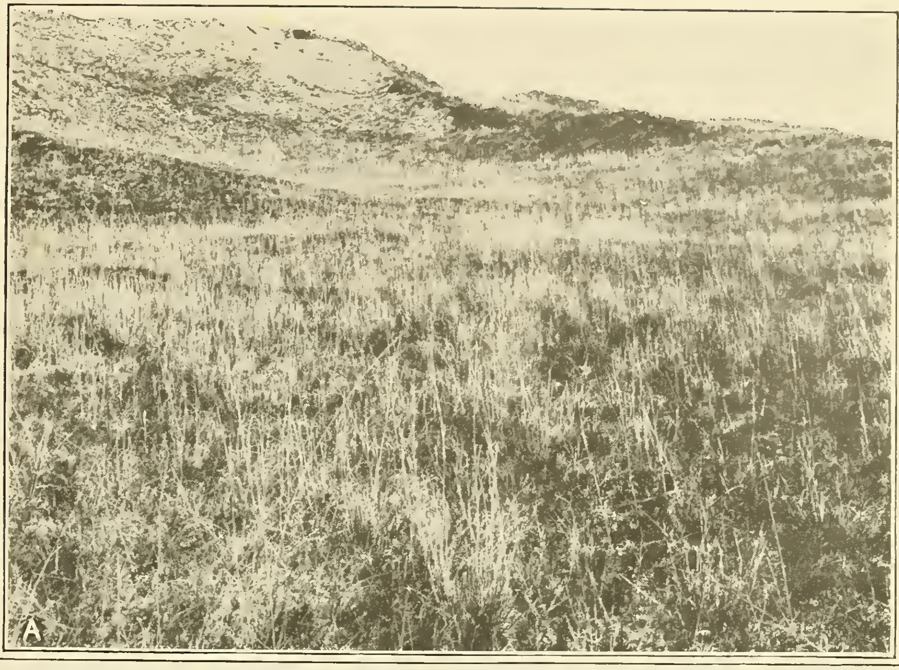
The other two groups of aeration indicators consist of plants which grow normally in well-aerated soil. Hence they lack special adaptations for aeration, and consequently serve to indicate a lack of oxygen by their growth or distribution. Those which are somewhat tolerant of water-logged and poorly aerated soils respond to reduced oxygen content by decreased growth and reproduction. Intolerant species drop out, and their reduced number or absence serves as an indicator of conditions. Field studies of aeration or acidity have been few in the region concerned here. The most important is that of Sampson (1912 : 51) in the Wallowa Mountains of northeastern Oregon.

**Indicators of factor-complexes.**—While indicators are concerned most immediately with direct factors, they are also definitely related to the indirect ones. Since the water-content is profoundly influenced by the nature of the soil, water indicators often serve as indicators of soil also. In practice, the character of the soil is more readily recognized than the amount of water in it, and the indicators of good soil represent not merely an adequate water-content and air-content, but a proper supply of nutrients as well. Slope or exposure and altitude are similar factor-complexes, in which the relation of the indicator to the complex is often clearer than it is to any one of the factors in it. In all of these, however, it is understood that the correlation is with one or two limiting factors, which are controlled or modified by soil, exposure, or altitude (plate 16, A).

**Soil indicators.**—Since the soil is the seat of water-content, salts, oxygen, and acids, as well as of numberless organisms, it may be related to the indicators of any of these. This is the case in ordinary practice, and plants are spoken of as indicators of moist soil, alkaline or acid soil, as the case may be. In the stricter sense, indicators refer to the soil as defined by its physical properties, though this necessarily includes water-content. On this basis, plants may be indicators of sand, clay, loam, or humus soils. When their growth and distribution are taken into account, they may serve to indicate even finer divisions of each of these types. In such cases, however, local variations in water-content are often more potent than soil texture, and correlation with one does not necessarily mean correlation with the other. Since the physical character of the soil is of primary importance in determining the echard, soil indicators may be used to distinguish high and low echard. The plants of clay and humus soils are indicators of the one, those of gravelly and sandy soils of the other. In humid regions this distinction is of little importance, except possibly in relation to drainage, but in arid climates or during seasons of drought it is frequently a vital matter. This has been emphasized by Shantz (1911 : 87) in his indicator studies in eastern Colorado:

"Many of the older settlers in eastern Colorado have moved from short-grass onto wire-grass land, or even bunch-grass land, where they claim there is much less likelihood of crop failure; but the newcomer in the region or the speculator almost invariably chooses the hard or short-grass land because it is darker in color, and looks more like the soil he has been accustomed to farm successfully in the East."

**Slope-exposure indicators.**—While slope and exposure are regarded as distinct topographic features, they are so intimately combined on every hill and mountain that their separation is undesirable, so far as indicators are concerned at least. Both modify the direct factors, water-content, humidity, light, and temperature, and through them nearly all other factors of the habitat. Exposure is of the most immediate importance, as it determines the exposition toward the sun or away from it, but is itself determined in large measure by the angle of slope. Exposure directly affects the temperature and humidity, and through them the water-content, and consequently the nutrients and aeration. A northerly exposure also reduces the amount of direct sunlight, but this is perhaps felt only in transpiration. An increase in the angle of slope has a marked effect in increasing the runoff and correspondingly reducing the



A. *Andropogon hallii* indicating stable sandy soil in sandhills, Agate, Nebraska.

B. Albernes of sagebrush and aspen-Douglas fir forest indicating various slope-exposures, King's Ranch, Colorado.

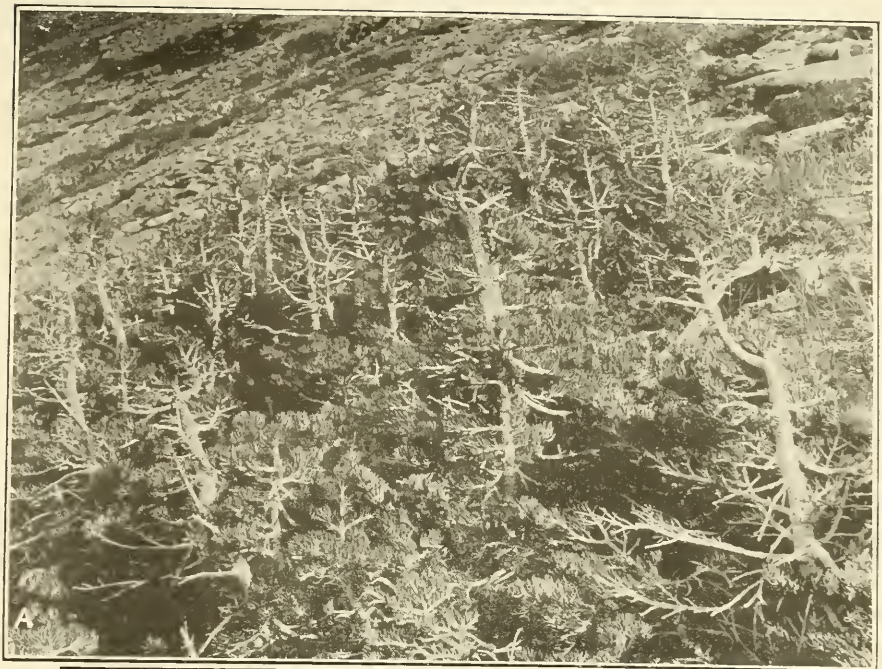
water-content. Perhaps its most significant effect lies in emphasizing the effects of exposure toward or away from the sun. Together the two increase temperature and evaporation, and decrease humidity and water-content on all southerly exposures, while they have just the opposite effect on northerly ones. In arid regions, the effects upon plants are often most pronounced. Succession moves much more rapidly and the climax is reached much sooner on the north side, with the result that the communities often differ greatly on the north and south slopes of the same hill. Growth usually begins earlier on south slopes, but the plants are taller and denser on north ones. The indicator differences deal with the presence or absence of various species and the corresponding communities, and with the growth and abundance of the individuals. Such indications are related primarily to water-content and evaporation, though temperature plays a direct rôle of some consequence (plate 16, B).

Alternation in vegetation is largely a matter of slope-exposure (Clements, 1904 : 165; 1905 : 285; 1907 : 289). Much attention has been given to the alternation of dominants and subdominants on different slopes in the rolling prairies of Nebraska and the mountains of Colorado. Shantz (1906 : 25) has shown the variation in temperature and light intensity during the day for different slopes in the short-grass association at Colorado Springs. Weaver (1917 : 43; 1919) has made a detailed study of the evaporation, water-content, and temperatures of northeast and southwest slopes in the Palouse region of Washington and adjacent Idaho. All the factors agree in showing that the southerly slopes are much more xerophytic, and readily explain the absence of a large number of species, or their greater abundance on the northerly slopes. Spalding (1909 : 43) studied the occurrence of species on two opposite slopes in the desert scrub at Tucson. He found that they had 15 perennial species in common, while the northeast slope had 24 not found on the southwest, and the latter 9 not present on the other. Shreve (1915 : 97, 61) has given a detailed account of the differences in the vegetation of the Santa Catalina Mountains due to slope-exposure, and in the factors concerned.

Altitude indicators.—Altitude is not so much an edaphic factor-complex as the expression of a specialized climate, of which elevation above the sea-level is the remote cause. This expression occurs in some degree at all altitudes, but its accumulation becomes most striking at the higher ones and especially above timber-line. Because of the close relation between altitude and latitude, the actual level of a particular effect, such as timber-line, varies from sea-level at the northern tree-limit to 12,000 feet or more in the southern Rocky Mountains. As is well known, the direct effect of increased elevation is seen in reduced pressure and a correspondingly rarefied atmosphere, which is the primary cause of most of the changes. The factor most affected is temperature, the rays passing readily through the rarer air during the day, while for the same reason radiation is very rapid at night. As a consequence, the soil and the air immediately above it may become very warm on a sunny day and then drop to freezing at night. On Pike's Peak the surface of the soil may show a temperature of 140° F., while in the air 5 feet above, the temperature is but 70° F. Probably still more important is the shortness of the growing season. The frostless season is nearly 5 months long at Colorado Springs (6,000 feet), while on the top of Pike's Peak (14,100 feet) frost occurs frequently throughout the summer. The light changes little in quality or intensity with the altitude in the Rocky Mountain region generally, though this may be due to low humidity. The relative humidity increases, but evaporation and transpiration are greater at higher elevations, owing to reduced pressure, wind, etc. The annual precipitation rises steadily with altitude, and an increasing amount of it occurs as snow. The excessive snowfall of subalpine and alpine regions accounts for many of their characteristic features and explains the generally high water-content. Winds are usually prevailing and forceful, and have both a direct and indirect effect in the dwarfing of trees at timber-line. The indicator values associated with high altitudes are primarily due to temperature or water, or usually to both acting together. With the exception of the wind and snow forms of trees and shrubs, all alpine and subalpine indicators are related to these factors in the region concerned.

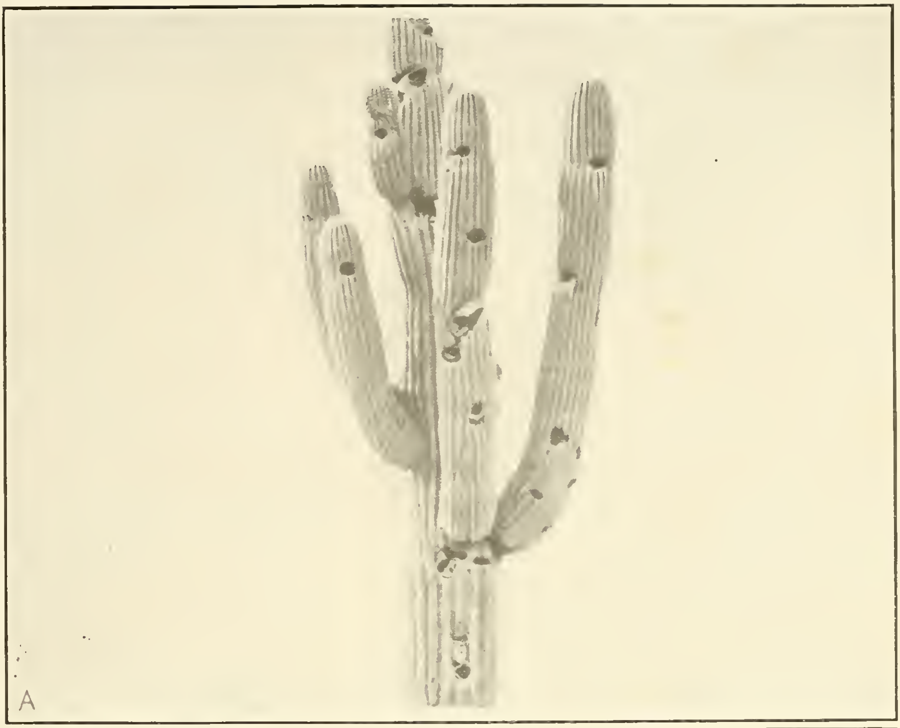
The sharp changes of climate with altitude produces a corresponding sequence of climaxes, which serve as the most outstanding of indicators. These are considered in more or less detail in the following chapter. In addition, the majority of montane and alpine species have rather definite lower and upper limits, and may be used as indicators of altitude, though a correction is necessary for those of wide range in latitude. Cockerell (1906 : 861) has made an analysis of the alpine species of Colorado, based upon Rydberg's Flora of Colorado (1906), which brings out their altitudinal relations clearly, and makes it possible to use many of them as altitude indicators for the central Rocky Mountains (plate 17).

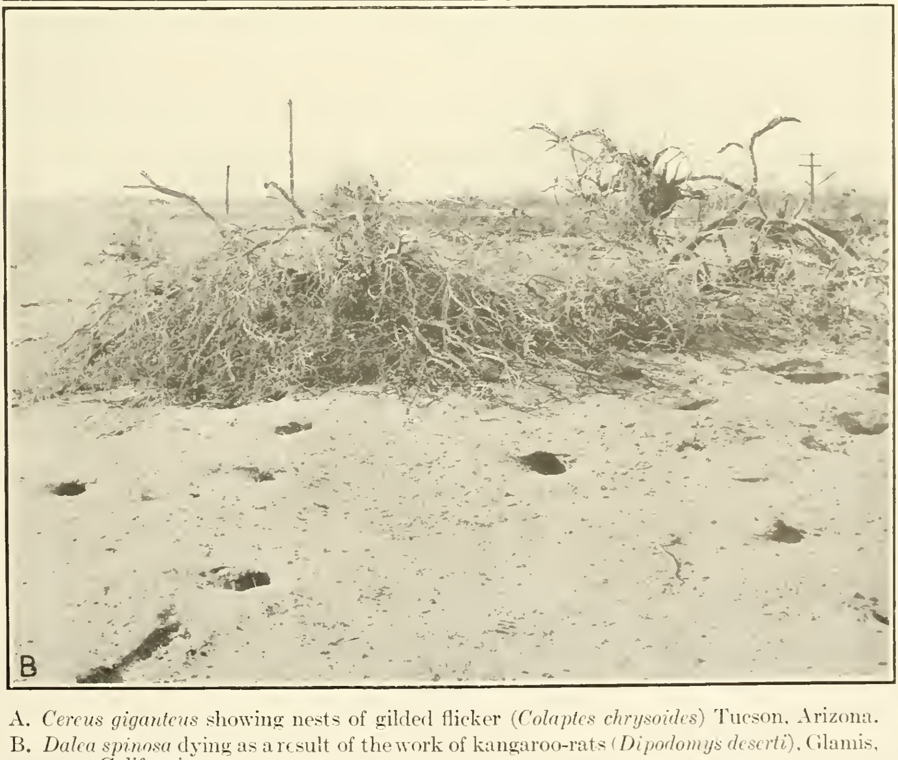
Organism indicators.—The many basic relations between plants and animals make it clear why the plants often serve as definite indicators of animals. Animals may also act as indicators of plants, but to a less degree and in a less definite manner. In addition, plants regularly serve as indicators of such other plants as bear a distinct nutritional relation to them. This is particularly true of the fungi and bacteria, of which one of the most striking indicator relations, the fairy ring, has already been discussed (p. 12). The use of plants as indicators of animals is based upon the relation of food, shelter, disturbance, or pollination. In all of these the indications may be very definite, a certain plant or community denoting a particular animal, but as a rule the relation is necessarily more general. In some cases, moreover, the relation may be concomitant rather than causal, as in the case of the alpine conies and marmots, where the control seems to be rather one of climate than of the alpine plants upon which they feed. Furthermore, the indicator relation varies from region to region with the range of local occurrence of the species concerned. A striking example of this occurs in the relation of the kangaroo rat (*Dipodomys deserti*) to the shrubs about which it makes its mounds. In the savannahs of the desert plains it occupies every clump of *Celtis pallida* as its first choice. In the usual desert mixtures of *Larrea* and *Prosopis* where *Celtis* is absent, the preference is almost exclusively for *Prosopis*, but when the latter is lacking or has been destroyed by the rats, the mounds are made about *Larrea*. In portions of the Colorado Desert, mounds of remarkable size are built about *Dalea spinosa*, and both *Prosopis* and *Larrea* are practically ignored. Throughout the desert scrub, one or the other of these four genera will be the indicator, depending upon their grouping.



A. Alpine fir (*Abies lasiocarpa*) at timber line, showing the dwarfing effect of high altitudes, Long's Peak, Colorado.

B. An alpine dwarf (*Rydbergia grandiflora*), Pike's Peak, Colorado.




A. *Cereus giganteus* showing nests of gilded flicker (*Colaptes chrysoides*) Tucson, Arizona.
B. *Dalea spinosa* dying as a result of the work of kangaroo-rats (*Dipodomys deserti*), Glamis, California.

Food and shelter relations are naturally often combined in the same community. When they are found in the same species, the indicator value of the latter is distinctive. This is not infrequent for mammals and birds, as in the case of *Neotoma* and *Yucca* or *Opuntia* in their respective communities, but it is best seen in the case of insects. The classic example is afforded by *Yucca* and *Pronuba*, but *Xyloscopa*, *Megachile*, and other genera of pollinators furnish similar instances, while the host-plants of gall-producing insects exhibit a like relation. Such examples are naturally rare among birds, but a close relation exists in some cases. Taylor (1912 : 414) has called attention to this in the case of *Artemisia tridentata* and the sage-thrasher, *Oreoscoptes montanus*, and it occurs also between the cylindric opuntias and the cactus wren, *Heleodytes brunneicapillus*, as well as between the giant cactus, *Cereus giganteus*, and the gilded flicker, *Colaptes chrysoides* (plate 18).

The indicator relations between plants and animals arising out of the disturbances caused by the latter are numerous, and play a large part in the study of secondary succession. Among the striking examples are ant-hills, rodent burrows, prairie-dog towns, and beaver dams. The indicators of this type are considered further in the section on paleic indicators.

## PROCESS INDICATORS.

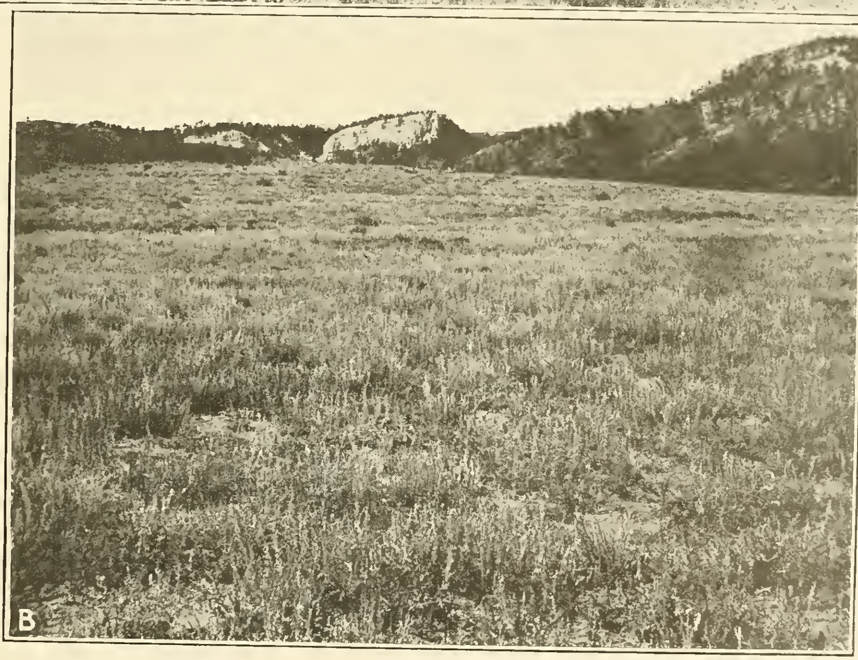
Nature.—Process indicators comprise those plants and communities which indicate definite processes in the habitat. Such processes may be natural, as when they are topographic or climatic, or artificial, when they are the result of disturbances due to man. Such a distinction is convenient rather than essential, since there is no real difference in the overgrazing due to a herd of bison and that caused by a herd of cattle, or in disturbances of the soil produced by primitive or civilized man. The latter, however, does cause disturbances in vastly greater number and on a much greater scale, with the result that the majority of process indicators ordinarily encountered are related to his activities. While the two have much in common, the more vital distinction is based upon the nature of the area, and the vegetational development which results (Plant Succession, 33, 60). Primary areas are represented by water-bodies, rock, dune-sand, etc., in which extreme conditions prevail, and a long line of development occurs. Secondary areas are due to disturbance by man or animals, or to superficial erosion or deposition. The conditions are usually much less extreme for the initial invaders, and the development is correspondingly short and simple. Both are alike, however, in that the successional development progresses by more or less well-marked stages, in which there is a definite relation between the dominants and the factors. Each stage or associes thus serves as a community indicator of the conditions of the habitat, each consocies as an indicator of smaller habitat differences, and each socies of still finer differences.

Kinds.—Process indicators are grouped primarily upon the nature of the process itself. They are all indicators of the successional process in vegetation, and hence this relation is taken for granted. The great majority of them are concerned with unit successions or seres related to physiographic processes or disturbances, but many of them have to do with climatic processes or cycles, as found in potential succession, and in coseres and cliseres. Hence it is desirable to distinguish the indicators of primary processes, such as climatic and physiographic cycles, and those of secondary processes such as superficial disturbances which result in denudation merely, whether produced by man or other agencies. The major secondary processes are fire, lumbering, cultivation, grazing, engineering operations which involve cutting or filling, irrigation, drainage, and superficial erosion and deposition due to natural agencies. These are all alike in that they initiate secondary seres, but they differ sufficiently in detail to be characterized by more or less distinctive indicators. This is so true of some that it is possible to distinguish different kinds of cultivation, grazing, etc., by means of their indicators.

Process indicators serve not only to denote the kind of process, as well as certain variations in it, but they can also be used to approximate the time of origin and the rate of movement. This is the natural outcome of the sequence of stages in sere and habitat which marks succession. Moreover, they possess the further advantage peculiar to all successional dominants of indicating communities and conditions which have preceded, as well as those which are to follow, including the final climax. As already indicated, this is often of the greatest practical value in enabling one to restore an earlier condition or community, to hasten a later one, or to hold the succession in the stage desired. Accurate determinations of the rate of progress can be made only by the use of permanent quadrats, but it can often be closely approximated, in woody communities especially, by ascertaining the age of the dominants in relation to the life-history.

Fire indicators.—While fire has some points in common with other agencies which cause denudation, it differs especially in its action upon the surface soil and in the more or less complete destruction of plants and germules, as well as in the fact that the soil is not actually disturbed. These differences are reflected in the large number of indicators either peculiar to it or more typical of it than of other processes. Certain vegetation-forms appear to owe their character or at least their dominance to fire. This is particularly true of scrub, where the form and consequently the dominance are due to the root-sprouts produced after fire. This relation is practically universal in the Coastal chaparral, and explains the greater massiveness of this association in comparison with the other scrub communities. It is general in the Petran chaparral and the desert scrub, and is poorly developed only in the Basin sagebrush. The response to fire is typical of the subclimax chaparral in California and Oregon, as well as of that which occurs in the prairies of the Middle West. The bush or scrub type is a characteristic fire indicator in forest climaxes the world over, and throughout the northern hemisphere it often consists of the same genera and even species (plate 19, A).

Fire has played a similar rôle in making certain genera and species of trees almost universal indicators of its action. The best known examples are found in *Populus* and *Betula*. *Populus tremuloides* and *Betula papyrifera* are the characteristic indicators of fire in forest communities throughout boreal North America, as well as in many mountain regions. They owe this to their ability to form root-sprouts, and the trees often or regularly consist of several stems in consequence. In the Old World, corresponding species of the same genera play a similar part. A second striking group of indicators is found among the conifers, and especially the pines. The latter are characterized by cones which may remain closed upon the branches for many years, but open



A. Aspen indicating an early fire, and sagebrush alternes, a recent one, Strawberry Canyon, Utah.

B. *Artemisia frigida* indicating an old fallow field, Warbonnet Canyon, Pine Ridge, Nebraska.

readily after fire, thus furnishing a large number of seeds for immediate ecesis. Three important species of this type occur in western North America, namely, lodgepole pine, *Pinus contorta,* jack pine, *P. divaricata,* and knobcone pine, *P. attenuata.* These are all typical fire trees, and form subclimaxes of great extent and duration in areas frequently swept by fire (Clements, 1910). In the Coast forest, *Larix occidentalis* and *Pseudotsuga mucronata* likewise owe their dominance in large measure to fire, though for reasons partly connected with their intolerance.

Among herbaceous plants the number of fire indicators is legion. A large number of these are annuals and biennials, but some of the most widespread are perennials, such as *Epilobium spicatum* and *Pteris aquilina.* They are not restricted to flowering plants, but are represented by *Pyronema confluens* among the fungi, *Marchantia polymorpha* among the liverworts, and *Bryum argenteum* and *Funaria hygrometrica* among the mosses. The most typical fire-grass is *Agrostis hiemalis,* while among the composites, *Anaphalis margaritacea, Achillea millefolium, Arnica cordifolia, Erigeron acris,* and species of *Carduus, Senecio,* and *Solidago* are especially important. In severe burns, the germules may be largely destroyed, and the resulting subsere shows distinct stages of which *Agrostis hiemalis* is the first community and *Epilobium* the second. Very often, however, the dominants of the various stages appear during the first two years, and the successional movement consists chiefly of the successive dominance of annuals, biennials, perennials, bushes, and trees, as they replace or overtop each other. Many of the herbs and bushes persist as layers if the shade permits, suggesting that they were originally derived from such. In most cases, their continued persistence as societies is connected with occasional ground fires. In such instances, the evidence furnished by their presence can be checked by means of fire-scars, the age of burned seedlings, and the presence of charcoal in the soil.

Lumbering indicators.—As a general rule, the indicators of lumbering operations are of much less importance than those of fire. This is due to the fact that the direct evidence afforded by stumps and relict trees is altogether conclusive, and that furnished by the herbs and shrubs is superfluous. In spite of this, there are not infrequent cases where the clearing has been so complete that the usual woody relicts are absent. Many of these are complicated by fire or cultivation, and some by both. However, in the midst of virgin forest, clearings occur in which the evidence as to the agent must be sought from the species in possession. In all clearings due to the ax, whether the direct evidence is still available or not, many of the dominants are the same as in burns. The chief difference in the two communities lies in the greater selection exerted by fire, with the result that the dominants are fewer in number and more controlling. For the same region, the major dominants are the same for both, particularly where fire has followed lumbering, as has been the rule.

Cultivation indicators.—As suggested previously, these might well be called indexes rather than indicators, since they are the consequence of cultivation instead of an indication of its possibility. The number of such indicators is very large and they vary from one climax to another in accordance with the flora. Many of them are introduced weeds, but the majority are subruderal species derived from the adjacent vegetation. The relative importance of the two elements varies greatly, but the introduced species decrease rapidly in number toward the interior as well as upward into mountain ranges. For a number of reasons, the prairies and plains exhibit the largest number of cultivation indicators, but they occur in all climaxes with the exception of the alpine meadow.

Especial attention has been paid to the subsere originating in fallow and abandoned fields, and on timber claims throughout the grassland climax. In the more arid portions of this vast region, there have been several waves of settlement, coinciding more or less closely with the wet phases of the sun-spot cycle. These waves have receded during the drought phases of the early seventies, the early nineties, and of 1916–1918. However, the recession has been less each time, owing largely to better methods of tillage and to the diversification of crops. In the drought of 1893–1895, the Niobrara region of northeastern Nebraska was nearly depopulated, where to-day there exists an assured agricultural practice. As a consequence, also, the belt of abandoned fields and farms has moved westward, and the indicators have changed to correspond. Many of them occur over much of the region, however, and these are still those of greatest importance and almost universal occurrence. A large number are annuals, and the pioneers are all annual or biennial. As is typical of weeds and subruderals, they occur in dense stands of a single dominant, or a mixture of but two or three major dominants (plate 19, B).

The widespread dominants of the fallow fields of the prairies and plains are *Salsola* and *Helianthus*, the latter represented by *H. annuus* in the eastern portion, and *H. petiolaris* in the western. Both genera occur from Montana to Texas, but are more abundant southward. *Erigeron canadensis* is perhaps next in importance in fields, while *Grindelia*, *Gutierrezia*, and *Artemisia frigida*, though abundant, are of still greater importance in pastures. *Coreopsis tinctoria* and *Polygonum pennsylvanicum* are typical of moister fields in the eastern half, while *Anogra albicaulis*, *Oenothera rhombipetala*, *Eriogonum annuum*, and *Cycloloma platyphyllum* characterize fallow areas with more or less sandy soil, especially in the West. Other indicators of common occurrence are *Euphorbia marginata*, *E. geyeri*, *Ambrosia artemisifolia*, *Iva xanthifolia*, *Chenopodium album*, *Panicum capillare*, *Eragrostis pectinacea*, *Cenchrus tribuloides*, etc. A similar wealth of indicators of fallow or abandoned fields is found in California. *Eschscholtzia californica* is by far the most striking of these, though it is less widely distributed than *Amsinckia intermedia*, *Eremocarpus setigerus*, *Sisymbrium altissimum*, *Rhaphanus sativus*, *Brassica nigra*, *Bromus maximus*, etc.

Grazing indicators.—Like the species which indicate cultivation, grazing indicators mark disturbance in varying degree. It is likewise necessary to distinguish such indicators or indexes from those which denote the kind of grazing possible or desirable, and the carrying capacity as measured by number of animals. The latter are among the most direct of practice indicators, and might well be taken for granted, if their value did not change critically from one community to another, or in different portions of the same community. There is much less difference in the nutritive value of the ordinary grass dominants, for example, than in their palatability, but the latter varies greatly with the choice possible.

A considerable number of cultivation indicators are also indicators of overgrazing. This is explained by their common relation to disturbance. In the case of cultivation, the disturbance is much greater and usually operates in a shorter time. The disturbance produced by overgrazing is gradual and accumulative, and requires several years or more to attain definite expression. In the case of breaking and tilling in a new region on the plains, the original vegetation is completely or mostly destroyed, and a distinct subsere beginning with annuals is initiated. On the other hand, overgrazing changes the competition relations between the dominants as its primary effect, and the actual disturbance of the soil is usually secondary. The grasses and herbs that are not eaten gradually secure an advantage over the others, and correspondingly increase in dominance or importance. In most cases, they are already present in the community, but where they are not, their invasion from roadsides or other disturbed places into the trampled soil is a simple matter. There are in consequence two general types of indicators of overgrazing, *i. e.*, those due primarily to the fact that they are not eaten, and those which invade because of disturbance. There is naturally no hard-and-fast line between them, as is shown in the detailed discussion in Chapter VI (plate 20, A).

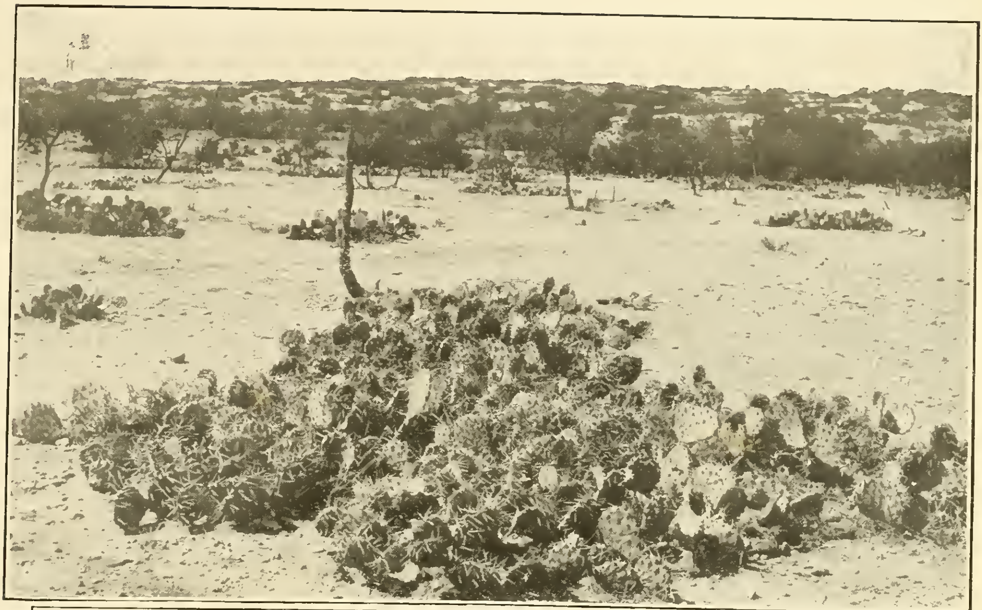
As a consequence of the difference in the successional process, the indicators of overgrazing resemble those of old fallow fields, and there are instances in which careful scrutiny is needed to distinguish the initial cause. However, when trampling has destroyed the control of the dominants and greatly disturbed the surface soil, as happens frequently in sandy areas, a subsere beginning with annuals results. Throughout the grassland climax, there occur three overgrazing indicators which outrank all others in importance. These are *Gutierrezia sarothrae*, *Aristida purpurea*, and *Artemisia frigida*. There are many others of great significance, especially among the species of *Grindelia*, *Opuntia*, *Psoralea*, *Petalostemon*, *Verbena*, *Vernonia*, *Euphorbia*, *Carduus*, *Solidago*, etc., which are discussed in Chapter VI.

**Indicators of irrigation and drainage.**—These are related in that they are connected primarily with a decisive disturbance in the water relations, though they are more or less opposite in nature. Plants which register the effects of irrigation are numerous, and are to be found along every irrigation ditch and field. Those which indicate the possibility or desirability of irrigation are less definite and have received much less attention. Many of them are of great importance in denoting good soils of sufficient depth, *e. g.*, *Artemisia*, *Prosopis*, etc., or sufficiently free from alkali, *e. g.*, *Artemisia*, *Atriplex canescens*, etc. The disturbance of the soil in constructing irrigation canals and ditches, coupled with the abundant water supply, has permitted the development of a large and varied plant population along them. This is composed largely of the weeds of cultivated fields and roadsides, but it also contains many subruderals developed from the natural communities. Macbride (1916) has made an interesting study of the successional changes which occur under irrigation, and his results serve to indicate the general indicator value of the dominants.

Plant communities serve as excellent indicators of the need of drainage, as well as of its progress and success. The need for drainage is clearly indicated by the presence of any one of the stages of the hydrosere or oxysere. The latter also indicates the necessity of liming the soil, or employing some other method of securing aeration and neutralization. Drainage hastens the movement and reaction of the succession in swamps and bogs, and the later seral stages clearly indicate when the successive points have been reached at which the area can be used for grazing, forestation, or crop production. However, in extensive drainage operations, the areas concerned are put into commission so rapidly that the natural communities are destroyed.

Construction indicators.—Practically all engineering and other construction operations in nature disturb the soil, often in a most striking fashion. The most common and important are the building of roads and the construction of railways and canals. The construction of buildings and similar operations belong in the same category, but the effects are usually masked by the subsequent activities of man. The general relation of engineering operations to succession and hence to indicators is best exemplified in the case of a railway cut and fill. In addition to the cut and the corresponding fill, there is often a dump of new earth on each side of the cut. These three secondary areas for succession have much in common, but the loose soil of the dump and the fill is invaded much more rapidly than the firm soil of the sloping sides of the cut. This difference is even more striking when the track runs through a level stretch and the bed is built up from soil scraped out from both sides. The moist depressions are readily invaded by the more mobile or vigorous species of the original community. The bed is not only more xerophytic, but also is disturbed from time to time. Moreover, invasion proceeds along it more readily than into it across the depressions which separate it from the native community. As a consequence, the bed remains more or less permanently in the early stages of succession, which consist of annual and perennial weeds, some of which are derived from the native population. The depressions, on the other hand, pass more or less rapidly through the usual stages to the climax, unless the sere is kept in the subclimax by burning or cutting. Their indicators are often of the most exceptional value in regions where the native vegetation has been greatly modified or largely destroyed (plate 20, B).

Roads resemble railways in their general relation to succession and indicators. This is particularly true of highways in which cutting and filling, though less extensive, are as frequent as in the case of railroads. Roadsides usually show a typical zonation from the bare trackway to the natural community on either side (Clements, 1897 : 968). The sequence of zones summarizes the successional movement, and the latter is shown in especial detail when there are many parallel roads of different ages (Shantz, 1917 : 19). In addition to indicating the disturbance caused by roads, plants may be used as indicators in connection with road-building and even in traveling. The correlation between certain communities and good roads is as striking as it is gratifying, and in actual travel it is often a matter of much importance to be able to determine the character of the road from the vegetation which stretches for many miles ahead. During the constant field travel of the past five summers, many communities have been recognized to have some value for road construction as well as travel, but there are a few of the greatest importance and the widest extent. Throughout the mixed prairies, *Stipa* generally indicates good upland roads, *Agropyrum*, poor lowland ones, while the presence of short-grass on the hills and ridges usually means a road made rough by the matted roots of *Carex*. In the sagebrush climax, sagebrush, *Artemisia tridentata*, indicates excellent natural roads, *Atriplex confertifolia*, much poorer



A. *Opuntia comanchica* indicating overgrazed pastures, Sonora, Texas.
B. *Euphorbia marginata* marking roadways, Walsenburg, Colorado.

ones, and *Atriplex nuttallii* and *A. corrugata*, very poor ones. Throughout the desert scrub, *Larrea* is an index of good roads, *Prosopis* of poorer ones, and the saline subclimax of the very poorest, except where the presence of sand makes some improvement.

**Physiographic indicators.**—Plant communities owe their significance as indicators of physiography or physiographic processes to the influence of the latter upon the direct factors, especially water and solutes. It is clear that the indicators of factor-complexes, such as slope-exposure and altitude, have a distinct physiographic correlation also. However, the basic relation between physiography and indicators is through such processes as erosion and deposition which directly control the soil and its water-content. Since physiographic processes are the universal causes of primary bare areas, their indicators occur in successional communities that mark the progressive change of the area from the initial condition to one of relative stability. As has been emphasized elsewhere (Plant Succession, 35), causes other than physiography may produce similar bare areas and initiate the same sere, the successional movement being due to the reaction of the communities alone, or to this and physiographic processes working together. In the great majority of primary areas, however, physiographic causes or processes are so important or controlling that the seral indicators are readily correlated with them and their changes.

The most outstanding and best-known series of indicator communities of physiographic processes is that of ponds and lakes. In these, physiography is normally the initial cause of the body of water, and deposition the process which controls or promotes the seral movement. The primary stages of the process are marked by the well-known associes of submerged plants, floating plants, reed-swamp, and grassland, or scrub. Pearsall (1917 : 189) has recently pointed out that still other associes should be recognized, and these would serve as indicators of somewhat smaller changes. Finally, each consocies indicates a more or less definite set of conditions within the associal stage. The succession in dunes, sandhills, and blowouts is almost equally well known. In these the physiographic processes are very active, and the indicators of the different degrees of reaction or stabilization well-marked (Cowles, 1899; Gleason, 1907; Pool, 1914). The indicators of sandhills, and of river and coastal dunes have received much attention during the studies of the past five years. The dominants and seral communities are identical or similar throughout the West, except along the Pacific Coast, where a very different flora is concerned. During the same period, a special study has been made of succession in Bad Lands, and this has permitted the correlation of a large number of indicators with erosion and deposition, and the resulting differences in water-content and salt-content. Similar though less extensive investigations have been made of the indicators of saline bolsons and playas, and of the geyser and mud-volcano areas of Yellowstone Park. Finally, the seral indicators of cliffs, rock-fields, and gravel-slides have been worked out for the central Rocky Mountains in particular (Clements, 1905 : 270; 1916 : 225).

**Climatic indicators.**—The value of climax communities as climatic indicators has already been emphasized. Formation, association, consociation, and society are correlated with different climates or climatic subdivisions, and their general values as indicators are pointed out in the succeeding chapter. In addition to this, plants and communities have striking significance as indicators of climatic cycles and hence may become of great value in determining the proper practices in production for the arid and semi-arid regions of the West. The existence of such cycles has been demonstrated beyond a doubt by the work of Douglass (1909, 1914), Arctowski (1912), Huntington (1914), Kapteyn (1914), and Clements (1916). The relation of climatic cycles to succession and hence to indicators has been discussed at some length in "Plant Succession," and an extensive study of the relation of the 11-year cycle to grazing and dry-farming has been made during the drought of 1916–1918 (Clements, 1917, 1918). A complete summary of the relations between cycles of rainfall, sun-spots, and tree-growth has recently been made by Douglass (1919).

Trees and shrubs are the best indicators of minor climatic cycles by virtue of the annual record of growth in rings. It is also probable that height-growth furnishes a correlated record, but little study has as yet been made of the cyclic nature of the latter. It has been found that the height-growth and the reproduction of dominant grasses and halfshrubs, such as *Bouteloua, Agropyrum, Gutierrezia,* and *Isocoma,* show a close correspondence with the rainfall of the dry and wet phases of the sun-spot cycle. It is, moreover, a matter of general experience that the carrying capacity of the western ranges varies 100 per cent or more from wet periods to times of drought. Even more striking variations in the yield of field crops are shown for similar periods (Ball and Rothgeb, 1918 : 49). Since wet phases usually offer the best conditions for germination and growth, and drought periods the poorest, the ecesis of dominants often affords striking indications of climatic phases. This is especially well seen in the ecotone between two adjacent communities such as grassland and scrub, woodland and sagebrush, or forest and grassland. In the majority of cases so far investigated in which a woody dominant is extending into another community of smaller water requirements, the annual rings indicate its establishment during the wet phase of the cycle.

The general significance of climatic cycles and of cycle indicators in practice is discussed in the next section. Their fundamental value in paleo-ecology is dealt with under paleic indicators at the close of the chapter.

## PRACTICE INDICATORS.

Nature.—Practice indicators are those plants or communities which point out the possibility or desirability of a particular practice. This is the original as well as the general use of the word "indicator," and there are good reasons for restricting it to this sense, and designating the so-called indicators of factors and processes as "indexes." However, two cogent reasons have caused the word indicator to be retained in the general as well as the special sense. The first of these is the impossibility of drawing a line between actual practices, as in agriculture, and the combination of human practice and natural process in forestry and grazing. The second is that the value of an indicator for practice rests upon the factor or process which it denotes. Furthermore, the term indicator has become so generally understood that it would be unfortunate to restrict its meaning, though it has been found convenient to employ "index" as a partial synonym.

Kinds.—The basic practices concerned in a system of indicators are agriculture, grazing, and forestry. The primary consideration, however, is which of these is possible or most desirable in a particular area or region. Since successful agriculture brings the largest returns per unit area, the first question is whether the land is agricultural. If not, the next question deals with its value for forestry or grazing, or for a combination of the two. The methods employed in reaching a decision as to the most desirable of the three practices constitute land classification, which in a new region at least is to be regarded as a practice prerequisite to the others. It is preeminently dependent upon plant indicators, as is shown by the first serious endeavor to classify the lands of the western United States upon anything approaching a scientific basis (Shantz and Aldous, 1917). It is obvious that similar methods, refined by quantitative methods and increasing experience, must sooner or later be used in all the new regions of the world where maximum economic returns are desired.

In addition to distinguishing areas as primarily agricultural, grazing, or forest land, practice indicators serve also to indicate particular types of agriculture, grazing, or forestry, as well as to suggest the crop of the greatest promise. Thus, in the case of agriculture, indicators may be used to denote the greater feasibility of humid, dry, or irrigation farming, or the importance of combining grazing with dry-farming. Where grazing is concerned, the type of vegetation not only determines whether cattle, sheep, or goats are preferable, or a combination of two or three possible, but it also indicates whether the introduction of other dominants is possible or desirable. In similar fashion, indicators may be employed to determine the possibility of afforestation or reforestation, as well as the most promising dominants for any particular region. Finally, practice indicators have more or less value for reclamation projects and other engineering operations, especially road-building, and they are of the first importance for indicating the course and intensity of climatic cycles and the modifications of current practice which they demand.

Because of their direct economic importance, a chapter is devoted to the indicators of each of the great basic practices, agriculture, grazing, and forestry, respectively. Land classification is considered in the following chapter in connection with agriculture, and the relation of climatic cycles to optimum production is discussed in connection with each type of practice.

## PALEIC INDICATORS.

Paleo-ecology.—The significance of paleic indicators rests upon the conviction that ecologic processes were essentially the same during the geological past as they are to-day (Clements, 1916 : 279; 1918 : 369). It is assumed that the vegetation of the globe was differentiated into climax formations corresponding to the primary climates. Such formations possessed a development and structure strictly comparable with that of present-day climaxes. They were divisible into associations, consociations, and societies, and they exhibited primary and secondary seres wherever bare areas occurred. The control of the direct factors, water, light, temperature, etc., must have been just as to-day, and this is equally true of their modification by physiographic processes and climatic changes, as well as by the competition and reaction of plant communities. Then, as now, the latter furnished food and shelter to the land animals, and these modified plant and community as a result of various kinds of distrubance. The conception of the biome, or biotic social unit, seems even clearer for past periods than for the present, owing to the lack of confusing detail, especially in the remoter eras. Finally, there is positive evidence of the minor climatic cycles, such as the 11-year sun-spot cycle, in the rings of fossil trees, and of greater cycles in the coseres of peat-bogs. Paleo-ecology is characterized, moreover, by great changes of flora and vegetation such as are unknown for ecology to-day. These are expressed in great successions, such as the clisere and eosere, which correspond with the grand deformational cycles.

Nature of paleic indicators.—While all the types of indicators now recognized must have existed in the past, especially if the Recent period is included, paleic indicators show one essential difference. This lies in the fact that communities were but rarely fossilized, and that the community itself must be inferred often from the merest fragments of its total population. Fortunately, the conception of the community as a complex organism with characteristic parts and processes furnishes an adequate method of interpretation. The great majority of species not only play a definite rôle in the climax or in its development as a dominant, subdominant, or concomitant, but each species also bears distinct relations to other species. When its rôle is interpreted in the light of its vegetation-form and habitat-form, it can be placed in the vegetation with something of the certainty possible in existing communities. As a consequence, the indicator values which have been taken for granted in all the preceding discussion, namely, the indication of other species, or even a whole community or sere by a single dominant or subdominant, play a paramount part in paleo-ecology. The smallest fragment of a fossil may thus become an indicator of the greatest significance, providing only that its generic identification be certain. In the case of plants at least, even this is not absolutely necessary if the vegetation-form or habitat-form be sufficiently distinctive to determine its habitat, and consequent position in climax or sere.

The methods of interpretation employed in paleo-ecology have been discussed in "Plant Succession" (p. 280), and summarized in a later paper (1918 : 371). Because of its importance for the understanding of paleic indicators, this summary is quoted in full:

"The methods by which the ecological results of to-day can be carried back into the past have been briefly discussed in 'Plant Succession' and it will suffice to pass them in review here. For the most part these are methods with which the paleontologist is already familiar, since they have to do primarily with the translation of facts from the present to the past. The foremost is the *method of causal sequence*, already mentioned, with its basic relation of habitat, plant, and animal. This is well illustrated by the occurrence of *Stipa* in the Miocene of Florissant, which indicates not merely the existence of prairie, but also, of course, a grassland climate and a grazing population. A similar but even more fundamental sequence begins with deformation and passes through gradation, climate, and vegetation to exhibit its final effects in the fauna. The *method of phylogeny* which has been the most serviceable of taxonomic tools is likewise of great value in the reconstruction of the life-forms and communities of the past. It shares with the method of succession the credit of permitting us to give more and more detail to the bold outlines of past vegetations and vegetation movements. The *method of succession* is based on the great strides made by the developmental study of vegetation during the last twenty years. When successional studies become the rule in zoo-ecology as well, there will seem to be no limit to the increasing perfection of detail in picturing the rise and fall of past populations and communities. In the case of vegetation, this method has already gone so far as to bring conviction that all the essential features of successional processes and climax communities as seen to-day already existed in the past.

"As indispensable corollaries of the methods of phylogeny and succession are inferences from distribution in space and in time, and from association. The former enables us to close many a gap in the fossil record and to fill in the areas outlined by the known distribution of dominants. Inference from association, for example, aided by phylogeny, makes it all but certain that swamps of reed-grass, bulrushes, and cattails existed as far back as the Cretaceous, though *Phragmites* is the only one of the three dominants recorded for that period. The most recent is the *method of cycles*, which gives promise of becoming one of the most important. It is perhaps too soon to insist that cyclic processes are universal in time and in space; but the great mass of evidence from geology and climatology is matched by an increasing body of facts from biological succession."

Kinds.—The indicator values of a fossil plant or animal clearly depend upon the accuracy of its identification and stratigraphic position. With reference to the former, its generic position, together with the vegetation-form and habitat-form, is of paramount importance, partly because specific determinations are often very uncertain among plants at least, and partly because the majority of genera are uniform as to the ecological type of their constituent species. While definite stratigraphic allocation is necessary for finer analysis, the assignment of a plant to a particular era or period has much value, owing to the fact that many dominant genera persist throughout most or all of an era. The indicator value also depends greatly upon whether the plants were fossilized in position and hence in their community relations, or whether they have been scattered and carried to points more or less remote from their home. The distinction between the corresponding deposits, termed stases and strates, is discussed at some length in "Plant Succession" (291). Here it will suffice to point out that the water stase as exemplified in peat-bogs has nearly the complete indicator values of an existing sere, while those of the much more universal strate are usually incomplete and subject to interpretation.

It is evident that fossil plants, and animals also to a lesser degree, may serve as indicators of factors, processes, or practices, in essentially the same way that existing species do. Practice indicators are naturally connected with the presence of man, and hence are restricted to the Pleistocene and Recent periods. Grazing must have been the earliest of these, perhaps reaching back into the late Pleistocene, but agriculture was relatively well-advanced by the time of the Lake-dwellers, and construction, as well as a crude sort of forest utilization, was at least begun. Moreover, it must be recognized that, while grazing took on some new features as herds came under the control of man, it must have existed as a natural process throughout the Tertiary at least. In the case of fire, this agency must have begun its modifying influence upon vegetation as early as the Paleozoic, but its effect must have greatly increased with the differentiation of deciduous forest and grassland in early

Tertiary times. It could hardly have become a universal process until the pastoral phase became general, and its greatest extension has doubtless taken place during the last 1,000 years. The primary processes involved in physiographic and climatic changes must have had much the same indicators as to-day, allowing for the differences in flora during the various eras. While such changes seem much greater and more frequent during the geological past than to-day, this is almost certainly the result of a short perspective. With respect to factor indicators, the plant genera concerned during the Cenozoic era were largely those which characterize marked differences in water, light, and temperature to-day, and this was particularly true after the Miocene. During the earlier eras, the genera were mostly different, but the vegetation- and habitat-forms the same.

The fragmentary nature of the fossil record makes it necessary to emphasize certain existing indicator relations, as well as to employ some not needed in actual vegetation. These are derived from the methods of interpretation already discussed. The use of indicators based upon the successional sequence is much the same, except that a single dominant or stage must often serve to denote the presence of the entire sere. Even this is not so different from conditions to-day, since there are many swamps in arid regions especially in which the reed-swamp associes is represented by *Scirpus* or *Typha* alone. The method of causal sequence furnishes many of the most striking and significant of paleic indicators. Habitat, plant, and animal are linked together in a fundamental cause-and-effect relation, in which each one serves as an indicator of the other. The importance of the plant in this relation has been emphasized elsewhere. It may be said to have a double indicator value, since it indicates the habitat directly by its response, and the animal directly by virtue of the control exerted through food and shelter. Thus, while there are numerous examples of definite relations between habitat and land animals, most of these take the plant community for granted. The indicators of cycles comprise both those derived from succession and from causal sequence. In fact, they are the indicators of the grand successions recorded in the clisere and eosere, and consist chiefly of shifting formations and floras. Fossil genera and families often possess great indicator values which arise from their phyletic relationships. While phylogeny must long remain a field for varied opinions, certain great lines of relationship receive increasing recognition, and can be employed with corresponding certainty. Thus, while *Juncus* is not recorded until the Eocene, the presence of both *Carex* and *Phragmites* in the Cretaceous makes it all but certain that the more primitive *Juncus* was already in existence. In connection with phylogeny and succession, plants may indicate distribution in space and in time as well as the presence of associated dominants (Plant Succession, 352).

Since the field of indicators has been developed wholly with reference to plants and with particular application to agriculture, the importance of reciprocal indicators has not been recognized. However, in paleo-ecology where the body of definite facts is relatively small, it is of the greatest aid to secure all possible indications from every fact, and to check these by the indications of related facts. Fossil plants and animals constitute the best of reciprocal indicators, but topography and climate are often of great service also. When all four can be employed as indicators in a particular period or region, it is possible to reconstruct the biome in much detail and with the greatest possible certainty. For example, the geologic evidences of arid climates at different periods must be regarded as more or less tentative until confirmed by plant or animal indicators of aridity. When both occur, as in the Miocene, the chain of evidence is complete. It then becomes possible with the aid of the indicator relations discussed here to present a fairly detailed and complete picture of the structure and development of the biotic climaxes of the past. The general features of this have already been done for animals by Osborn (1910), and much progress has been made in doing this for the associated plants and animals of the Bad Land horizons of the West.

**Paleic indicators of climates and cycles.**—The evidences of past climates and climatic changes have been summarized from the geologic, botanic, and zooic aspects (Plant Succession, 313). Since plants are the most immediately responsive to climatic influences and constitute the best indicators, they are chiefly considered here. The grand climates of geologic time are indicated by corresponding great floras and faunas, which have served as the basis for the division into eras. During each of the latter, climatic differentiation in both space and in time has been faithfully reflected in the vegetation, and the combined effect of climate and vegetation in the fauna. It seems highly probable that a considerable differentiation of climates and climaxes took place during the Paleophytic era, and that this was increased during the Mesophytic era to become the most outstanding feature of the biosphere during the Cenophytic. Thus, while each era is indicated by a particular climax flora, it also exhibits climax formations as indicators of more or less distinct climates, just as is the case to-day. While the grand deformation cycles which produced the eras were marked by a changed flora and fauna, the major deformation cycles and grand sun-spot cycles are thought to correspond with shiftings of climate and vegetation, such as are indicated for the Pleistocene. These have to do with climaxes as indicators, and it seems a fair assumption that the series of climaxes found in the Pleistocene shiftings likewise occurred in some degree in the earlier cliseres of the Mesophytic and Paleophytic eras. The constitution of the climaxes during the various eras and their relation to climatic cycles is discussed in some detail in "Plant Succession" (356, 406, 419) and need not be repeated here.

**Paleic indicators of succession.**—Apart from the great successional movements involved in the change of floras and the shifting of climaxes, there must have been innumerable examples of seres and coseres in every era. Primary areas of erosion and deposition were probably more abundant than to-day, and primary succession must have been the rule, though secondary seres were not unknown. Coseres resulting in the formation of coal or peat have occurred repeatedly from the Paleophytic to modern times, while in periods of great volcanic activity, such as the Miocene, they were produced by deposits of volcanic dust. While each era possessed its particular flora, all the life-forms were represented. Thus, while the genera typical of the various seral stages during the Paleophytic and Mesophytic are practically all different from those of the Cenophytic and to-day, the vegetation-forms and habitat-forms are the same or nearly so. With reference to the genera which constituted the seral dominants and hence served as indicators of habitats and of succession, the life-forms have been discussed in "Plant Succession" (pp. 354, 405, 420). Throughout the major portion of the Cenophytic, the seral genera as well as the life-forms were essentially the same as those of to-day, and their indicator value is readily inferred from existing conditions.

**Plant indicators of animals.**—The general indicator relations of fossil plants and animals have long been recognized and utilized by paleontologists, but chiefly on the animal side. The correlation between the appearance of a dominant angiospermous flora and the evolution of mammals is the most outstanding example of this, but the rise of the cursorial ungulates in response to an expanding grassland climax is hardly less striking. Such correlations must be superlatively general before the Cenophytic, though the existing relations between seral and climax communities and the great groups of animals must have had analogies at least during the Mesophytic era. Since the larger animals were all totally different, and the dominant genera of plants practically all different likewise, the use of plant and animal indicators as a basic method in paleo-ecology must be confined chiefly to the Cenophytic era for the present. Here, however, it seems to offer great possibilities, some of which must wait upon the further study of communities as biotic units with development and structure. The indicator value of plants in this connection is limited only by our knowledge of existing correlations with animals. This is due to the fact that a large number of modern genera of plants have existed since the Cretaceous. The evolution of animals has been much more rapid, and the number of existing genera of mammals, for example, which reach back to the Eocene is very small. However, among the rodents and ungulates, where plant correlations are most important, nearly half the families contain both modern and fossil genera. With respect to the birds and insects, our knowledge is much less complete, but it appears highly probable that many existing families and orders had arisen at least by the Tertiary. As a consequence, it becomes possible to scan the rapidly growing list of plant indicators, and to extend their correlations as far into the past as the recorded existence of the genera or related genera permits.

**Animal indicators of plants.**—The reciprocal relation of plants and animals as indicators, whether as communities or species, greatly extends the use of indicators in geological times. In many horizons, animals have been preserved to a much larger degree than plants, while in some, plant remains are entirely lacking. Fossil animals are especially significant in the reconstruction of upland life, since the cursorial forms of the uplands were preserved in fairly large number, while the record of the associated plants is exceedingly fragmentary. Moreover, animals may serve to indicate the presence of plants in regions or in periods where they are not yet actually found. Outside of the insects, there are few extinct animals in which there is an indicator correlation with a single species of plant. On the other hand, the correlation of herbivores with plant communities, both climax and seral, is practically universal, and they serve to indicate with a high degree of probability the development and extension of sedgeland and grassland from the Cretaceous to the Pliocene. The general correlation of browsing ungulates with forest and scrub, of the earlier types of grazing animals with sedgeland and meadow, and of the highly specialized upland types with the climax grassland of xerophytic grasses (Osborn, 1910 : 9, 237) is fundamental, and has been used to furnish the basis for the treatment of the development and structure of the biotic communities in the Bad Lands of the West.

## IV. CLIMAX FORMATIONS OF WESTERN NORTH AMERICA.

**Nature.**—The vegetation of a continent falls into a number of major divisions or units. These are known as plant formations, and are regarded as complex but definite organic entities with a characteristic development and structure (Plant Succession, 124). They are the product of climate and are controlled by it. Each formation is the highest expression of vegetation possible under its particular climate, and hence it is also termed a climax. As here understood, the formation and climax are identical, and the terms are essentially synonymous. For the sake of emphasis as well as of convenience, however, the two are used together. Hence the same unit may be referred to as a climax, a formation, or a climax formation. Since it exhibits a development as well as structure, it is further necessary to recognize that the successional areas in the great grassland formation, for example, are an integral part of the climax, however much they may differ from it. Whatever seems inconsistent in this is apparent and not real, since it is a matter of common knowledge that the same organism may appear in two or more unlike forms, such as the seedling and adult plant, or the larva, chrysalis, and butterfly.

Climaxes owe their character to the controlling species or dominants which make them up. These climax dominants belong to the same vegetation-form, which represents the highest type possible under the prevailing climate. In grassland the climax dominants are all grasses or sedges, in forest they are trees, in chaparral, shrubs, and so forth. The exceptions to this rule all seem to be merely apparent. They are well illustrated by the so-called savannah in which the trees or shrubs are more noticeable than the grasses, but the latter are in actual control of the habitat. Moreover, in the prairies the dominant grasses may be concealed for much or all of the growing season by tall herbs, such as *Psoralea*, *Amorpha*, and *Solidago*. These are called subdominants and characterize minor communities subject to the control of the grasses. In addition to the climax dominants are the other species which mark particular stages in the development of the climax. These are developmental dominants, and are usually termed successional or seral because of their rôle in the succession or sere which reestablishes the climax on a bare area.

**Tests of a climax.**—Each climax is regarded as the direct and complete expression of its climate. The climate is the cause, the climax the effect. So close is this relation that the climax must be regarded as the final test of a climate. From the standpoint of vegetation at least, climates are to be recognized and delimited only by means of climaxes, and not the reverse. No matter how complete his equipment of meteorological instruments, the ecologist must learn to subordinate his determination of climate to that of the plant if his results are to be reliable and usable. The paramount importance of formations in indicating climates makes their objective recognition of the first importance. In the search for criteria which would permit an objective and consistent basis for formations, several guiding principles have become evident. The first of these is that the climax dominants must all belong to the same great vegetation-form, since this indicates a similar response to climate.

The second is that one or more of the dominant species must range throughout the formation as a dominant to a larger or smaller degree. The importance of this lies in the fact that while no two dominants are exactly alike, those of the same formation are so nearly equivalent that the presence of one indicates the possibility of others. This is well illustrated by the behavior of *Bouteloua gracilis*, which ranges as a dominant from the Missouri River to California and from Saskatchewan to Mexico. While the climate of this vast stretch varies greatly in physical or in human terms, the conclusion is unavoidable that the extensive areas covered with *Bouteloua* have the same or a similar grassland climate. This obviously permits the application to vegetation of the principle that things equal to the same thing are equal to each other. This approximate equivalence of dominants receives its best proof in the grassland formation, in which the mixed prairie shows *Bouteloua gracilis* in intimate mixtures with *Stipa*, *Agropyrum*, *Bulbilis*, *Carex*, or *Koeleria*. The third criterion is that the majority of the dominant genera extend throughout the formation, though represented by different species. This is well exemplified by the chaparral climax, in which *Quercus*, *Prunus*, *Rhus*, *Cercocarpus*, and *Ceanothus* are found in the several associations. A corollary of this is that most of the subdominants likewise belong to the same genera, as, for example, *Astragalus*, *Erigeron*, *Psoralea*, *Petalostemon*, *Solidago*, *Eriogonum*, and *Artemisia* in the grassland associations. The fourth criterion is developmental or successional and has several aspects. It is seen in the behavior of such subclimax dominants as *Aristida purpurea*, which characterizes certain types of disturbed areas in all the grassland associations, and later yields to the climax dominants of each. It is equally well shown by *Andropogon scoparius* and *Bouteloua racemosa*, which are subclimax in rough areas as well as in meadows to the final dominants of the four most extensive grassland associations. Finally, the degree of equivalence of dominants is indicated by their mingling but is checked by their successional alternation. The position of *Andropogon* in meadows, *Agropyrum* and *Stipa* on slopes, *Bulbilis* and *Bouteloua* on the crests of the rolling prairies, is not only significant of their physiological and successional relations, but also of their associational positions. *Andropogon furcatus* and *scoparius* are typical of the subclimax prairie of the Mississippi Valley, *Stipa* and *Agropyrum* of the climax prairies, and *Bulbilis* and *Bouteloua* of the still drier plains.

Structure and development.—By far the greater portion of a climatic region is occupied by the climax characteristic of it. But all through it occur areas of varying size in which new or denuded soils are available for colonization and the development of the climax as a consequence of succession (Plant Succession, 3). As a result, every formation shows subdivisions or communities of two sorts, namely, climax, and successional or seral. Initial seral communities, such as the colonies of water-plants in ponds and streams and of lichens and mosses on cliffs and boulders, are readily distinguished from climax ones. As succession proceeds, however, the communities more and more nearly approach the climax in appearance. In the last analysis, they can be distinguished only by the fact that each stage slowly yields to the next until the climax is reached, when the succession stops. In many cases where the disturbance due to fire, grazing, or cultivation is continuous or periodic, the subclimax may persist for a long period and appear to be a true climax. In the great majority of cases, however, the successional movement though slow is constant, and there can be no question of the climax, especially when the permanent quadrat is employed to reveal changes.

Each climax formation falls readily into two or more major subdivisions known as associations. Toward their edges these blend into each other more or less, making a transition area or ecotone. The latter is broad in the case of relatively level regions, and narrow in that of the climax zones of mountain ranges. The associations have one or more dominants in common, or at least belonging to the same genus, and there is a certain degree of similarity as to subdominants also. Each association consists of several dominants as a rule, though there may sometimes be as many as eight or ten or more, as in scrub and chaparral. Each dominant constitutes a consociation. It may occur alone, though as a rule it mixes and alternates with the other dominants of the same association. This is the direct outcome of the similar requirements of the dominants, and hence it is a guiding principle that two or more consociations are regularly associated in the larger unit. This is emphatically true of the associations covering a large area and possessing a rich flora, such as prairie, chaparral, and forest. It is less striking in desert associations where the dominants are often few, but even in the case of sagebrush and desert scrub an extensive survey indicates that mixing of dominants is the rule. Since no two consociations are exactly equivalent, there are often large areas in which a single one occurs, such as the yellow pine in Arizona and the Douglas fir in Oregon. Such areas are often due as much to migration and successional factors as to differences in climatic requirements (cf. Zon, 1914 : 124).

As will be seen later, there are more groupings of consociations than are represented by the associations actually named. This is illustrated most clearly by the basic association of the grassland climax, the *Stipa-Bouteloua poion*. This association is named from the two most characteristic consociations, but it contains several dominants, *e. g.*, *Stipa comata*, *Agropyrum glaucum*, *Koeleria cristata*, *Bouteloua gracilis*, *Bulbilis dactyloides*, *Carex filifolia*, and *C. stenophylla*. It seems clear that a community of *Stipa* and *Bouteloua*, or *Agropyrum* and *Bulbilis*, differs in nature and in indicator value from one containing most or all of these. When detailed mapping of vegetation is undertaken on a large scale, all of these actual groups will demand recognition as well as definite names. But for the present, it seems sufficient to give names to the association and to each consociation, while recognizing that the former will often be represented by groups containing only two or three of the several dominants.

Societies.—A subdominant is a species which controls an area within that of a dominant or group of dominants. The actual community formed by a subdominant is called a society. Its exact nature is best seen in forest or prairie, where the control of the dominant vegetation-form, tree or grass, is complete, though at the same time it permits a secondary control by a dominating species of a different vegetation-form. Thus the yellow pine consociation of Oregon frequently shows a typical layer or society of *Purshia tridentata*, the Douglas fir forest of the Rocky Mountains one of *Thalictrum fendleri*, and the *Stipa spartea* prairies, mixed societies of *Psoralea*, *Amorpha*, and *Petalo-*

*stemon.* The striking feature of a society, that of a control within a control, often apparently greater than that of the consociation itself in the case of grassland at least, is due to the difference in vegetation-forms and hence in ecological requirements. A society may conceivably belong to the same vegetation-form as the consociation or association in which it occurs, but such cases are practically unknown. Apparent examples of this have all been readily referred to successional causes, as where a localized area of *Hordeum jubatum* occurs in prairie, or one of *Aristida purpurea* on the plains. The almost invariable rule is that the society belongs to a vegetation-form of lower requirements than that of the consociation. The forest will have societies of shrubs, herbs, mosses, etc., the chaparral of undershrubs, grasses, and herbs, and the prairie of herbs principally. In this connection, it is especially important to recognize that savannahs do not represent tree or shrub societies in grassland, but are an incomplete expression of the next stage in succession.

The degree of control exerted by the society clearly depends upon the life-history relations of the dominant and subdominant concerned. This is largely a matter of the height and extent of the shoot, but the root also plays a large part. In forest the societies of varying rank, from shrub to moss or lichen, are wholly and obviously subordinate to the trees. In chaparral this is also true to a large extent, but societies of undershrubs and grasses often play a conspicuous part. As to grassland, the societies are frequently much more conspicuous than the dominant grasses, and at times they appear to be in control. In such cases the control is seasonal. Each subdominant reaches a maximum in spring, summer, or fall, when it seems to dominate, but the real relations are disclosed at the other seasons. This tendency of societies to appear during a particular season further explains the relation of dominants to subdominants. They not only make different demands by virtue of their vegetation-forms, but these demands are also made at different times. Societies exhibit a similar seasonal relation in forest and scrub, in which their time of appearance is almost wholly controlled by the dominants. In most cases, this relation is so striking that it is possible to distinguish two or more aspects during a season, marked by particular societies (Clements, 1905 : 296 ; 1916 : 132). From the preceding discussion, it is clear that various kinds have already been distinguished (Clements, 1916 : 132), and it is highly probable that still others will demand recognition as the study of vegetation becomes more detailed and accurate.

The society is not a subdivision of the consociation in the same way that this is of the association. The latter consists of its consociations, grouped or single; they occupy its total area. The consociation does not consist of societies, but the latter merely occur in it or through it to a larger or smaller degree. This is readily seen to be due to the basic difference in vegetation-forms and to the seasonal nature of societies. As a consequence, a particular society may occur not only in two or more different consociations, but also in two or more associations of the same formation. It may extend more or less continuously over wide stretches, or it may recur as successional processes or physical factors determine. A typical example of this is *Psoralea tenuiflora*, which occurs in nearly every association and consociation of the grassland climax, while the closely related society of *P. argophylla* is restricted to the prairie associations. *Gutierrezia sarothrae* forms similar communities of even wider range, but this is probably to be explained by the assumption that it is really a subclimax consocies as described below, and persists as an apparent society well into the climax. In general, however, the climatic and floristic differences between associations are sufficiently marked to restrict each society to a particular association.

When a species exhibits a local or restricted subdominance covering a few square yards or a few acres, it constitutes a clan. It is clear that the difference between society and clan is merely one of degree. Theoretically, there is a point at which they are indistinguishable, but practically very few difficult cases have been encountered. The best examples of clans are species of gregarious habit, especially stoloniferous ones, and of low growth. Such clans are capable of holding ground very tenaciously, and of slowly extending it, but they are able to make only limited headway against the double control of dominants and subdominants. Clans are best exemplified by *Delphinium penardi* and *Erigeron flagellaris* in grassland, and by *Pirola*, *Goodyera*, *Heuchera*, etc., in forest.

**Names of climax communities.**—An endeavor has already been made to devise a system of names for plant communities, in which the names would be short, significant, and usable, as well as international in character (Clements 1916 : 127, 129, 133, 137, 138). Some such system will be indispensable as ecology becomes more and more definite in nature as well as international in scope. In the present treatise, which is purposely limited to the western half of the United States, the technical terms are unnecessary and are used only as an occasional convenience. Hence, the practice will be to secure the maximum of definiteness consistent with brevity and clearness by uniformly distinguishing between associations, consociations, societies, and clans by means of the one or two most characteristic genera or species. At the same time, an endeavor is made to furnish a somewhat more usable equivalent in vernacular terms, in the expectation that these will come into practical use. Thus the *Stipa-Bouteloua poion* will be referred to as the *Stipa-Bouteloua climax* or formation, or as the grassland climax or formation, and the *Stipa-Koeleria* association as the *Stipa-Koeleria* prairie or true prairie. The alternative terms for the various formations and associations are given in the summary on page 114.

**Seral communities.**—The limits of space make it impossible to give an adequate account of the basic process of succession as exhibited in the development of climax formations, and for this the reader must be referred to "Plant Succession," especially Chapters I, V, VI, and VII. Here it must suffice to point out that succession is a universal phenomenon by which bare areas become colonized by plants and slowly develop through successive stages into the climax formation which surrounds them. Bare areas are initially bare, as in the case of bodies of water, rock ridges, and fields and sand-dunes, or they are denuded of vegetation by various forces, especially fire, lumbering, grazing, and cultivation. The course of succession is much longer and slower in the former case than in the latter, but the essential features of development are the same. Each population or community reacts upon the area or habitat in such a way as to make conditions less extreme and correspondingly more favorable to species of greater requirements. These enter gradually and compete successfully with the occupants, finally driving them out or compelling them to take a subordinate rôle. This dominance of the invaders marks a new stage in the succession, which persists until its reaction upon the habitat permits the invasion of new-comers of still greater demands. This process continues until the climax stage is reached, when no further change occurs, unless denudation again intervenes to produce a new bare area for succession.

The course of development in each succession or sere is marked by a series of stages or communities of progressively higher requirements, determined largely by the characteristic vegetation-form. While they differ in nature and composition, they are alike in being more or less temporary as well as in playing an intrinsic part in the development of the climax. As a consequence, they are termed developmental, successional, or seral communities, in contrast with the final and permanent climax communities. Apart from this basic distinction, a seral community exhibits much the same structure as a climax one. Both are associations of two or more dominants, and exhibit societies of subdominants. Practically as well as developmentally, however, the distinction between temporary and seral communities and permanent climax ones is so important that it has proved desirable to use terms which at once place each in its proper developmental position. Accordingly, each seral stage or community is termed an associes—*i. e.*, it is a temporary or developmental association. Similarly, the community formed by each dominant is called a consocies and that by each subdominant a socies, corresponding respectively to consociation and society. In addition, the terms family and colony are used for initial stages in which dominance is lacking or little developed. The colony is the community formed by two or more pioneer species, while the family consists of individuals belonging to a single species. The colony is regularly characteristic of the initial stages of succession.

An associes consists, like an association, of two or more dominants or consocies. The most familiar example is the reed-swamp, which usually comprises three consocies, *Scirpus lacustris*, *Typha latifolia* or *T. angustifolia*, and *Phragmites communis*. In extensive swamps, all of these occur, usually alternating or sometimes mixed, and in northern regions with a fourth consocies, *Zizania aquatica*. Over much of the West, *Scirpus* and *Typha* alone are found together and in many localized areas only one or the other is present. Some socies, such as *Heleocharis*, *Sagittaria*, and *Alisma*, are practically coextensive with the dominants, though not always to be found in each local area. Other subdominants are more restricted, and some are more frequently associated with one consocies than with the other. Other well-marked associes are *Nymphaea-Potamogeton* in ponds, *Ammophila-Elymus* on sand-dunes, *Redfieldia-Muhlenbergia* in blow-outs, *Spirostachys-Dondia* in salt marshes, *Populus-Betula* in burns, and *Gutierrezia-Artemisia frigida* in disturbed areas.

The designation of seral communities is essentially like that of climax ones. The associes is distinguished by the use of its two most important consocies, as the *Scirpus-Typha* associes or reed-swamp, while consocies and socies are named from the dominant or subdominant, as the *Scirpus* consocies, *Nymphaea* consocies, *Populus tremuloides* consocies, *Sagittaria* socies, *Pentstemon* socies, etc. Colonies are like associes in requiring the names of the two most important species for designation.

**Indicator significance of climax formations.**—The formation is the greatest of all indicators. In its climax form, it not merely indicates but actually delimits plant climates. In its developmental stages, it sets a definite mark on each successional habitat, and indicates the rate and degree to which these approach the final condition. In practical terms, the climax indicates climate, and its successional stages indicate soil or edaphic conditions. The climax indicates the range of natural and cultural possibilities of a region, the successions point out the possibilities of localized areas and soils. In a particular locality the climax denotes the general limits of production, and the seres suggest the ways by which maximum production may be reached. Thus, while it is necessary to keep the climatic limitations in mind, the concrete problem in any region is to utilize the indications furnished by the various successions. In the case of agriculture, the facts derived from succession can only be indications, since the vegetation is removed. With grazing and forestry, however, as well as irrigation, reclamation, and many engineering problems, succession itself becomes an instrument by which the desired natural crop can be indefinitely maintained, or by which one crop can be supplanted by another.

As stated in a former chapter, succession is the universal key to the practical as well as the technical use of indicators. The stages of a sere are regularly linked together in such a definite and organic process of development that the presence of one serves as a record of those preceding and as a prediction of those to follow. In every stage lies a record of the past and a prophecy of the future. In practice, this means that a sere can be held in any stage desired, that its progress can be retarded or accelerated, or that it may be destroyed in part or in whole, and a new stage or sere produced. Succession thus becomes a tool of the greatest utility wherever natural crops are concerned. Even in agriculture, it has considerable value quite apart from its indicator significance in meadow and pasture crops and in all those where weeds are a serious factor. It is hardly necessary to point out that such a use of succession is possible only through a good understanding of its processes. For a complete treatment of this subject, the reader is again referred to "Plant Succession." Here it must suffice to point out the general types of succession and to emphasize their indicator significance.

**Significance of succession.**—Since succession is the development, or usually the redevelopment of the climax in a particular spot, it is clear that the actual successions or seres will differ in accordance with the climaxes in which they occur. In other words, each sere is an integral part of the development of the climax and its indicator value pertains primarily or wholly to that climax. As to origin, all seres arise on a bare or on a denuded area. But bare surfaces differ profoundly in nature and hence in the kind of plant community which they can support. Some, such as rock and water, present extreme conditions for plant growth and require a long period of reaction and development before an actual soil is formed and land communities can thrive upon them. Other areas, such as fallow fields and burns, have well-developed soils into which plants can invade immediately. Rock and water are regarded as primary areas, while burns, fields, etc., are secondary ones. A primary area shows a primary succession or prisere, characterized by extreme conditions as to water-content in particular, by a correspondingly slow reaction and soil formation, and by a long series of stages leading very gradually to the climax. Such priseres are found in lakes, ponds, and streams, and on rock cliffs, ridges, lava flows, and cinder cones. They usually occur also in salt marshes and basins, and in shifting dune-sand, both of which regularly afford extreme conditions for colonization, in spite of the presence of a soil. A secondary area is one in which an existing vegetation has been destroyed or removed without destroying the soil. Its water relations are never extreme, and a large number of herbs or shrubs can invade in the first few years, often indeed during the first year. The secondary succession or subsere which results is short, consists of relatively few stages, and passes rapidly into a climax. Subseres are the most conspicuous and easily understood of all successions. Since they are largely due to human disturbance, they are most abundant in settled regions and hence are of the most immediate practical importance.

The nature of the succession in both priseres and subseres is further determined by the water relations of the bare areas. This is best illustrated by the prisere, which may begin in water or on rock. In the first case, the reactions of the successive communities are chiefly concerned with reducing the amount of water and increasing the amount of solid material. In the second case just the reverse is true. The amount of water is increased and the rock is broken down into actual soil. The one begins with submerged aquatics of the highest water requirements, the other with the rock lichens of the lowest water requirements. The former is called a hydrosere, the latter a xerosere. Subseres are similarly divided, since they regularly begin in conditions wetter or drier than the final climax. It is further desirable, especially for indicator purposes, to recognize hydroseres in which the lack of oxygen is a critical factor, and xeroseres in which the abundance of alkali or the instability of the sand is decisive. For the sake of convenience, these are called respectively oxysere, halosere, and psammosere (Clements, 1916 : 182).

Indicator value of disturbed areas.—As has already been suggested, the most usable of all successions are subseres, which occur typically in areas disturbed by man or as a result of his activities. Even a relatively new country, such as ours, has been the seat of widespread and almost universal disturbance. Arable lands have been cleared, broken, cultivated, permitted to lie fallow or to "go back." Forests have been lumbered, burned, or grazed, while grasslands and deserts have been constantly grazed and burned. Even in the most inaccessible parts of the West it is difficult to find wholly primitive conditions, even though by comparison most of the vegetation may fairly be called natural. As a consequence, practically all regions show many areas of disturbance marked by secondary successions. These furnish an enormous amount of indicator material, which only needs interpretation in the light of successional knowledge to be of the greatest practical importance. Every burn, every clearing, every pasture or open range, each fallow field, irrigation ditch, roadside, or railway fill or cut, in fact every place of whatever size from a square foot to a township, in which the soil has been disturbed or removed, has indicator evidence of value to offer. Indeed, the problem is often to find primitive areas for determining the original conditions of the vegetation and thus permitting a proper correlation of the subsere. As long ago as 1898, a systematic search was made in several counties of eastern Nebraska for prairie that had never been pastured or mowed. Only an insignificant rocky triangle of a few yards was discovered. Even areas which were mowed but unpastured were very rare and of small extent. If it were not for the unintentional protection afforded by fencing railroad right-of-ways, it would often be impossible to determine the original vegetation of many regions. The appreciation of this fact has led to the development of a method which has been of the utmost value during the last five years in reconstructing the primitive vegetation of regions where it has been greatly modified or almost entirely displaced. This method has yielded surprising results throughout grassland, sagebrush, and desert scrub, but its most striking success has been in the great interior valleys of California, where ruderal grasses have almost undisputed sway. The constant examination of fenced right-of-ways and other chance protected areas the past three years has confirmed the theoretical assumption that this was formerly a vast *Stipa* association. This determination of the original climax might well seem to be without practical importance, but it is actually of the greatest value in indicating the proper method and the objectives in restoring overgrazed areas to their normal productiveness, as is shown in detail in Chapter VI.

The relation of the subsere to the climax is so definite and organic that, once established for a single locality, it can be extended to all others where the subsere occurs. Obviously the reverse is true also, namely, that a particular climax will exhibit the same subsere wherever similar or identical disturbances occur. This same organic correlation applies likewise to the prisere. The succession in water, on rock, or in sandhills is essentially the same throughout the vast area of the grassland formation, for example. The relation between climax and prisere once established, it is possible to predict the climax from the prisere or the prisere from the climax wherever either is absent. There is also a close correlation between subsere and prisere, especially in the later stages, and it is further possible to anticipate the effect of disturbance in a region where the prisere is present, or to prophesy the course of the slowly moving prisere from that of the subsere. When it is clearly recognized that practically all human activities in nature result in disturbed areas, the correlations between climax, subsere, and prisere will be seen to be of the greatest practical importance.

Summary of the climax formations.—In presenting a sketch of the climax formations as a background against which indicator values may stand out more clearly, the treament is purposely limited to the western half of the country. This is chiefly for the reason that indicator values are greatest in newer regions, but partly also because the climax relations are simpler and hence more certain. For this reason the prairie is the most eastern association considered, though this necessarily involves occasional reference to the deciduous climax. It is also recognized that some of the western climaxes are not confined to the United States, but occur also in Canada and Mexico. Our knowledge of vegetation and especially of succession in these countries is so scanty that only occasional reference to them is warranted.

The following outline will serve to show the climax formations and their associations, and will also serve as a guide to the discussion of each in its proper sequence. The treatment of each formation and association is necessarily brief, as the primary object is not a detailed account of the vegetation, but only such as will serve the general purposes of indicator studies. This account is based chiefly upon the special investigations of the last six years, since these were undertaken for the express purpose of determining the structure and development of the climaxes and their indicator values. These have been supplemented by the earlier work from 1896 to 1912, and by the results of the writer's associates and students.

1. The Grassland Climax: Stipa-Bouteloua Formation.
    1. True Prairie: Stipa-Koeleria Association.
    2. Subclimax Prairie: Andropogon Associes.
    3. Mixed Prairie: Stipa-Bouteloua Association.
    4. Short-grass Plains: Bulbilis-Bouteloua Association.
    5. Desert Plains: Aristida-Bouteloua Association.
    6. Bunch-grass Prairie: Agropyrum-Stipa Association.
2. The Sagebrush Climax: Atriplex-Artemisia Formation.
    1. Basin Sagebrush: Atriplex-Artemisia Association.
    2. Coastal Sagebrush: Salvia-Artemisia Association.
3. The Desert Scrub Climax: Larrea-Prosopis Formation.
    1. Eastern Desert Scrub: Larrea-Flourensia Association.
    2. Western Desert Scrub: Larrea-Franseria Association.
4. The Chaparral Climax: Quercus-Ceanothus Formation.
    1. Petran Chaparral: Cercocarpus-Quercus Association.
    2. Subclimax Chaparral: Rhus-Quercus Associes.
    3. Coastal Chaparral: Adenostoma-Ceanothus Association.
5. The Woodland Climax: Pinus-Juniperus Formation.
    1. Piñon-cedar Woodland: Pinus-Juniperus Association.
    2. Oak-cedar Woodland: Quercus-Juniperus Association.
    3. Pine-oak Woodland: Pinus-Quercus Association.
6. The Montane Forest Climax: Pinus-Pseudotsuga Formation.
    1. Petran Montane Forest: Pinus-Pseudotsuga Association.
    2. Sierran Montane Forest: Pinus Association.
7. The Coast Forest Climax: Thuja-Tsuga Formation.
    1. Cedar-hemlock Forest: Thuja-Tsuga Association.
    2. Larch-pine Forest: Larix-Pinus Association.
8. The Subalpine Forest Climax: Picea-Abies Formation.
    1. Petran Subalpine Forest: Picea-Abies Association.
    2. Sierran Subalpine Forest: Pinus-Tsuga Association.
9. The Alpine Meadow Climax: Carex-Poa Formation.
    1. Petran Alpine Meadow: Carex-Poa Association.
    2. Sierran Alpine Meadow: Carex-Agrostis Association.

## THE GRASSLAND CLIMAX.

### STIPA-BOUTELOUA FORMATION.

General relations.—The grassland is much the most extensive of all the western formations. It ranges from central Saskatchewan and Alberta in the north to the highlands of central Mexico on the south, and in its subclimax form at least from Illinois on the east to California on the west. From its great extent geographically and climatically, a question naturally arises as to its unity. It may at once be said that any division of the vegetation of the North American continent into major units would include this as one of the most outstanding. The real question is not so much as to its unity as to whether it should be called a formation or not. The study of vegetation is still in such a stage that each ecologist will answer as his experience and insight make possible. In attempting to arrive at a basic and subjective concept founded upon development as the only real guide to relationship, it seemed best to employ the term formation for the major unit of vegetation, as usage was coming to do more and more (Plant Succession, 124), and to use association for the major subdivision, a relation likewise warranted by usage as well as by the action of the Brussels Congress. Whatever the final solution of this matter may be, there would seem to be no doubt that the grassland is a major unit, coordinate with deciduous forest, sagebrush, chaparral, etc.

When we turn to the internal proof of the unity of the grassland climax, the evidence is more complete. In the first analysis of the grassland, Pound and Clements (1898 : 243, 1900 : 347) recognized two prairie formations, viz, the prairie-grass and buffalo-grass formation, a bunch-grass formation of the sandhills, and a meadow formation. In the light of successional studies, the last two are to be regarded as subclimaxes. In a few years (Clements, 1902) it had become clear that the buffalo-grass or *Bulbilis-Bouteloua* formation and the prairie-grass or *Stipa-Agropyrum* formation were the two great communities of the prairie-plains region. This was essentially the view of Shantz (1906, 1911) and of Pool (1914). This conception was still maintained in "Plant Succession" (180 : cf. note) after many additional years of successional research. However, the developmental concept of the formation had broadened its scope and afforded a clearer view of its structure. As a consequence of a special study of these relations, it became necessary to abandon the view of two separate grassland formations, and to recognize a single formation composed of several associations. Meanwhile, it had become increasingly evident that the *Agropyrum spicatum* consociation of the Northwest was closely related to the *Stipa-Agropyrum* prairie (Weaver, 1917 : 40). This was first suggested by frequently finding the three dominants associated in the field work of 1914 from Washington to Montana. It was confirmed in 1917, but the true relationship was obscure until it became certain in 1918 that *Stipa setigera* and *S. eminens* were the original bunch-grasses of California. As a consequence, it proved possible to recognize a fourth grassland association, composed of bunch-grasses and characteristic of the Pacific region of winter precipitation.

Unity of the grassland.—The conclusion that the grassland is a single great climax formation is based in the first place on the fact that the three most important dominants, *Stipa*, *Agropyrum*, and *Bouteloua*, extend over most of the area, and one or the other is present in practically every association of it. This would seem the most conclusive evidence possible, short of actual vegetation experiments, that the grassland is a climatic vegetation unit. Equally cogent is the fact that these dominants, together with *Carex*, *Bulbilis*, and *Koeleria*, mix and alternate in various groupings throughout the *Stipa-Bouteloua* association. Indeed, this association appears so conclusive as to the general formational equivalence of these seven dominants that it is regarded as the typical or base association. In addition, the characteristic societies either extend through several of the associations or are represented by corresponding communities belonging to the same genus. The relation of the associations to such subclimax species as *Andropogon scoparius*, *Calamovilfa longifolia*, *Aristida purpurea*, and *Elymus sitanion* further confirms the relationship of the dominants. The most obvious difference between the various associations are exhibited by the tall-grass prairies, *Stipa-Koeleria poium*, and the short-grass plains, *Bulbilis-Bouteloua poium*. Yet these are closely related, as shown not only by the criteria given above, but also by their geographical contact. Still more eloquent is the fact that overgrazing favors *Bouteloua* and *Bulbilis* at the expense of *Stipa* and *Agropyrum*, and thus frequently converts the base association of *Stipa-Bouteloua* into a pure short-grass cover. Concrete evidence of this has been obtained in widely separated areas and has led to the working hypothesis that a pure short-grass cover is partly if not largely a response to grazing animals. The evidence for this is discussed in Chapter VI.

Correlation with climate.—The apparent objection to the view of the grassland advanced here is that the climates of Saskatchewan, Nebraska, Arizona, and California, for example, are vastly different, and hence the same climax can not exist in all of them. This objection is partly met by the fact that it is impossible to speak of *the* climate of Arizona or California in particular, since even from the human viewpoint each shows several climates. The conclusive answer, however, is that the objection is based upon a definition expressed in human terms or in physical measures. The everyday conception of climate emphasizes temperature, especially the extremes, and rainfall. It ignores water relations very largely and in particular the compensating rôle of water-content. Humanly, the Palouse region of Washington and the prairies of Kansas possess distinct climates, but in terms of wheat production and grassland vegetation they are very similar. Likewise, the winter in Saskatchewan is long and the summer short, while in Texas just the reverse is true. But the short growth period of *Bouteloua gracilis* fits into the short summer of Saskatchewan as readily as it does into the early summer of Texas, with the result that this dominant covers large areas in both.

Examples of this sort can be multiplied almost indefinitely to prove that in the study of vegetation the plant must be taken as the best if not the only judge of climate. However sympathetic one may be with the use of physical factor instruments, he can not afford to minimize the unique importance of the plant for the analysis of climates. To do otherwise is to substitute human judgment for plant judgment in the plant's own field. Hence, in the correlation of vegetation and climate, it has seemed imperative to determine at the outset and at first hand just where each formation or association is found. The next step is to accept the judgment of the formation as final, and to regard the climatic region as identical with the area of the formation. This done, it at once becomes possible to correlate climate and vegetation by means of phytometers and permanent quadrats, and to check the correlations in some degree by means of physical instruments.

Use of weather records.—The tendency to approach the problem by the use of weather records and floristic reports is almost irresistible, especially in view of the time and effort involved in obtaining an adequate first-hand knowledge of climaxes. However, the latter not only seems indispensable, from the vantage ground of a continuous study of the problem, but its paramount importance seems to be shown also by the endeavors to correlate an unknown vegetation with imperfect records of climate. The most interesting attempts have been those of Merriam (1898) and Transeau (1905), partly because they have endeavored to determine the limits of vegetational zones by means of climatic lines. In so far as Merriam's life-zones dealt with natural vegetation, they are necessarily unsatisfactory, since temperature is far less critical than water for native species.


Fig. 3.—Monthly and total rainfall for representative localities in the various associations of the grassland climax.

As a botanist, Transeau properly emphasized the water relations, employing the percentages found by dividing the mean annual rainfall by the depth of evaporation. The unavoidable errors due to the imperfection of the record (Livingston, 1913 : 272) are so great, however, that his results only served to emphasize the well-known fact that in North America forest yields to prairie, prairie to plains, and plains to desert from east to west, as rainfall decreases and evaporation increases. Probably the author did not intend that his climatic lines should be taken for the limits of vegetation units, but such an outcome was unavoidable. In referring to Transeau's work, Waller (1918 : 49, 59) says:

"The map makes an acceptable working basis for outlining the vegetation of the North American continent and remains still the best climatic chart that has been published on forest and prairie distribution."

It will suffice to point out that no climatic chart, no matter how accurate, can hope to outline the vegetation of North America. The formations and associations can never be outlined except as a result of painstaking reconnaisance and survey, after which alone will it be possible to determine the coincidence or correlation of the lines showing climatic factors or ratios. The very general relation of the 60 per cent line of Transeau to the one-hundredth meridian and the course of the upper Missouri River has led to the feeling that this is the most important line climatically and vegetationally in North America. It would seem that even the existence and location of this line must be regarded as purely tentative at the present time. As to its vegetational value, it can be stated unreservedly, after crossing and recrossing it repeatedly from Saskatchewan to Texas during the past six years, that it does not exist. While there can be no question of the interest and stimulus to be derived from "trying on" all sorts of climatic correlations, this is certain to be unfortunate if it does not lead to the conviction that causal relations between vegetation and climate can only be discovered after we know exactly where plant communities are and what they are doing. With this must also go a realization of the fact that climax climates necessarily fall into subclimaxes, that a climate may vary greatly and inconsistently within itself, that the variations of one climate during a climatic cycle may be greater than the difference between contiguous climates, and, finally, that it is the critical phases of a climate which count most, and not its averages or sums. It must be more fully understood that the growing season is the critical time for the vast majority of species, and that some parts of this are more critical than others. Furthermore, we must make more adequate use of our knowledge that plants stand better conditions much more complacently than they do worse ones (fig. 3).

Relationship of associations.—The associations of the formation exhibit relationships which may be considered from various angles. Geographically, they are grouped in the Great Plains with a narrow interrupted band stretching across the north to the Palouse region of Washington, Idaho, and Oregon, and a broader one at the south, reaching through New Mexico and Arizona almost to California. Both of these connect the bunch-grass association with the Great Plains mass. Climatically, the *Andropogon* subclimax is the wettest, with a rainfall of 30 to 40 inches, largely as summer rain, and the short-grass and the bunch-grass associations driest, with 10 to 20 inches. In the hotter regions, where evaporation is great, such as Texas and California, the efficiency of an inch of rainfall is naturally less. These are merely general correlations which apply to the mass and not to its limits. In view of the ecological requirements of grasses, the most suggestive correlation is with the line of 70 per cent of the annual precipitation occurring between April 1 and September 30 (fig. 4). With the exception of the winter rainfall region of the Pacific Coast, the general agreement as to limits is good. There appears to be no evident correlation as to temperature or altitude, as is well illustrated by the range of *Bouteloua gracilis* from Mexico to Saskatchewan, and from 3,000 to 9,000 feet.

**Floristic relations.**—The floristic relationship of the associations is evident. Of the five great dominant genera, *Stipa, Agropyrum, Bouteloua, Aristida,* and *Koeleria,* all occur throughout the formation, though *Bouteloua* is rare in the Coast region and *Stipa* in the southeast. Each of these is represented by a species of peculiarly wide range, namely, *Stipa comata, Agropyrum glaucum, Bouteloua gracilis, Aristida purpurea,* and *Koeleria cristata,* all of which occur from Saskatchewan to Texas, California, and British Columbia or Alberta. With the exception of *Koeleria,* which is monotypic as well as the least important of the five, each genus has one or more corresponding species in different portions of the area. Thus *Stipa comata* as a dominant is largely replaced in

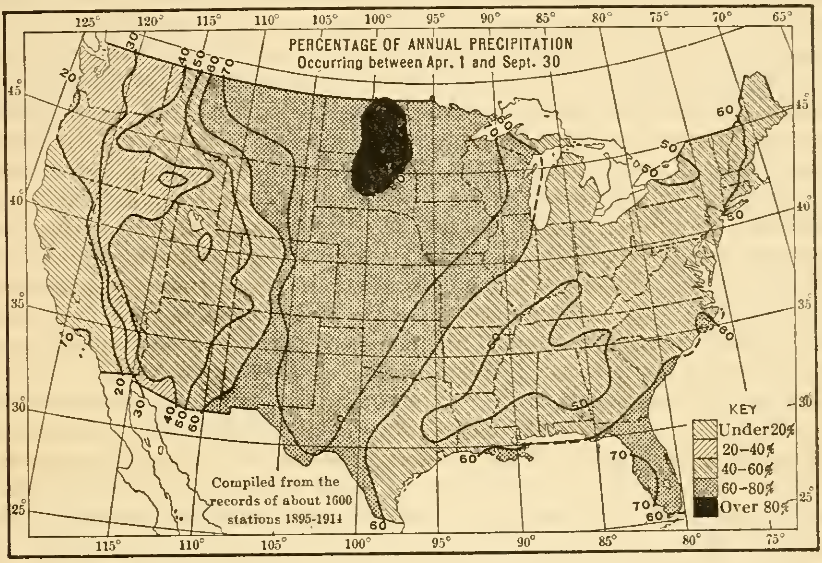



FIG. 4.—Map showing the percentage of annual precipitation between April 1 and September 30. After the U. S. Weather Bureau.

the Missouri Valley by *S. spartea* and in California by *S. setigera* and *S. eminens.* *Agropyrum glaucum* yields almost wholly to *A. spicatum* in Idaho, Oregon, and Washington. In southern Texas, New Mexico and Arizona, and in Mexico, *Bouteloua gracilis* gives way largely to *B. eriopoda, B. hirsuta, B. rothrockii,* and *B. bromoides,* while *Aristida purpurea* is represented for the most part by *A. divaricata, A. californica,* and *A. arizonica.* Of the ten most important subclimax dominants, such as *Andropogon scoparius, Bouteloua racemosa, Sporobolus airoides, Stipa viridula,* etc., all but one or two are found from Canada to Texas and California.

A similar relationship is shown by the climax subdominants which constitute the societies of the formation, though this is naturally somewhat less close so far as species are concerned. The most important societies are constituted by about 35 genera, of which practically all range throughout the formation, though they are naturally little in evidence in the California grassland to-day, owing to the intensive cultivation and the almost universal invasion of ruderal grasses. The number of such societies is 45, represented by as many species. Most of these are found in each of the associations, though many of them are more characteristic of some associations than others. The number of societies common to the whole formation or the major portion of it is several times greater than the number peculiar to any one association. The behavior of the subdominants seems fully as significant as that of the dominants, when their much greater number and plasticity are taken into account.

Ecological relations.—The ecological relationship is indicated primarily by the vegetation-form. All of the grass dominants are sod-formers, with the exception of those of the bunch-grass association. These are all bunch-grasses, and appear to be correlated with a winter precipitation which is 60 to 80 per cent of the total annual. The dominants of the prairie associations possess a tall growth-form, usually 2 to 3 feet and often 3 to 5 feet high. As the name indicates, the short-grass association consists of dominants regularly 1 to 2 feet high. These heights refer to the flowering stems, and the difference between the tall-grass prairie and short-grass plains is even more striking when the significant growth relations of the leaves are concerned. The leaves of the buffalo-grass, *Bulbilis dactyloides*, are normally within 4 inches of the soil, and those of grama, *Bouteloua gracilis*, within 4 to 8 inches. This applies likewise to *Carex filifolia* and *Carex stenophylla*, which are often very important constituents of the short-grass association and are sometimes more abundant than the grasses. On the other hand, the basal leaves of *Stipa* and *Agropyrum* are usually 8 to 15 inches high, and the leafy stems reach a height of 2.5 to 3.5 feet. This difference appears to be primarily one of water-content, more or less emphasized by grazing. The height and leaf-length of *Bouteloua* in particular can be doubled or trebled under irrigation. In nature, the height of the stems has been found to vary 100 per cent from a wet to a dry year. Striking as this difference between short-grasses and tall-grasses appears to be in the Great Plains, it disappears to a large extent in the desert plains of New Mexico and Arizona, where *Bouteloua* and *Aristida* regularly reach heights of 18 to 40 inches. The general ecological equivalence of the two forms is also well shown in the *Stipa-Bouteloua* association, where *Bouteloua* is frequently associated with *Stipa* as a layer, and *Bulbilis* with *Agropyrum*. As would be expected, the tall-grasses tend to have deep roots and the short-grasses shallower ones. In both cases this is largely determined by the depth of available water and by the compactness of the soil (Shantz, 1911 : 40; Weaver, 1915 : 274; 1917 : 56, 1919).

Subdominants.—The subdominants are practically all long-lived perennial herbs, in which the shoot and root have solved the problem of successful competition with the grasses. Four fairly well-defined types may be recognized. Perhaps the commonest is the type with tall bushy stems, such as *Psoralea tenuiflora*, *Amorpha canescens*, *Glycyrhiza lepidota*, and *Carduus undulatus*, which both shade and overtop the grasses in some degree. A second type is shown by such species as *Petalostemon candidus*, *P. purpureus*, *Solidago rigida*, *Lepachys columnaris*, etc., in which several tall strict stems come from one root. A third is illustrated by *Eriogonum annuum*, *Helianthus rigidus*, and *Gilia aggregata*, with a single slender shoot overtopping the grasses. In the fourth type, the stems form a tuft or mat-like mass, which dominates the grass shoots; this is seen in *Astragalus crassicarpus*, *Aragalus lamberti*, *Artemisia frigida*, and *Opuntia polyacantha*. In *Balsamorhiza*, *Solidago*, *Carduus*,

## True Prairie

A. *Stipa-Andropogon* association, Lincoln, Nebraska.
B. *Stipa spartea* consociation, Halsey, Nebraska.
C. *Andropogon scoparius* consociation, Medora, North Dakota.

and *Brauneria* a somewhat similar result is secured by means of the basal rosette. The roots of the great majority of these are deep-seated, apparently for the purpose of escaping the competition of the grass roots in so far as possible. Most of them place their roots at depths of 5 to 12 feet, and some penetrate as deeply as 15 to 20 feet.

Developmental relations.—From what has been said of the range of subclimax dominants, it follows that the several associations are closely related in successional development. The consocies and socies belong chiefly to the same genera, and a large number of species, especially those in water, saline areas, and Bad Lands, occur throughout. Phylogenetically, the formation shows evidence of having derived its dominants originally from two distinct vegetations. *Stipa, Agropyrum,* and *Koeleria* appear to have come from an original northern climax, which was forced southward during glacial times into the steppes of Eurasia and the prairies and plains of North America. *Bouteloua, Bulbilis, Aristida,* and *Andropogon* are genera of southern origin, which had probably pushed into the prairies and plains during the Miocene. It seems likely that the four most vigorous species, *Bouteloua gracilis, Aristida purpurea, Bulbilis dactyloides,* and *Andropogon scoparius* pushed still farther northward after the Pleistocene, and came to be at home with the tall-grasses of the northern prairies of the Dakotas, Montana, and Saskatchewan. The ecological unity of this particular association is emphasized by *Carex filifolia* and *C. stenophylla,* which resemble the short-grasses in life-form, but are holarctic in origin. To the east of this central matrix was differentiated the *Stipa-Koeleria* and to the west the *Agropyrum-Stipa* association, the one in response to a moderate rainfall of the summer type, the other to winter precipitation. Within these there was a further tendency to separate into a northern *Agropyrum* area and a southern *Stipa* one. This was well-marked in the Pacific region, but it has completely stopped as a consequence of settlement. In the south, a similar differentiation resulted in the *Aristida-Bouteloua* association, which still finds its best expression in Mexico, and the *Andropogon* subclimax of the Mississippi Basin.

## THE TRUE PRAIRIE.

### STIPA-KOELERIA ASSOCIATION.

Extent.—The true prairies occupy a distinct belt between the subclimax and mixed prairies, reaching from Manitoba to Oklahoma. This position as well as their relationship is shown by the presence of *Andropogon scoparius* derived from one and *Stipa comata* from the other. The ecological relation is well illustrated in northeastern Nebraska, where *Andropogon furcatus* and *A. scoparius* occupy the meadows and moister slopes, and *Stipa comata* and *Bouteloua gracilis* the drier upper slopes and crests of the *Stipa-Koeleria* hills. To the southeast, increasing rainfall enables first *Andropogon scoparius* and next *A. furcatus* to extend over the rolling hills, while to the west and northwest reduced rainfall causes *Stipa comata* to dominate and then replace *S. spartea,* and permits *Bouteloua* and *Bulbilis* to become constant associates of the prairie grasses (plate 21).

Cultivation has perhaps destroyed this association to a larger extent than any other community of the grassland, and its limits are accordingly difficult to trace. This difficulty is increased by the breadth of the two ecotones between the three parallel associations. However, the general limits of the area may be drawn with some definiteness. The eastern edge runs southward from Manitoba along the western boundary of Minnesota and then swings southeastward with the Minnesota Valley, reaching its limit between 92° and 93° W. It stretches across northern and central Iowa in the vicinity of the ninety-third meridian, and then trends southwestward across northwestern Missouri and eastern Kansas, where it turns south to the Oklahoma line. The western boundary begins in Manitoba between the one hundredth and the one hundred and first meridians and continues more or less due south to near the Nebraska line, where it turns southeast around the sandhill region, beyond the ninety-ninth meridian. It then follows this in a general way into northern and central Kansas, and finally approaches the Oklahoma line in the vicinity of the ninety-eighth meridian. The association reaches its greatest breadth of 7° of longitude along the forty-third parallel, and it tapers more or less irregularly in both directions to a width of 1° to 2° in Manitoba and in Kansas.

CONSOCIATIONS.

Stipa spartea. Agropyrum glaucum.
Koeleria cristata. Andropogon scoparius.
Stipa comata.

Each of the 5 species may occur as a pure dominant, though this is exceptional for *Koeleria.* The latter has been found in pure communities covering several square miles only in the Dakotas, where this condition was also found by Griffiths (Williams, 1898 : 22). *Koeleria* is sometimes dominant in meadows and swales, but it is usually associated with *Stipa* or *Agropyrum.* While it possesses the most extensive range of any of the 5 dominants, it is generally the least important locally, its abundance rarely being more than 30 per cent and often as low as 10 per cent. *Stipa spartea* and *S. comata* are complementary species which overlap as dominants in northeastern Nebraska and the central Dakotas. The ecotone between them runs in a general way along the ninety-ninth meridian, though either occurs locally beyond this line. In Kansas, *Stipa spartea* ranges over the eastern half of the State, while *S. comata* is reported for only five counties in the extreme west. It is probable, however, that the consociations are in contact with each other in the central portion. Both occur as pure communities over large areas in their respective regions, but they are generally associated with *Andropogon scoparius* or *Agropyrum glaucum. Stipa spartea* is the most typical dominant of the true prairies, while *S. comata* belongs primarily to the mixed prairies.

*Andropogon scoparius* is the normal associate of *Stipa spartea* and *Koeleria cristata,* giving the grass tone to the prairies during late summer and autumn, as they do in spring and early summer. It is one of the most widespread of dominants, and plays a climax or seral rôle in all the grassland associations except that of the Pacific Coast. It shows two life-forms, appearing as a sod-grass in the true and subclimax prairies, and as a bunch-grass in the sandhills and "breaks" of the mixed prairies and the plains. Like *Stipa comata, Agropyrum glaucum* is found throughout the West, but its dominance is local or subclimax in nature outside of the prairie association. It exerts a greater control on the habitat than any of its associates, owing largely to its many and vigorous rootstocks. It is purest on the gumbo plains and rolling hills of south-central South Dakota, where it stretches like fields of wheat as far as the eye can reach. Like *Stipa spartea*, it often meets and mixes with *Andropogon scoparius* or *A. furcatus* in low prairies or subclimax regions. In such places, as well as in local areas of higher rainfall, *Andropogon furcatus* and *A. nutans* often become controlling. When this is the case, however, the community is always to be regarded as subclimax. It need occasion no surprise to find extensive outposts of subclimax grassland in the true prairies, if account be taken of the close requirements of the dominants and the considerable variation in normal rainfall at places not very distant from each other. Thus Lincoln and Peru, Nebraska, are less than 60 miles apart, but one has a rainfall of 28 inches and is in the true prairies, while the other with a rainfall of 34 inches lies in the subclimax prairie (plate 22, A).

Factor relations.—*Koeleria* is a bunch-grass, while the other four dominants, as well as the subclimax *Andropogon furcatus*, are sod-formers in the prairie. All of the latter become bunch-grasses with the decreasing rainfall, such as is characteristic of the sandhill areas to the westward. Their water relations have been worked out for but a few regions as yet, but enough has been done to indicate the general requirements. These agree well with the growth-form and with the successional sequence, as well as with the physiographic relation where this controls the distribution of water. Studies of water-content in the *Stipa-Koeleria* prairies at Belmont, north of Lincoln, from April 22 to May 25, 1901, gave the following results at 5, 10, and 15 inches:

| Depth. | Crests. | Upper slopes. | Lower slopes and ravines. |
|---|---|---|---|
| *ins.* | *p. ct.* | *p. ct.* | *p. ct.* |
| 5 | 12 to 6 | 20 to 6 | 32 to 15 |
| 10 | 15 to 5 | 23 to 10 | 34 to 16 |
| 15 | 12 to 3 | 20 to 6 | 28 to 16 |

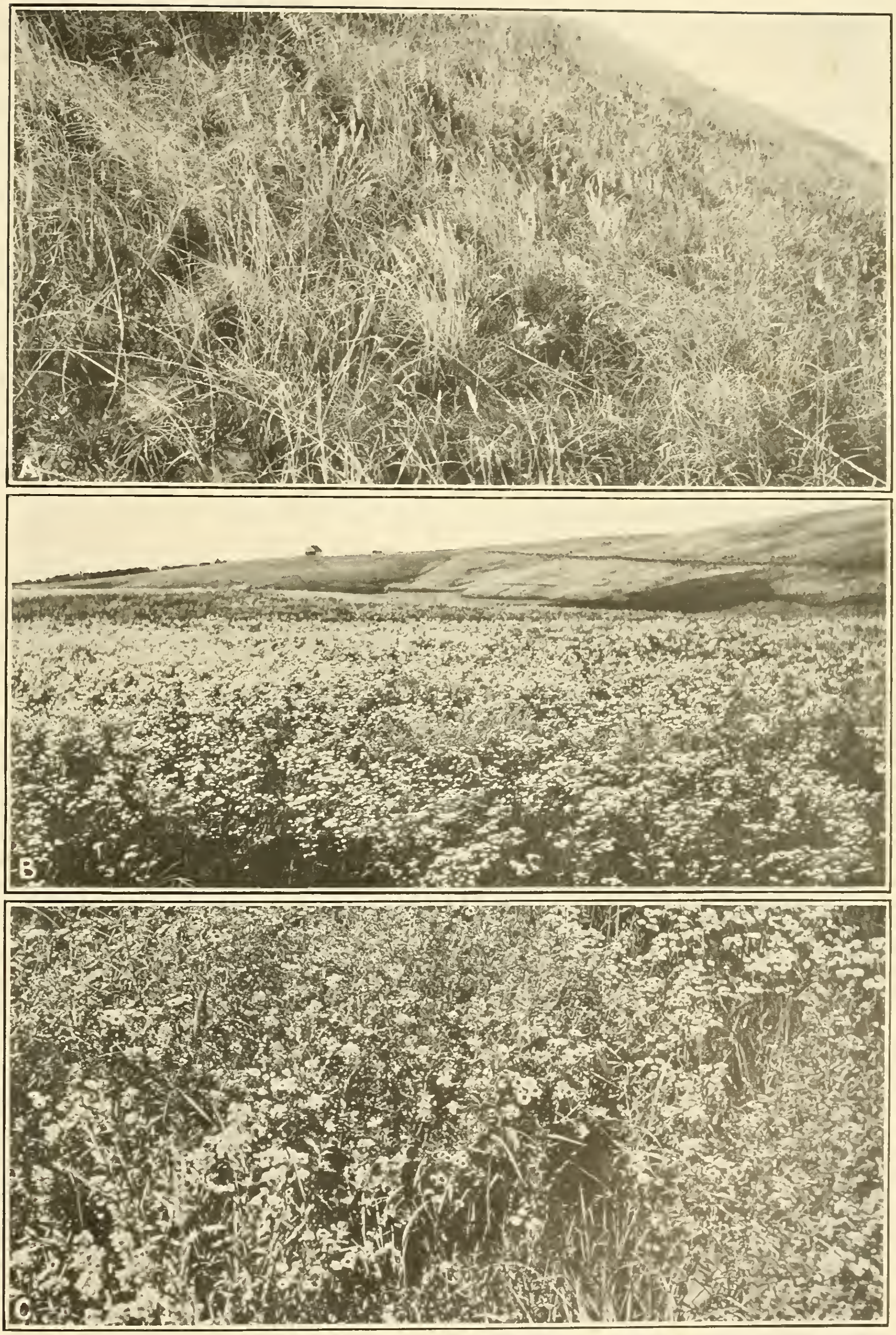
The three levels, which were represented by 7 stations, correspond with *Bouteloua*, *Stipa-Koeleria*, and *Andropogon* respectively. Weaver and Thiel (1917 : 15) found the water-content of *Stipa-Koeleria* prairie near Minneapolis to range for the most part between 5 per cent and 15 per cent during the summers of 1915 and 1816. In the low prairie of *Andropogon furcatus* and some *A. scoparius*, the variation in 1915 was 27 to 45 per cent, and in 1917 chiefly from 20 to 55 per cent. In the Belmont prairies in 1916, the range of soil-moisture in the high prairie was chiefly between 10 per cent and 25 per cent on the slope, while on the ridge it fell for the most part between 5 per cent and 15 per cent. The high prairie at Minneapolis and Belmont gave an evaporation rate nearly twice as great as that of the low prairie. The evaporation rate on a ridge of the Belmont prairie was usually 2 to 4 c.c. higher than on the slope.

Sequence of dominants.—These results confirm the water sequence as indicated by the successional and topographic relations. The subclimax *Andropogons* have the highest water-content requirement, a fact further attested by the readiness with which they are invaded by scrub or woodland. *Agropyrum* follows closely, often being nearly equivalent to *Andropogon scoparius*. After it come *Koeleria*, *Stipa spartea*, and *S. comata* in this order, with the extra-associational *Bouteloua gracilis* occupying the dry crests. The average range of water-content for the *Andropogons* is 25 to 35 per cent, for *Agropyrum* 20 to 30 per cent, for *Stipa spartea* and *Koeleria* 15 to 20 per cent, and for *Stipa comata* 10 to 15 per cent. It is clear that these values will vary greatly from the dry to the wet phase of the climatic cycle, and that their efficiency will change with the factors controlling evaporation and transpiration.

While extensive quantitative studies will refine these values and will definitize them for different regions, it seems clear that they will also further verify the successional sequence indicated above. In applying the latter, it must be borne in mind that the mixing of two or more of the dominants over a certain area by no means invalidates the sequence. The requirements of two successive dominants are more alike than different, and under minor disturbances in the habitat-complex are actually or apparently equivalent, for a time at least. These differences are modified by climatic fluctuations from year to year. When variation of slope, exposure, and soil are taken into account, it is readily understood why pure consociations extending over many miles are impossible. The largest area of *Agropyrum* seen was in the valley of Dog Ear Creek in South Dakota, but whenever the valley rose into hills, *Agropyrum* gave way to *Stipa comata* or *Stipa spartea*. Likewise, on the rough hills of the Pine Ridge reservation of South Dakota, *Stipa comata* appears like fields of golden grain for miles in every direction, but the lower valleys, swales, and roadways are characterized by *Agropyrum*. *Stipa spartea* shows a similar behavior on a smaller scale. However pure the community appears, it is regularly mixed with *Koeleria* or interrupted by *Agropyrum* or *Andropogon*.

The mixing of dominants within an association differs only in degree and extent from the mixing of dominants at the edge of contiguous associations or formations. But it would be a serious mistake to assume that the associations or formations concerned were essentially a unit because of the broad ecotone that exists between them. There is a complete sequence of dominants with overlapping ranges in the grassland from *Andropogon furcatus* on the east to *Bouteloua gracilis* on the west. This corresponds with a gradual decrease of rainfall from 30 to 40 inches to 10 to 15 inches. In spite of the equalization brought about by physiography, the two species practically never come in contact with each other as dominants. Between them lies the whole region of the climax prairies, 200 to 400 miles wide, along which *Andropogon* makes a broad ecotone on the east and *Bouteloua* on the west. A similar situation exists where grassland comes in contact with the sagebrush or the woodland climax. There is often a complete and more or less equal mixture for a width of several to many miles. From the superficial evidence, the dominants might well be placed in the same formation, but a study of the successional relations or a comparison of the ecotone with the formation proper on either side will at once disclose the real facts. As a rule the careful study of the ecotone will show that most of it can be referred to one or the other of the two formations or associations, and that the area of actual equilibrium is relatively small. In fact, increasing familiarity with vegetation shows that most transitions are due to disturbance or climatic cycles and are actually a part of succession.

True Prairie



A. *Koeleria cristata-Andropogon scoparius* association, Agate, Nebraska.
B. *Erigeron ramosus* society, Lincoln, Nebraska.
C. Detail of society of *Psoralea tenuifolia* and *Erigeron ramosus*, Lincoln, Nebraska.

## SOCIETIES.

**Nature.**—The societies of the grassland formation are constituted by perennial herbs which give a distinct impress to large areas of the grass cover. As already indicated, they show a dominance which is subordinate to that of the grasses, and hence are termed subdominants. Originally the term was employed for all conspicuous subdominants of wide range (Clements, 1905). As the importance of the distinction between climax and developmental communities became manifest, the society was restricted to the climax, and the corresponding term socies was used for the successional subdominants. In the superficial study of an association, subdominants of all sorts will be found to alternate and mix with each other. All such communities appear to be societies, until a study of succession reveals the fact that some are relatively permanent while others are temporary, and many indeed persist for only a few years. Where disturbance is continuous or recurrent, as in grazing, temporary societies or socies persist as long as the disturbance lasts, and their real character can be determined only by protected quadrats or by comparison with undisturbed areas. In the majority of such cases, however, socies can be recognized by the fact that they are composed of species of annual or biennial habit.

**Control of dominants.**—The subdominance of a society is necessarily limited by that of the grass dominants. In grassland, water is the primary limiting factor, and determines the competition between dominants and subdominants as well as within the corresponding communities. The fact that the two belong to distinct vegetation-forms means that they avoid competition in so far as possible by making different demands and at different times. Theoretically, the grass dominants should gradually gain the advantage over the subdominants and replace the latter completely. This is especially true of legume societies, the reaction of which greatly stimulates the growth of grasses. Such an outcome is frequent in the *Bouteloua gracilis*, *Bulbilis*, and *Agropyrum glaucum* consociations, wherever the dense turf holds the water in the upper soil layer. In such cases, the grass roots absorb practically all of it and leave little or none for the deeper-rooted herbs (Shantz, 1911 : 51; Weaver, 1919 : 51). As a consequence, the number and extent of societies depend primarily upon rainfall. Where the rainfall is from 25 to 40 inches and the evaporation correspondingly low, societies will usually be so numerous and luxuriant as to conceal or at least obscure the dominant grasses during much of the growing season. As the rainfall decreases and the evaporation increases to the westward, the dominants will take more and more of the water-content, and the number and extent of the societies will steadily diminish. The result is that the true prairies (*Stipa-Koeleria* association) show the best development of societies. The wealth of subdominants is partly due also to the fact that the prairies have been able to draw almost equally upon the eastern and the western floras. The mixed prairies have the same societies for the most part, but they are reduced in number and even more in extent and density. This is due partly to reduced rainfall and partly to the presence of the lower layer of short-grasses and sedges.

The bunch-grass prairie is much poorer in societies, on account of a low winter precipitation. The poorest of all is the short-grass plains (*Bulbilis*-

*Bouteloua* association). This seems to be related to three interacting causes. Perhaps the most important is the small amount and the character of the summer rainfall, and the rapidity of evaporation. Coupled with this are the dense sod and the fine mass of shallow roots which limit penetration largely to the upper foot or two. A third factor is the extensive grazing which has supplemented the first two by decreasing the competitive vigor of the subdominants or by actually destroying them. In the desert plains (*Aristida-Bouteloua* association), somewhat similar conditions prevail, and societies are relatively few. This essential water relation between the consociations and the societies is well shown in regions where the rainfall or water-content is locally increased. The number, extent, and dominance of societies are greatly augmented in the case of mixed prairies along the Pine Ridge escarpment in Northern Nebraska, the east edge of the Black Hills, and the Front Range of the Rocky Mountains in Colorado. This is likewise true in the sandhill region of central Nebraska, where the chresard or available soil-water is exceptionally high.

Relation to consociation.—While there is no necessary connection between consociation and society, there is a more or less evident correlation based upon water requirements and floristics. It must be clearly recognized, however, that consociations are not divided into societies as associations are into consociations. The entire area of the association is occupied by its consociations, in pure alternes or in mixtures, except where succession is in process. The same area will likewise show societies, but they will mix and alternate, or replace each other without any clear relation to the consociations. This is partly due to their large number and partly to the fact that subdominants are naturally susceptible to variations in the composition, density, and vigor of the grass communities as well as to local differences in the habitat. For example, *Psoralea tenuiflora* is one of the most important of grassland societies. It is essentially a formational subdominant in that it occurs in all of the associations with the probable exception of the bunch-grass prairie. Yet its height and density, and hence its degree of dominance, differ in practically all of them. It reaches its best expression in the *Stipa spartea* consociation, but is usually replaced in the related *Agropyrum* and *Andropogon* consociations by its complementary subdominant, *Psoralea argophylla*. Of the hundred or more societies, the majority occur in at least three associations, and usually three contiguous ones. So closely related are the associations in conditions and floristics that hardly a single society is known to be restricted to one association. The societies of the most limited extent are those which have been recently derived from other formations. They naturally occur in the subclimax, the desert plains, or in the bunch-grass prairie, since these are the marginal associations of the grassland.

Origin.—This fact corresponds with a general grouping of societies with reference to the flora from which they come. The grassland has approximately 100 societies, of which more than 40 are derived from the southwest, and about 30 from the east or southeast. Some of the latter were doubtless from the south or southeast originally. A few are apparently indigenous and a small number are Pacific, and hence probably southern also. The large number of southern elements agrees with the southern derivation of most of the grassland dominants. The fact that *Bouteloua, Aristida,* and *Bulbilis* have pushed so far north explains why the societies of desert plains, short-grass plains, and the mixed prairie are so largely southwestern. The more mesophytic eastern prairie affords a readier area for the invasion of the eastern and southeastern species from regions of greater rainfall. The result is that the prairies are largely characterized by eastern elements. This is particularly true of the spring societies and those of the low prairies, as these are especially mesophytic. The summer and particularly the autumn societies are increasingly xerophytic, and are accordingly largely southwestern and western in origin.

Mixed societies.—Subdominants either alternate or mix with each other in the grassland fundament. Their large number explains why mixing is the rule. The degree will vary, however, in the different associations in accordance with the water relations, as well as the wealth of the flora. Mixed societies are regularly characteristic of the true prairie, less so of the mixed prairie, and still less so of the short-grass plains, where alternation of pure societies seems rather more frequent. Mixed societies may consist of 2 to 3 dominants, one of which is controlling, or of several dominants, of which 2 or 3 may be equally important. The most characteristic society of the rolling *Stipa-Koeleria* prairie about Lincoln consists of *Psoralea tenuiflora*, *Amorpha canescens*, *Petalostemon candidus*, *P. purpureus*, and *Brauneria pallida*. At Mandan, North Dakota, this is represented by *Psoralea argophylla*, *Brauneria*, and *P. candidus*, while along the Rawhide Hills, in eastern Wyoming, *Psoralea tenuiflora* and *P. purpureus* form the chief society. In the Pine Ridge region of northwestern Nebraska and South Dakota, *Psoralea* occurs as a pure society, as is frequently the case throughout the Great Plains. While these subdominants may occur in nearly all possible combinations, the example given illustrates the uniform tendency to reduction wherever local factors or climatic conditions decrease the water-content. As a consequence, the pattern woven by the subdominants upon the grass fundament is a complex one and it can be traced only by a careful study of the interaction of competition and the water-content. When layer societies occur in the grassland, they are the outcome of competition for light primarily. They are naturally restricted to the prairies.

Aspects.—The most helpful clue to the structure and grouping of societies is furnished by the study of seasonal aspects and of alternation. These are chiefly expressions of the relation to water-content differences as brought about by season and topography. The success of each subdominant depends upon the extent to which it avoids competition with others. This has led to the multiplication of the number of societies up to the limit set by the water relations. As a corollary, the number of societies and the degree of mixture are indicative of the water relations of a particular area or region. Species have necessarily made use of both methods of avoiding competition, namely, alternation in time and in space. Alternation in time results in periods of maximum development termed aspects (Pound and Clements, 1900 : 143, 349; Thornber, 1901 : 57; Shantz, 1906 : 26). Aspects are based primarily on the flowering period of the subdominants, upon the assumption that the total requirements of a plant are greatest at the time of flowering and fruiting. Moreover, the subdominants are most characteristic at this time, and the corresponding societies stand out sharply. The number of aspects naturally depends upon the length of the growing season. At Lincoln, the mean duration of the latter is 234 days, and it is possible to recognize four aspects, early spring, spring, summer, and fall. As the season grows shorter, the early spring and fall aspects merge into the spring and summer respectively. These two aspects persist even when the season is reduced to two months or less, as is the case on Pike's Peak (Clements, 1904 : 349).

The early spring or prevernal aspect is largely a matter of temperature and light, the water-content being high and the demands upon it slight. The plants are chiefly low mat and rosette plants, which must bloom early to avoid the overshading produced by later species. The maximum water-content occurs in the spring and evaporation is lowest then also, though pronounced fluctuations are of frequent occurrence. As a general result, the more mesophytic species appear in the spring and the more xerophytic ones in late summer and autumn. The maximum development occurs during the summer aspect in high prairie, and somewhat later in low prairie, the temperature necessary for mature growth playing some part in this. In the case of high prairie the growing season is gradually closed by drought, with low prairie it is usually terminated by frost. With the passing of each aspect, its principal species decrease their activity greatly. Accordingly, while the number of mature plants constantly increases during the summer, the demands for water and light increase less rapidly, and the supply is conserved at the requisite level. It is hardly necessary to point out that there are no sharp distinctions between the various aspects. The one passes gradually into the next, and the change is not perceptible from day to day. If, however, the prairie is visited in early April, late in May, in early July and early September, it will present a wholly different appearance at each time.

Zones and alternes.—The structure of the prairie during a particular aspect is largely due to alternation and zonation. These are both caused by slight differences in the requirements of the species concerned. This is best illustrated by corresponding species of the same genus, such as *Petalostemon purpureus* and *candidus*, *Psoralea tenuiflora* and *argophylla*, *Solidago missouriensis* and *rigida*, *Artemisia frigida* and *gnaphalodes*, *Aster multiflorus* and *sericeus*, and *Liatris punctata*, *scariosa*, and *pycnostachya*. In each case the first species is more xeroid than the second, with the consequence that one regularly occurs above the other in more or less zonal arrangement over the rolling prairies. In many areas the zones are obscure or interrupted, and the two species occur in drier and moister areas respectively, or the one will be more abundant in high prairie and the other in low prairie. This relation is confirmed by their successional behavior in that the xeroid species usually shows a marked tendency to appear just before the climax. *Petalostemon* and *Psoralea* have been studied as to their water relations in the Lincoln prairies, where *Psoralea argophylla* characterizes the valley plains and lowermost slopes with an average water-content of 25 to 35 per cent, while *P. tenuiflora* dominates the slopes and broad middle ridges with a water-content of 15 to 20 per cent. The two touch, but only occasionally overlap or mingle to any considerable degree. *Petalostemon* has been more adequately studied. The sharp ecotone between the two species was carefully traced on two opposite slopes in 1901, and the water-content limit between them was found to be 13 per cent. In 1917, Loftfield studied the water relations of the two species under control, and succeeded in modifying plants of *P. purpureus* in high water-content so that they could not be distinguished in shoot characters from those of *P. candidus*. The three species of *Liatris* are especially striking in their relations. About Lincoln, *L. pycnostachya* is confined to low prairies and meadows, *L. scariosa* takes middle levels and lower slopes, while *L. punctata* is found on upper slopes and crests. As would be expected, this agrees with the difference in growth-form; *L. punctata* averages 1 to 2 feet in height, *L. scariosa* 2 to 3 feet, and *L. pycnostachya* 3 to 4 feet. It is also in accord with their distribution westward. The hydroid *L. pycnostachya* finds its limit in the prairies and the intermediate *L. scariosa* in the mixed prairies, while *L. punctata* occurs throughout the plains as well as in the bunch-grass prairies of the Northwest.

The alternation of unrelated subdominants is often more striking. This is true of *Anemone* and *Viola* in the spring aspect, of *Psoralea* and *Erigeron* in the summer, and of *Aster*, *Solidago*, and *Vernonia* in the fall. The most conspicuous alternation of this sort is that of *Psoralea tenuiflora* and *Erigeron ramosus*, owing to the dominance and extent of each, as well as the outstanding difference in color. The areas of each broaden and contract with the wet and dry phases respectively of the climatic cycle. In the wet year of 1915 the *Erigeron* society covered the lower slopes and vales of the Lincoln prairies like fields of snow, while the upper slopes and edges were marked out in the purple-green of the *Psoralea* society. At Weeping Water, where the prairie is largely subclimax, the grass openings on the oak hills were snow-white with *Erigeron*, thus confirming its topographic and cyclic relation to *Psoralea* in the prairie region (plate 22, B, C).

Studies of prairie societies.—As an adequate treatment of the prairie societies is impossible, owing to the limits of space, it must suffice to refer to the work that has been done upon them and to list them in the general order of importance under the different aspects. The first attempt to deal with the structure of the grassland was made by Pound and Clements (1898 : 244; 1900 : 349, 244, 299), who distinguished and characterized the various subdominants, determining their rank largely upon the basis of the quadrat method. Thornber (1901 : 73, 96, 137) made a thorough analysis of the structure of a subclimax prairie at Nebraska City, paying especial attention to the alternation of the principal and secondary species. Harvey (1908 : 81) has traced the seasonal development of the various societies in the prairies at Yankton, South Dakota. In a careful study of climaxes and their successional development in the sandhills of Nebraska, Pool (1914 : 221) has distinguished the principal and secondary species of the subclimax bunch-grass prairie. Recently Weaver and Thiel (1917 : 9, 32) have dealt with the aspects and societies of the prairie at Minneapolis and Lincoln, and Pool, Weaver, and Jean (1919) with the root relations of dominants and subdominants in subclimax prairie at Peru, Nebraska, and climax prairie at Lincoln. Naturally, the following lists are based chiefly upon the structural and quantitative studies made in the Nebraska prairies from 1895 to 1907. They have been checked and extended throughout the true prairies from North Dakota to Kansas in the special studies made during the summers of 1913 to 1918. All of the important societies that occur in the prairies are listed here, though many of them are found also in other associations.

*Societies of the True Prairie.*

*Prevernal Societies:*
Carex pennsylvanica.
Antennaria dioeca.
Anemone patens.
Anemone caroliniana.
Lomatium foeniculaceum.
Draba caroliniana.
Androsace occidentalis.

*Vernal Societies:*
Astragalus crassicarpus.
Aragalus lamberti.
Tradescantia virginiana.
Phlox pilosa.
Anemone canadensis.
Fragaria virginiana.
Viola pedatifida.
Viola cucullata.
Baptisia leucophaea.
Callirrhoe alcaeoides.
Vicia americana.
Thalictrum purpurascens.
Ranunculus ovalis.
Zizia aurea.
Anemone cylindrica.
Equisetum arvense.
Comandra umbellata.
Senecio aureus.
Sisyrinchum angustifolium.
Lithospermum linearifolium.
Lithospermum canescens.
Lithospermum hirtum.
Agoseris cuspidata.
Achillea millefolium.
Hosackia americana.
Viola pedata.
Sieversia ciliata.
Hypoxis hirsuta.
Oxalis stricta.
Castilleia sessiliflora.
Houstonia angustifolia.

*Estival Societies:*
Psoralea tenuiflora.
Amorpha canescens.
Petalostemon candidus.
Petalostemon purpureus.
Psoralea argophylla.
Erigeron ramosus.
Glycyrhiza lepidota.
Brauneria pallida.
Lepachys columnaris.
Helianthus rigidus.
Dalea laxiflora.
Verbena stricta.
Verbena hastata.
Linum sulcatum.
Equisetum levigatum.
Equisetum hiemale.
Veronica virginica.
Allium mutabile.
Pentstemon grandiflorus.
Euphorbia corollata.
Coreopsis palmata.
Rosa arkansana.
Lespedeza capitata.
Monarda fistulosa.
Heliopsis scabra.
Pycnanthemum lanceolatum
Pentstemon gracilis.
Silphium integrifolium.
Steironema ciliatum.
Teucrium canadense.
Teucrium occidentale.
Amorpha nana.
Callirrhoe involucrata.

*Serotinal Societies:*
Solidago rigida.
Aster multiflorus.
Solidago missouriensis.
Solidago speciosa.
Artemisia frigida.
Grindelia squarrosa.
Gutierrezia sarothrae.
Kuhnia glutinosa.
Aster oblongifolius.
Artemisia graphalodes.
Artemisia dracunculoides.
Salvia azurea.
Rudbeckia hirta.
Solidago serotina.
Aster sericeus.
Aster paniculatus.
Aster novae-angliae.
Aster azureus.
Nabalus asper.
Eupatorium altissimum.
Liatris pycnostachya.
Liatris punctata.
Liatris scariosa.
Carduus undulatus.
Solidago nemoralis.
Solidago canadensis.
Vernonia baldwinii.
Vernonia fasciculata.
Helianthus maximiliani.
Helianthus grosse-serratus
Silphium laciniatum.

## CLANS.

Clans are climax communities of limited area or dominance. They usually occur as secondary areas in societies, but are occasionally found where the dominance of grasses is too great to permit the appearance of societies. A clan may consist of a species which is locally important or conspicuous, but does not occur generally. The most common type is represented by a gregarious species which grows in small patches of a few square yards or a few rods. Another common type is exemplified by subsparse secondary species which are more or less frequent throughout the association. Some of these naturally become so sparse that they no longer give any impression of a community. Clans are perhaps best regarded as communities of the third degree of dominance, in which the control is necessarily slight as a consequence of being subordinated to the primary control of the grass dominants and the secondary control of the subdominants. Near the edges of an association, societies of adjoining areas enter in reduced abundance and dominance. As a result, they have the appearance of clans and would pass for such where a single locality is studied. Since the fluctuations of societies are of great importance for indicator studies as well as for climatic correlation, it seems clear that they should always be treated as such, with the proper statement as to their reduced significance. It is perhaps even more necessary to maintain the distinction between fragmentary consocies or socies, and clans. A host of minor disturbances may denude a small spot or displace the dominants sufficiently to start a minute succession. To the unpracticed eye, the community will appear as a clan, while it is really a stage in succession. Its real nature is readily disclosed by comparison with other areas where disturbance is obvious, or by following its development during a few years.

Because of their subordinate importance, the factor relations of clans have secured little attention. They are clearly controlled by water relations, as is shown by their topographic position, and their seasonal appearance. They are also more or less influenced by light as an outcome of their competition with the subdominants.

*Vernal Clans:*
- Delphinium penardi.
- Oxalis violacea.
- Oxalis stricta.
- Scutellaria parvula.
- Astragalus canadensis.
- Specularia perfoliata.
- Pentstemon cobaea.
- Pentstemon albidus.
- Onosmodium molle.
- Baptisia leucantha.
- Erigeron philadelphicus.

*Estival Clans:*
- Asclepias syriaca.
- Asclepias sullivantii.
- Asclepias tuberosa.
- Asclepias verticillata pumila.
- Lactuca pulchella.
- Desmodium illinoense.
- Schrankia uncinata.
- Desmanthus illinoensis.
- Lathyrus ornatus.
- Acerates viridiflora.
- Psoralea esculenta.
- Potentilla arguta.
- Physalis lanceolata.
- Physalis virginiana.
- Dalea aurea.

*Estival Clans*—continued.
- Evolvulus argenteus.
- Gerardia purpurea.
- Gerardia aspera.
- Cacalia tuberosa.
- Lythrum alatum.
- Lechea minor.
- Ruellia ciliosa.
- Triosteum perfoliatum.

*Serotinal Clans:*
- Liatris squarrosa.
- Hieracium longipilum.
- Gentiana puberula.
- Gentiana andrewsii.
- Solidago graminifolia.

## THE SUBCLIMAX PRAIRIE.

### ANDROPOGON ASSOCIES.

Nature.—East of the *Stipa-Koeleria* association lies a belt of prairie more or less interrupted by woodland. In general character the two are very similar, so much so that at first thought it seems impossible to draw a valid distinction between them. The difficulty arises from the very gradual increase of rainfall from 30 to 40 inches and the correspondingly broad transition from the one to the other. In spite of this, the two communities are at least as different as the other associations of this formation. The climatic difference of 10 inches of rainfall is reflected in the close sod and the taller growth-form, both more typically developed than in any other association of the grassland. The greatest distinction arises from the fact that the dominants are nearly all different, though their similarity in requirements is attested by the degree to which they mingle and alternate. *Andropogon* is typical of the community to an almost exclusive degree, but the species often mix with *Stipa*, *Agropyrum*, and *Koeleria* to such an extent as to make the exact relationship of a particular area difficult to determine. All of these differences are summed up in the fact that the *Andropogon* prairie over most of the region is subclimax in character, *i. e.*, it will be replaced by scrub, woodland, or forest wherever cultivation, fire, or grazing does not prevent. Here again much of the broad transition between the two prairies would probably develop into forest where disturbing processes are not too great, but the *Stipa-Koeleria* prairie is a climax association through practically its entire area. In a few especially favorable locations and during the wet phase of the climatic cycle, forest may encroach upon it, but not to an important degree. Finally, the societies of the subclimax prairie differ from those of the climax in containing more eastern species and fewer western. The majority of the societies, however, are the same for both, and this is likewise true of their luxuriance and complexity (plate 23).

Range.—The *Andropogon* associes has never been clearly recognized before, and in consequence it has received little direct attention. The few studies have been local ones dealing chiefly with succession in dunes or swamps, and have consequently emphasized the seral stages more than the climax. The region lies east of the Missouri River for the most part and has been visited but little in the course of the special survey of the past six years. As a consequence, its outlines can be traced only in the most general manner. The area includes southeastern Nebraska, eastern Kansas, northern Missouri, eastern Iowa, small areas in southeastern Minnesota and southern Wisconsin, and more considerable areas in Illinois and Indiana. In addition, it runs into Oklahoma and Texas, but little is known of the extent covered. As successional fragments, it is found also in Arkansas and Mississippi, but these are wholly extra-regional. Similar extensions occur throughout the valleys of the prairies and well into the plains, but here they are subclimax to the less mesophytic grass associations. A remarkable development of this sort occurs in the great sandhill region of Nebraska, where *Andropogon* is again the dominant genus. Here the important dominants are bunch-grass, as demanded by the more rigorous water conditions, and the climax is the *Stipa-Bouteloua* prairie.

The western limit of the subclimax prairie as known at present is fairly well indicated by the isohyete of 30 inches, as it runs through Minnesota, Iowa, Nebraska, and Kansas, and northern Oklahoma. It is impossible to draw the limits in the east, north, or south, not merely because of lack of knowledge, but also because its occurrence is more and more local in character and successional in nature the farther east one goes.

CONSOCIATIONS.

| | | |
|---|---|---|
| Andropogon furcatus. | Andropogon saccharoides. | Panicum virgatum. |
| Andropogon nutans. | Bouteloua racemosa. | Spartina cynosuroides. |
| Andropogon scoparius. | Elymus canadensis. | |

The *Andropogons* are by all odds the most important dominants of this association. They give it the distinctive impress everywhere except in transition areas. Because of its characteristic alternation as a subclimax with forest on the one hand and true prairie on the other, it often contains subdominants from the former and dominants from the latter. In the low prairies and meadows of Nebraska, Iowa, and Minnesota, practically any of the above may be found intimately mixed with *Stipa spartea, Agropyrum glaucum* or *Koeleria cristata* (Pound and Clements, 1899, 1900 : 345; Thornber, 1901 : 66, 86; Weaver and Thiel, 1917 : 11). As a consequence, the

Subclimax Prairie

A. Association of *Andropogon furcatus, nutans, scoparius* and *Bouteloua racemosa*, Peru, Nebraska.

B. Society of *Silphium laciniatum* in *Andropogon-Agropyrum* association, Salina, Kansas.

dominants of the subclimax run the whole gamut of water-content from wet meadow to true prairie.

**Factor relations.**—Because of its ability to grow in saturated soil, *Spartina* often serves as the last consocies in the wet meadow stage of the hydrosere. During most of the summer, the soil in which it grows is usually moist rather than wet, and this, with its tendency to mix with the other dominants, warrants putting it in the subclimax for the present. In the regions with more rainfall, it is properly to be regarded as a wet-meadow dominant. It clearly has the highest water requirements of all its associates and is apt to be the most localized, as well as in the purest stands. The water-content of *Spartina* ranges from saturation to about 45 per cent, while that of *Elymus* and *Panicum* is from 60 to 30 per cent. The last two are nearly equivalent, though *Elymus* will grow in somewhat moister soil. *Andropogon furcatus* and *A. nutans* are the most mesophytic of the four *Andropogons*, and are nearly equivalent to *Panicum* and *Elymus*. They form a much more perfect sod than these two, and as a result are more successful in competition and less susceptible to annual fluctuations. The normal range of water-content for *A. furcatus* is 50 to 25 per cent. *Andropogon nutans* is slightly less mesophytic and *A. scoparius* still less so, though all three frequently occur together. The water values of *A. saccharoides* are unknown, but its constant association with *A. scoparius* in Kansas, Oklahoma, and Texas indicates an intermediate position between this and *A. furcatus*. *Bouteloua racemosa* has essentially the same water requirements as *A. scoparius*, and the two are regularly mixed, not only in the subclimax, but in rough places throughout the prairies, plains, and desert plains. For a more detailed account of the ecological factors, the reader is referred to Thornber (1901 : 32), Weaver (1919), and Pool, Weaver, and Jean (1919).

Three other species of grasses occur with such abundance or frequence as to require notice, though none of them can be properly ranked as dominants. The most important is *Poa pratensis*, which displaces the native grasses in many places where grazing, mowing, or other disturbances have given it the advantage. In sandy soils, and especially in sandhills, *Andropogon hallii* is frequently associated with *A. scoparius* and occasionally with *A. furcatus*. *Panicum scoparium* is abundant throughout the subclimax and also in the transition to the true prairies, but it can hardly be regarded as a dominant because of its low stature. In essence, it is a layer society of the first importance, but it is hardly to be treated as an actual society because of its vegetation-form. Its broad leaves, however, do give it much the value of a subdominant herb.

**Sequence.**—The factor relations of the dominants are confirmed by their topographic position and seral sequence. Hundreds of localities in boldly rolling prairies will show the fundamental sequence from wet meadow to crest of ridge. This is (1) *Spartina*, (2) *Elymus*, (3) *Panicum virgatum*, (4) *Andropogon furcatus*, (5) *A. nutans*, (6) *A. scoparius*, (7) *Bouteloua racemosa*, with *Poa pratensis* appearing almost anywhere between *Spartina* and *A. scoparius* as disturbance permits. In sandy meadows of the sandhill region, disturbance often initiates a subsere in which the early grasses are *Eriocoma cuspidata*, *Andropogon hallii*, and *A. scoparius*, followed by *A. furcatus*, *Panicum* *virgatum*, and *Elymus canadensis*, with *Spartina* in the moister areas (cf. Pool, 1913 : 298). The growth-forms are in almost perfect accord with the factor and seral sequence. *Spartina*, which is both hydroid and the earliest in appearance, has a growth-form usually 5 to 7 feet and sometimes 8 to 10 feet high. *Andropogon furcatus* and *A. nutans* are normally 4 to 6 feet and occasionally 6 to 8 feet tall, while *A. saccharoides* is a little shorter. *Elymus canadensis* and *Panicum virgatum* are practically the same height, from 3 to 5 feet. *Andropogon scoparius* is usually about 3 feet in height and *Bouteloua racemosa* generally somewhat less. In size and habit, *A. scoparius* is the transition form to the true prairies, in which the dominants are between 2 and 3 feet high. This also explains why it is such a constant associate of *Stipa* and *Koeleria*. The root relations are less distinctive, as would be expected. *Andropogon furcatus* and *Panicum virgatum* are the most deeply rooted, *A. nutans* and *A. scoparius* come next, while *Elymus canadensis* resembles *Koeleria* and *Stipa* in having shallow roots (Weaver, 1919).

Grouping.—The dominants which constitute the greater part of the association are *A. furcatus, A. nutans*, and *A. scoparius*. Mixed or alternating, they occupy nine-tenths of the area and form the pattern in which the others play minor parts, except in localized areas. The actual groupings are best shown by the records of 33 quadrats charted by Thornber (1901 : 95) in the southeastern corner of Nebraska, and ranging from wet meadow to hilltops. Of 6 quadrats in the wet meadow, 4 contained *Spartina cynosuroides* and 5 *Poa pratensis* as dominants. The 5 quadrats in the meadow or low prairie all contained *A. furcatus* and *A. scoparius;* 3 contained *A. nutans*, and 3 showed *Elymus* and *Panicum*. With regard to the number of dominants, 2 quadrats showed all five; 1 showed four, and 2 showed three. *A. furcatus* and *A. scoparius* occurred as dominants in every one of the 22 quadrats on the slopes and crests, *Bouteloua racemosa* in 4, *Koeleria cristata* in 2, *Panicum scoparium* in 2, and *P. virgatum* in 1. *P. scoparium* also occurred in more or less abundance in 17 other quadrats, *B. racemosa* in 14, *Stipa spartea* in 12, and *Koeleria cristata* in 9, suggesting the transition to the true prairie. Southward from Kansas into Texas, similar groupings of the dominants occur, but *A. furcatus* is partly or largely replaced by *A. saccharoides*, while *A. hallii* plays a rôle of some importance.

## SOCIETIES AND CLANS.

These are all but identical with those found in the *Stipa-Koeleria* prairie and it is unnecessary to repeat the lists on pages 130 and 131. A few additions might be made, but these are nearly all invaders from woodland and thicket and do not properly belong in the prairie. Likewise certain societies derived from the west or southwest, as *Gutierrezia sarothrae, Grindelia squarrosa*, and *Artemisia frigida*, are limited to the western edge or are altogether lacking. An excellent idea of the societies and clans of the subclimax prairie can be gained from Thornber's treatment (1901). This author gives a detailed account of aspects and treats the grouping and behavior of the subdominants on pages 54 to 95. This is followed by an account of the many quadrats in both list and chart form (pp. 95 to 136), and a phenological record of practically all the species for 1899–1900 (cf. Gates 1912 : 300, 327).

# THE MIXED PRAIRIE.

## STIPA-BOUTELOUA ASSOCIATION.

Nature.—Since the first recognition of a prairie and a plains formation (Pound and Clements, 1898 : 244; 1900 : 347) it has been assumed that the one passed into the other through a broad transition region. In the summer of 1914 it was found that *Stipa*, *Agropyrum*, and *Koeleria* did not begin to yield to the short-grasses in the central Dakotas and Nebraska and then give way to the plains formation, as had been generally assumed. On the contrary, the three prairie dominants continued across the plains and into the foothills of the mountains of Montana, Wyoming, and Colorado (Clements, 1916 : 180). It was also found that, while *Bouteloua*, *Bulbilis*, and the two species of *Carex* became increasingly abundant, it was as an under-story in the tall-grasses, especially *Stipa* or *Agropyrum*. Moreover, where *Bouteloua* occurred as a pure consociation, or with *Bulbilis*, this was discovered to be the usual result of overgrazing. This has forced the recognition of a mixed association composed of the dominants of both prairies and plains, but essentially prairie in its tall-grasses, numerous societies, and successional relations (plate 24).

In order to test this assumption fully, the region has been crossed from east to west during 1915, 1916, and 1917, and in 1918 it was traversed from Colorado to North Dakota on the west and from North Dakota to Kansas on the east. Especial attention was paid to the community relations of the dominants and the climatic and topographic correlations, particularly where the association touched the prairies and the short-grass plains. As a consequence, the conclusion has become unavoidable that these northwestern prairies represent a distinct association. They are not a transition community in structure, as they exhibit seven dominants in various combinations throughout the area. Nor are they transitional in position, since the short-grass plains lie south of them, while their major western contact is with the sagebrush formation. They are primarily prairie in character, since the tall-grasses are codominant throughout, the root systems are relatively deep-seated, and the numerous societies are identical or similar in floristic and character to those of the true prairies. The most significant difference is the practically universal presence of one or more of the short-grasses or sedges as a lower layer.

The constant association of *Stipa* or *Agropyrum* with *Bouteloua* or *Bulbilis* throughout the community is shown by the following summary: During 1914 the climax grassland was studied in 88 localities east of the Rocky Mountains, and tall-grasses and short-grasses were associated as dominants in 83 of these. In 136 local stations the same grouping was found in all but 12. During 1915, of 76 localities visited, 73 showed both types. In 1916, of 65 localities, 64 showed *Stipa* or *Agropyrum* with *Bouteloua* or *Bulbilis*. In 1917 the number was 61 out of 64, and in 1918 tall-grasses and short-grasses were associated in 97 out of 100 localities. During the six years, without allowing for duplicate localities, at least one tall-grass and one short-grass were found together as dominants in all but 15 of the 393 localities studied.

Effect of grazing and climatic cycles.—The study of grazed and protected areas in 1914 disclosed the fact that *Stipa* and *Agropyrum* were much more readily affected by grazing than the short-grasses, and that *Stipa* in particular could be completely eliminated by overgrazing. During the succeeding years a careful search was made for protected areas, especially along railways, in regions where *Stipa* or *Agropyrum* would be expected. The result was the discovery of one or both in or near practically all pure *Bouteloua* or *Bulbilis* communities found in the Dakotas, Montana, Wyoming, Nebraska, and Colorado. Similar results were obtained for both dominants over a large part of the sagebrush association from Oregon to Colorado, and for *Stipa* throughout California. Indeed, what was once the climax association of *Stipa* over the interior valleys from San Diego to Mount Shasta is now represented by widely scattered relicts enabled to persist by chance protection. It was to be expected that such widespread response to grazing would have been noticed by other observers, and this has proved to be the case. Williams (1898 : 54, 55) found that *Agropyrum*, when too closely grazed, made most of its growth by underground stems, and very few if any fertile culms were developed. He also observed that *Stipa*, when kept closely grazed, seldom seeded in quantity. Wooton (1912 : 58) says that *Stipa pennata neomexicana* and *S. comata* "are relished by stock and are of especial importance because they appear at a time when most of the other grasses are dead and dry. Apparently they do not reproduce readily and since they are now rarely allowed to go to seed, they are probably being gradually exterminated wherever stock can get at them." The Forest Service bulletin on range grasses (1914 : 175) states that in parts of northern New Mexico *Stipa comata* is in danger of extermination because it is so closely grazed in spring and early summer that it is not given a chance to seed. Wooton and Standley (1915 : 66) make the following statement about these species: "Both are valuable range grasses; neither, however, reproduces well, but is soon killed by overstocking and replaced by needle grasses."

The fact that *Stipa* and *Agropyrum* are taller and more conspicuous in wet seasons suggested the possibility that they were greatly reduced or lacking in dry years. Throughout the association, however, they proved as abundant and universal in the dry years, 1916 to 1918, as in the exceedingly wet year of 1915. The only evident response to drought was a marked reduction in height and in the number of flower stalks, a reduction which affected *Bouteloua* as much as *Stipa*, though hardly as much as *Agropyrum*. This was further confirmed by a scrutiny of reports on grassland in the Great Plains from 1889 to 1915 and by field notes from 1897 to 1918. All of these agreed in showing the constant association of tall-grasses and short-grasses throughout the region, not only for the wet phases of the three climatic cycles but for the dry periods as well. Since the latter included two of the severest drouths recorded, it is certain that the tall-grasses and short-grasses are regularly codominants of the association, except where grazing interferes. In connection with the grazing experiments discussed later, permanent protected quadrats have been established in representative areas of the association for the purpose of securing an exact record of the effect of grazing and of protection, as well as of the dry and wet phases of the climatic cycle (plate 24).

Range.—The mixed prairies occur from central North and South Dakota, central Nebraska, and northwestern Kansas, throughout Montana and Wyoming to the Rocky Mountains, and southward in Colorado along the foothills of the Front Range. They extend well north into Saskatchewan and Alberta

Mixed Prairie

A. *Stipa comata* consociation, Pine Ridge, South Dakota.

B. *Agropyrum glaucum* consociation, Winner, South Dakota.

C. Detail of association of *Stipa comata*, *Sporobolus cryptandrus*, and *Bouteloua gracilis*, Colorado Springs, Colorado.

and are known to have covered much of northern New Mexico before the period of intensive overgrazing. On the east, the association is found in more or less typical form at Medicine Hat in Saskatchewan, Minot and Mandan in North Dakota, Winner in South Dakota, and Long Pine and McCook in Nebraska. Along the west, it occurs from near Calgary, Alberta, southward to Lewiston and Billings, Montana, Douglas and Laramie, Wyoming, and Colorado Springs and Trinidad, Colorado. Beyond the eastern limit, *Bouteloua* and *Bulbilis* merely persist as alternes in xerophytic situations in the midst of the prairie.

CONSOCIATIONS.

| | | |
|---|---|---|
| Stipa comata. | Stipa viridula. | Carex filifolia. |
| Agropyrum glaucum. | Bouteloua gracilis. | Carex stenophylla. |
| Koeleria cristata. | Bulbilis dactyloides. | |

The distinctive feature of the association is the intimate mixing of the tall-grasses and short-grasses. This is the direct consequence of their relative heights, the short-grasses regularly occurring as a layer beneath the tall ones. The persistence of this relation is explained by the fact that the roots of both types work at much the same level, and there is little opportunity for one to get more water than the other. Moreover, while the tall-grasses shade the others more or less, this is offset by their greater handicap from grazing. The constant mixture is conclusive testimony to the sufficiency of the rainfall and to the close equivalence of the two types of dominants. If the water relations and root penetration were such as Shantz (1911 : 32) has found in the short-grass plains at Akron, the tall-grasses would soon give way to short-grasses, especially during the dry phase. This has nowhere been found to be the case, and the vast area over which they live together not only speaks eloquently of their associational equivalence under the particular subclimate, but is also a compelling argument for the unity of the formation.

Grouping.—At the edge of the association, the dominants tend to become pure and hence to alternate instead of mingling in layers. This is to be expected in the southwest, where it passes into the short-grass association, and on the west, where there is a broad transition to the sagebrush formation, since both of these mark drier climates in which the competition for water is necessarily keener. Any one of the dominants may appear as a pure consociation over limited areas in such regions. *Bouteloua* and *Bulbilis* show this tendency chiefly on the southwest, and *Stipa*, *Agropyrum*, and *Carex filifolia* on the west. Nearly every possible combination of dominants occurs within the association, but certain ones are the rule. In eastern Wyoming, in Montana and western North Dakota, the ruling group is *Stipa-Agropyrum-Bouteloua* or *Stipa-Bouteloua*. In the moister region south and east of the Black Hills and through South Dakota to the Missouri River, *Agropyrum-Bulbilis-Stipa-Bouteloua* is the typical mixture. The essential basis of this is formed by *Agropyrum* and *Bulbilis*, and hence either of the other two may be lacking. *Stipa* in particular is much more general than appears to be the case in summer and autumn after it has been grazed down. *Carex filifolia* or *C. stenophylla* appears commonly in nearly all the groups but usually in reduced abundance. This is also true of *Koeleria* in less degree. Other frequent groups are *Stipa-Koeleria-Bouteloua*, *Stipa-Carex-Bouteloua*, *Stipa-Bulbilis-Bouteloua*, and *Agropyrum-Bulbilis-Bouteloua*. Combinations of four or five dominants are often found over large stretches also. The most common are *Stipa-Agropyrum-Bouteloua-Bulbilis* and *Agropyrum-Stipa-Koeleria-Bouteloua-Carex*. *Stipa viridula*, as a sod-former, is the typical dominant of broad swales and shallow valleys. It is more or less subclimax in habit and hence is usually associated with *Agropyrum*.

Sequence of dominants.—The factor correlations of the dominants have received little attention. For the present it must suffice to infer them from the topographic and successional relations, and to check this by reference to the behavior of the tall-grasses in the prairie and the short-grasses on the plains. This establishes a fairly definite and practical sequence, though it is impossible to assign accurate values to the correlations with water-content, evaporation, and light. In addition to succession and topography, range, growth-form, and subclimax dominants, such as *Andropogon*, *Calamovilfa*, and *Bouteloua racemosa*, are all in agreement in indicating that *Stipa viridula* and *Agropyrum* are the most mesophytic and *Bouteloua* the most xerophytic. The actual sequence is (1) *Stipa viridula*, (2) *Agropyrum*, (3) *Koeleria*, (4) *Stipa comata*, (5) *Bulbilis*, (6) *Carex stenophylla*, (7) *C. filifolia*, and (8) *Boutelona gracilis*. While the rainfall is 5 to 10 inches less and the evaporation rate correspondingly greater than in the prairies, the water-content is but little lower, owing chiefly to the lessened transpiration resulting from a smaller population and a shorter season. This appears to be confirmed by the deep roots, even of the short-grasses, indicating a fairly adequate water-supply. It is the similarity of the root behavior which explains the close equivalence of the seven dominants, as shown by the fact that four or more frequently occur in the most intimate mixture and that practically every one has been found with each of the others. This also explains why pure consociations are rare (plate 25).

While the existence of the *Stipa-Bouteloua* association has not been recognized before, it is now clear that the bunch-grass formation and the grass formation of high prairies and plains of Pound and Clements (1898; 1900: 354, 380–386) are essentially this association. Even at that time the close similarity with the true prairies was clearly recognized, as the following shows:

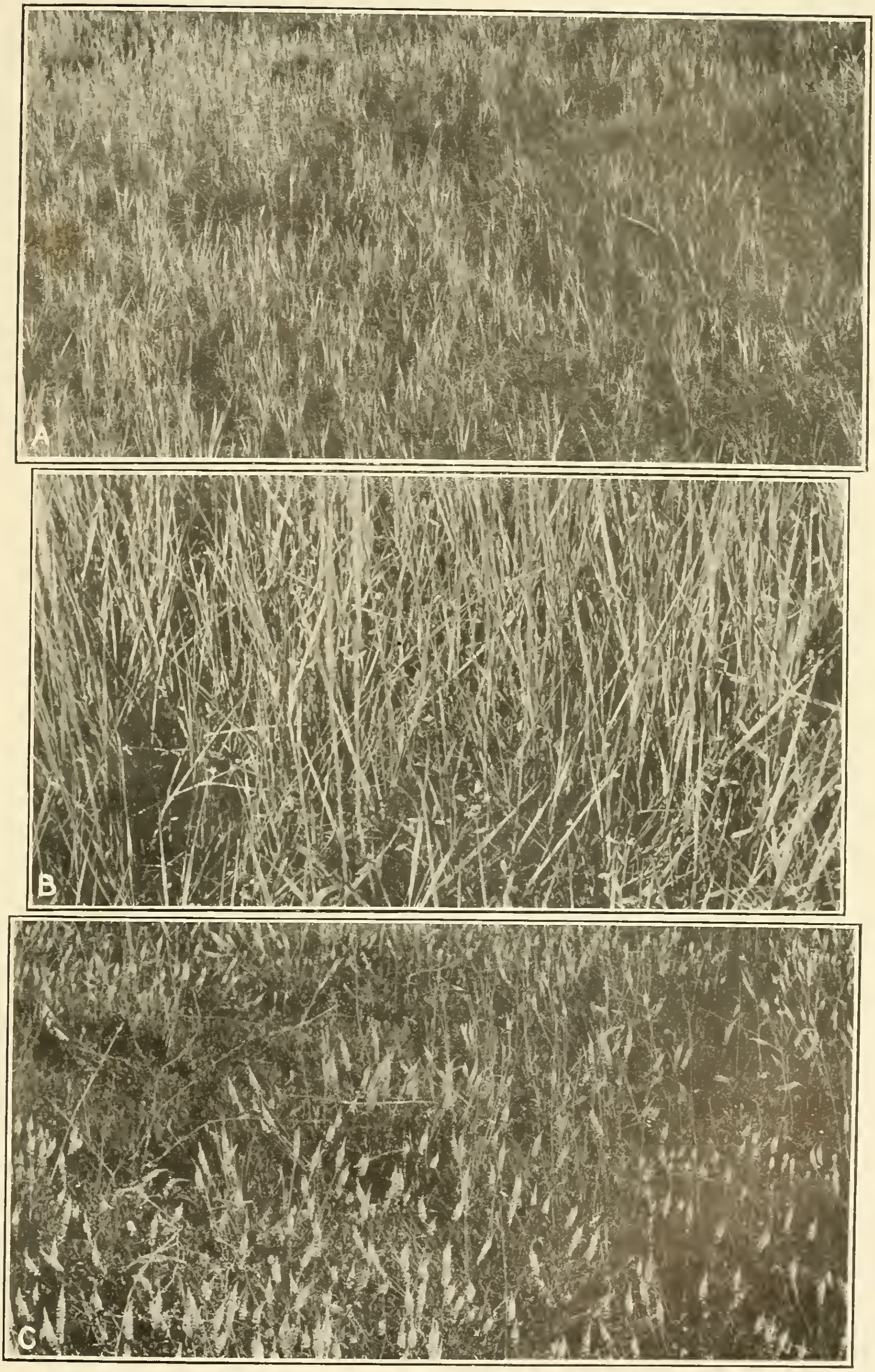
"The foothill grass formation has much in common with the prairie formation of region II. As one looks at the high rolling prairies in region IV covered with *Stipa comata*, from a distance the carpet of *Stipa*, variegated with the profusely flowering astragali, lupines, and psoraleas which abound in it, appears to be a piece out of the familiar prairie of the eastern portion of the State."

This similarity is further emphasized by the fact that the societies are largely the same, as shown by the following list.

### SOCIETIES OF THE MIXED PRAIRIE.

By far the major number of subdominants is the same for the *Stipa-Koeleria* and the *Stipa-Bouteloua* associations. This would be expected from the dominance of tall-grasses in both, indicating a deep penetration of water and roots and hence a favorable soil for deep-rooted herbs. The mixed prairies naturally lack such societies as *Phlox pilosa*, *Baptisia leucophaea*, *Anemone canadensis*, etc., which are typically eastern, and they have added a few from the west. The chief difference lies in the fact that the societies are less lux-

Mixed Prairie




A. *Agropyrum glaucum-Bouteloua gracilis* association, Vermejo Park, New Mexico.
B. Detail of *Agropyrum-Bulbilis* association, Winner, South Dakota.
C. *Polygala alba* society in *Bouteloua* consociation, Interior, South Dakota.

uriant and less mixed, and the growth-form is smaller as a rule. It is also significant that most of the societies are found in the eastern half with a rainfall above rather than below 15 inches. In the western portion the societies are better developed in the valleys and along the lower slopes, and are much reduced in number and dominance on the upland.

*Prevernal Societies.*
- Carex pennsylvanica.
- Antennaria dioeca.
- Anemone patens.
- Leucocrinum montanum.
- Androsace occidentalis.
- Draba caroliniana.

*Vernal Societies.*
- Astragalus crassicarpus.
- Aragalus lamberti.
- Erysimum asperum.
- Fragaria virginiana.
- Viola pedatifida.
- Comandra umbellata.
- Vicia americana.
- Anemone cylindrica.
- Sieversia ciliata.
- Achillea millefolium.
- Hosackia americana.
- Sophora sericea.
- Senecio aureus.
- Sisyrinchium augustifolium.
- Lithospermum linearifolium.
- Castilleia sessiliflora.
- Astragalus drummondii.
- Krynitzkia virgata.
- Agoseris cuspidata.

*Estival Societies:*
- Psoralea tenuiflora.
- Petalostemon candidus.
- Petalostemon purpureus.
- Amorpha canescens.
- Psoralea argophylla.
- Brauneria pallida.
- Glycyrhiza lepidota.
- Lepachys columnaris.
- Erigeron ramosus.
- Tradescantia virginiana.
- Polygala alba.
- Lupinus ornatus.
- Astragalus bisulcatus.
- Astragalus adsurgens.

*Estival Societies*—continued.
- Delphinium menziesii.
- Yucca glauca.
- Helianthus rigidus.
- Monarda citriodora.
- Malvastrum coccineum.
- Erigeron pumilus.
- Rosa arkansana.
- Hymenopappus tenuifolius.
- Opuntia mesacantha.
- Opuntia polyacantha.
- Dalea laxiflora.
- Meriolix serrulata.
- Linum rigidum.
- Phlox douglasii.
- Pentstemon grandiflorus.
- Pentstemon gracilis.
- Aster ericoides.
- Gaura coccinea.
- Astragalus mollissimus.
- Gilia pungens.
- Gilia aggregata.
- Verbena stricta.
- Verbena hastata.
- Lygodesmia juncea.
- Hedeoma drummondii.
- Steironema ciliatum.
- Castilleia integra.
- Rudbeckia hirta.
- Haplopappus spinulosus.
- Psoralea cuspidata.
- Balsamorhiza sagittata.

*Serotinal Clans:*
- Solidago rigida.
- Solidago missouriensis.
- Aster multiflorus.
- Artemisia frigida.
- Artemisia cana.
- Grindelia squarrosa.
- Gutierrezia sarothrae.
- Senecio douglasii.
- Artemisia filifolia.

*Serotinal Societies*—continued.
- Liatris punctata.
- Chrysopsis villosa.
- Carduus undulatus.
- Artemisia dracunculoides.
- Artemisia gnaphalodes.
- Artemisia canadensis.
- Kuhnia glutinosa.
- Eriogonum annuum.
- Thelesperma gracile.
- Thelesperma trifidum.
- Eriogonum microthecum.
- Eriogonum alatum.
- Solidago speciosa.
- Liatris scariosa.
- Liatris pycnostachya.
- Gymnolomia multiflora.

*Vernal Clans:*
- Delphinium penardi.
- Pentstemon albidus
- Specularia perfoliata.
- Oxalis stricta.
- Oxalis violacea.
- Viola nuttallii.

*Estival Clans:*
- Asclepias speciosa.
- Asclepias verticillata pumila.
- Lactuca pulchella.
- Lathyrus ornatus.
- Psoralea esculenta.
- Potentilla pennsylvanica.
- Evolvulus argenteus.
- Dalea aurea.
- Cactus viviparus.
- Acerates viridiflora.
- Allionia linearis.
- Gerardia aspera.
- Verbena bipinnatifida.

*Serotinal Clans:*
- Solidago graminifolia.
- Liatris squarrosa.

## THE SHORT-GRASS PLAINS.

### BULBILIS-BOUTELOUA ASSOCIATION.

Nature.—The short-grass plains owe their distinctive impress to grama and buffalo-grass. These are sod-formers with dense root systems. As Shantz has shown at Akron (1911 : 33), the water below 12 inches is non-available for much of the growing season, with the result that the roots are usually confined to the first foot of soil.[1] A further consequence is that the short-grasses mature in July. Thus, the soil beneath a short-grass cover is often without available water below 18 inches, and the water-content in the upper foot is low after mid-summer. As a consequence, the deeper-rooted tall-grasses and subdominant herbs are practically excluded and the typical short-grass cover is very uniform and monotonous as a result.

[1] Cf. Weaver, 1919, 1920.

Shantz (l. c., 62) has traced the succession in sandhills and in secondary areas, and finds that the depth of water penetration is the decisive factor In sandy soils, the deep-rooted *Andropogons* are dominant and with them occur many deep-rooted perennial herbs, such as *Psoralea tenuiflora, Artemisia filifolia*, and *Ipomoea leptophylla.* With the entrance of *Aristida purpurea* and the *Boutelouas*, the water is used chiefly in the 1 to 2 foot layer, and the deeper species gradually die out. As the *Bouteloua* sod becomes denser, *Aristida* and its associates disappear, and the short-grass climax is established. When the cover is destroyed by cultivation or overgrazing, the water penetrates more deeply, permitting the entrance of *Aristida, Gutierrezia, Grindelia, Artemisia frigida,* and other deeper-rooted species. With the return of the gramas, the depth of penetration decreases and the invaders are displaced. Shantz (1917 : 19) has lately shown that the secondary succession in abandoned roads is due to the same cause, though *Bulbilis* largely takes the place of *Bouteloua* in effecting the return to the climax (plate 26).

Range.—The short-grass association ranges from southwestern Nebraska and the western half of Kansas through eastern Colorado into northwestern Texas, northern New Mexico, and Arizona. It is also developed to some extent in southeastern Utah and southwestern Colorado. The chief dominant throughout is *Bouteloua gracilis.* In the eastern part its usual associate is *Bulbilis dactyloides;* in the western part it is *Muhlenbergia gracillima* or *Hilaria jamesii.* In sandhill and foothill areas, it is often associated with *Bouteloua hirsuta.* The chief contacts of the short-grass plains are with the other associations of the grassland formation. On the north, in Colorado and Nebraska, they meet the mixed prairies, in Kansas the subclimax prairie, and in west-central Texas, central New Mexico, and Arizona the desert plains. On the west this community comes in contact with the sagebrush association of the Great Basin, while throughout the Southwest generally it is frequent in park-like savannahs of pine and piñon-cedar.

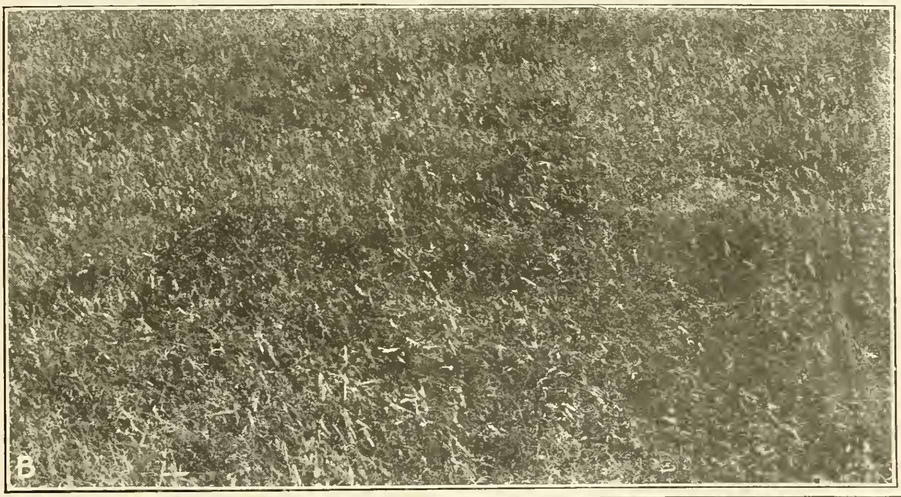
As already indicated, nearly pure communities of *Bouteloua gracilis* occur well outside the area outlined above. All of these appear to have resulted from the elimination of the tall-grasses by overgrazing. It is an open question what part grazing has played in the short-grass association proper. There is considerable evidence to show that *Stipa* and *Agropyrum* were more abundant formerly, but whether they were sufficiently so to rank as codominants is uncertain. It is possible that a detailed survey of the short-grass region will settle this point, but it is more probable that an adequate idea of the original vegetation will be obtained only from the fenced quadrats established in connection with the grazing investigations. At any event, it is practically certain that grazing, especially in connection with the former annual movement of cattle from the south to the north, has played an effective part in maintaining the characteristic short-grass cover.

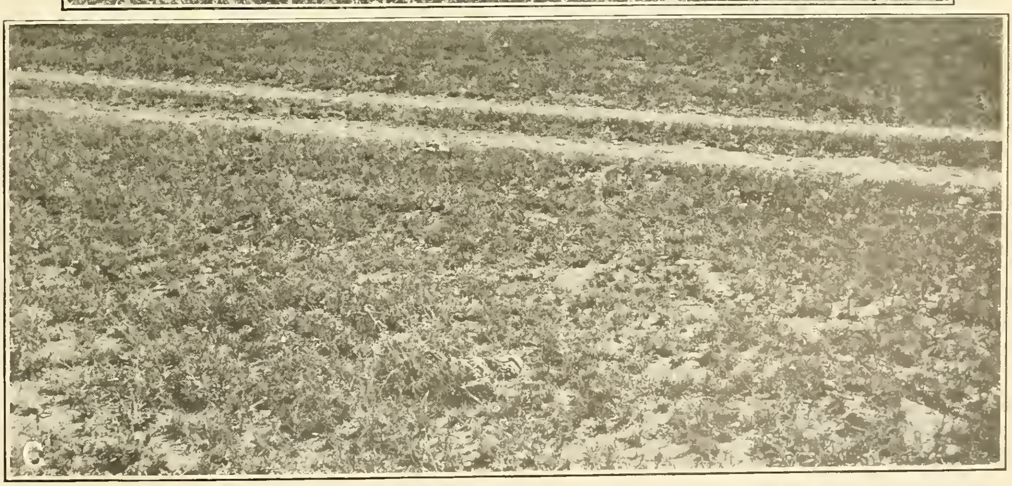
CONSOCIATIONS.

| | |
|---|---|
| Bouteloua gracilis. | Muhlenbergia gracillima. |
| Bulbilis dactyloides. | Hilaria jamesii. |
| Bouteloua hirsuta. | |

*Bouteloua gracilis* is regarded as the chief consociation. It is almost universally present throughout the association, though it varies considerably in abundance. It not only occurs mixed with each of the others and some-

Short-grass Plains





A. *Bouteloua-Bulbilis* association, with subclimax of *Andropogon scoparius* and *Bouteloua racemosa* on butte, Stratford, Texas.

B. Dense sod of *Bulbilis* and *Bouteloua*, Goodwell, Oklahoma.

C. Open sod of *Bouteloua*, Dumas, Texas.

times with two of them, but also as a pure dominant over large areas. *Bulbilis* stands next to *Bouteloua* in importance, and the two, singly or together, constitute the fundament of the association. *Bulbilis* is largely restricted to the eastern part of the area, while *Muhlenbergia* and *Hilaria* are found chiefly in the western. This results in a differentiation into two halves, an eastern, consisting almost wholly of *Bouteloua* and *Bulbilis*, and a western, made up of *Bouteloua* with *Muhlenbergia* or *Hilaria*. The former is typical of western Kansas and Oklahoma and the Panhandle of Texas; the latter is found in southern Colorado and the northern half of New Mexico and Arizona.

Any one of the five dominants may appear as a pure community, but this is rare for *Muhlenbergia* and infrequent for *Bouteloua hirsuta*. *Hilaria* often dominates extensive areas in New Mexico and Arizona, and in the Great Basin where the sagebrush and short-grass are in contact. In the latter, especially, it is more or less subclimax in nature and mixes with *Bouteloua gracilis* as the climax is approached. *Bouteloua hirsuta* is characteristic of sandy areas and rough gravel or limestone hills, and is most abundant in sandhills. While it is an important dominant in the desert plains association, it is secondary on the plains proper, and is often to be regarded as subclimax. *Muhlenbergia* is a fairly constant associate of *Bouteloua gracilis* in Colorado, New Mexico, and Arizona. It has been found in pure stands of considerable extent only in the latter. It bears much the same relation to *Bouteloua* that *Bulbilis* does, and hence rarely occurs with the latter.

The southern Great Plains are characterized by *Bouteloua gracilis* and *Bulbilis dactyloides* in varying relations. As a rule they are associated, but either may occur as a pure dominant. They may meet on nearly equal terms or may exhibit varying degrees of relative abundance. In the eastern portion of the association *Bulbilis* is usually controlling and *Bouteloua* secondary, though this relation is often reversed on the Staked Plains of Texas and New Mexico. From Colorado southward, *Bouteloua* is generally controlling and *Bulbilis* secondary. Where *Bulbilis* is predominant the sod is dense and the grama grass is scattered through it more or less abundantly. Grama typically forms an open sod, even where it is dominant, but the persistent sod habit of the buffalo-grass causes the latter to appear in compact mats a few feet to several yards or more in diameter. The open grama turf dotted with mats of *Bulbilis* is so characteristic over much of the Great Plains that it was supposed to be the rule. In the summer of 1918, however, buffalo-grass was found to be either controlling, and sometimes pure, or to meet grama on equal terms throughout southwestern Kansas and western Oklahoma. This is in accordance with the water relations, as discussed below.

Grouping of dominants.—The groupings of short-grasses are relatively few and simple. *Bouteloua gracilis* is normally present in all of them and usually as the predominant species. Most of the groups consist of two dominants only, for example, *Bouteloua-Bulbilis*, *Bulbilis-Bouteloua*, *Bouteloua-Hilaria*, *Bouteloua-Muhlenbergia*, and *Bouteloua gracilis-B. hirsuta*. *Bouteloua gracilis* also occurs with *B. hirsuta* and *Muhlenbergia*, and with *Hilaria* and *Muhlenbergia*. On the plains of Oklahoma and Texas, *Bouteloua racemosa* is a frequent associate of *Bulbilis-Bouteloua* and sometimes appears to be a codominant. North and northeast of the associational area *Bouteloua* and *Bulbilis* become constituents of the mixed prairie, forming a layer beneath *Stipa* and

*Agropyrum.* In central Kansas they play a similar part, but usually occur with *Andropogon.* Toward the southern limits of the area, *Bulbilis* mixes with *Hilaria cenchroides, H. mutica,* and *Aristida purpurea* in Texas, and *Bouteloua gracilis* with *B. eriopoda* and *A. purpurea* in New Mexico and Arizona.

When *Bouteloua* and *Bulbilis* meet the tall-grasses, both or either may become dominant as a result of overgrazing. There is increasing if not conclusive proof that overgrazing is the cause of the pure areas of short-grass found in the mixed prairie from Saskatchewan to Kansas, and sometimes covering many square miles. The study of this problem has also led to the plausible assumption that the widespread but erroneous belief in the disappearance of the buffalo-grass is likewise due to the changed conditions following settlement. The disappearance of the enormous herds of buffalo gave the tall-grasses a chance to reappear and to conceal the short-grasses beneath them. At least, it is undeniable that buffalo-grass and grama still grow abundantly in many places where they were said to have disappeared in the late sixties and early seventies. This also explains the frequent statement that the bluestems and other tall-grasses entered the Middle West, or at least became much more abundant, after settlement began. A detailed discussion of this point may be found in Chapter VI.

Factor relations.—While the factor relations of the dominants have received almost no attention quantitatively, the habitat of the association has been studied by both Shantz and Weaver. The former (1911 : 32; 1906 : 28) found the average chresard from June 7 to September 27 at a depth of 0 to 6 inches to be 4.8 per cent, at 6 to 12 inches 2.7 per cent, at 12 to 18 inches 1.25 per cent, at 18 to 24 inches 0.56 per cent, and at 24 to 30 inches 0.23 per cent. He also dealt with the distribution of the rainfall, and the relation of runoff, penetration, and evaporation to water-content. Weaver (1919) has measured the water relations on the plains at Colorado Springs, but it is probable that this area belongs to the mixed prairie rather than to the short-grass community. Briggs and Belz (1911) have made a thorough digest of rainfall and evaporation records for the West, which has much significance for the climatic relations of these contiguous associations. A study of their figures makes it clear why grassland goes little beyond the isohyete of 20 inches at the Canadian boundary, but extends to that of 25 inches in central Texas (fig. 3). The change from mixed prairie to short-grass plains, moreover, is in accord with the evaporation values for the respective regions. Over the northern Great Plains, these values are 30 to 39 inches, and over the southern they are 52 to 62 inches.

Sequence of dominants.—The evidence drawn from both the habitat and from succession indicates that *Bouteloua* is the most and *Bulbilis* the least xerophytic of the dominants. This agrees essentially with their general distribution, in that *Bulbilis* becomes more controlling to the east with increasing rainfall, or to the north with decreasing evaporation. As already noted, *Bouteloua* forms the matrix over most of the south-central Great Plains, and *Bulbilis* makes dense mats in depressions of all sorts, abandoned roadways, dry pools, playas, etc. The topographic evidence is fully confirmed by the successional, as Shantz has shown in the case of old roadways (1917 : 19), and is especially well exhibited in the playa subsere. While the playa is a

Short-grass Plains

A. *Muhlenbergia gracillima* and *Bouteloua gracilis*, Manitou, Colorado.
B. Detail of *Bouteloua gracilis*, Vermejo Park, New Mexico.
C. *Hilaria jamesii* on a saline plain, Delta, Colorado.

pond, it is bordered by a zone of hydroid ruderals and subruderals, followed by a broad band of pure buffalo-grass, the whole set in a matrix of grama. In the fall or in years of drought the pond dries to a bed of mud or moist soil, over which the ruderals extend, followed by the slower invasion of *Bulbilis*. When drought, cultivation, or drainage leads to the final drying-up of the playa, the buffalo-grass sooner or later takes entire possession. It is invaded at the same time by grama along the upper edge, but the ordinary drainage into the depression keeps the center more or less permanently in the *Bulbilis* stage.

The other dominants are also subclimax to *Bouteloua gracilis*, and hence, in an arid climate, are somewhat more mesophytic. The equivalence of *Muhlenbergia* is very close to that of *Bouteloua gracilis*, while that of *B. hirsuta* is less so. Even in the latter instance, the difference in requirements must be regarded as slight, since the two are often associated. As in all such cases, however, it must be borne in mind that the mixing is due rather to the ability of *B. gracilis* to invade slightly better conditions than that of *B. hirsuta* to enter slightly poorer ones. While *Hilaria jamesii* is clearly subclimax, its factor relations are somewhat obscured by its more or less halophytic nature (plate 27).

## SOCIETIES.

The density of the sod and the effect of the superficial roots upon water penetration explain the relatively small number of societies and the general lack of conspicuous or distinctive character. These factors naturally owe their effectiveness to the low rainfall, the average over much of the area being from 10 to 15 inches, and to the high evaporation. As a consequence, while many of the subdominants of the other associations occur in the short-grass plains, they attain a relatively feeble expression, and then only where the dominants have been more or less disturbed. It is not at all infrequent to find a *Bouteloua* plain stretching in all directions without a single conspicuous society to relieve the monotony. Wherever the soil becomes somewhat sandy or the rainfall greater, the water penetration increases correspondingly, and societies become more prominent. As a consequence, the actual number of subdominants throughout the association is much greater than their diminished importance or extent would indicate. There are fewer mixed societies, and both the growth-form and abundance of particular subdominants are reduced.

*Prevernal Societies:*
- Leucocrinum montanum.
- Anemone patens.
- Townsendia exscapa.

*Vernal Societies:*
- Senecio aureus.
- Astragalus drummondii.
- Aragalus lamberti.
- Euphorbia robusta.
- Sophora sericea.
- Pentstemon unilateralis.
- Pentstemon coeruleus.
- Arenaria fendleri.
- Erysimum asperum.
- Lithospermum linearifolium.
- Krynitzkia virgata.

*Estival Societies:*
- Psoralea tenuiflora.
- Petalostemon candidus.
- Petalostemon purpureus.
- Lepachys columnaris.
- Malvastrum coccineum.
- Opuntia polyacantha.
- Opuntia mesacantha.
- Lupinus argenteus.
- Thelesperma gracile.
- Carduus plattensis.
- Helianthus pumilus.
- Chrysopsis villosa.
- Polygala alba.
- Zinnia grandiflora.

*Estival Societies*—continued.
- Astragalus bisulcatus.
- Ipomoea leptophylla.
- Gaura coccinea.
- Erigeron pumilus.
- Linum rigidum.
- Dalea laxiflora.
- Meriolix serrulata.
- Artemisia canadensis.
- Actinella richardsonii.
- Haplopappus spinulosus.
- Hedeoma drummondii.
- Lepachys tagetes.
- Gymnolomia multiflora.
- Aster bigelovii.
- Aster tanacetifolia.

*Serotinal Societies:*
Artemisia frigida.
Gutierrezia sarothrae.
Senecio douglasii.
Grindelia squarrosa.
Carduus undulatus.
Artemisia dracunculoides.
Solidago missouriensis.
Liatris punctata.
Aster multiflorus.
Kuhnia glutinosa.
Vernonia baldwinii.

*Prevernal Clans:*
Cympoterus acaulis.
Phellopterus montanus.

*Vernal Clans:*
Erigeron flagellaris.
Lappula texana.
Antennaria dioeca.
Erigeron canus.
Pentstemon jamesii.
Physalis lobata.
Allium cernuum.
Astragalus lotiflorus.

*Estival Clans:*
Lathyrus ornatus.
Aster ericoides.
Asclepias v. pumila.
Cactus viviparus.
Evolvulus argenteus.
Dalea aurea.
Potentilla pennsylvanica.
Allionia linearis.

*Serotinal Clan:*
Eriogonum jamesii.

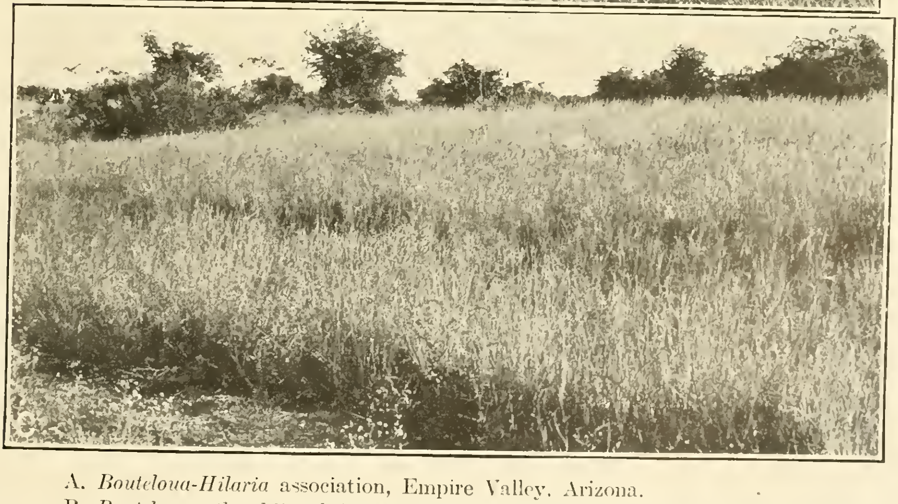
## THE DESERT PLAINS.

### ARISTIDA-BOUTELOUA ASSOCIATION.

Nature.—The grassland of the Southwest derives its character primarily from *Aristida* and *Bouteloua.* In general appearance it closely resembles the short-grass plains, but the grasses are taller, more numerous, and the groupings more varied. The sod-forming habit is much less developed. It is absent in *Aristida* and in *Bouteloua rothrockii.* While it is more or less evident in *Bouteloua eriopoda, B. hirsuta,* and *B. bromoides,* the sod has no continuity, but is broken into many small mats. Although this condition obtains in some parts of the short-grass plains, the sod is much more complete as a rule. No single species of this association possesses the importance shown by *Bouteloua gracilis* in the short-grass region. Probably *Bouteloua eriopoda* is to be regarded as the most dominant species of this genus, and *A. purpurea,* in its several forms, of *Aristida.*

The close relationship between the two associations is shown by the long contact from Texas through New Mexico and Arizona and by their similar appearance. They are also alike in their successional relation to such subclimax dominants as *Andropogon scoparius, A. saccharoides,* and *Bouteloua racemosa.* Their chief relationship, however, lies in the fact that certain dominants occur in both, although usually with different values. These are *Bouteloua gracilis, B. hirsuta, Aristida purpurea,* and *Bulbilis dactyloides. B. gracilis* may be more or less subclimax in nature and restricted to mountain valleys or it may be intimately mixed with *B. eriopoda, hirsuta* or *racemosa. B. hirsuta* is one of the important dominants, usually with *B. bromoides or Hilaria cenchroides* on foothills and on mountain slopes. *Bulbilis* usually occurs only in small scattered patches, except in Texas, where it meets *Hilaria cenchroides, Bouteloua eriopoda,* or *Aristida purpurea* on more or less equal terms. *Aristida purpurea* changes from subclimax to a climax dominant, especially important in Texas and New Mexico. The similarity as to societies and clans is less than that between the prairies and plains, but this is due chiefly to the proximity to the original center of the flora. However, as the lists show, there is much agreement as to the genera concerned (plate 28).

The desert plains are in close contact with but one other association of the grassland formation, namely, the short-grass plains. It is probable that there was formerly a second contact, with the *Stipa* bunch-grass prairie of California, but to-day there is a wide gap between, bridged to a certain extent by *Hilaria jamesii H. rigida* and *Boutelona gracilis.* The contact mentioned is from Snyder and Big Springs in the Staked Plains of Texas to Roswell and Socorro



A. *Bouteloua-Hilaria* association, Empire Valley, Arizona.
B. *Bouteloua rothrockii* and *Aristida divaricata*, Santa Rita Reserve, Tucson, Arizona.
C. *Bouteloua racemosa* consociation, Oracle, Arizona.

in New Mexico and to Prescott in Arizona. It was perhaps much broader at one time, as *Bouteloua eriopoda* still occurs in some abundance about Albuquerque and from Adamana to Winslow in Arizona.

**Range.**—The desert plains association extends from Snyder and Sweetwater in Texas on the northeast through the southern two-fifths of New Mexico into southeastern and south-central Arizona. In Texas and New Mexico, it is the typical community of the regions indicated, with saline associes in the lower valleys and the mesquite along the benches and upper levels. From southwestern New Mexico through southern Arizona, it occupies a broad belt several to many miles wide around the major mountain chains, and covers the broad intermountain plateaus. Its general range in altitude is from 3,400 to 5,500 feet.

The association sweeps southward through Chihuahua, Sonora, and Durango into the high tablelands of central Mexico. It has received no ecological study beyond a few miles south of the boundary, and its nature and extent in Mexico must be inferred from floristic and grazing sources. The inference seems clear that Mexico is the real center of the desert plains grassland and that it is richer in dominants and more varied in structure there than in the United States. This is confirmed by the fact that the best expression of the community is found in southern Arizona near the border. The extent of this grassland in Mexico is probably much greater than in this country, but nothing definite is known about it.

The name "desert plains" is thought to indicate the nature and location of the association. As to the kind of grassland and topography, "plains" is clearly the best term to be applied. This conclusion is emphasized by the relationship with the short-grass plains. In addition, this is not only the characteristic grassland of the desert region of the Southwest, but it is also in direct contact with the desert all along its lower edge. A further reason is found in the fact that there exists a broad transition region between the scrub desert and the *Aristida-Bouteloua* grassland. Indeed, *Larrea* or *Prosopis* is scattered over so much of the latter that it has often been regarded as mesquite rather than grassland. Finally, relict patches of *Bouteloua rothrockii*, *Aristida divaricata*, or *Muhlenbergia porteri* have been found in various protected places in the desert, at altitudes as low as 2,400 feet, especially at Tucson. These indicate that the desert grassland once extended well down into the scrub desert, and that it was replaced by scrub as a consequence of overgrazing. The significance of these relict areas is confirmed in some degree by the statements of stockmen to the effect that the desert was formerly well-grassed.

### CONSOCIATIONS.

| | | |
|---|---|---|
| Bouteloua eriopoda. | Bouteloua gracilis. | Aristida californica. |
| Bouteloua rothrockii. | Bouteloua racemosa. | Aristida arizonica. |
| Bouteloua bromoides. | Aristida divaricata. | Hilaria cenchroides. |
| Bouteloua hirsuta. | Aristida purpurea. | Muhlenbergia porteri. |

All of these may form pure consociations, but *Bouteloua eriopoda* and *Aristida purpurea* are the only ones known to do so for long stretches. Both are dominant over the northern and lower areas, particularly in New Mexico and Texas. In these they mix somewhat, but as a rule either one is much more important than the other wherever they occur together. The others rarely form pure communities more than a few acres or at least a few miles in extent. *Bouteloua rothrockii* might be regarded as an exception to this, for while usually mixed with *Aristida*, it covers areas of several to many miles as a practically pure dominant. The most frequent groupings are those in which *Bouteloua* and *Aristida* occur together, probably because grazing favors the latter at the, expense of the former.

Rank of dominants—The general rank of the dominants and some of their subclimax associates is indicated by the following table of occurrences in trans-Pecos Texas, southern New Mexico, and Arizona:

| | | | |
|---|---|---|---|
| Bouteloua eriopoda | 56 | Aristida californica | 4 |
| Bouteloua gracilis | 40 | Aristida arizonica | 2 |
| Bouteloua racemosa | 35 | Hilaria cenchroides | 10 |
| Bouteloua hirsuta | 23 | Muhlenbergia porteri | 9 |
| Bouteloua rothrockii | 16 | Hilaria mutica | 33 |
| Bouteloua bromoides | 8 | Scleropogon brevifolius | 23 |
| Aristida divaricata | 28 | Andropogon saccharoides | 15 |
| Aristida purpurea | 20 | Sporobolus flexuosus | 11 |

The abundance of a dominant is not necessarily in accord with its frequence. As a result, *Bouteloua racemosa* is less important than its occurrence indicates, while *B. rothrockii*, *B. bromoides*, and *Aristida californica* are much more frequent. It is these species, moreover, which appear to be among the most characteristic of the grasslands of northern Mexico. The last four dominants of the list are all really subclimax, with the probable exception of *Sporobolus flexuosus*. This is particularly true of *Hilaria* and *Scleropogon*, which are typical of "swags" and other valley-like depressions throughout the *Larrea-Flourensia* scrub. Both occur so frequently with *Bouteloua*, and especially *B. eriopoda* and *B. hirsuta*, that they can not be ignored in a treatment of the desert plains. This *Hilaria-Scleropogon* subclimax covers thousands of square miles from the Pecos River to central Arizona.

Grouping of dominants.—While all the dominants range more or less throughout the association, with the exception of *Bouteloua rothrockii* and *Aristida californica*, they vary greatly in importance and grouping in the three States. This depends upon the altitude and the distance from the center in Mexico. In Texas *Aristida purpurea*, in various forms, is the chief dominant at the lower levels; toward its northern limit it is much mixed with *Bulbilis* and *Bouteloua gracilis* as a lower layer. *Hilaria cenchroides*, *B. eriopoda*, *A. divaricata*, and *Muhlenbergia porteri* occur more or less frequently with it. In the mountain ranges of western Texas, from the Davis and Guadalupe Mountains to the Sierra Blanca, *Bouteloua gracilis*, *B. eriopoda*, and *B. racemosa* are the climax dominants, with which *Aristida* and *Muhlenbergia* occur more or less abundantly. Between these ranges lie extensive bolsons or bolson-like valleys, characterized in the center by *Hilaria-Scleropogon* swags in a more or less open scrub desert. The grama grasses extend far down the gradual slopes of the bolson, and mix with the subclimax grasses over a wide zone (plate 29).

The chief dominant in New Mexico is *Bouteloua eriopoda*, often much mixed with *Aristida purpurea*, as in the valley of the Pecos. They occur abundantly on the marl hills north of Albuquerque with *B. gracilis* and *Muhlenbergia gracillima*, and to a smaller degree in northern Arizona. All of the evidence available indicates that this is the northern edge of the ecotone and that the

Desert Plains

A. *Bouteloua-Aristida* association, Sweetwater, Texas.

B. *Bouteloua gracilis, Scleropogon brevifolius,* and *Hilaria mutica* valley, *B. eriopoda, gracilis, racemosa* hills. Van Horn, Texas.

C. *Bouteloua gracilis, hirsuta, eriopoda,* and *Aristida divaricata,* Jornada Reserve, Las Cruces, New Mexico.

region generally belongs to the short-grass association. The desert plains of southern and southwestern New Mexico are characterized by *Hilaria* and *Scleropogon* in the subclimax stage, and *Bouteloua eriopoda* in the climax. In the Jornada del Muerto the latter is usually associated with *Sporobolus flexuosus*, and with *S. cryptandrus* where the soil is somewhat more sandy. *B. racemosa* is not infrequent, but it is rarely dominant at this level. On the slopes of the Organ and San Andreas Mountains at 5,000 to 6,000 feet, the dominants are *Bouteloua hirsuta*, *B. gracilis*, and *B. racemosa*, with considerable *Aristida divaricata* and little *B. eriopoda*.

All of the 12 dominants occur abundantly between elevations of 3,500 to 5,500 feet in southern Arizona, and as a consequence the grouping is more varied and complex than in any other part of the association. Since all the dominants are present in northern and central Mexico as well, it is practically certain that the same groupings will be found there. The lowermost community is typically *Bouteloua rothrockii* and *Aristida divaricata*, often with some *A. purpurea* and *Muhlenbergia porteri*. *Aristida californica* or *A. arizonica* may occur as a dominant with either *B. rothrockii* or *B. eriopoda* alone or together. *Bouteloua eriopoda* and *Aristida divaricata* are frequently associated also. *Bouteloua bromoides* tends to become controlling at 4,000 feet and is often the major dominant for the next 1,000 feet, where its usual associates are *B. racemosa* and *A. divaricata*, with more or less *B. hirsuta* and *B. eriopoda*. This is the typical condition on the upper levels of the Santa Rita Range Reserve near Tucson. *Hilaria cenchroides*, *Bouteloua hirsuta*, and *B. gracilis* become abundant at about 4,500 feet and with *B. bromoides*, *B. racemosa*, and more or less *Aristida divaricata*, constitute the grassland until it gives way to the *Andropogon* community of the oak savannah at 5,500 to 6,000 feet. Altogether, nore than 30 different groupings of the dominants have been found in Arizona; 9 of these consist of two dominants, 12 of three, 8 of four, and 7 of five. These varying combinations furnish invaluable material for the determination of equivalences.

Sequence of dominants.—No study has yet been made of the habitat relations of the desert plains grassland, and these must be inferred from the groupings and the topographic position, as well as the behavior under disturbance. No definite sequence can be suggested without factor measurements for such a large number of closely equivalent dominants, but certain general relations will serve as a helpful basis for future work. These have to do with altitude, topography, range, grazing, and succession. The chief dominants of lower altitudes are naturally those of the greater range northward in the association. These are *Aristida purpurea*, *Bouteloua eriopoda*, *A. divaricata*, and *B. rothrockii*. The most xerophytic of these is *B. eriopoda*, which finds its best development in southern New Mexico in a rainfall of 10 to 15 inches, and the least xerophytic, *A. purpurea*, with a rainfall of 15 to 20 inches in western Texas. At higher altitudes, *B. hirsuta*, *B. bromoides*, *Hilaria cenchroides*, *B. racemosa*, and *B. gracilis* are the dominant species. The first three mix intimately and probably are to be regarded as the most nearly equivalent of the many dominants. *B. hirsuta* is the only one of the three which ranges far to the northward, where it is a regular associate of *B. gracilis* in sandy soils. In the Empire Valley, and probably in the heart of the association generally, it is intermediate in requirements between *B. gracilis* and *B. racemosa*, which occupy valleys and north slopes, and *B. bromoides* and *Hilaria* which take upper slopes and tables. It mixes with the former in the valleys and runs up the slopes to mingle with the latter on equal terms. From a number of similar transects the sequence as to water relation seems to be (1) *B. racemosa*, (2) *B. gracilis*, (3) *B. hirsuta*, (4) *B. bromoides*, (5) *Hilaria cenchroides*. This corresponds well with the successional sequence, so far as known, and also with the climatic relations.

In the secondary succession due to disturbance, and especially to grazing, it is apparent that the *Aristidas* are subclimax to the *Boutelouas* as a general rule. Overgrazing and trampling tend to destroy the more xerophytic species, such as *B. rothrockii* and *B. eriopoda*, and to permit the entrance of *Aristida*, especially *A. divaricata*. *Bouteloua rothrockii* and *Muhlenbergia porteri* are particularly susceptible to grazing injury and have consequently disappeared over large areas. *Muhlenbergia*, in fact, is rarely found at present, except in the protection of a catclaw or mesquite clump. A similar tendency for *Aristida* to replace *Bouteloua* occurs at the higher altitudes also, but is much less marked. One would expect disturbance to bring about the replacement of *B. gracilis* and *B. hirsuta* by *A. purpurea*, as is the case in the short-grass plains, but no important areas of this sort have been seen. *A. divaricata* sometimes plays this rôle, but much less frequently than at lower levels.

## SOCIETIES.

The desert plains have two groupings of subdominants. The most characteristic consists of those found in the heart of the association in southern Arizona and New Mexico. The second group comprises those found along the north, where the association meets the short-grass plains. The latter are those species which constitute the typical societies of the prairies and plains. While they are largely southwestern in origin, they have had time and opportunity to migrate throughout the formation east of the Rocky Mountains. The more characteristic societies appear to be of relatively recent derivation from the Mexican center, and they are best represented in the region along the boundary.

The desert plains resemble the short-grass plains in the relatively small number of societies, and especially of mixed societies. This is readily explained by the low rainfall over much of the area and the thoroughness with which the water available is utilized by the associated dominants of slightly different demands. Wherever the rainfall increases materially, as in the *Aristida* consociation of Texas or toward the mountains, the number and complexity of the societies increase also.

*Vernal Societies:*
- Antennaria dioeca.
- Calliandra eriophylla.
- Astragalus bigelovii.
- Krameria secundiflora.
- Zinnia pumila.
- Eschscholtizia mexicana.
- Malacothrix fendleri.
- Lithospermum linearifolium.
- Psilostrophe cooperi.
- Eriogonum abertianum.

*Estival Societies:*
- Psoralea tenuiflora.
- Petalostemon purpureus.
- Petalostemon candidus.
- Dalea laxiflora.
- Linum rigidum.
- Meriolix serrulata.
- Malvastrum coccineum.
- Thelesperma gracile.
- Hymenopappus filifolius.
- Aster tanacetifolius.

*Estival Societies*—continued.
- Chrysopsis villosa.
- Eriogonum wrightii.
- Verbesina encelioides.
- Haplopappus gracilis.
- Yucca radiosa.
- Yucca baccata.
- Eriogonum polycladum.
- Gaillardia aristata.
- Lepachys columnaris.
- Plantago elata.

*Serotinal Societies:*
Gutierrezia sarothrae.
Grindelia squarrosa.
Isocoma hartwegii.
Kuhnia rosmarinifolia.
Vernonia baldwinii.
Liatris punctata.

*Serotinal societies*—continued.
Artemisia gnaphalodes.
Carduus undulatus.

*Clans:*
Argemone platyceras.
Aster ericoides.

*Clans*—continued.
Lesquerella fendleri.
Lotus mollis.
Evolvulus argenteus.
Desmanthus jamesii.
Hofmanseggia stricta.

## THE BUNCH-GRASS PRAIRIE.

### AGROPYRUM-STIPA ASSOCIATION.

Nature.—The grasslands of the Northwest and of the Pacific coast differ from those already described in the characteristic bunch-grass habit of the dominants and in their relation to winter precipitation. The first visit to them in 1914 led to the suggestion that they were essentially prairies, resembling in many respects the climax prairies of the Missouri Valley. The difference in habit appears greater than it really is, since the prairies of the great sandhill region of Nebraska are characterized by bunch-grasses also. This association consists of tall-grasses, which are species of *Agropyrum* and *Stipa*, as in the eastern prairies. Three of the dominants of the latter, *Stipa comata*, *Agropyrum glaucum*, and *Koeleria cristata*, occur throughout the bunch-grass prairies, though the latter is the only one of much importance. *Aristida purpurea* is likewise important, especially in California, while *Stipa viridula*, *Elymus sitanion*, and *Eriocoma cuspidata* all play a part as subclimax dominants. *Bouteloua gracilis* and *Bulbilis* are the only ones of the great dominants of the formation that are rare or lacking. The closer relationship with the prairies shown by the dominants is explained by the fact of a fairly continuous connection on the north, while the bunch-grass prairies are separated from the plains by the wide stretch of the Colorado and Mohave deserts. This fact is further reflected in the societies and clans. In the *Agropyrum* consociation, the genera and many of the species of subdominants are identical with those of the mixed prairie. These generally change southward, and in southern California many of the genera and practically all of the species which form societies are different. However, it is difficult to draw exact comparisons here, since the relict areas of *Stipa* are too small to permit the original structure to reach full expression.

Range.—The bunch-grass prairies find their best expression to-day in the Palouse region of southeastern Washington and adjacent Idaho. Typical areas also occur in northern and eastern Oregon, but these are only fragments of what were once extensive stretches. Cultivation, grazing, and fire have combined to destroy bunch-grass or to handicap it in competition with the invading sagebrush. In the form of outposts, this association is found eastward in Montana to Helena and Livingston, in western Wyoming from Yellowstone Park to the Green River region and southward through northwestern Colorado and northeastern and northern Utah. Over most of this region, it occurs on dry rocky hillsides surrounded by sagebrush, indicating that it formerly covered much larger areas. This is confirmed by the fact that burning or clearing the sagebrush from an area permits the development of typical bunch-grass prairie (plate 30).

The southern part of the association is much more fragmentary, so much so in fact that it has had to be reconstructed from widely scattered relicts. The

*Agropyrum* and *Stipa* consociations meet in southern Oregon and northern California, though here fire, grazing, and the invasion of ruderal grasses have almost completely destroyed the native grassland. The *Stipa* consociations seem formerly to have dominated the interior valley from Bakersfield to Mount Shasta and from the foothills of the Sierra Nevada and Cascade Mountains, through and over much of the Coast Range. The successive invasions of European weedy grasses, the extensive cultivation of the land, and the repeated burnings which favored chaparral at the expense of grassland, have operated to practically eliminate the original grasses. A special search has been made for relict patches of *Stipa* during the past three years, with the result that such areas have been found more or less continuously or at frequent intervals from La Jolla and San Diego northward to Sisson and Weed. Further information as to the original extent of the *Stipa* grassland has been obtained from collections, ranges, the statements of early settlers, and the accounts of earlier collectors and explorers.

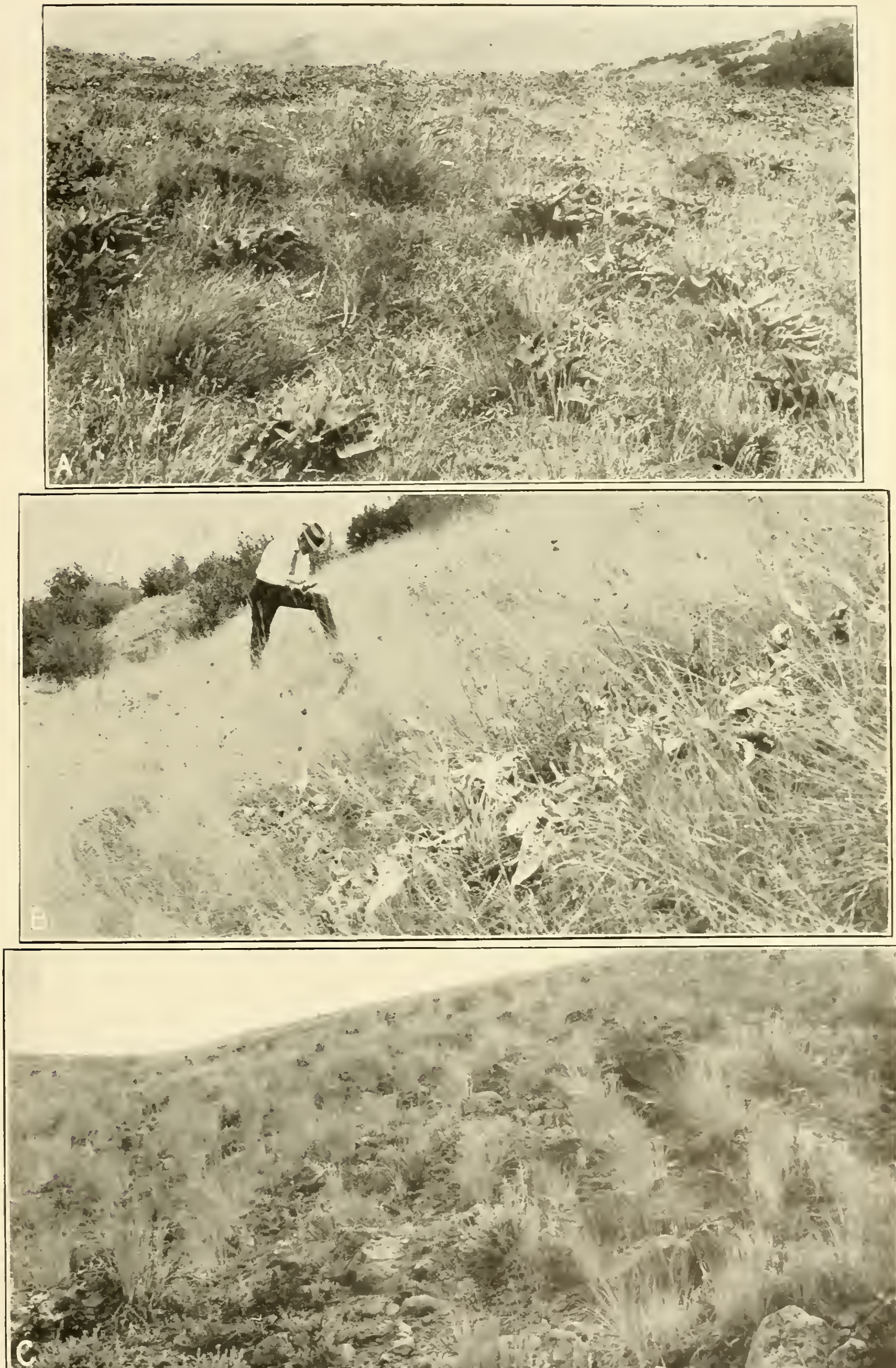
The bunch-grass prairie passes so gradually into the mixed prairie in central Montana that no line can be drawn between them. This is readily understood when it is known that *Stipa comata*, *Koeleria cristata*, and *Agropyrum glaucum* occur in both, and that a large number of the societies are identical. The change is marked chiefly by the appearance and increasing importance of *Bouteloua*, and the transfer of the major dominance from *Agropyrum spicatum* to *Stipa comata* and *Agropyrum glaucum*. As already mentioned, there is no connection between the bunch-grass prairies, and the short-grass and desert plains in the south. The Colorado and Mohave Deserts have proved an effective barrier, which was probably in existence before the Pleistocene. It thus appears probable that the bunch-grass prairies were derived from the northeast and spread southward along the Pacific Coast.

CONSOCIATIONS.

| | |
|---|---|
| Agropyrum spicatum. | Stipa setigera. |
| Poa tenuifolia. | Stipa eminens. |
| Festuca ovina. | Stipa comata. |
| Koeleria cristata. | Elymus sitanion. |

The two most important dominants are *Agropyrum spicatum* and *Stipa setigera*. The first is the major and often the exclusive dominant throughout the Palouse, southward into Oregon and California and eastward into Idaho and Montana. The second is, or rather was, the great dominant throughout California, and it extends well into Oregon. The others are all secondary to these in importance. *Festuca* is the only other one which frequently makes pure stands, and there is some question as to its true relationship. It seems to attain the maximum development at higher elevations, as is true also in the Rocky Mountains, and to have recently made its way into the bunch-grass prairies. However this may prove to be, it is impossible to ignore it as a dominant member of the latter (Weaver, 1917 : 42). In California, *Stipa eminens* stands next in importance to *S. setigera*. It is usually mixed with the latter, but may constitute a pure community. *Elymus sitanion* has been found in pure stands also, but as a rule it is mixed with *Stipa setigera* or *Agropyrum spicatum*. *Poa tenuifolia* is a fairly constant associate of *Agropyrum* and *Festuca*, but is never a pure dominant. This appears to be the rule also for *Koeleria* and *Stipa comata*. They may be expected throughout

Bunch-grass Prairie



A. *Agropyrum-Festuca* association' The Dalles, Oregon.
B. *Agropyrum* consociation, Missoula, Montana.
C. *Agropyrum* consociation on "scab" land, John Day Valley, Oregon.

Bunch-grass Prairie



A. *Stipa setigera* consociation in trackway, Fresno, California.

B. *Avena fatua* consocies, with relicts of *Stipa setigera* and *eminens*, Rose Canyon, San Diego, California.

the association, but nowhere in it have they been found in pure communities. At the present, they are more characteristic of the *Agropyrum-Festuca* community.

The rôle of *Agropyrum glaucum* in the bunch-grass association is still in question. As a rule, it is subclimax in lowlands and especially in moist saline areas. In northern California and in Oregon, it often meets *Stipa setigera* or *Agropyrum spicatum* on what appear to be more or less equal terms. In the Hampton Valley in Central Oregon, the removal of the sagebrush results in the establishment of an *A. glaucum* sod instead of the usual bunch-grass community. In fact, repeated observations in Oregon and Idaho during the past summer indicate that *Agropyrum spicatum* frequently loses its bunch habit under certain conditions, and comes to be almost indistinguishable from forms of *A. glaucum.* Through the same region, *Elymus condensatus* is a frequent associate of the bunch-grass. It reaches its best development in saline lowlands, however, and must be regarded normally as a subclimax dominant. *Eriocoma cuspidata* and *Stipa speciosa* likewise occur now and then with the dominants when the soil is looser or sandy, but they are clearly subclimax consocies of the xerosere.

Factor relations and sequence.—The presence of a prairie of tall-grasses in a region with 10 to 12 inches of precipitation annually is due to several facts. Perhaps the most important is the bunch habit, which enables each plant to draw upon a relatively large area of soil for its water supply. The second is that 60 to 90 per cent of precipitation comes during winter, with the result that penetration and conservation of the water are at a maximum. As a consequence, the root systems are mostly deep-seated, and their efficiency is high. Along the coast of southern California, moreover, the low precipitation is offset by the high humidity and reduced evaporation to the extent that *Stipa setigera* and *S. eminens* reach a high development here. The best expression of bunch-grass prairies to-day occurs in that part of the Palouse with 15 to 25 inches rainfall (plate 31).

Weaver (1917) has made a careful study of the physical conditions of the *Agropyrum* and *Festuca* consociations in this region, as well as of the root-systems of the dominants and subdominants. From June to September, at Colfax, the evaporation in the former averaged 8 to 10 c. c. higher than in the latter, while the water-content at 10 inches was 5 to 10 per cent lower. Since the differences between northeast and southwest slopes of the *Festuca* consociation were 9 to 10 c. c. and 5 to 12 per cent, respectively, it is evident why the two consociations are frequently mixed. As would be expected from the behavior in other associations, *Koeleria* stands close to *Festuca* in its water requirements, while *Poa* is somewhat more xerophytic than *Agropyrum.* These relations are confirmed by the successional sequence (Weaver, 1917: 68). Of the Stipas, *Stipa comata* is the most mesophytic, followed closely by *S. setigera* and this by *S. eminens*. *Elymus sitanion* is more xerophytic than *S. setigera* and probably slightly more so than *S. eminens.*

SOCIETIES.

The bunch-grass prairies contain three groups of subdominants: (1) those derived from the mixed prairie; (2) those characteristic of the Washington-Idaho center; and (3) those found in central and southern California. The destruction of the association over wide stretches and the fact that the societies have not been made the subject of definite study throughout the season render the following lists more or less provisional. It has been especially difficult to determine the subdominants of the *Stipa* communities in California, as the fragmentary areas are almost completely overrun with annuals. The societies of such grassland areas at present are essentially the same as for the chaparral (p. 193). The following list for the *Agropyrum-Festuca* community of Washington and Idaho has been contributed by Dr. J. E. Weaver:

*Societies of the Agropyrum-Festuca community.*

*Prevernal Societies:*
- Carex geyeri.
- Erythronium grandiflorum.
- Claytonia linearis.

*Vernal Societies:*
- Lupinus wyethii.
- Balsamorhiza sagittata.
- Leptotaenia multifida.
- Phlox speciosa.

*Estival Societies:*
- Wyethia amplexicaulis.
- Geranium viscosissimum.
- Astragalus arrectus.
- Astragalus collinus.
- Astragalus spaldingii.
- Castilleia lutescens.
- Helianthella douglasii.
- Lupinus leucophyllus.
- Lupinus ornatus.

*Estival Societies*—continued.
- Lupinus sericeus.
- Gaillardia aristata.
- Achillea millefolium.
- Galium boreale.
- Arnica fulgens.

*Serotinal Societies:*
- Hoorebekia racemosa.
- Solidago missouriensis.
- Solidago serotina.

*Prevernal Clans:*
- Viola adunca.
- Ranunculus glaberrimus.
- Fritillaria pudica.
- Sisyrinchium grandiflorum.

*Vernal Clans:*
- Synthyris rubra.
- Collinsia parviflora.

*Estival Clans:*
- Carduus foliosus.
- Carduus palousensis.
- Potentilla convallaria.
- Potentilla blaschkeana.
- Sidalcea oregana.
- Penstemon confertus.
- Agoseris heterophylla.
- Agoseris grandiflora.
- Eriophyllum lanatum.

*Serotinal Clans:*
- Hieracium scouleri.
- Aster fremontii.
- Aster levis geyeri.
- Erigeron corymbosus.
- Carum gardneri.
- Gentiana oregana.

## THE SAGEBRUSH CLIMAX.

### ATRIPLEX-ARTEMISIA FORMATION

Nature.—The sagebrush climax owes its character to the dominance of low shrubs or bushes, of which *Artemisia tridentata* is the most important. It is essentially a scrub desert, in which the dominants seem to have acquired their distinctive vegetation-form as a rather recent adaptation to the arid climate itself. In other words, they are shrubby adaptations of herbaceous families, and not dwarf forms of shrubs or trees, as is true of chaparral and mesquite. The formation is regarded as composed of 17 dominants, of which 11 belong to the *Asteraceae*, 4 to the *Chenopodiaceae*, 1 to the *Polygonaceae*, and 1 to the *Lamiaceae*. These families agree in showing a high systematic development, and doubtless the dominants owe some part of their success to the highly specialized one-seeded fruit typical of all of them. Their success is due even more largely to the acquisition of the woody habit in some degree at least, and especially to the accompanying ability to sprout more or less readily from the base. As a consequence, the sagebrush dominants are not only well adapted to their habitat, but they are also particularly well fitted to invade other habitats, wherever fire or other disturbance has weakened the hold of the occupants. The result has been a widespread extension of sagebrush into all of the contiguous formations, the grassland, desert scrub, chaparral, and woodland, and even into the pine consociation of the montane forest. These transitions are often very broad, and hence the actual delimitation of the formation on the map is a matter of peculiar difficulty. They also give the sagebrush a varied aspect, and seem to call in question its value as a distinct formation, especially in hilly and mountainous country, where it mixes or alternates constantly with fragments of other climax communities. As is shown below, however, the great central mass of the community leaves no doubt as to its formational unity and rank.

Unity of the formation.—The geographical unity is greater than that of most other climaxes in that the sagebrush occupies a natural physiographic unit, the Great Basin. While the most representative species, *Artemisia tridentata,* extends far beyond the limits of the latter, the formation proper does not. The Great Basin is likewise a climatic unit, and hence naturally corresponds to its climax. It is hemmed in by the high mountains, and contains by far the most extensive area with 5 to 10 inches of rainfall to be found on the continent. The general rainfall limits are from 5 to 15 inches in the interior, though to the eastward sagebrush mixes with or yields to grass as the rainfall rises above 12 inches (fig. 5).

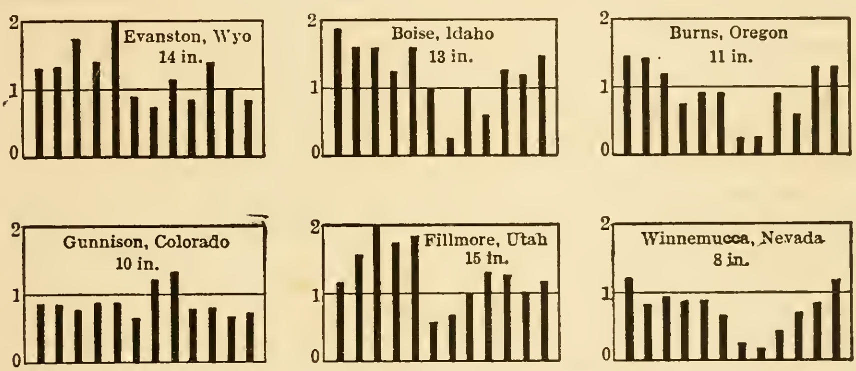



FIG. 5.—Monthly and total rainfall for representative localities in the Basin sagebrush association.

With respect to the component species, the unity of the climax is proved by such widely ranging dominants as *Artemisia tridentata, Chrysothamnus nauseosus, Atriplex confertifolia, A. canescens, Gutierrezia sarothrae,* and *Eurotia lanata.* Of the 17 dominants, only 4 fail to occur throughout the central mass of the formation as indicated by the limits of the Great Basin. As to origin, the formation is characteristically southwestern. The main body of dominants, which constitute the *Atriplex-Artemisia* association of the Great Basin, seem to have moved northward at an early period, perhaps before the Pleistocene, though they have probably undergone considerable differentiation since that time. A more recent lateral development has produced the *Salvia-Artemisia* association of southern California and Lower California. The latter found itself between the chaparral on the one hand and the rapidly desiccating desert on the other, and has covered but a limited area in comparison with the main association. Its relationship, however, is clearly indicated by its frequent contact with *Artemisia tridentata,* and especially by its occupying the same position between the desert scrub or grassland and the chaparral formations that the *Atriplex-Artemisia* association does. The floristic unity of the formation is conclusively indicated by the fact that *Artemisia tridentata* has been found in 314 of the 416 localities where the community has been studied.

The ecological unity of the climax is due especially to the fact that all of the 17 dominants are half-shrubs or bushes. They range in height from an average of 3 to 5 feet in *Artemisia tridentata, A. californica, Chrysothamnus nauseosus, Atriplex canescens, Eriogonum fasciculatum,* and *Salvia mellifera,* while in *Artemisia trifida, Gutierrezia,* and *Eurotia* the range is 1 to 2 feet. They are typically deep-rooted, and this, with their bushy habit and perennial woody stems, accounts for their success in competing with other dominants. For their region, most of them have a further advantage in being able to endure a more or less highly saline soil. The close similarity in their nature and requirements is shown by the fact that they are replaced by such turf-forming grasses as *Agropyrum, Bouteloua,* and *Hilaria,* wherever conditions permit the formation of a sod. All of the dominants, without exception, are marked xerophytes in which transpiration is decreased by reduction of the leaf-surface, a hairy epidermis, or succulence. This similarity in habit is confirmed by their association. While the sagebrush in particular forms pure stands, mixed communities are the rule. Of the 416 communities studied, 145 contained two dominants and 143 contained three; in 44 there were four, in 5 five, and in 1 six, or a total of 339 mixed communities in contrast with 75 pure ones.

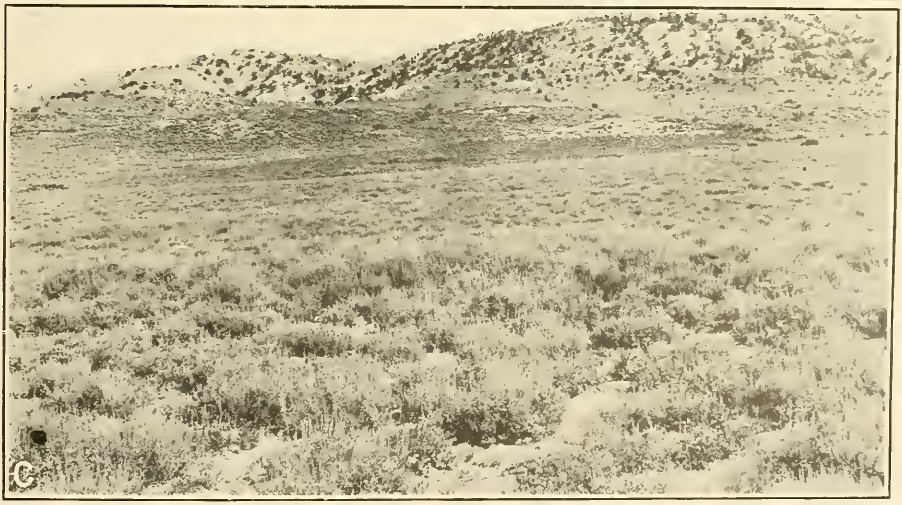
Successionally, the sagebrush climax is perhaps more uniform than any other formation. This is due to the low rainfall, the high evaporation, and the rapid drying-out of bodies of water. Since its area is a great intermountain basin composed of several smaller lake basins, the lakes and ponds are either saline or they form salt marshes as they dry out. As a consequence, the typical succession is the halosere, originating in salt marshes, or on the saline shales and clays, which are especially frequent. In fact, the successional correlation of the seral and climax dominants is so fundamental that the development of a local subclimax of *Atriplex* and *Artemisia* occurs widely throughout the Bad Lands of the Great Plains and the prairies, in spite of the fact that these are several hundred miles from the sagebrush climax proper.

Range.—It is impossible to draw the limits of the sagebrush climax with accuracy, owing to the extent to which it mixes with contiguous formations. The general tendency is to use the conspicuous dominants, such as *Artemisia tridentata* and *A. cana,* to outline its area, but these extend far beyond the limits of the formation proper. Since ecotones are areas in which dominants meet on more or less equal terms, it follows that the limit of a particular climax must be drawn at the line where it is still controlling. As a matter of convenience, a formation is called dominant where it covers three-fourths of a particular area or region. Outside of this climax mass occur many outposts of the community as well as of individual dominants, but these are merely expressions of topographic or climatic diversity in the area of adjoining climaxes. For example, the erosion valleys of the Bad Lands of northwestern Nebraska are covered with luxuriant sagebrush, but this is really subclimax to the mixed prairie which ultimately replaces it (plate 32).

If the limits are set as indicated above, the sagebrush climax will include all of Nevada except the southeast, practically all of Utah, Colorado west of the Continental Divide, central and southwestern Wyoming, a part of southwestern Montana, all of south-central Idaho, Oregon south of the John Day

Basin Sagebrush






A. *Artemisia tridentata* consociation, Henefer, Utah.
B. *A. tridentata* consociation. Garland, Colorado.
C. *A. arbuscula* consociation, Evanston, Wyoming.

Valley and east of the Cascades, and California east of the Sierra Nevada. Disregarding the interruption due to isolated mountain ranges, this constitutes the largest central mass exhibited by any formation west of the prairies and plains. Tongues of sagebrush stretch out from this mass into eastern Montana, central Colorado, northern New Mexico, and Arizona, southern California and Mexico, while climax outposts are found in southeastern and eastern Washington, and even in southernmost British Columbia. These are practically all extra-regional, persisting because of peculiar local conditions or because the proper climax has not yet occupied all of its climatic region.

Subclimax sagebrush.—Much if not all of this marginal portion of the formation is subclimax in nature. This seems to be true also of long stretches which are apparently an intrinsic part of the central mass. This relation is obvious where sagebrush comes in contact with the true woodland climax or with the montane forest, because of the dominating relation of the trees. It is less clear in the case of transitions between sagebrush and chaparral or desert scrub, where the dominants are more nearly of the same size and nature. In such instances, the mixed community not only seems but actually is a fairly permanent community, of which the real climax relationship can only be determined by prolonged study.

The longest contact of the sagebrush is with grassland. It meets the bunch-grass prairies in Washington, Oregon, Idaho, Montana, and Utah, the mixed prairies in Montana, Wyoming, and Colorado, and the short-grass plains in western Colorado, northern New Mexico and Arizona, and southeastern Utah. The ability of the sagebrush and grassland to live together is shown not only by the very broad transition between them all along the line of contact, but also by the fact that such dominants as *Agropyrum glaucum* and *Stipa comata* are found more or less abundantly throughout the climax area of the formation.

The actual relation between sagebrush and grasses is readily disclosed wherever sagebrush has been cleared and often also where it has been burned. When the short subsere which results ends again in sagebrush after a few years, the area may well be regarded as a part of the sagebrush climax. This can usually be anticipated by the vigor with which the shrubs form root-sprouts, as well as by the failure of the grass dominants to appear in abundance during the first two or three years. If the grasses do develop abundantly during the first few years and especially the first year, so that they dominate the root-sprouts of the shrubs, the area is to be regarded as belonging to the grassland. Examples of this sort have repeatedly been found since 1913 in what appeared to be typical sagebrush areas. *Festuca ovina*, *Agropyrum glaucum*, and *A. spicatum* have frequently been found to replace cleared or burned sagebrush in Oregon. *Agropyrum glaucum* and *Stipa comata* have been seen in the same rôle in many parts of Idaho, northern Utah, and southwestern Wyoming. In addition, the grass dominants have been found killing out the sagebrush as a direct result of competition for water. This is not surprising along the eastern edge in Wyoming where the grasses have a definite climatic advantage, but it is unexpected in Utah and Nevada, where the advantage is reversed. Sagebrush has been seen nearly dead or dying as the result of water competition with *Agropyrum glaucum*, *A. spicatum*, *Bouteloua gracilis*, and *Stipa* *comata*. *Atriplex canescens* shows a similar behavior where *Bouteloua* forms a closed sod, and *A. confertifolia* wherever *Hilaria jamesii* tends to become dominant. The evidence of the replacement of sagebrush by the grasses during the dry years of 1917 and 1918, either as a result of fire or clearing, or in consequence of competition, has been so abundant as to indicate that a broad marginal belt of the climax is really subclimax, or at least tends to become such during the dry phase of the climatic cycle. This subclimax belt is from 100 to 300 miles wide and extends all along the grassland contact from Oregon to Montana and from Wyoming to Arizona. If placed under proper treatment, it is felt that it can again be converted into the original grassland community. The significance of this for grazing is indicated in Chapter VI.

The conversion of contiguous grassland into sagebrush has undoubtedly been caused by overgrazing during the past fifty years, aided in a large measure by repeated fires. This is confirmed not only by evidence of the controlling part formerly played by grasses in regions now covered by sagebrush, but also by the persistence of the grass covering in areas more or less protected. This is particularly the case in the John Day Valley of eastern Oregon, where the original *Agropyrum spicatum* is almost completely displaced by *Artemisia tridentata* over the range generally, while it persists in its former dominance on rocky or inaccessible slopes. More recent evidence is afforded by pastures in which *Agropyrum* has practically disappeared and weeds abound, while contiguous protected areas show the pure stand of grass.

Associations.—The sagebrush formation is composed of two communities, the *Atriplex-Artemisia* and the *Salvia-Artemisia* association. When the climax formation was first recognized, it was supposed that it consisted of a single association, the *Atriplex-Artemisia halium*. In attempting to determine the relation of sagebrush to chaparral in California, it was found that the community formed by *Artemisia californica*, *Salvia*, and *Eriogonum fasciculatum* showed a closer relationship to sagebrush than to chaparral. This was first suggested by its constant position below the true chaparral and by its more xerophytic nature. Further study showed the frequent contact with the *Artemisia tridentata* association and confirmed the evidence afforded by the similarity of the vegetation-forms with that of the sagebrush, and not the chaparral. This was further supported by the discovery that the California association bore the same relation to the *Stipa* grassland that the Great Basin association does to the grasslands that touch it. As a consequence, while the *Salvia-Artemisia* association is of limited extent in comparison with the main association, it possesses all the characteristics of a distinct but related community. It is less conspicuous because it has been more generally disturbed by fire and overrun by such ruderal grasses as *Avena* and *Bromus*. In protected areas where it retains its original character, it displays a marked resemblance to some communities of the main association.

## THE BASIN SAGEBRUSH.

### ATRIPLEX-ARTEMISIA ASSOCIATION.

Range.—Most of what has been said of the climax formation applies in particular to this association. It covers the whole of the climax region, except southern California and Lower California, and its outposts extend into British Columbia, North Dakota, Kansas, and Mexico, as represented

Basin Sagebrush

A. Subclimax sagebrush in badland valleys, Hat Creek, Nebraska.
B. Alternes of *Artemisia* and *Kochia*, Strevell, Idaho.
C. *Sarcobatus, Chrysothamnus, Atriplex* and *Artemisia*, Vale, Oregon.

by *Artemisia tridentata*, *A. cana*, and *Gutierrezia*. Few other associations of the West exhibit such a large number of dominants or such a variety of groupings. It is also the most xerophytic of all climax associations, with the exception of the *Larrea-Prosopis* desert, and is unique in its general halophytic character. The greatest development of dominants is in the climax mass, from which they shade out toward the margins, being represented in the outpost communities by a single species. The haloid dominants are the least extensive, and the lower non-haloid forms, such as *Gutierrezia*, have the widest range. In fact, *A. cana*, *A. trifida*, *Eurotia lanata*, and *Gutierrezia sarothrae* are so completely at home in the mixed prairies or short-grass plains that it has seemed desirable to treat them as societies where they occur in these associations. Like most of the western associations, the sagebrush has received little quantitative study as yet, and it is possible to deal only with its outstanding features and to suggest some of its more obvious correlations.

CONSOCIATIONS.

| | | |
|---|---|---|
| Artemisia tridentata. | Artemisia cana. | Grayia spinosa. |
| Atriplex confertifolia. | Artemisia arbuscula. | Gutierrezia sarothrae. |
| Chrysothamnus nauseosus. | Artemisia trifida. | Tetradymia spinosa. |
| Chrysothamnus viscidiflorus. | Artemisia rigida. | Eurotia lanata. |
| Atriplex canescens | Artemisia spinescens. | |

The most important as well as characteristic of all the dominants is *Artemisia tridentata*. It is also one of the most widespread, ranging from Saskatchewan to Nebraska, Mexico, California, and British Columbia. In this respect it is equaled by *Eurotia lanata* and *Chrysothamnus nauseosus*, and excelled by *Gutierrezia sarothrae*, which extends eastward to central Kansas. *Atriplex canescens* is of nearly as wide range, but it appears to be lacking in Canada. *Atriplex confertifolia* and *Chrysothamnus viscidiflorus* are somewhat more limited, as is the case with *Grayia spinosa*, *Artemisia cana*, and the remaining species of *Artemisia*. Naturally, the range of these as climax dominants is much more restricted, and is almost wholly confined to the Great Basin proper (plate 33).

**Rank and grouping.**—The number of dominants in the association is so large and their equivalences so close that a large number of groupings occur. In the endeavor to determine the relative importance of the dominants and of the various mixtures, a summary has been made for all localities visited in the sagebrush association in 1907, 1909, and from 1913 to 1918. The total number of localities was 416, including a few duplicated in different years. The sequence of the various dominants is shown by the following table:

| | | | |
|---|---|---|---|
| Total number of localities | 416 | Grayia spinosa | 54 |
| Artemisia tridentata | 314 | Gutierrezia sarothrae | 45 |
| Atriplex confertifolia | 142 | Tetradymia spinosa | 37 |
| Chrysothamnus | 140 | Eurotia lanata | 15 |
| Atriplex canescens | 56 | Artemisia spp. (except A. tridentata) | 61 |

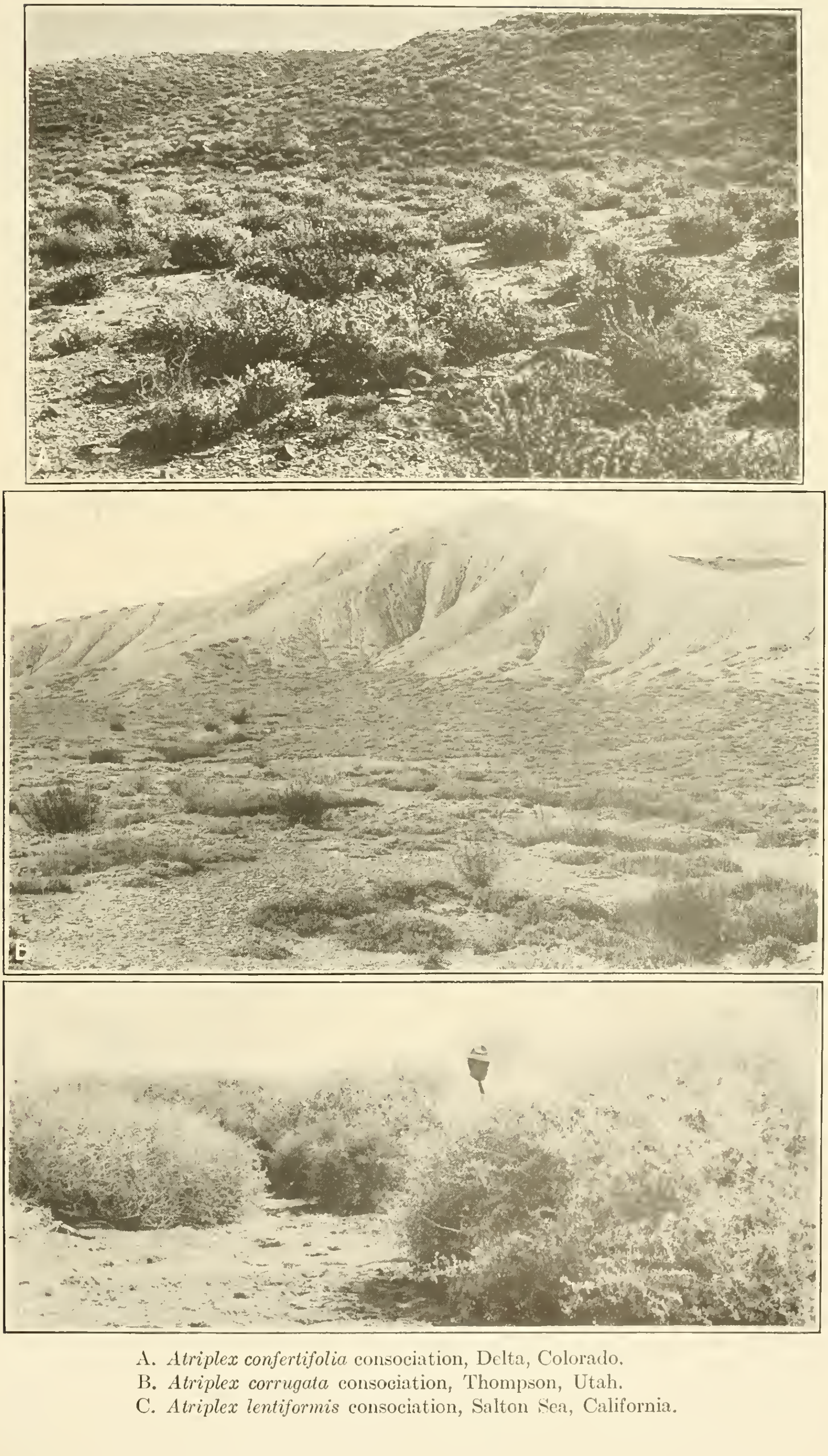
*Artemisia tridentata* was found 60 times in pure stands stretching over many miles, often for 20 to 30 miles without interruption. *Atriplex confertifolia* was met but 10 times in extensive pure areas, though it is very often found on hillsides and mountain slopes in pure communities a few miles long. While the more halophytic and hence subclimax species of *Chrysothamnus* make pure stands, sometimes covering several to many square miles, the climax ones are regularly found in mixture, or as narrow band-like alternes. *Artemisia cana* has several times been met as a pure zone below *A. tridentata*, but it is much more frequent in the mixed prairies. The tendency to form pure stands of small extent is naturally more marked outside of the climax area, since the other dominants of similar equivalence are usually lacking.

In spite of the major dominance shown by *Artemisia tridentata*, the association is typically mixed in character. Of 406 instances, pure stands occurred in but 75, while 331 were mixtures. Two and three dominants are the rule, the former occurring in 142 cases, the latter in 139. Four dominants were found in 44 localities, five in 5, and six in 1. The frequency of the most important groupings is as follows:

| | |
|---|---|
| Artemisia tridentata-Atriplex confertifolia, alone | 24 |
| A. tridentata-A. confertifolia, with other species | 74 |
| A. tridentata-Chrysothamnus nauseosus or C. viscidiflorus | 31 |
| A. tridentata-Chrysothamnus, with others. | 79 |
| A. tridentata-Grayia ± others | 41 |
| A. tridentata-A. confertifolia, Grayia ± others | 18 |
| A. tridentata-A. confertifolia, Chrysothamnus ± others | 23 |
| A. tridentata-Gutierrezia ± others | 30 |
| A. tridentata-A. canescens | 28 |
| A. tridentata-Sarcobatus ± others | 23 |
| A. confertifolia-Grayia ± others, but no A. tridentata | 10 |

Correlations.—The dominants of the sagebrush association show the most striking relation to the amount of salt in the soil. While they are essentially xerophytes, the water relation is so obscured by the presence of salt that the specific requirements and the successional sequence are most readily indicated by the latter. Our knowledge of the salt relations of the dominants is due chiefly to the work of Kearney, Briggs, Shantz, McLane, and Piemeisel (1914), and of Shantz (Clements, 1916:237). The most saline of the species considered here is the subclimax *Sarcobatus vermiculatus* with a mean of 0.8 per cent. *Atriplex confertifolia* possesses a mean of 0.5 per cent and *Artemisia tridentata* of 0.04 per cent. *Grayia*, *Tetradymia*, *Atriplex canescens*, and *Artemisia spinescens* center about *Atriplex confertifolia*, while *Chrysothamnus nauseosus*, *C. viscidiflorus*, *Eurotia*, *Gutierrezia*, and the several species of *Artemisia* resemble the sagebrush more nearly. In spite of the excellent work which has been done in the salt relations of the dominants of the sagebrush association, these results do not suffice to explain their varied groupings, nor are they in full harmony with what seems to be the successional sequence. When two deep-rooted species, such as *Artemisia tridentata* and *Sarcobatus vermiculatus* are found 23 times in intimate mixture, this relation does not seem consistent with the mean salt-content for each. This discrepancy appears even more striking in the case of *Artemisia tridentata* and *Atriplex confertifolia*, which occur intimately associated in 98 localities. This relation is further complicated by the fact that *Artemisia tridentata* not only occurs in 278 of the 338 mixed communities, but is also repeatedly associated with every one of the saline dominants from *Sarcobatus* to *Atriplex canescens*. As a consequence, it seems certain that we are not at the bottom of the salt relation. For a complete understanding, it will be necessary to determine the root relations of each dominant alone as well as in mixed stands, and to ascertain the extremes of salt-content for it in the various mixed communities and at the different working levels of the roots as well. Here, as everywhere else, the behavior of the plant or community must be accepted as conclusive as to the

Basin Sagebrush



A. *Atriplex confertifolia* consociation, Delta, Colorado.
B. *Atriplex corrugata* consociation, Thompson, Utah.
C. *Atriplex lentiformis* consociation, Salton Sea, California.

equivalence and sequence, and the instrumental results as of secondary importance. The latter are indispensable but never paramount.

Successional sequence.—A question naturally arises as to the possibility of succession in a region of such low rainfall and in basins of such high salt-content. Shantz (1916 : 235) has shown conclusively that succession is a normal process, even in the most saline areas about Great Salt Lake:

"Two lines of development are initiated by the *Allenrolfea* association. The more natural line is brought about largely by the gradual lowering of the ground-water level. As a result water is less and less supplied from the ground-water, and more and more from the surface as rain. *Allenrolfea*, when the ground-water is not too close, is gradually replaced by *Sarcobatus*, *Suaeda moquinii* may follow *Allenrolfea* and be replaced in turn by *Sarcobatus*. As a rule, *Sarcobatus* and *Suaeda* are mixed, the former being the most important plant. *Sarcobatus*, which often forms a pure association in this valley, usually forms a scattered growth, the interspaces being occupied by *Atriplex*. This mixed association finally gives way to pure *Atriplex* when the ground-water is no longer within the reach of *Sarcobatus* roots. The *Atriplex* association is not readily replaced in the Tooele Valley. The soil is rather strongly alkaline and is very slowly leached. No permanent type of vegetation stands between this and the alkali-avoiding *Artemisia* in this Valley. *Artemisia* and *Atriplex* are not sharply separated at the ecotone, and, although *Artemisia* is never luxuriant along this line, there is no doubt that it is gradually replacing the *Atriplex* as the conditions become more favorable for plant growth.

"*Kochia*, which occurs on land of unusually heavy texture, represents the most extreme conditions in the Valley in regard to the shortage of water, and indicates the presence of 0.5 to 1 per cent salt below the first foot. The run-off in this land is very great, and it is very slowly leached. If a salt flat could be lifted above the level influenced by ground-water, and slightly leached, especially in the surface foot, the conditions would be very similar to those in the larger *Kochia* areas of the Valley. Since such conditions are not markedly different from *Atriplex* land, *Atriplex* is slowly advancing along the broad ecotone. In time, *Atriplex* will probably replace much of the *Kochia*. The ecotone between *Kochia* and *Artemisia* is very sharp, and a great change occurs in salt-content and the physical texture of the soil. When water drains over land of this type, and where unusual leaching occurs, *Artemisia* enters directly on *Kochia* land. This is due to the proximity of the *Artemisia* and *Kochia* areas. A more natural change would be from *Kochia* to *Atriplex*, and from *Atriplex* to *Artemisia*.'

This account conforms essentially to the course of the halosere throughout the sagebrush association. *Sarcobatus* and *Chrysothamnus n. glabratus* are the chief subclimax dominants in saline valleys, though this rôle is usually taken by *Atriplex corrugata* and *A. nuttallii* over the extensive gumbo plains derived from such deposits as the Mancos and Steele shales. These are followed by *Tetradymia spinosa* and this by *Atriplex confertifolia*, or by *Chrysothamnus nauseosus*. The latter is next invaded by *Grayia* in some regions, and by such low *Artemisias* as *A. trifida* or *A. arbuscula* in others. In still other areas, *Atriplex confertifolia* is followed directly by *Artemisia tridentata*, often with more or less *Eurotia*, *Atriplex canescens*, *Chrysothamnus viscidiflorus*, or *Gutierrezia*. The general sequence, more or less modified by local conditions, recurs in hundreds of valleys throughout the association. It not only confirms the successional movement, but explains the characteristic mixing throughout (plate 34).

SOCIETIES.

These are poorly developed in the climax portion generally, but they become more and more abundant through the marginal subclimax zone leading to the adjacent formations, particularly the grassland. This is readily explained by the fact that the sagebrush societies are largely drawn from the grassland associations, and hence the two groups are similar to a large degree. The sagebrush likewise contains a number of grasses derived from the various grass associations. These play a rôle essentially similar to that of societies, though they are properly to be regarded as extra-formational examples of the particular consociation. The societies peculiar to the sagebrush are largely constituted by halophytic species which persist from the subclimax. Pure stands of *Artemisia tridentata* are to be regarded as the final condition of the climax. They are characteristically dense and closed, and are often practically destitute of other species, except for a few plants of such ruderals as *Sisymbrium altissimum*, *Lepidium perfoliatum*, and *Bromus tectorum*. The latter regularly simulate striking societies over large areas, but they are properly understood as pioneer annuals of a subsere due to fire or grazing, or usually to both.

*Grass Communities appearing as Societies:*
- Agropyrum spicatum.
- Agropyrum glaucum.
- Stipa comata.
- Stipa viridula.
- Festuca ovina.
- Elymus condensatus.
- Koeleria cristata.
- Bouteloua gracilis.
- Hilaria jamesii.
- Aristida purpurea.
- Elymus sitanion.
- Eriocoma cuspidata.

*Vernal Societies:*
- Anemone patens.
- Antennaria dioeca.
- Anemone globosa.
- Sieversia ciliata.
- Potentilla arguta.
- Astragalus flexuosus.
- Astragalus drummondii.
- Astragalus crassicarpus.
- Allium cernuum.
- Senecio fendleri.
- Comandra umbellata.
- Aragalus speciosus.
- Aragalus deflexus.
- Erysimum parviflorum.
- Krynitzkia virgata.
- Heuchera parvifolia.

*Estival Societies:*
- Balsamorhiza sagittata.
- Balsamorhiza deltoidea.
- Castilleia miniata.
- Achillea millefolium.
- Cordylanthus wrightii.
- Linum perenne.
- Opuntia polyacantha.
- Opuntia mesacantha.
- Eriogonum umbellatum.
- Calochortus gunnisonii.
- Allium cernuum.
- Potentilla pennsylvanica.
- Potentilla hippiana.
- Potentilla gracilis.
- Galium boreale.
- Erigeron canus.
- Erigeron pumilus.
- Eriogonum racemosum.
- Pentstemon confertus.
- Pentstemon unilateralis.
- Pentstemon strictus.
- Geranium caespitosum.
- Delphinium scopulorum.
- Lupinus argenteus.
- Malvastrum coccineum.
- Campanula rotundifolia.
- Campanula parryi.
- Gaura coccinea.
- Aster bigelovii.
- Artemisia canadensis.
- Actinella floribunda.
- Orthocarpus purpureus albus.
- Stanleya pinnata.

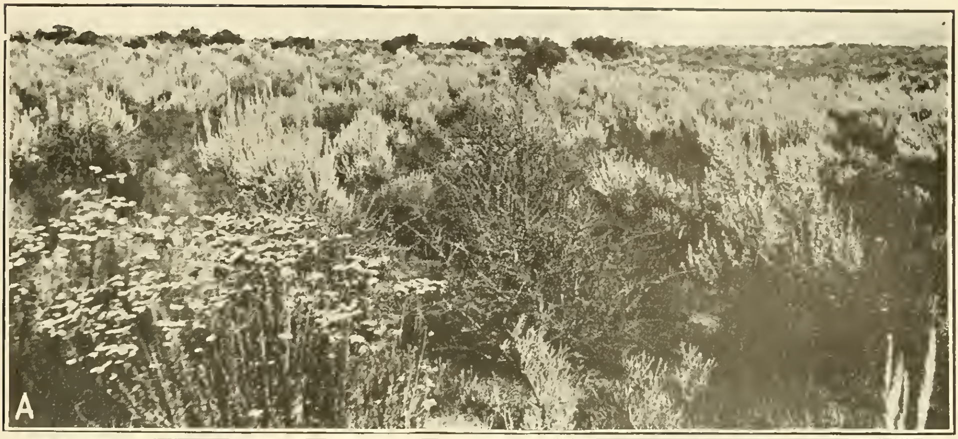
*Serotinal Societies:*
- Artemisia frigida.
- Grindelia squarrosa.
- Carduus undulatus.
- Carduus plattensis.
- Wyethia amplexicaulis.
- Wyethia arizonica.
- Wyethia helianthoides.
- Wyethia scabra.
- Chaenactis douglasii.

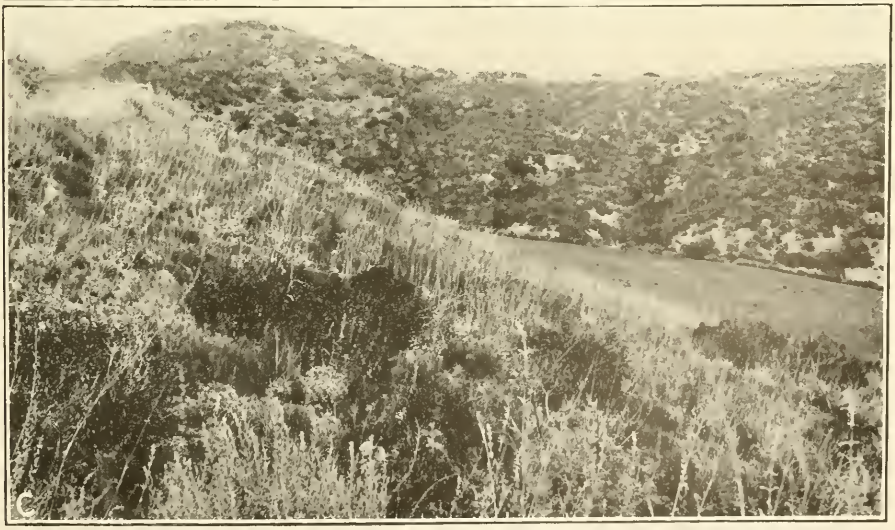
## THE COASTAL SAGEBRUSH.

### SALVIA-ARTEMISIA ASSOCIATION.

Range.—The association is limited to the region from northern Lower California to San Francisco Bay, and from southwestern Nevada to the Pacific Coast. It is characteristic of the lower foothills, between the *Stipa* grassland or the *Larrea* desert, and the *Adenostoma* consociation of the chaparral. It occurs with the latter so much in southern California that it has been regarded as a particular southern type of chaparral, but it now seems that this view can no longer be maintained. The first recognition

## Coastal Sagebrush





A. Contact of Basin Sagebrush with Coastal sagebrush and chaparral, Campo, California.

B. *Artemisia californica, Salvia mellifera,* and *Eriogonum fasciculatum* association, Elsinore, California.

C. Coastal sagebrush with *Adenostoma* in ravines, Temecula, California.

of this as a sagebrush association was made in 1918, and as a consequence it has received little or no special study. It owes its character to *Artemisia californica* as the major dominant. This is a typical sagebrush, resembling *Artemisia filifolia* closely in habit and *A. tridentata* in climax qualities, especially when it occurs as a pure consociation.

CONSOCIATIONS.

| | |
|---|---|
| ARTEMISIA CALIFORNICA. | SALVIA APIANA. |
| SALVIA MELLIFERA. | ERIOGONUM FASCICULATUM. |
| SALVIA LEUCOPHYLLA. | |

The most important consociation is *Artemisia californica*. It not only occurs in most of the groupings, but it also ranges widely along the Coast hills as a pure community. *Eriogonum fasciculatum* is the most frequent associate of the sagebrush, often with *Salvia mellifera*. *Salvia apiana* is restricted to the southern part of the area, and is more subclimax in nature than the others. *Eriogonum fasciculatum*, with the variety *polifolium*, has much the widest range, forming extra-associational communities in the *Larrea* desert, and the southwestern edge of the main sagebrush association. In southern California and Lower California, four dominants are frequently associated. Farther north the community is regularly constituted by *Artemisia californica*, *Eriogonum fasciculatum* and *Salvia mellifera*, or *leucophylla*. This is the typical grouping of the association, though any two of the dominants may occur together in this area. The association shows the usual tendency to break into pure consociations toward its borders. Along the edge of the desert it is represented chiefly by *Eriogonum fasciculatum*, and on the western slopes of the Coast Range by *Artemisia californica* (plate 35).

The Coastal sagebrush association is in intimate contact with the *Adenostoma-Ceanothus* chaparral and the *Larrea* desert. In former times it must have touched the *Stipa* bunch-grass community along much of the interior valley, and to-day the two are much mixed in southern California. Throughout its area, the sagebrush lies just below the *Adenostoma* consociation of the chaparral. The ecological requirements of the latter are so nearly equivalent to those of *Salvia* and *Eriogonum* in particular that these often seem an integral part of the chaparral. All the dominants mix so intimately with *Adenostoma* along the ecotone, owing to the characteristically diverse topography, that an absolute line of separation is out of the question. This is so often true of ecotones, however, that it does not affect the validity of the sagebrush association, as is readily seen when typical areas of the two formations are compared. This conclusion is supported likewise by a characteristic difference in the shrub form, and by the systematic relationships, as pointed out before. Toward the desert the intrusion is even greater and is best illustrated on the south side of the Mohave, where *Eriogonum fasciculatum* is regularly mixed with such desert dominants as *Larrea*, *Salvia carnosa*, *Salazaria mexicana*, *Trichostema lanatum*, and *Yucca*, as well as frequently with *Artemisia tridentata*, *Chrysothamnus nauseosus*, and *Atriplex canescens*.

No factor studies have been made in this association and the sequence of the dominants is a matter of inference. The five species are closely equivalent, though the topographic and seral relations indicate a definite and constant sequence. *Artemisia californica*, like *A. tridentata*, is the most mesophytic and under static climatic conditions would tend to form a pure climax. *Salvia mellifera* and *S. leucophylla* follow closely in requirements, while *Eriogonum* *fasciculatum* has a wider range of adjustment, from climax conditions with 15 to 20 inches of rainfall to desert ones at 5 to 10 inches, where it is represented by *Eriogonum f. polifolium*. *Salvia apiana* seems the least mesophytic and consequently is more or less subclimax, growing on rocky slopes or in other more or less disturbed areas.

## THE DESERT SCRUB CLIMAX.

### LARREA-PROSOPIS FORMATION.

Nature.—The desert scrub, or mesquite, resembles sagebrush and chaparral in both appearance and character. As the name indicates, it is distinctly the most xerophytic of the three, reaching its best development in a rainfall of 5 to 12 inches. The dominants are bushy shrubs, 3 to 6 feet high for the most part. The chief exceptions are *Prosopis* and *Acacia*, which often form trunks and become small trees on flood-plains and in other favorable situations. Most of the dominants possess the ability to produce root-sprouts, though to a smaller degree than the chaparral. To this they doubtless owe the many-stemmed habit as well as their dominance. With the exception of the typical dominant, *Larrea*, most of the species are deciduous, though many are imperfectly so and a number have evergreen stems or branches, as in *Opuntia*, *Parkinsonia*, and *Koeberlinia*. The characteristic feature which distinguishes the desert scrub most readily from chaparral and sagebrush is its very open structure. The bushes usually stand 10 to 30 feet apart in typical situations, and it is altogether exceptional that the crowns touch each other, even in the case of the less xerophytic *Prosopis* and *Acacia*. The spacing is evidently a consequence of low rainfall and resultant low water-content, necessitating a large area for adequate absorption by the roots. As would be expected, this seems to be correlated with the root habits of the various dominants. The individuals of *Larrea* are more widely separated than those of *Prosopis*, by reason of a shallow root system as well as a lower chresard. This produces three results generally typical of the desert scrub, all due to the large intervals in which more or less water is available superficially. The first is the presence of tall undershrubs which occupy the intervals in greater or less abundance, such as *Franseria*, *Isocoma*, *Parthenium*, *Gutierrezia*, *Hilaria*, etc. A second consequence is the development of a characteristic population in the intervals during the winter rains in February and March. A third result, which has an important bearing upon the relation of desert scrub to contiguous formations, especially the grassland, is the readiness with which it forms parks or savannahs. Such parks are an especial feature of the Southwest, where they mark the broad transition between the desert scrub and the grassland.

With respect to systematic relationship, the desert scrub is less homogeneous than chaparral or sagebrush. The three chief dominants belong to as many different families, *Larrea* to the *Zygophyllaceae*, *Prosopis* to the *Mimosaceae*, and *Flourensia* to the *Asteraceae*. The *Asteraceae* and *Leguminosae* are most important, and the *Rhamnaceae* next, while the *Liliaceae* are represented by *Yucca*, the *Gnetaceae* by *Ephedra*, the *Chenopodiaceae* by *Atriplex*, and the *Poaceae* by a shrubby grass, *Hilaria rigida*.

This particular type of scrub is known by various names in the different sections. In Texas it is called chaparral or mesquite, the latter being the usual name where *Prosopis* is prominent or predominant. From New Mexico westward, where *Larrea* is the chief dominant, the general name is greasewood. None of these will serve as a desirable name for the formation as a whole or for either of its associations. As previously suggested, it seems best to restrict the use of the word chaparral to the *Quercus-Ceanothus* climax. Mesquite is of too limited application in so far as the scrub community is concerned, being applied only to *Prosopis* or to *Prosopis* with some other related dominant, such as *Acacia*. The word has the further disadvantage of being used for a number of grasses, *Bouteloua*, *Bulbilis*, and *Hilaria*, probably because of their frequent association with the mesquite in grassy parks. Greasewood is the designation of several shrubs, but the common usage seems to agree with the scientific in confining the word to *Sarcobatus vermiculatus*. Hence, in seeking a readily usable name for this extensive formation, it has appeared necessary to employ two words, *i. e.*, desert scrub, the latter referring to its nature, the former to its typical habitat.

Range.—The area characterized by the desert scrub climax is difficult to delimit for two reasons. It shares with the sagebrush and chaparral formations the habit of breaking up along the line of contact with grassland or other scrub communities, and thus forming a broad ecotone of mixed or alternating communities. In addition, it is especially given to forming parks or savannahs with grassland, particularly along its northeastern edge and on the bajada slopes of mountains. This is typical of *Prosopis*, but it is also true to a large degree of *Yucca* and *Flourensia*, and, to a much smaller one, of *Larrea*. In Texas, for example, while the three dominants have not been seen together east of Ozona and Odessa, *Prosopis* is a regular feature in the grassland as far north as Lubbock, and it occurs frequently farther north, finally disappearing in southwestern Kansas. It also occurs generally, but more or less sparsely, in the desert plains grassland, from the mountains of western Texas and southern New Mexico to those of southern and central Arizona, where it is frequently associated with *Yucca radiosa*.

If the limits of the formation be determined by the presence of two of the three dominants in more or less complete control, its area will comprise southwestern Texas west of Odessa and Ozona, and the southern quarter of New Mexico. In Arizona the formation is limited to the southern third of the State, owing to the barrier of the central mountain ranges, and to the northwestern part beyond the Hualpai Mountains and the Grand Canyon. It is typical in general of southeastern California, east of the Laguna, San Jacinto, San Bernardino and Tehachapi Mountains, and the Antelope Valley. It occupies the southern portion of Nevada south and west of Caliente and also the extreme southwestern part of Utah. Its range in Mexico is unknown, but it is the typical formation of the northern part from the mouth of the Pecos westward through Lower California (MacDougal, 1904, 1908; Goldman, 1916 : 334, 338). A related community of *Prosopis* and *Acacia* extends eastward along the Rio Grande plain as far as the coast, but too little is known of it to warrant assigning it definitely to the desert scrub formation.

Unity of the formation.—The geographical unity of the desert scrub is perhaps greater than that of any other western formation. It constitutes a broad band 500 to 1,000 miles wide from trans-Pecos Texas to southern California and and Lower California. This suffers two great interruptions, one due to the Sierra

Madre Mountains, the other to the Gulf of California. Its greatest extension northward is found in Nevada, while it ranges southward in Mexico through Chihuahua and Durango. In altitude it reaches its major expression between 1,000 and 3,000 feet, but it occurs from sea-level to 4,000 feet or higher.

With respect to climate, the desert scrub is especially distinct. This is true of both temperature and rainfall. It has the lowest rainfall, the greatest evaporation, and the highest mean temperature of all the western climaxes, though the sagebrush approaches it closely in the matter of rainfall. The precipitation ranges from 2 to 12 inches, with the major portion of the formation lying between 5 and 10 inches. The highest rainfall occurs in trans-Pecos Texas, with 15 inches, and the lowest in the Colorado Desert with 2 inches. There is a general but irregular decrease from east to west, correlated with changes in the structure of the formation itself (fig. 6).

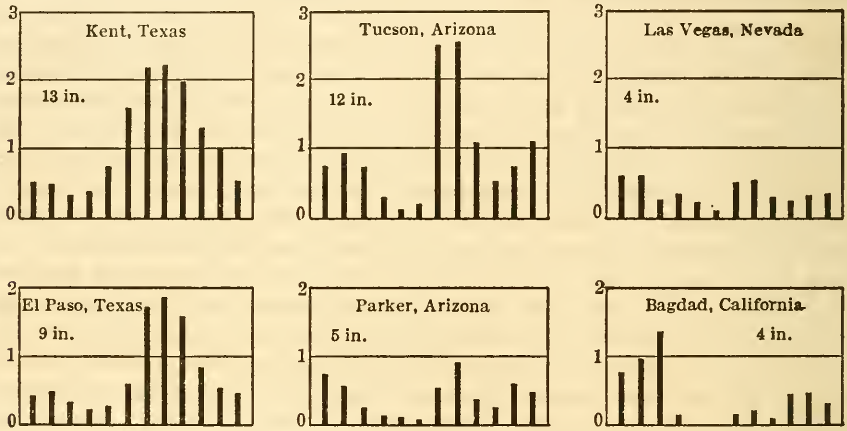



FIG. 6.—Monthly and total rainfall for representative localities in the associations of the desert scrub climax.

The floristic unity of the desert scrub is even greater than that of the other two scrub climaxes. The two most important dominants, *Larrea mexicana* and *Prosopis juliflora*, occur throughout. This is likewise true of *Atriplex canescens* and *Fouquiera splendens*, though these are probably subclimax in character. *Acacia*, *Yucca*, and *Ephedra* extend throughout the area, but the species change to some degree. *Acacia greggii* is found from western Texas to Lower California, while *A. constricta* ranges nearly as widely. *Yucca radiosa* and *Y. macrocarpa* are present from western Texas through Arizona, but are largely replaced in California and Lower California by species ecologically equivalent. While four or five species of *Ephedra* occur in the formation, these are essentially similar if not identical in ecological character. Among the undershrubs, *Gutierrezia*, *Isocoma*, *Krameria*, and *Zinnia* are distributed over most of the formational area.

The ecological unity of the desert scrub is indicated by the fact that practically all of the dominants are many-stemmed, bushy shrubs, usually with the habit of root-sprouting well developed. This is essentially true of *Yucca*, especially the most important species, *Y. radiosa*, in spite of its very different appearance. *Prosopis* and *Acacia* usually constitute exceptions, particularly when found on flood-plains and in washes. However, on uplands and on dunes, these too are regularly many-stemmed. As would be expected, the taller dominants are uniformly deep-rooted, the depth of the roots being determined largely by that of the soil. Naturally all are intense xerophytes, in which the chief adaptations are the reduction and loss of leaves and twigs, the development of evergreen leaves or branches, or of a thick or glutinous cuticle. The great majority are deciduous, *Larrea* and *Yucca* furnishing the most important exceptions. Nearly all agree likewise in being somewhat resistant to alkali. This is a direct outcome of the prevalence of halophytic areas in the valleys and bolsons. Many of the most striking playa regions occur within the area of the formation. The succession on saline soils is essentially identical from one end of the area to the other. This is true also of the sand-dune and hummock succession, which is probably the most widespread of all. The third important succession is that of rocky ridges and slopes. While this shows the same stages in both associations, it is characterized by *Agave, Yucca, Opuntia,* and *Dasylirium* in the east, and by *Fouquiera, Parkinsonia, Cereus,* and *Encelia* in the west. The close equivalence of these two subclimaxes is shown by the presence of *Fouquiera, Dasylirium,* and *Yucca radiosa* in both.

With respect to its origin, this formation is one of the most homogeneous. The dominants are all subtropic or Mexican in distribution, with the exception of *Atriplex canescens,* while this and *Gutierrezia* are the only ones that range far beyond the formational limits to the north. This conforms to its occurrence as a broad belt on both sides of the Mexican boundary. The gradual differentiation of this formational mass has reached a point where it seems desirable to recognize two associations, the one centering about the Rio Grande and the other around the Colorado. The reasons for this are discussed in the following section.

Structure of the formation.—The general abundance of *Larrea* throughout the formation gives the impression that the latter contains a single association. A scrutiny of the various groupings discloses a number of constant differences between the eastern and western portions, which warrant the recognition of two corresponding associations. The statistical evidence from more than 250 localities is supported by the comparative studies made in 1918, when the formation was examined in its entirety from Texas to California. In the table on the following page the occurrence of the dominants and their major groupings are shown for the two associations. The line which separates them is in general that of the Galiuro and Dragoon ranges in southeastern Arizona.

It is evident that *Larrea, Prosopis,* and *Flourensia* far outrank all of the others in importance, and that *Franseria* is three times as frequent as *Acacia* in the association where they meet, in addition to being much more abundant. *Acacia, Atriplex, Yucca, Ephedra, Fouquiera,* and *Condalia* are all more or less regular associates of the primary dominants in both associations. While typically less abundant, they sometimes equal or exceed them in number. The division into two associations rests chiefly upon the complete absence of *Flourensia* in the one, as a dominant at least, and of *Franseria* in the other, and upon the more uniform distribution of *Prosopis* in the *Larrea-Flourensia* type. These differences are reflected in the figures showing the occurrence of the four groupings. Of the other dominants, *Atriplex* is more important in the west, and *Yucca* and *Ephedra* in the east, while *Fouquiera* varies but little between the two. *Parkinsonia, Cereus,* and *Dalea* are confined to the western, and *Rhus* to the eastern association. Of the undershrubs, *Gutierrezia* is much more important in one, and the corresponding genus, *Isocoma,* in the other. *Hilaria* and *Encelia* are confined to the *Larrea-Franseria* association, *Microrhamnus* and *Parthenium* practically to the *Larrea-Flourensia,* while *Krameria* and *Zinnia* show little difference. All in all, the evidence supports the recognition of two recently differentiated but fairly distinct associations.

*Summary of dominants.*

| | Larrea-Flourensia (Texas-New Mexico). | Larrea-Franseria (Arizona-California). | | Larrea-Flourensia (Texas-New Mexico). | Larrea-Franseria (Arizona-California). |
|---|---|---|---|---|---|
| Total number of localities | **168** | **100** | Fouquiera | 14 | 12 |
| Larrea | 110 | 82 | Condalia | 16 | 8 |
| Prosopis | 110 | 43 | Rhus | 4 | 0 |
| Flourensia | 97 | 0 | Koeberlinia | 7 | 2 |
| Franseria | 0 | 35 | Microrhamnus | 9 | 0 |
| Acacia | 26 | 12 | Parkinsonia | 0 | 10 |
| Larrea-Prosopis | 75 | 35 | Cereus | 0 | 8 |
| Larrea-Flourensia | 67 | 0 | Dalea | 0 | 8 |
| Flourensia-Prosopis | 50 | 0 | Hilaria | 0 | 8 |
| Larrea-Flourensia-Prosopis | 30 | 0 | Encelia | 0 | 8 |
| | | | Parthenium | 7 | 1 |
| Larrea-Franseria | 0 | 31 | Gutierrezia | 38 | 3 |
| Atriplex | 15 | 28 | Isocoma | 6 | 15 |
| Yucca | 31 | 8 | Krameria | 5 | 6 |
| Ephedra | 15 | 3 | Zinnia | 7 | 11 |

Associations.—The desert scrub formation consists of two associations, the *Larrea-Flourensia* and the *Larrea-Franseria.* In addition there is the closely related community of *Prosopis* and *Acacia,* typical of the lower valley of the Rio Grande and probably to be regarded as a subclimax. Besides the differences in composition already noted, the two associations differ much in structure. In the *Larrea-Flourensia* type, the three dominants are of nearly equal importance, as is shown by their respective frequence, viz, *Larrea* 110, *Prosopis* 110, and *Flourensia* 97, as well as by that of the four major groupings. Moreover, the latter show that the dominants are frequently or regularly mixed on more or less equal terms. *Gutierrezia* is the characteristic undershrub. In the *Larrea-Franseria* community the ground-tone is given chiefly by *Larrea.* The uniform olive-brown color is less broken by *Prosopis,* except where the two mix along the line of contact in valleys and draws, or in sandy soils. *Flourensia* is altogether lacking. *Franseria,* though an undershrub, often ranks next to *Larrea* in importance, and gives a distinctive impress to the community. In some places a similar rôle is taken by *Hilaria,* and not infrequently *Franseria, Hilaria,* and *Encelia* are to be found mixed or alternating with each other. A further distinction between the two associations is found in the much greater frequency of *Yucca* and *Ephedra* in the *Larrea-*

*Flourensia* type. Over much of the area one or both will regularly occur in abundance with *Prosopis* or *Flourensia*, though rarely with *Larrea* where it is most typical.

Their relation to the subclimaxes of rocky slopes and ridges marks another difference between the two associations. In the east the subclimax consists of *Yucca*, *Agave*, *Dasylirium*, and *Fouquiera* chiefly, and this explains why *Yucca radiosa* and *macrocarpa* are such frequent constituents of the scrub below. In the west *Yucca* is largely confined to the grasslands, and the subclimax consists primarily of *Parkinsonia*, *Cereus*, and *Fouquiera*. All of these mix with *Larrea* to a considerable extent, and are sometimes found in the heart of the association, where they are often to be regarded as relicts. Another distinctive feature of the *Larrea-Franseria* type is the presence of the cylindric *Opuntias*, such as *O. fulgida*, *O. spinosior*, *O. versicolor*, etc. While *Opuntia* occurs sparsely in the eastern association, it has nowhere been found in the abundance which characterizes it in Arizona. Here the species of *Opuntia* make important communities on the lower bajada slopes with *Larrea* or in the broad washes with *Prosopis*.

Finally, a unique feature of the *Larrea-Franseria* scrub is the development of a more or less continuous cover of winter annuals from January or February to April. This is the direct consequence of a secondary maximum of rainfall at this time, and is very similar to what occurs in southern California. This transitory community of annuals is little if at all developed in Texas and New Mexico. Here the rainfall from January to April is less than 15 per cent of the annual, while in Arizona and southeastern California it is 30 to 60 per cent of the total. The distribution of the rainfall seems also to explain the change from one association to the other in eastern Arizona. New Mexico and western Texas receive 60 to 75 per cent of their annual rainfall between April 1 and September 30, while the *Larrea-Franseria* region of Arizona and California receives but 20 to 50 per cent during the same period. Furthermore, the greater tendency of the eastern type to form savannahs is explained by the fact that the seasonal distribution of the rainfall is practically the same as that for grassland.

**Relation to other formations.**—The chief contact of the desert scrub is with the grassland formation. This is the case in trans-Pecos Texas, New Mexico, and Arizona, where the contact is with the desert plains association. This is especially true of elevated plains and of bajadas with northerly slopes. On slopes with southerly and westerly exposure or rocky surface the scrub is usually separated from chaparral or woodland by a broad band of the *Yucca-Agave* community in the east or one of *Parkinsonia-Cereus-Fouquiera* in the west. The lines of contact are often broad ecotones and, in the case of the grassland, they regularly develop into parks of scrub and grass several miles wide along the mountain ranges and hundreds of miles in length over the southern Great Plains. In Nevada and adjacent Arizona and Utah, the *Larrea* scrub yields to the sagebrush formation, and in California it lies in touch with the sagebrush or chaparral, or less frequently with woodland. At the western edge of the Edwards Plateau in Texas, desert scrub meets the chaparral of oak, and *Prosopis* becomes the typical shrub of the level valleys and washes throughout the region.

## THE EASTERN DESERT SCRUB.

### LARREA-FLOURENSIA ASSOCIATION.

This community consists primarily of *Larrea mexicana*, *Prosopis juliflora*, and *Flourensia cernua*, though other species often play a dominant part in it, as shown by the following table:

| Dominants (total number of localities, 168). | No. | Halfshrub dominants. | No. |
|---|---|---|---|
| Larrea mexicana | 110 | Gutierrezia sarothrae | 38 |
| Prosopis juliflora | 110 | Microrhamnus ericoides | 9 |
| Flourensia cernua | 97 | Zinnia pumila | 7 |
| Yucca radiosa and macrocarpa | 31 | Opuntia chlorotica | 5 |
| Acacia greggii and constricta | 26 | Opuntia phaeacantha | 3 |
| Ephedra torreyana | 15 | Parthenium incanum | 7 |
| Atriplex canescens | 15 | Isocoma hartwegii | 6 |
| Condalia lycioides | 16 | Krameria glandulosa | 5 |
| Fouquiera splendens | 14 | Chrysoma laricifolia | 1 |
| Koeberlinia spinosa | 7 | Psilostrophe cooperi | 2 |
| Opuntia arborescens | 5 | | |

While any of the shrub dominants may occur alone, this is rarely the case, even with the three chief species. In the great majority of cases, two of the latter occur mixed in varying proportions, usually with a smaller quantity of one of the lesser dominants. This is shown by the occurrence of the four principal groupings, as follows:

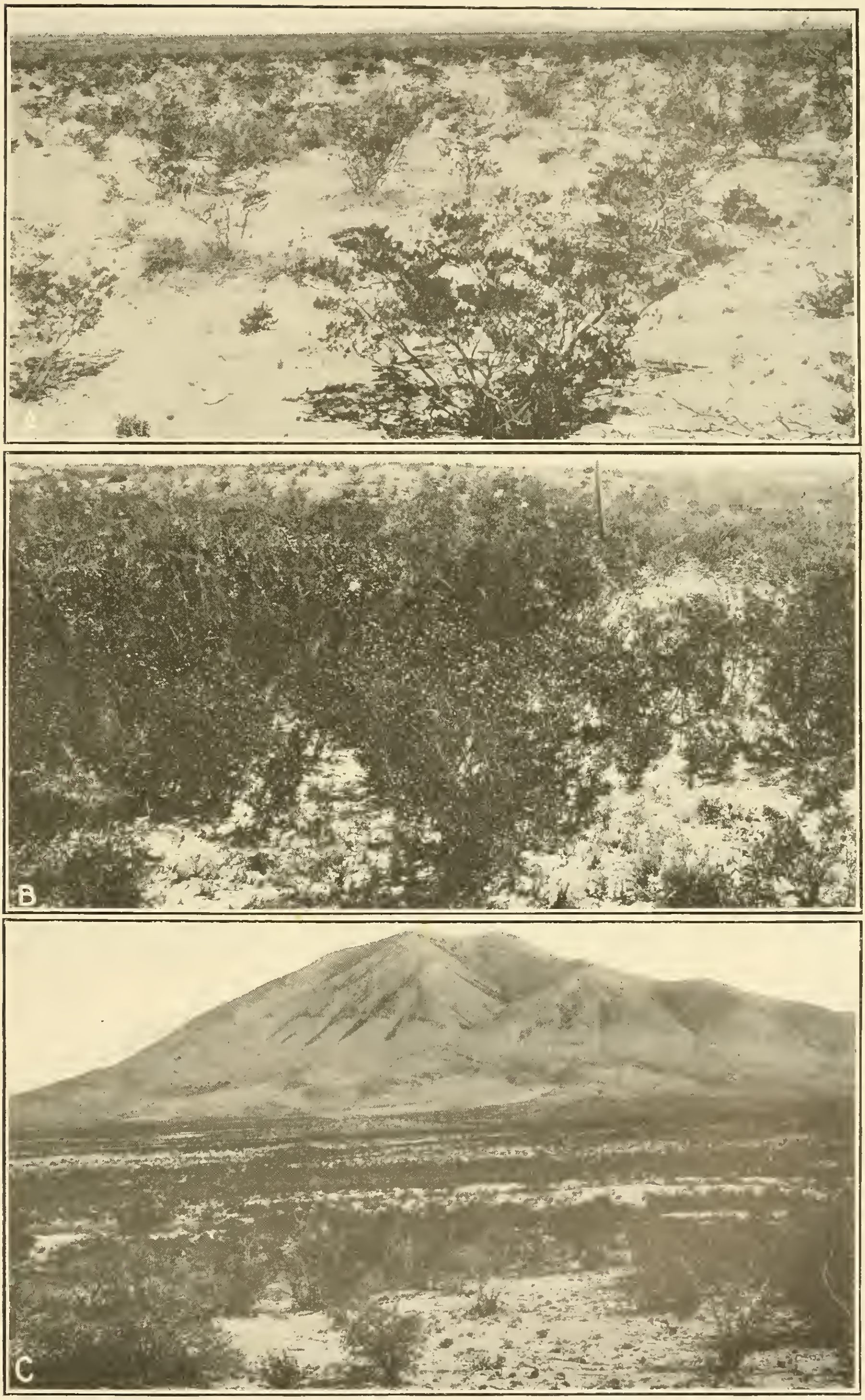
| Species. | No. | Species. | No. |
|---|---|---|---|
| Larrea-Prosopis | 75 | Flourensia-Prosopis | 50 |
| Larrea-Flourensia | 67 | Larrea-Flourensia-Prosopis | 30 |

Other important groupings are *Acacia* with *Prosopis* and *Larrea*, *Atriplex* with *Prosopis*, and *Yucca-Ephedra* or either alone with *Prosopis*, or with various mixtures of the primary dominants. A layer of undershrubs is more or less constantly present. Usually this consists of *Gutierrezia*, less frequently of *Isocoma*, *Krameria*, or *Zinnia*, or two or three of these may be mixed in varying degree (plate 36).

This association occupies the levels above the saline valleys and playas to altitudes of 3,500 to 4,000 feet, where it passes into grassy parks in which the shrubs are secondary. It occupies trans-Pecos Texas, as well as a considerable area northeast of the great bend of the Pecos River, adjacent Mexico, southern New Mexico, and eastern Arizona. Two of the dominants, *Prosopis* and *Acacia*, form an extensive community on the plain of the lower Rio Grande and extend over much of the Panhandle region as a low open scrub in the grassy plains.

Correlations and sequence.—The general correlation of the *Larrea-Flourensia* scrub is with an annual rainfall varying from 16 inches along the Pecos to 8 inches in south-central and southwestern New Mexico. Over the same area, the annual evaporation ranges from 40 to 60 inches. The distribution

Eastern Desert Scrub




A. *Larrea* consociation, Stockton, Texas.
B. *Larrea-Flourensia* association, Pecos, Texas.
C. *Larrea* plain, Sierra Blanca, Texas.

of the rainfall is peculiar to this general region in that less than a third of the total usually falls in the first six months, while July, August, and September receive more than half. On the higher levels near the mountains, May and June are marked by more rain and the climate there becomes adapted to grassland. Since relatively high ranges occur at intervals of 50 to 100 miles from the Davis and Guadalupe Mountains on the east to the Santa Catalina and Whetstone chains on the west, it is evident why the desert scrub constantly mixes and alternates with grassland throughout the region.

While factor studies of the dominants are lacking, their successional relations are brought into evidence repeatedly by changes in altitude, topography, and soil. These have to do chiefly with water-content, but salinity must frequently be taken into account as well. The basic sequence of the association is shown by *Prosopis*, *Flourensia*, and *Larrea*, wherever ridges and valleys occur. This is especially marked in the valley of the Pecos River from Fort Stockton and Grandfall to the foothills of the Davis Mountains. The primary sequence is *Prosopis* in the middle of the valley, a mixture of *Prosopis* and *Flourensia*, in which *Flourensia* becomes more and more abundant until *Larrea* appears as the slope begins, followed by mixed *Flourensia-Larrea*, which becomes pure *Larrea* on the ridges or *Larrea* with sparse *Flourensia* and *Prosopis*. More frequently, the valleys are shallower and poorly drained, with *Flourensia* in the center, followed by a zone of *Flourensia-Larrea* on the slope and of nearly pure *Larrea* on the ridge. In the case of valley washes, where the soil is more or less sandy, *Prosopis* and *Larrea* exhibit a similar relation from valley to ridge. This typical relation to water-content is also found in sandy soils where *Prosopis* forms hummocks and dunes. As the soil becomes more stable and the available water decreases, *Flourensia* enters and finally *Larrea*, or where *Flourensia* is absent, *Larrea* enters directly. Of the other dominants, *Yucca radiosa* and *Acacia greggii* most nearly resemble *Prosopis* in their water use. The former has a wider margin of adjustment to more xerophytic conditions, and the latter a narrower one. *Yucca macrocarpa* is more xerophytic than *Y. radiosa* and is more often associated with *Larrea* as a consequence. *Ephedra torreyana* makes much the same demands as *Prosopis* and *Yucca radiosa*, often occurring in sandy soils with them, as well as in gumbo valleys with *Flourensia*. *Condalia* and *Koeberlinia* usually occur sparsely though generally in the harder soils. They have been seen but rarely in dominant or pure communities, and such cases were in small closed valleys or "swags," often with a gypsum soil. *Acacia constricta* has in general somewhat higher water requirements than *Larrea*, while *Fouquiera* approaches the latter closely in many places. Its preference, however, is for rocky slopes in which the available water should be higher.

The undershrub dominants are all more xerophytic than the shrubs with which they are associated. This is indicated by their lower stature and the location of their root-systems at a higher level. *Gutierrezia* and *Isocoma* are nearly equivalent and are regularly associated with *Prosopis*, or a mixture of it with *Yucca*, *Atriplex*, or *Acacia*, usually in sandy soil. They are essentially corresponding species, occasionally occurring together, but found for the most part in their respective associations. *Zinnia* and *Krameria* are typical associates of *Larrea*. *Parthenium* is found more frequently with *Larrea*, but occurs in various mixtures of the three primary dominants.

*Prosopis* is the most tolerant of salinity, though practically all the dominants posssess this ability in a large measure. *Prosopis* occurs regularly with *Sporobolus airoides* over great saline flats, especially in the valley of the Pecos. It is constantly associated with *Atriplex canescens* on sandy dunes and hummocks throughout. Typical areas of great extent occur from Sierra Blanca to El Paso along the Rio Grande, and northward through the Jornada del Muerto and the Tularosa Desert. *Prosopis* also associates with *Atriplex canescens* and *A. polycarpa* on alkaline plains and occasionaly thrives in saline meadows of *Distichlis spicata.* Its ability to withstand high concentrations is most conclusively shown by its intimate association with *Spirostachys occidentalis* and *Dondia moquini* in the Pecos Valley. *Flourensia* and *Ephedra* are both more halophytic than *Larrea* as a rule. In the pure gypsum soils of the Pecos Valley, *Larrea* is the first shrub to enter in the drier areas, and *Condalia* the first in the swales. Both of these are followed by *Prosopis,* and this by either *Flourensia* or *Acacia.*

The seral sequence of *Prosopis, Flourensia,* and *Larrea* is confirmed by their climatic relations in regions of greater rainfall, such as Texas. In the form of savannah or forest-like thicket, *Prosopis* occurs generally in the western half of Texas under a rainfall of 20 to 30 inches. *Flourensia* first appears at about 20 inches, but does not become dominant until a rainfall of 16 inches is reached. *Larrea* appears last at a rainfall of about 16 inches, where it quickly takes rank as a dominant.

*Prosopis* also differs from *Larrea* and *Flourensia* is being a characteristic dune-former, a habit doubtless related to its more mesophytic nature. Mesquite dunes and hummocks are a typical feature of the formation from the Panhandle of Texas to the Salton Sea. They are due to the ability of *Prosopis* to grow faster than the sand accumulates, a property almost wholly lacking in both *Larrea* and *Flourensia.* It is shared in greater or less degree by *Atriplex canescens, Ephedra torreyana, Yucca radiosa, Artemisia filifolia,* and *Dalea scoparia,* with the result that one or more of these are usually associated with *Prosopis* in such areas. The much wider range of the mesquite is due to the fact that its sugary pods are eagerly eaten by animals, which scatter the well-protected seeds. It suffers some disadvantage in that it is often browsed by stock, while *Flourensia* is rarely eaten, and *Larrea* practically never. This becomes a marked handicap where the kangaroo rats are abundant, as they make their mounds in mesquite bushes almost exclusively and feed upon both branches and roots.

### SOCIETIES.

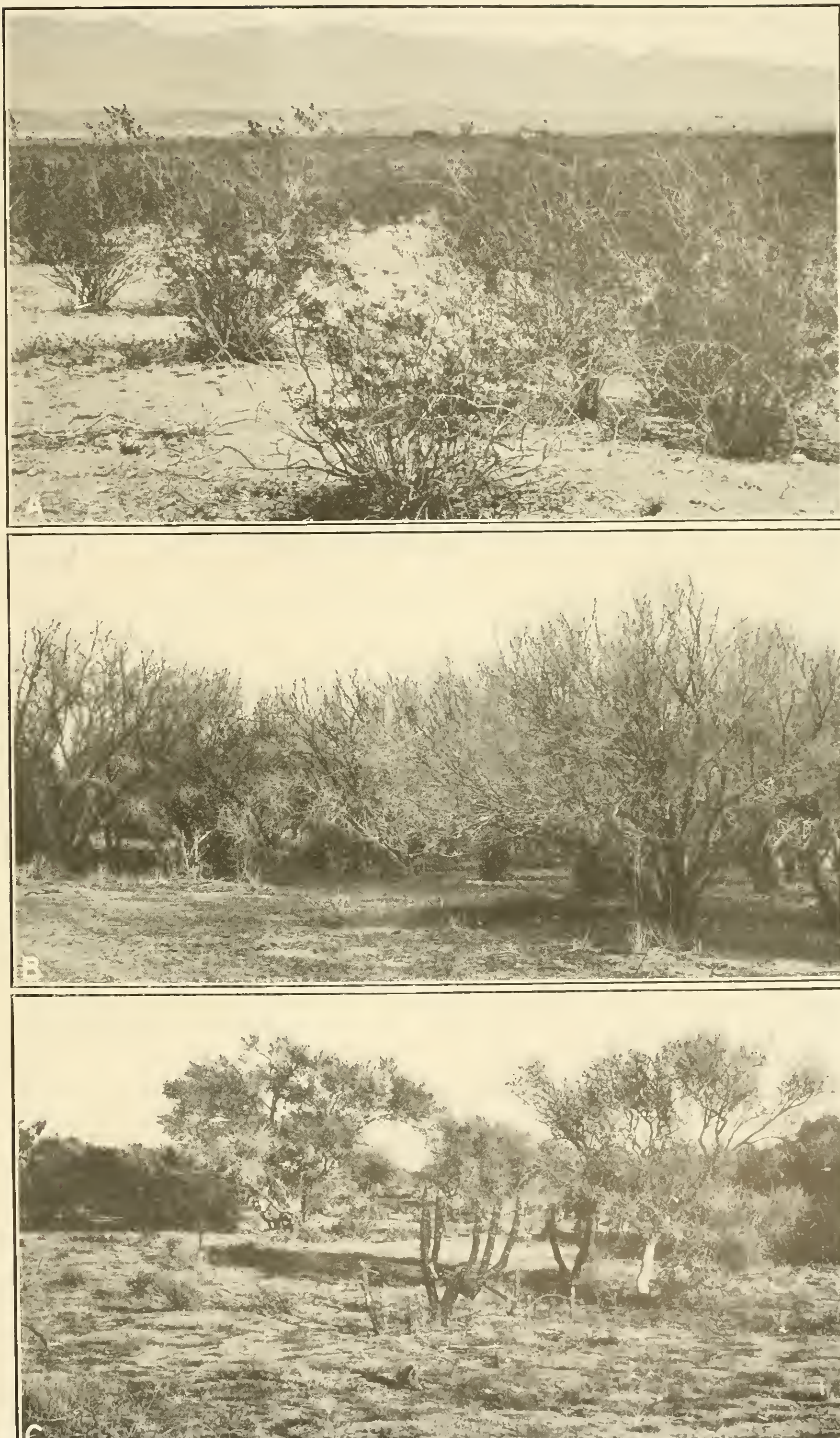
No study has yet been made of the seasonal aspects of the eastern desert scrub and an adequate treatment of its societies is impossible. Since the majority are alike for both associations, a fair understanding of them may be obtained from the list on page 176.

## THE WESTERN DESERT SCRUB

### LARREA-FRANSERIA ASSOCIATION.

Nature.—This association is regarded as the more typical one of the formation. The evidence of this is found chiefly in the larger number of dominants and in the more extensive continuous areas occupied by them. The western scrub also exhibits much more of the traditional appearance of desert, due

Western Desert Scrub



A. *Larrea* consociation, Tucson, Arizona.
B. *Prosopis* consociation, San Pedro Valley, Arizona.
C. *Parkinsonia torreyana* and *Acacia greggii*, Tucson, Arizona.

largely to the abundance of cacti in it. In this respect it resembles closely the deserts of Mexico, of which it is probably a continuation. At present it likewise differs from the eastern type in general absence of grasses, though this may be largely the work of animals. While *Larrea* is still the most typical dominant, the community shows extensive differentiations in which it is nearly or entirely lacking. However, it also appears to have a wider range of adaptation and often becomes a shrub 10 to 15 feet tall in washes. This seems to be connected with the greater abundance of tall shrubs or low trees, such as *Parkinsonia*, *Olneya*, and *Dalea*. As already indicated, a characteristic feature is the great development of communities of low winter annuals, the many species of which cover the ground with a brilliant carpet (plate 37).

Extent.—The eastern limits of the *Larrea-Franseria* community are indicated by the Galiuro, Whetstone, and Huachuca Mountains in Arizona. It extends northward in the valleys of the San Pedro, Gila, Salt, and Verde Rivers to find its northern limit along the mountains of central Arizona. On the west the desert scrub occupies the Colorado Desert and reaches into southwestern Utah and southern Nevada, though greatly reduced in number of dominants. In California it is the climax vegetation of the Mohave Desert and Death Valley, though much of the area is covered with the halophytic subclimax of *Atriplex* and related dominants. West of the Salton Basin several of the dominants reach the lower slopes of the San Jacinto and Laguna Mountains. Desert scrub is the most important association throughout Lower California, while in Mexico proper it occurs as far south as Zacatecas and San Luis Potosi. The occurrence of both *Prosopis* and *Larrea* southward to Argentina indicates a still greater range for this or some related associations.

DOMINANTS.

*Shrubs:*
- Larrea mexicana.
- Prosopis juliflora.
- Acacia constricta.
- Parkinsonia microphylla.
- Acacia greggii.
- Opuntia fulgida.
- Opuntia f. mamillata.
- Opuntia spinosior.
- Parkinsonia torreyana.
- Parkinsonia aculeata.
- Dalea spinosa.
- Olneya tesota.
- Cereus giganteus.
- Fouquiera splendens.
- Celtis pallida.
- Opuntia versicolor.
- Opuntia arbuscula.
- Condalia lycioides.
- Condalia spathulata.
- Simmondsia californica.
- Atriplex canescens.

*Shrubs*—continued.
- Atriplex polycarpa.
- Prosopis pubescens.
- Yucca radiosa.
- Koeberlinia spinosa.
- Mimosa biuncifera
- Ephedra trifurca.
- Ephedra nevadensis.
- Salazaria mexicana.
- Dalea emoryi.
- Dalea schottii.
- Lycium spp.
- Cereus thurberi.
- Adelia phyllarioides.
- Holacantha emoryi.
- Canotia holacantha.

*Halfshrubs:*
- Franseria dumosa.
- Franseria deltoidea.
- Isocoma coronopifolia.
- Isocoma c. hartwegii.

*Halfshrubs*—continued.
- Isocoma veneta.
- Opuntia discata.
- Opuntia chlorotica.
- Zinnia pumila.
- Hymenoclea salsola.
- Calliandra eriophylla.
- Chrysoma laricifolia.
- Lippia wrightii.
- Baccharis wrightii.
- Trixis californica.
- Opuntia phaeacantha.
- Opuntia engelmannii.
- Encelia farinosa.
- Encelia frutescens.
- Krameria glandulosa.
- Hilaria rigida.
- Psilostrophe cooperi.
- Yucca baccata.
- Gutierrezia sarothrae.
- Bebbia juncea.
- Parthenium incanum.

In addition to the above, a large number of other shrubs, halfshrubs, and succulents occur frequently but sparsely, or in occasional clan-like groups. Others are dominant at higher levels, such as species of *Agave*, *Dasylirium*, or at lower ones, *Atriplex*, *Hymenoclea*, etc. The relation of all of these is either actually or potentially successional, or they are of minor importance and can not be further considered in a brief account.

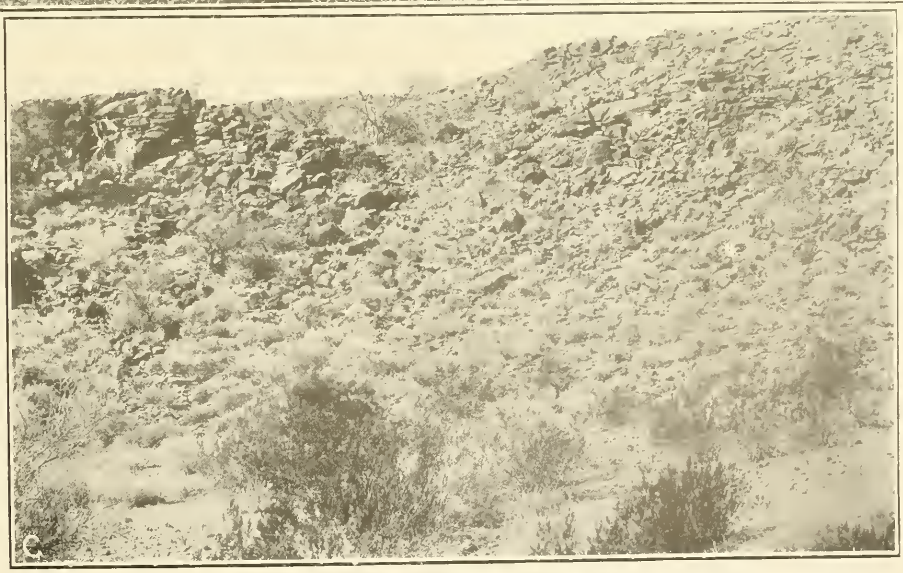
Structure.—The general structure of the desert scrub is clearly revealed by the color-tones, as seen in a bird's-eye view of one of the great intermountain valleys. Such a view of the Santa Cruz Valley from the Tucson Mountains shows three clear differentiations of the scrub mass. The long dissected bajada slopes are olive-green with *Parkinsonia*, *Cereus*, *Fouquiera*, and their associates. The flood-plains of the valley are vivid green with *Prosopis* and *Acacia*, and the central mass on the general level of the plain is bronze with *Larrea*. The courses of the streams are marked chiefly by *Populus*, *Sapindus*, *Fraxinus*, *Juglans*, and *Celtis*, while a nearer view reveals seral communities of *Hymenoclea*, *Baccharis*, and *Chilopsis* in the sandy washes and of *Atriplex* and *Dondia* in saline areas. Finally, there is a striking inversion of the species of the valleys, by which *Prosopis*, *Acacia greggii*, *Parkinsonia torreyana*, *Olneya tesota*, and others are carried up the bajada slopes or up broad canyons into the zones above.

As a consequence, the general zonation of the regions is as follows: (1) subclimaxes of the river-bed and salt-spots; (2) the valley community of *Prosopis*, *Acacia greggii*, and *Parkinsonia torreyana;* (3) the central mass of the midland plain, consisting chiefly of *Larrea*, often with much *Acacia constricta;* (4) the community of bajadas and foothills, characterized by *Parkinsonia microphylla*, *Cereus*, and *Fouquiera;* (5) the *Prosopis-Acacia* areas of the canyons and savannahs of the mountain ranges. The same zonal relations are seen in miniature throughout the area wherever changes of soil, drainage, or elevation occur to modify the control of the dominants. As these features recur constantly, owing to the more or less torrential nature of the rainfall, each zone is much modified by the mingling or alternation of dominants which normally grow above or below it. Such alternation is a regular feature of the association and explains the variety and frequence of the groupings as shown below (plate 38).

Groupings.—A special study has been made of the grouping of the major dominants over the Tucson plain and the bajadas and foothills of the surrounding ranges. The primary purpose was to throw light upon the degree of equivalence of the various dominants, based upon *Larrea* as the final dominant. It serves also to give a clear idea of the relative importance of the different species, and the frequence and complexity of the various groupings. The area covered is about 40 miles in length from the Santa Catalina Moun-

| Species. | Dominant. | Present. | Species. | Dominant. | Present. |
|---|---|---|---|---|---|
| Larrea mexicana | 60 | 8 | Koeberlinia spinosa | 0 | 4 |
| Prosopis juliflora | 60 | 9 | Isocoma coronopifolia | 40 | 4 |
| Parkinsonia microphylla | 41 | 5 | Franseria deltoidea | 18 | 4 |
| Acacia (constricta, greggii) | 37 | 5 | Encelia farinosa | 6 | 2 |
| Cereus giganteus | 34 | 8 | Zinnia pumila | 5 | 1 |
| Fouquiera splendens | 22 | 9 | Krameria glandulosa | 4 | 2 |
| Opuntia (fulgida, spinosior, versicolor) | 22 | 20 | Larrea-Prosopis | 35 | 10 |
| Olneya tesota | 10 | 4 | Larrea or Prosopis with Acacia | 34 | 7 |
| Atriplex (canescens, polycarpa) | 7 | 5 | Larrea-Parkinsonia | 24 | 7 |
| Condalia lycioides | 7 | 3 | Larrea with Cereus, or Fouquiera | 15 | 5 |
| Celtis pallida | 6 | 7 | Parkinsonia with Cereus, Fouquiera or both | 37 | 5 |
| Simmondsia californica | 6 | 1 | | | |
| Yucca radiosa | 0 | 5 | | | |

Western Desert Scrub



A. *Larrea* and *Franseria dumosa*, Ajo, Arizona.
B. *Larrea*, *Prosopis* and *Hilaria rigida*, Ajo, Arizona.
C. *Encelia farinosa* on lava ridge, Ajo, Arizona.

tains on the north to the Santa Rita on the south, and about 30 miles wide from the Rincons to the Tucson Range at the west. It was traversed in all directions and the results are thought to be representative. The total number of localities considered is 110.

The number of dominants in each grouping, irrespective of those of secondary importance, varies from 2 to 6, with the following frequency: two dominants, 24; three, 28; four, 38; five, 14; six, 5.

**Factor relations.**—The wide adaptability of the desert scrub climax is shown by its occurrence in a region where the rainfall varies from 2 to 16 inches. In this respect it excels even the sagebrush formation. The desert scrub of Texas and New Mexico is found in a rainfall of 7 to 16 inches. The western type has a much wider range. In southeastern Arizona it occurs in a rainfall as high as 12 to 14 inches, while in the Colorado Desert it is still dominant under a rainfall of 2 to 3 inches. The evaporation is also much higher in the western association. From April to September it ranges from 54 inches at Tucson to 71 inches at Calexico, in comparison with 40 to 54 inches in Texas and New Mexico. The contrast would be even greater if the total annual evaporation were considered, as should be the case with a community containing so many evergreen or nearly evergreen dominants. The more xerophytic nature of the climate is clearly reflected in the greater number of cacti in the *Larrea-Franseria* scrub, though this probably has a direct relation to winter temperatures as well (Shreve, 1914 : 194). In so far as the leafy shrubs are concerned, the lower rainfall and higher evaporation are compensated in large measure by the distribution of rain during the year. In southeastern Arizona nearly 60 per cent of the rain falls during the period from April 1 to September 30, and the dominant vegetation is grassland savannah, as already pointed out for much of the area in southern New Mexico. The percentage of spring and summer rain decreases rapidly across southern Arizona to become 30 per cent at Yuma and 20 per cent at Calexico. The latter represents the typical winter rainfall of California, which finds expression at the lower levels in the characteristic sclerophyll chaparral. Thornber (1910; cf. Spalding, 1909 : 96) has pointed out the relation of this difference of rainfall in eastern and western Arizona to the abundance of winter annuals as well as that of grasses. He also shows that there is a constant difference throughout the year of one-half to one inch of rainfall between the desert scrub and the desert plains grassland (l. c., 256).

While a number of quantitative studies have been made of the desert scrub in the region of Tucson, those of Spalding (1909 : 91) are the only ones which bear directly upon the comparative factors for different dominants or communities. The curves showing the march of water-content from October 1907 to April 1908 are of the most significance. These are given for the *Parkinsonia-Fouquiera* community of Tumamoc Hill, the *Larrea* consociation of the slope, the community of *Parkinsonia torreyana* and *Acacia greggii* in a wash, and the *Prosopis* consociation of the flood-plain. These are in general agreement with the topographic and successional evidence in that the hill and flood-plains show the highest water-content and the slope and wash the lowest. However, it seems certain that the *Larrea* slope or plain is typically drier than the wash containing *Parkinsonia*, *Acacia*, and *Prosopis*, in spite of the figures. This is clearly indicated by the author himself in his discussion of conditions in the wash (l. c., 14). A comparison of the curves for the hill and the flood-plain are especially instructive. The former are regularly higher, due partly to the fact that they were taken on the north slope, but the two sets are sufficiently alike to furnish a ready explanation of the characteristic inversion by which *Prosopis* and *Acacia greggii* in particular occur in the foothills (plate 39).

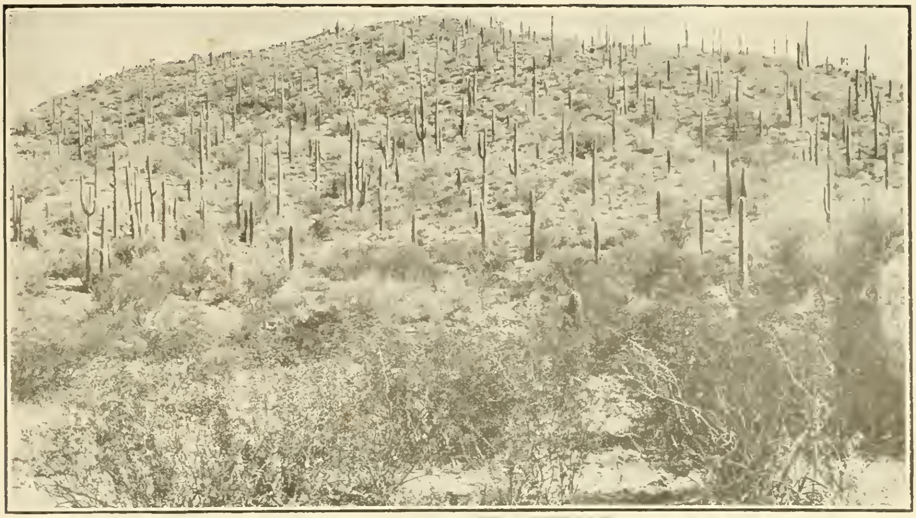
Successional relations.—No quantitative studies have been made of the actual or potential succession in the desert scrub climax. While the movement is necessarily slow in a region so arid, there can be no question of the general occurrence of succession in flood-plains, especially in salt-spots, dunes, and washes, and in secondary areas. Even in what seem stable areas, the movement toward the *Larrea* consociation as the final climax dominant is clear. Spalding (1909 : 16, 30) has noted this tendency on Tumamoc Hill as well as in the wash, and it can be discovered wherever topographic or biotic factors produce bare areas or otherwise modify existing ones.

The type of succession is peculiar to desert. Succession is regularly mesotropic, *i. e.*, developing in hydrophytic or xerophytic habitats which constantly become more mesophytic to the final climax (Clements, 1916 : 182). In the desert scrub the seres are all xerotropic, in that the earlier stages are less xerophytic than the climax. This results in the sere being exceptional in having a small number of stages and a slow rate of movement. Moreover, while the topographic relations of erosion and deposition to the climax plain are essentially as in ordinary succession, the climax itself is xerophytic. Consequently the *Larrea* plain is to be regarded as the threefold baseline for topography, climate, and succession, toward which all the others are tending slowly but nevertheless surely. In a region where permanent streams and lakes are all but impossible, the hydrosere is absent or is quickly converted into a halosere (MacDougal, 1914). The latter begins in a soil more arid than that of the climax, but its position seems normally to result in a habitat which is less xerophytic, since *Prosopis* usually enters before *Larrea*. Apart from this, the hill and valley communities are both less xerophytic than the *Larrea* plains and hence show similar sequences.

Of the valley dominants, *Prosopis* is the least xerophytic. This is shown by its form, which is often that of a tree, capable of forming continuous woodlands, and by its association with such mesophytic river-bank species as *Fraxinus*, *Sapindus*, etc. *Acacia greggii* follows *Prosopis* closely in its water requirements, and is followed in turn by *Condalia lycioides* and *Acacia constricta*. While their association is much less frequent, *Olneya* and *Parkinsonia torreyana* appear but little more xerophytic than *Prosopis*, and this is likewise true of *Dalea spinosa*. The three lowland chollas, *Opuntia fulgida*, *O. f. mamillata*, and *O. spinosior* have a wide range of equivalence. In general they are most abundant in the ecotone between *Prosopis* and *Larrea*, but they extend well into both consociations, especially the latter. The three cacti are often the dominants in *Larrea* plains on which subaerial processes are active. *Yucca*, *Ephedra*, and *Koeberlinia* resemble *Prosopis* more nearly in their demands, but the latter is often found in the lower *Larrea* levels also. *Atriplex canescens* and *A. polycarpa* are regularly associated with *Prosopis*, perhaps largely because of the ability of the latter to withstand salt.

The dominants of the foothills and the upper bajadas approach *Larrea* in requirements, as indicated by the frequence of their association. Here the

Western Desert Scrub




A. *Cereus-Encelia* in lava ridge with *Larrea* below, Tucson, Arizona.
B. *Parkinsonia microphylla* and *Cereus giganteus* on foothills of Tucson Mountains.
C. *Fouquiera splendens* consociation, Santa Rita Reserve.

sequence is nore difficult to determine because of the irregular topography and the confusing effect of temperature. Moreover, the hotter and drier southerly slopes are younger and less stable than the northerly ones, thus further complicating the problem. In general, it may be said that *Fouquiera* stands nearest *Larrea, Cereus* comes next, and *Parkinsonia microphylla* is last. Though *Parkinsonia* mixes with *Larrea* in scores of places, this is largely due to the wide adaptation of the latter.

The occurrence of the halfshrub dominants is correlated more or less closely with that of the shrubs, and they exhibit a similar zonation. *Isocoma* is habitually associated with *Prosopis*, but occurs also in the lower *Larrea* areas. *Opuntia discata* is an associate of the cylindric *Opuntias* and hence has a wide range. The most typical halfshrub associates of *Larrea* are *Franseria dumosa, Hilaria rigida, Krameria glandulosa, Zinnia pumila,* and *Psilostrophe cooperi. Franseria deltoidea* characterizes the *Larrea-Parkinsonia* ecotone, while *Encelia farinosa* is typical of the *Parkinsonia-Fouquiera* community. *Lippia wrightii, Chrysoma laricifolia, Parthenium incanum,* and *Bebbia juncea* are usually restricted to the latter also. *Calliandra eriophylla* is typical of the foothill areas of *Prosopis* and *Acacia* and reaches its greatest abundance on the *Prosopis* savannahs.

**Root relations.**—Cannon (1911) has made a comprehensive study of the roots of desert plants, in which he recognizes three types of root systems. The generalized type has the tap-root and laterals both well developed, while of the two specialized types, one has emphasized the tap-root and the other the laterals. The dominants with generalized root systems are *Larrea, Prosopis, Acacia, Parkinsonia, Fouquiera, Celtis, Lycium, Franseria,* and *Encelia.* Those with a well-developed tap-root are *Condalia, Ephedra,* and *Koeberlinia.* Practically all the cacti have superficial roots with prominent laterals, though the arborescent *Opuntias* approach the generalized type. As would be expected, the roots of annuals are the most superficial, penetrating the soil rarely more than 8 inches, and with the maximum development at about 2 nches.

In general, there is a tendency to form three layers of roots in the soil, the uppermost of annuals, followed closely by the root-layer of the cacti, and a much broader deep-seated layer composed of tap-root systems, with or without prominent laterals. The tendency to place roots at different levels minimizes the direct competition of the dominants, as Cannon has pointed out (l. c., 64). This is especially effective in the case of the superficially rooted annuals and cacti. The necessary compensation for the period of seasonal drouth is secured by drouth evasion in one and drouth resistance in the other. The wide spread of laterals in many of the dominants explains the characteristic open spacing of the desert scrub and the bush-like habit. The effect of a larger water supply is seen especially on the flood-plain, where *Prosopis, Acacia,* and *Parkinsonia* often become trees, and even *Larrea* may grow to a height of 15 feet or more. This is shown even more strikingly along the margins of roads, where the shrubs become remarkably vigorous as a result of the increased runoff and the freedom from competition. This effect is universally exhibited by the halfshrub, *Isocoma,* in which the plants along the roadside are often twice as tall as those in the midst of the community. Its response was especially graphic in 1918, when the roadside plants leafed out fully while those of the mass were still leafless (plate 40).

## SOCIETIES AND CLANS.

The desert scrub possesses an extraordinary wealth of herbaceous species. The great majority of these are annuals, owing to the existence of two rainy seasons separated by periods of drought. There are in consequence two clear-cut growing seasons which may be regarded for the present as aspects, though closer study may show that these are themselves divisible into aspects. The two seasons are winter-spring and summer. Since they depend wholly upon the incidence of the corresponding rains, the dates of beginning and closing are extremely variable. After the severe drought of 1917, the first winter annuals did not appear until March and the seasonal communities were exceptionally dwarf, sparse, and short-lived. The continuance of the drought brought about an almost complete failure of the summer annuals and many of the herbaceous perennials. The occurrence of unusual rains in the following autumn led to the first appearance of the most important annuals by the beginning of December, and the ensuing development was exceptionally complete and vigorous.

*Perennials:*
- Allionia incarnata.
- Aster spinosus.
- Bahia absinthifolia.
- Baileya multiradiata.
- Boerhaavia viscosa oligadena.
- Delphinium scaposum.
- Euphorbia albomarginata.
- Euphorbia capitellata.
- Franseria tenuifolia.
- Gutierrezia microcephala.
- Hoffmannseggia drepanocarpa.
- Hoffmannseggia jamesii.
- Hoffmannseggia stricta.
- Pappophorum wrightii.
- Pentstemon wrightii.
- Philibertella hartwegii heterophylla.
- Rumex hymenosepalus.
- Setaria composita.
- Sida lepidota sagittifolia.
- Solanum elaeagnifolium.
- Sphaeralcea cuspidata.
- Teucrium cubense.
- Triodia mutica.
- Triodia pulchella.
- Verbena ciliata.

*Long-lived Annuals:*
- Atriplex bracteosa.
- Atriplex elegans.
- Atriplex texana.
- Chenopodium fremontii.
- Eriogonum abertianum.
- Eriogonum deflexum.
- Eriogonum trichopodum.

*Long-lived Annuals*—continued.
- Euphorbia preslii.
- Helianthus annuus.
- Helianthus petiolaris.
- Heterotheca subaxillaris.
- Lepidium thurberi.
- Machaeranthera parvifolia.
- Machaeranthera tanacetifolia.
- Verbesina encelioides.
- Wislizenia refracta.

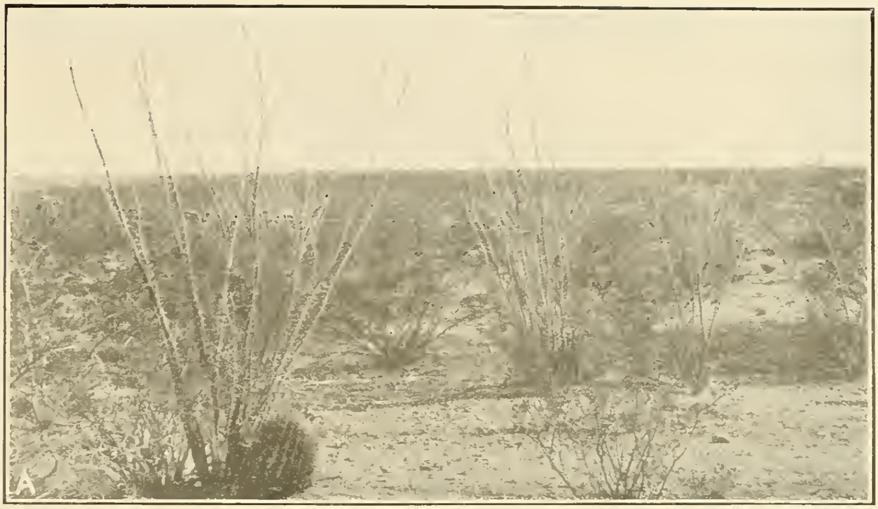
*Summer Annuals:*
- Amarantus palmeri.
- Aristida americana.
- Bouteloua aristidoides.
- Bouteloua polystachya.
- Chloris elegans.
- Cladothrix lanuginosa.
- Eragrostis neo-mexicana.
- Eragrostis pilosa.
- Eriochloa punctata.
- Kallstroemia brachystylis.
- Kallstroemia grandiflora.
- Leptochloa viscida.
- Panicum hirticaulum.
- Pectis papposa.
- Pectis prostrata.
- Physalis angulata linkiana.
- Trianthema portulacastrum.

*Winter Annuals*
- Actinolepis lanosa.
- Amsinckia intermedia.
- Amsinckia tessellata.
- Astragalus nuttallianus.
- Baeria gracilis.
- Bowlesia lobata.

*Winter Annuals*—continued.
- Chaenactis stevioides.
- Cryptanthe angustifolia.
- Cryptanthe pterocarya.
- Daucus pusillus.
- Eremiastrum bellidioides.
- Eschscholtzia mexicana.
- Evax caulescens.
- Festuca octoflora.
- Gilia filifolia.
- Harpagonella palmeri.
- Lappula redowskii.
- Lepidium lasiocarpum.
- Lesquerella gordoni.
- Lotus humistratus.
- Lupinus leptophyllus.
- Malacothrix glabrata.
- Malacothrix sonchoides.
- Malvastrum exile.
- Mentzelia albicaulis.
- Microseris linearifolia.
- Monolepis nuttalliana.
- Orthocarpus purpurascens.
- Pectocarya linearis.
- Pectocarya penicillata.
- Phacelia crenulata.
- Phacelia distans.
- Phalaris caroliniana.
- Plagiobothrys arizonicus.
- Plantago fastigiata.
- Plantago ignota.
- Polypogon monspeliensis.
- Salvia columbariae.
- Sophia incisa.
- Sophia pinnata.
- Streptanthus arizonicus.
- Thelypodium lasiophyllum.
- Veronica peregrina.

The more important herbs of the scrub are grouped in the following list under four heads, viz, perennials, long-lived annuals, summer annuals, and winter annuals. The first alone constitute true societies, the annuals representing the initial stage of a subsere which advances no further because of the

Western Desert Scrub






A. *Fouquiera* subclimax in *Larrea* plain, Tucson, Arizona.
B. *Opuntia fulgida* consociation, San Pedro Valley, Arizona.
C. *Opuntia discata, fulgida,* and *spinosior,* Tucson, Arizona.

annually recurrent drought of late spring and early summer. Hence, they are strictly pioneer socies and families, but by virtue of their annual recurrence they may well be treated as societies of annuals. In addition to these, there are the herbaceous communities of dunes, washes, and salt-spots, and of disturbed areas, which are successional in nature. A large number of these seral annuals are identical with those already mentioned. Finally, there are a number of perennial grasses, some of which have entered from the desert plains in contact with the scrub at its upper limit, and others which may be regarded as relicts of a former savannah condition of certain portions of the desert scrub. Such are *Muhlenbergia porteri*, *Aristida divaricata*, and *Bouteloua rothrockii* in particular. The lists given above are contributed by Professor J. J. Thornber and are based chiefly upon studies in southern Arizona, though the majority of species extend throughout the association.

## THE CHAPARRAL CLIMAX.

### QUERCUS-CEANOTHUS FORMATION.

**Nature.**—The chaparral formation is characterized by low shrubs of the same vegetation-form and for the most part of similar systematic relationship. In comparison with forest, it is xeroid in character, but distinctly less so than sagebrush and desert scrub, which resemble it in physiognomy. It is not dwarfed woodland, similar to that found at timber-line. It not only lacks the habit of "elfin" wood, but the characteristic species, with the exception of those of *Quercus*, do not belong to tree genera. In fact, there is little more reason for regarding chaparral as dwarfed forest than for treating sagebrush or *Larrea* desert as such. It represents a distinct ecological type, intermediate in character and requirements between grassland or scrub desert, *i. e.*, sagebrush and mesquite on the one hand and forest or woodland on the other. This is supported by its almost universal occurrence in front of forest or around it wherever it meets grassland or desert. While timber-line scrub has a general resemblance to chaparral at the first glance, it differs essentially in habitat, floristic, and physiognomy, and belongs to a wholly different category.

The term chaparral is in general use throughout the West and Southwest for scrub or thicket. It is most commonly applied to the mesquite of Texas and the *Adenostoma-Ceanothus* association of California, and less frequently to the *Quercus-Cercocarpus* community of the Rocky Mountains region. In spite of their general resemblance to chaparral, this term seems never to be used for sagebrush or for the creosote-bush desert (*Larrea* consociation). Naturally, it is in common use in those regions where Spanish influences are still felt, and it disappears gradually to the northward long before the community itself has disappeared. In restricting the word to one formation and in broadening it to cover all the associations of that climax, the thought has been to follow the major usage and at the same time to definitize it. As a result, all the associations of this formation from the Missouri Valley to the Pacific Coast are designated as chaparral on account of the essential ecological unity discussed below. A further refinement has been made in distinguishing climax and subclimax chaparral, both in the East and West. As indicated later, these are so closely related successionally and have so many points in common that a distinct term for the subclimax chaparral seems both unnecessary and unwise.

**Unity of the chaparral formation.**—In view of the exceptionally wide range, the floristic unity of the chaparral is remarkable. The major dominants belong to 10 genera, namely, *Quercus*, *Ceanothus*, *Cercocarpus*, *Rhus*, *Prunus*, *Amelanchier*, *Symphoricarpus*, *Rosa*, *Arctostaphylus*, and *Shepherdia*. With one or two exceptions, all of these occur as dominants in both associations, and in the subclimaxes as well. The relationship is even better shown by such species as *Rhus trilobata*, *Prunus demissa*, *Arctostaphylus pungens*, *Cercocarpus parvifolius*, and *Ceanothus cuneatus*, which are dominants in both associations. Still other species, such as *Amelanchier alnifolia*, *Holodiscus discolor*, *Symphoricarpus albus*, and *Philadelphus gordonianus* occur as dominants in one and are of secondary importance in the other. It is also a striking fact that of 25 genera which play a considerable part in the formation, all but two belong to the order *Rosales* or to the related *Acerales* and *Fagales*. This is reflected in the appearance or physiognomy of the formation. The dominants not only belong to the same vegetation-form, viz, shrubs, but also to the same general growth-form. Instead of being tall shrubs, as a rule practically all of them assume the bush-form or produce several ste ns. The latter is a consequence of the nearly universal habit of forming root-sprouts to which the chaparral owes much of its success, especially in competition with grassland. The regular occurrence of several dominants in mixture also explains the general uniformity in height and habit, which so often gives chaparral the appearance of a densely woven green carpet.

One evident difference between the Rocky Mountain and the Coastal chaparral lies in the fact that the former is deciduous, the latter evergreen or sclerophyll. This difference is probably to be correlated with winter as the most xerophytic period for the former and summer for the latter. While this distinction is characteristic, it is not thorough and must not be given too much importance. The most representative species of the Rocky Mountain chaparral is *Quercus undulata*, which exhibits deciduous forms in the north and evergreen ones in the south. Likewise, *Cercocarpus parvifolius* is a more northern deciduous species and *C. ledifolius* a southerly evergreen one, but in spite of this, both are found together over the foothills of the Wasatch Mountains and elsewhere. Moreover, the evergreen *Arctostaphylus pungens* and *Ceanothus cuneatus greggii* are found from northern Arizona to central Utah in intimate association with *Quercus*, *Rhus*, and *Amelanchier*. A similar condition is encountered in California, where most of the chief dominants are evergreen, but they are often associated with deciduous species, such as *Cercocarpus parvifolius*, *Holodiscus discolor*, *Prunus demissa*, and others. As a consequence, it must be recognized that there is nothing ontradictory in having deciduous and evergreen dominants in the same ormation and even in the same association.

**Climatic relations.**—Geographically, chaparral is a western formation, reaching its typical development on the foothills of the Rocky Mountans and its numerous secondary ranges, and on those of the Sierra Nevada, Cascade, and Coast Ranges of the Pacific Slope. This relation is strikingly shown by its appearance in the Black Hills of South Dakota and the Wildcat Mountains of western Nebraska at a distance of several hundred miles from the main range. This is naturally to be explained by the climatic relations. As the typical zone between forest and grassland or desert, chaparral has an intermediate climatic position. It resembles forest in the wide range of rainfall conditions in which it occurs, and only a general correlation with the latter is possible. In the Rocky Mountains the chaparral lies between 15 and 20 inches of rainfall. In southern California it ranges from 10 to 20 inches, and in northern California and Oregon it occurs on dry slopes under 50 to 60 inches. It seems clear that chaparral is possible in 10 inches of rainfall only where the proximity of the ocean cuts down evaporation, and at 50 inches only where insolation greatly increases it. Here, even more than in sagebrush and grassland, it will be necessary to determine water-content, evaporation, and especially transpiration relations before adequate correlations can be established (fig. 7).

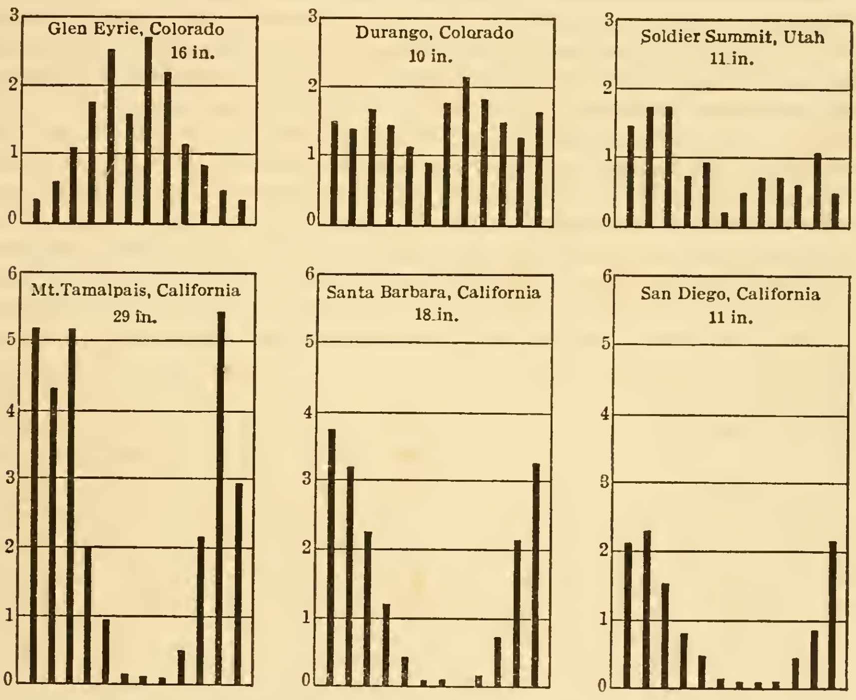



FIG. 7.—Monthly and total rainfall for representative localities in the associations of the chaparral climax.

Origin and succession.—The chaparral, like the grassland and desert scrub, is largely southwestern in origin. This would be expected from its general climatic relations as well as from its greater development in the south, and its uniform shading-out to the northward along both mountain systems. With the exception of a few genera such as *Prunus* and *Rosa*, all of the dominants are either southwestern or have reached their chief development in the Southwest. Thus, it seems probable that the chaparral has moved northward from an original southern center and has differentiated into two associations as a consequence of finding ecesis most successful along the two great mountain axes.

The successional relations of the chaparral are expressed chiefly in the xerosere and the subsere. The primary succession is found usually on rock outcrops and especially on talus slides, and exhibits the same essential stages in the various regions. The subsere is much the most frequent and important, especially from the practical side. It is regularly caused by fire, and it is probable that all chaparral areas, as they exist to-day, have resulted from fire. This does not mean, however, that all chaparral was originally developed in response to fire. Like grassland, it originated in response to a xeroid climate and followed the latter in its extension into new regions. Like grassland, also, it was able to develop its natural dominance after fire much more quickly than forest could, with the result that fire has constantly increased the area of chaparral at the expense of the forest. As a consequence, chaparral consists of two distinct types developmentally. The original and most typical is climax chaparral, corresponding to a climate whose water efficiency is lower than that demanded by forest. The most recent type is subclimax chaparral, which occupies a zone of variable width about the climax proper. It is not only the result of the destruction of the original forest by fire, or clearing and fire, but also owes its persistence to the periodic recurrence of these disturbing processes. While it is necessary to trace the process of succession in each region to determine the nature of the chaparral with complete certainty, the indicators left by the denuding agent as well as the development itself are usually sufficient to permit a trustworthy decision. The distinction between climax and subclimax chaparral is of the first importance in the treatment of a region, and this matter is further discussed on a later page.

Range and extent.—Chaparral does not dominate great areas, as is the case with grassland and sagebrush. While it occurs in considerable bodies under the most favorable conditions, it is generally found in relatively narrow and often much interrupted belts along the edge of forest formations. Consequently, while the formation has an exceedingly wide range, it posesses relatively little continuity, and hence is little impressive over much of its broad extent. It is poorly developed along the line of contact between the deciduous forest and grassland, attains fair expression along the base of the main range of the Rocky Mountains, becomes massive in the Wasatch Mountains of Utah, and reaches its fullest expression in California.

As a climax, the chaparral is found from Wyoming and the Black Hills of South Dakota southward along the Rockies into Texas and Mexico. It extends across Utah, New Mexico, and Arizona along the mountain ranges. It is greatly broken up by the mass of the sagebrush and desert scrub formations in Nevada and in the Mohave and Colorado Deserts, but it reappears on the mountain ranges of southern California and the Sierra Nevada. Chaparral is to-day perhaps the most characteristic association found in California, but it rapidly loses its importance with increasing rainfall and the consequent development of forest. In northern California and in Oregon it becomes limited to the drier slopes more and more and finally becomes a mere subclimax or completely disappears.

The chaparral dominants belong to 30 genera, the majority of which range throughout the formation. This is particularly true of *Quercus*, *Cercocarpus*, *Ceanothus*, *Rhus*, *Prunus*, *Amelanchier*, *Symphoricarpus*, *Rosa*, *Opulaster*, *Purshia*, *Ribes*, and *Cornus*. A striking group of genera is limited to the Southwest or finds its chief development there. This consists of *Peraphyllum*, *Fendlera, Fallugia, Cowania, Coleogyne, Robinia,* and *Garrya,* all but the last belonging to the rose order. Of 35 species of dominants more than half range from Saskatchewan, Manitoba, or the Dakotas to Texas or New Mexico, thence to Arizona and California on the southwest and to Oregon, Washington, or British Columbia at the northwest. While only a few are major dominants throughout this wide area, all are sufficiently important to show the basic unity of the formation and the close relationship of the various associations, both climax and subclimax.

Structure of the formation.—The studies of the last six years have revealed several different regions in which the chaparral type of vegetation reaches more or less complete expression. These are the Rocky Mountains, the Pacific Coast, the Southwest, the Northwest, the Missouri Valley, and Texas. In the last two, as in the mountains of the Pacific Coast, the chaparral is subclimax. These communities do not belong to the formation proper and are considered with it chiefly because of their contiguity and general relationship. They are properly associes of a climax forest. Of the four climax maxima, two stand out clearly, namely, the Rocky Mountain and Coastal. The other two have been regarded tentatively as associations during the course of the field work. In order to determine their real rank as well as the relationship of the several communities, a summary has been made of all the groupings of dominants recorded from 1900 to 1918, as well as in 1893, when a botanical reconnaissance was made along the Missouri and Niobrara Rivers. The summary comprises approximately 500 localities, of which 206 are in the Rocky Mountain region, 39 in the Northwest, 38 in the Southwest, 45 on the Pacific Coast, and 164 in the subclimax chaparral of the grassland formation. The occurrence of the dominants in the five regions is shown in the table on page 182. No account is taken here of the Californian subclimax, which is essentially different.

Grouping of dominants.—The unity of the formation is readily seen from the distribution of the genera especially. The first 7 genera occur in all the five areas, 5 others occur in three, and 6 are found in two. Three of the species are present in all five communities, 4 others in four of the areas, 5 in three, and 9 in two. The differentiation of the maxima is revealed by the presence of certain genera and species in one area and not in another, as well as by their frequence. For example, *Adenostoma* and *Quercus dumosa* occur only in the Coast chaparral, while *Ceanothus cuneatus* and *Arctostophylus pungens* are of the first importance in it alone. Likewise *Fallugia, Cowania, Coleogyne, Robinia,* and *Fendlera* are limited to the Southwest and the southern part of the Rocky Mountain association. The differentiation of the subclimax community is shown by *Quercus macrocarpa, Symphoricarpus occidentalis, Rosa arkansana, Elaeagnus argentea, Fraxinus viridis, Prunus americana,* and *Rhus glabra,* while a less distinct maximum in the Northwest is indicated by *Purshia, Opulaster, Philadelphus, Holodiscus,* and *Peraphyllum.*

The relationship of these five maxima is revealed by the frequence of the dominants as shown in the table. The italic numbers indicate those which occur in at least 10 per cent of the total number of localities visited. The Rocky Mountain chaparral exhibits 12 dominants which occur in 10 or more localities, and of these 8 are equally important in the Northwest, while but 2 are absent in the latter. The southwestern chaparral has 6 of the 12 most frequent dominants of the Rocky Mountain community. It also shows 6 other important dominants, 5 of which, *Cercocarpus ledifolius*, *Fallugia*, *Cowania*, *Coleogyne*, and *Arctostaphylus pungens*, are of greater significance than in the Rocky Mountains, while one, *Ceanothus cuneatus greggii*, is largely absent in the latter. A comparison of the subclimax chaparral with the Rocky Mountain likewise shows a close relationship; 4 of the chief dominants of the one are equally important in the other, and all but 2 of the 13 are present

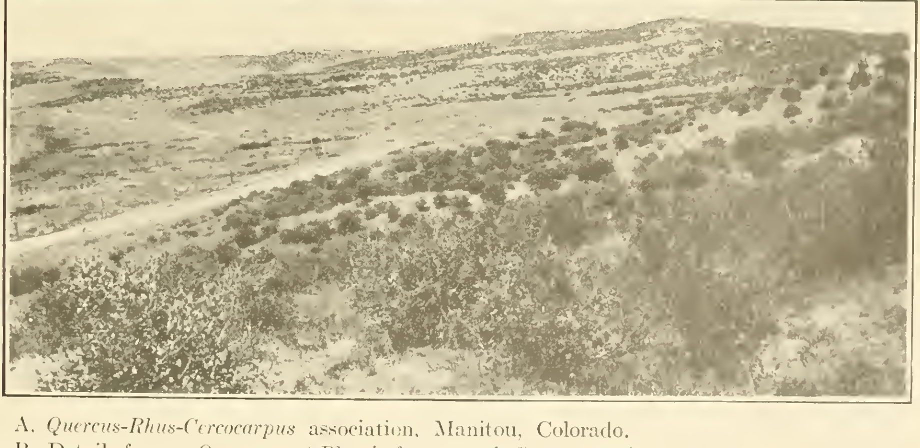
DOMINANTS.

| Species. | Rocky Mountain. | South-west. | North-west. | Sub-climax. | Pacific Coast. |
|---|---|---|---|---|---|
| Total | 206 | 38 | 39 | 144 | 45 |
| Quercus | 127 | 26 | 3 | 49 | 11 |
| Quercus undulata | *126* | *26* | ........ | 5 | ........ |
| Quercus macrocarpa | 1 | ........ | ........ | *29* | ........ |
| Quercus dumosa | ........ | ........ | ........ | ........ | *11* |
| Quercus virens | ........ | ........ | ........ | *15* | ........ |
| Cercocarpus | 109 | 23 | 3 | 2 | *11* |
| Cercocarpus parvifolius | *107* | *16* | ........ | 2 | *11* |
| Cercocarpus ledifolius | 2 | *7* | 3 | ........ | 2 |
| Rhus trilobata | *58* | *13* | *5* | *61* | *5* |
| Prunus demissa | *53* | *4* | *15* | *63* | *5* |
| Amelanchier alnifolia | *74* | *10* | *15* | *28* | *7* |
| Symphoricarpus albus, etc. | *28* | *4* | *11* | ........ | *5* |
| Symphoricarpus occidentalis | 1 | ........ | ........ | *65* | ........ |
| Rosa acicularis | *10* | 2 | *13* | ........ | 1 |
| Rosa arkansana | ........ | ........ | ........ | *47* | ........ |
| Ribes cereum | *11* | ........ | *5* | *4* | ........ |
| Ribes aureum | *1* | ........ | ........ | *16* | ........ |
| Peraphyllum ramosissimum | *24* | 1 | *4* | ........ | ........ |
| Opulaster opulifolius | 5 | p[1] | *11* | 2 | ........ |
| Holodiscus discolor | *15* | p | *5* | ........ | *6* |
| Purshia tridentata | *14* | p | *17* | ........ | *5* |
| Philadelphus gordonianus | 5 | p | *8* | ........ | ........ |
| Fendlera rupicola | 18 | p | ........ | ........ | ........ |
| Robinia neomexicana | 3 | 1 | ........ | ........ | ........ |
| Fallugia paradoxa | 2 | *10* | ........ | 3 | ........ |
| Cowania mexicana | 2 | *7* | ........ | ........ | ........ |
| Coleogyne ramosissima | p | *4* | ........ | ........ | ........ |
| Adenostoma fasciculatum | ........ | ........ | ........ | ........ | *21* |
| Ceanothus cuneatus | ........ | *4* | ........ | ........ | *26* |
| Ceanothus divaricatus | ........ | ........ | ........ | ........ | *5* |
| Arctostaphylus pungens | p | *6* | ........ | ........ | *24* |
| Arctostaphylus tomentosa | ........ | ........ | ........ | ........ | *5* |
| Shepherdia argentea | 6 | 1 | ........ | *15* | ........ |
| Elaeagnus argentea | ........ | ........ | ........ | *53* | ........ |
| Cornus stolonifera | ........ | ........ | ........ | *12* | ........ |
| Fraxinus viridis | ........ | ........ | ........ | *21* | ........ |
| Rhus glabra | 5 | ........ | ........ | *11* | ........ |
| Prunus americana | 3 | ........ | ........ | *24* | ........ |

[1] Merely present.

in the Rocky Mountain region. A lesser degree of resemblance is found between the Coast and the Rocky Mountain chaparral, though their formational relationship is clear. Of the 6 most typical dominants of the former, but 1 occurs in the latter, while the most characteristic dominant of the Rocky Mountains, *Quercus undulata*, is completely lacking, unless indeed it is represented by *Q. garryana*. On the other hand, the 2 communities possess 8 important dominants in common (plate 41).

Petran Chaparral



A. *Quercus-Rhus-Cercocarpus* association, Manitou, Colorado.
B. Detail of same, *Quercus* and *Rhus* in foreground, *Cercocarpus* behind, Manitou, Colorado.
C. *Cercocarpus parvifolius* consociation, Chugwater, Wyoming.

Associations.—A careful consideration of the above facts has led to the conclusion that the chaparral formation consists of but two climax associations. These are the Petran or *Cercocarpus-Quercus* association composed chiefly of *Quercus undulata, Cercocarpus parvifolius, Rhus trilobata, Prunus demissa, Amelanchier alnifolia, Symphoricarpus albus, Peraphyllum,* and *Fendlera,* and the Coastal or *Adenostoma-Ceanothus* association, consisting principally of *Adenostoma, Ceanothus cuneatus, Arctostaphylus tomentosa,* and *Quercus dumosa.* The fragmentary chaparral of the Northwest is clearly a shading-out of the Rocky Mountain association, since the chief difference is the absence of *Quercus undulata, Cercocarpus parvifolius,* and *Fendlera* in the former. The chaparral of the Southwest clearly shows its relationship to the Rocky Mountain association in the abundance of *Quercus, Cercocarpus, Rhus, Prunus,* and *Amelanchier.* In addition, it possesses two dominants from the Coastal association, viz, *Arctostaphylus pungens* and *Ceanothus cuneatus,* and exhibits certain genera more or less peculiar to it, such as *Fallugia, Cowania,* and *Coleogyne.* The latter, however, are gradually finding their way into the Rocky Mountain area. As a consequence, this type of chaparral is perhaps best treated as a transition between the Rocky Mountain and Coastal associations, but with a much closer relationship as a rule to the former. In some of the mountains of southern Arizona, however, the chaparral consists chiefly of *Ceanothus* and *Arctostaphylus,* and is clearly an extension of the Coastal type. In the following discussion, the chaparral of the Northwest and Southwest are considered as more or less differentiated portions of the *Cercocarpus-Quercus* association. Because of their general resemblance to them, the subclimax types are treated with the corresponding climax, the *Rhus-Prunus* community of the Missouri Valley with the Rocky Mountain, and the *Rhus-Ceanothus* subclimax of the Pacific Coast with the Coastal association. The oak chaparral of Texas resembles that of the Missouri Valley in its general relation to the eastern forest, but its dominants are derived from both the East and West.

## THE PETRAN CHAPARRAL.

### CERCOCARPUS-QUERCUS ASSOCIATION.

Nature and extent.—The Rocky Mountain or Petran chaparral consists almost exclusively of deciduous shrubs in more or less intimate mixture. It ranges in height from 2 to 20 feet, but attains its most characteristic expression at 5 to 10 feet. Under optimum conditions, it is massive in nature, covering many square miles with the density of a forest cover. Because of its intermediate position between forest and other formations and its occurrence in the diverse topography of foothills, it is much interrupted as a rule. The total number of dominants is large, and at least several regularly occur in any one grouping. They agree closely in vegetation-form and in the characteristic habit of root-sprouting, though some produce sprouts much more readily than others. In growth habit, they are normally bushy shrubs, though the range in size is considerable. *Quercus undulata* and *Prunus demissa* often become small trees; *Rhus trilobata* may form a gigantic bush 20 feet high and 25 to 30 feet in diameter, while *Cercocarpus parvifolius* is usually a slender erect shrub. It is interesting to note that all the dominants belong to the rose order, with the exception of *Quercus, Rhus,* and *Symphoricarpus.*

The *Cercocarpus-Quercus* association reaches its best development in Colorado, northern New Mexico, and eastern Utah. Its extreme limits on the east are the Black Hills of South Dakota and the Wildcat Mountains of western Nebraska, and the mountains of western Texas. On the south and west it runs through southern New Mexico and Arizona, extending more or less into northern Mexico. It is usually poorly developed in Nevada, and thence ranges much interrupted through Idaho and eastern Oregon to British Columbia and Alberta. Chaparral is fairly developed in southern Wyoming, but is reduced northward to disappear largely in the mountains of central Montana, where its place is taken chiefly by aspen, or by subclimax chaparral from the East. Its altitude limits are of the widest. In Colorado and New Mexico, the *Quercus* consociation is found well-developed in dry southern slopes as high as 9,000 feet, and small outposts exist at somewhat higher altitudes. These, however, are subclimax and will sooner or later yield to montane forest. The lowest limit is about 4,000 feet, but subclimax fragments are frequently found at much lower levels in the Northwest. The association attains its best development between 5,000 and 8,000 feet and as a climax is practically restricted to this zone.

Contacts—Along the eastern edge of the Rocky Mountains, the chaparral is in contact below with the grassland association, touching the mixed prairie in the north, and the short-grass plains in the south. The ecotone is often several miles wide, and is usually marked by a striking alternation of the two associations. On the south and southwest, the contact is usually with the desert plains, more rarely with desert scrub. In the West, it is typically with sagebrush, and in the Northwest with sagebrush, or bunch-grass prairie. The upper contact is with piñon-cedar woodland or with the montane forest, particularly the more xeroid *Pinus ponderosa* consociation or the aspen consocies. Its relation to woodland is puzzling at first, since it occurs both above and below the latter. The probable explanation is that climax chaparral regularly occurs below climax piñon-cedar woodland. The latter is often well developed as an open subclimax on lower rocky ridges and slopes at altitudes where it will ultimately be replaced by chaparral or sagebrush. This upper ecotone is frequently greatly confused in dry rocky country, where one or more dominants of the sagebrush, chaparral, woodland, and montane forest may be found in intimate mixture or alternation.

In comparing the rank of the various dominants, it must be borne in mind that the figures indicate frequence rather than abundance. As a matter of fact, however, there is so much correlation between the two in the case of chaparral dominants that the one is a fair indication of the other. This is especially true of the most massive communities found in the central and southwestern areas. In these more typical areas, *Quercus undulata* is by far the most important dominant, chiefly as the variety *gambelii*. *Cercocarpus parvifolius* is a close second, with *Rhus* and *Prunus* approximately half as important. *Amelanchier* is secondary to *Quercus* and *Cercocarpus*, but its frequence must be interpreted in the light of its absence over most of the eastern slope of the Rocky Mountains, where the other four dominants are so typical, and its correspondingly greater abundance on the western slope. It is significant that the four most important dominants are the same for the first two areas. *Prunus demissa* loses its rank in the Southwest, but regains

Petran Chaparral

A. *Quercus-Cercocarpus-Fallugia* chaparral, Milford, Utah.
B. Same showing contact with sagebrush, *Cercocarpus ledifolius* in foreground, Milford, Utah.

it in the Northwest. In the latter the absence of *Quercus* and *Cercocarpus* and the importance of *Purshia* suggests a greater differentiation from the central chaparral mass. However, this seems readily explained by the remoteness from the latter and by a less favorable northern climate, which find expression in the fragmentary character and the subclimax tendency of the northwestern chaparral (plate 42).

DOMINANTS.

| | |
|---|---|
| *Central Rocky Mountains* (206 localities): | |
| Quercus undulata | 126 |
| Cercocarpus parvifolius | 107 |
| Amelanchier alnifolia | 74 |
| Rhus trilobata | 58 |
| Prunus demissa | 58 |
| Symphoricarpus albus | 23 |
| Peraphyllum ramosissimum | 24 |
| Fendlera rupicola | 18 |
| Holodiscus discolor | 15 |
| Purshia tridentata | 14 |
| Ribes cereum | 11 |
| Rosa acicularis | 10 |
| Philadelphus gordonianus | 5 |
| Opulaster opulifolius | 5 |
| Robinia neomexicana | 3 |
| *Southern Area* (38 localities): | |
| Quercus undulata | 26 |
| Cercocarpus parvifolius | 16 |
| Rhus trilobata | 13 |
| Amelanchier alnifolia | 10 |
| Fallugia paradoxa | 10 |
| Cercocarpus ledifolius | 7 |
| Cowania mexicana | 7 |
| Arctostaphylus pungens | 6 |
| Prunus demissa | 4 |
| Symphoricarpus albus | 3 |
| Coleogyne ramosissima | 3 |
| Ceanothus cuneatus | 3 |
| *Northwestern Area* (39 localities): | |
| Purshia tridentata | 17 |
| Prunus demissa | 15 |
| Amelanchier alnifolia | 15 |
| Rosa acicularis | 13 |
| Opulaster opulifolius | 11 |
| Symphoricarpus albus | 11 |
| Philadelphus gordonianus | 8 |
| Holodiscus discolor | 5 |
| Rhus trilobata | 5 |
| Ribes cereum | 5 |
| Peraphyllum ramosissimum | 4 |
| Cercocarpus ledifolius | 3 |

Groupings.—The number of dominants is so large and their equivalence so close that they occur in the most varied groupings. In any particular locality, the number of associated dominants is usually 4 or 5, and often 6 or 7; 3 is also a frequent grouping, but communities of 1 or 2 dominants are usually found only near the limits of the association, where the latter is more or less fragmentary. While nearly all of the most important dominants do occur in pure communities, these are usually of limited extent and regularly alternate with other dominants, except toward the edge of the association as already noted. The actual groupings are so numerous and varied that a detailed summary of them possesses little significance. In the central mass, *Quercus*, *Cercocarpus*, *Rhus*, and *Prunus* constitute the groundwork in central and eastern Colorado and New Mexico. In western Colorado and adjacent regions, these four are still of the first importance, but *Amelanchier*, *Fendlera*, *Peraphyllum*, and *Cercocarpus ledifolius* often become equally important. These may mix with the first four or replace one or more of them. This condition persists into the Southwest, where *Fallugia* and *Cowania* enter to further complicate the grouping, and *Arctostaphylus* and *Ceanothus* appear to serve as an indication of the transition to the Coastal association. In the Northwest, the association is so interrupted and fragmentary that definite groupings are not obvious. In general, the ground plan seems to be furnished by *Amelanchier*, *Prunus*, *Opulaster*, *Philadelphus*, and *Symphoricarpus*, though with almost infinite variation in detail. In the drier regions, *Amelanchier*, *Purshia* and *Peraphyllum* mix and alternate in varying degree.

Equivalence of dominants.—The large number of dominants, their close equivalance and wide range, and the almost complete absence of quantitative results make the task of determining their factor relations peculiarly difficult. This task is further complicated by the ease and intimacy with which the dominants mix. In spite of this, however, the topographical and successional relations are sufficiently evident to indicate their general response to physical factors. Because of the wide range of climatic conditions, this must be done for each area rather than for the association as a whole. The basic relation is determined by the five great dominants, *Quercus, Cercocarpus, Amelanchier, Rhus*, and *Prunus*, which have had some factor and successional study in Colorado and Utah. Since one or more of these is found in practically all the important groupings, they serve as basing-points for all the other dominants.

*Prunus demissa* is the most mesophytic of the five dominants, as is shown by the regular occurrence along streams and in ravines and by its taller habit. *Rhus trilobata* comes next in its water requirements, followed closely by *Quercus undulata gambelii.* The latter not only stands midway in the series, but it is also able to adapt itself to a wider range of conditions than the others, locally at least. This explains its greater frequence in spite of its range being the most restricted of the five. *Quercus undulata* is somewhat more xeroid, as its evergreen leaves and southern distribution indicate. The two are so frequently mixed where their ranges overlap that the difference in their requirements must be slight. *Cercocarpus parvifolius* and *Amelanchier alnifolia* are the most xerophytic and to an almost equal degree. To a large extent thay are corresponding species, the former being most typical east of the Continental Divide, the latter west. As a rule, *Cercocarpus* occupies the newer or drier areas, though their relative position is sometimes reversed. Of the remaining dominants, *Robinia neomexicana* is somewhat more mesophytic than the oak, as is shown by its fondness for ravines and valleys. This is likewise true of *Symphoricarpus albus* and *Rosa acicularis*, which often form a layer in oak thickets especially. *Opulaster opulifolius* is rather more mesophytic than oak and frequently forms a layer in forests of *Pseudotsuga* which the oak can not enter. While all of the others occur mixed with *Quercus*, this is less true of *Purshia tridentata* and *Ribes cereum*, which are to be regarded as the most xerophytic. *Holodiscus* and *Philadelphus* are slightly more xeroid than oak. *Fendlera* and *Peraphyllum* have a wide range of adjustments. As tall shrubs, they often mix with oak on north exposures and at the base of slopes, but usually they are nearly equivalent to *Amelanchier* and *Cercocarpus*.

As would be expected, the other dominants of the southwestern chaparral are typically xerophytic. This is indicated by their origin and distribution as well as by their generally evergreen habit. From the evidence derived from groupings as well as from the habitat, *Cercocarpus ledifolius* is nearly equivalent to the oak, and *Fallugia paradoxa* and *Cowania mexicana* to *Cercocarpus parvifolius*, though all are slightly more xerophytic. *Arctostaphylus pungens* and *Ceanothus cuneatus* are more xerophytic than *C. parvifolius*, while *Coleogyne* seems the most xerophytic of all. It forms pure communities on shallow soil on rocky cliffs, but since it rarely mixes with the other dominants, its relative position is uncertain.

The dominants of the northwestern chaparral have already been considered, but it may be helpful to relate them to each other, since both *Quercus* and

*Cercocarpus parvifolius* are lacking. *Prunus* and *Rhus* are the most mesophytic, *Purshia* the most xerophytic. *Amelanchier, Holodiscus, Philadelphus,* and *Opulaster* are more or less intermediate between these two extremes, while *Cercocarpus ledifolius, Peraphyllum,* and *Ribes* are nearly equivalent to *Purshia,* as is shown by their frequent occurrence as outposts in dense sagebrush.

### SOCIETIES.

From its nature and position, the societies of the mountain chaparral are largely derived from the climax communities in contact with it. The majority of these come from the grassland, but a number enter also from sagebrush, woodland, and even from the montane forest. The societies of the sunny intervals between the bushes are chiefly those of the ecotone between chaparral and grassland or sagebrush. As a consequence, it is necessary to list here only those which grow in the shade of tall clumps or of a more or less continuous chaparral cover. Some of these have been derived from woodland or forest, but the majority are shade-forms of grassland and sagebrush subdominants. A few of them are grasses, *Elymus triticoides, Agropyrum caninum, Bromus ciliatus, Stipa comata,* etc., though by far the greater number are herbs. Low shrubs, such as *Symphoricarpus occidentalis, Rosa acicularis, Rhus radicans, Pachystigma,* and *Berberis* often form a characteristic layer. Ruderal annuals are frequent also, perhaps because the denser clumps afford them protection from grazing.

*Vernal Societies:*
- Anemone patens.
- Senecio aureus.
- Arenaria fendleri.
- Euphorbia montana.
- Aragalus lamberti.
- Erysimum asperum.
- Pachylophus caespitosus.
- Draba aurea.
- Pentstemon coeruleus.
- Arabis holboellii.
- Comandra umbellata.
- Mertensia lanceolata.
- Scutellaria resinosa.
- Tradescantia virginiana.
- Vicia americana.
- Erigeron glandulosus.
- Lithospermum multiflorum.
- Delphinium scopulorum.
- Allium reticulatum.
- Lappula texana.
- Smilacina stellata.
- Thalictrum fendleri.

*Vernal Societies*—continued.
- Heuchera parvifolia.
- Thermopsis montana.

*Estival Societies:*
- Geranium caespitosum.
- Chenopodium fremontii.
- Polygonum convolvulus.
- Polygonum douglasii.
- Calochortus gunnisonii.
- Potentilla arguta.
- Campanula rotundifolia.
- Pentstemon secundiflorus.
- Pentstemon barbatus.
- Pentstemon unilateralis.
- Pentstemon strictus.
- Galium boreale.
- Erigeron flagellaris.
- Gilia aggregata.
- Achillea millefolium.
- Monarda fistulosa.
- Castilleia integra.
- Castilleia miniata.
- Thelesperma gracile.

*Estival Societies*—continued
- Potentilla gracilis.
- Erigeron asper.
- Senecio fendleri.
- Lupinus pusillus.
- Sisymbrium incisum.
- Nepeta cataria.
- Epilobium paniculatum.
- Lactuca pulchella.
- Salvia lanceolata.
- Bidens tenuisecta.
- Erigeron canadensis.
- Hedeoma drummondii.

*Serotinal Societies:*
- Artemisia gnaphalodes.
- Artemisia frigida.
- Brickellia grandiflora.
- Kuhnia glutinosa.
- Solidago speciosa.
- Solidago missouriensis.
- Gymnolomia multiflora.
- Aster bigelovii.
- Mirabilis oxybaphoides.

## THE SUBCLIMAX CHAPARRAL.

### RHUS-QUERCUS ASSOCIES.

Nature.—The subclimax chaparral is a fragmentary community of stream valleys and bluffs, due to the shading-out of the eastern forest as it meets the prairies and plains. As a consequence, it is rarely massive, but extends as narrow belts for hundreds of miles along the upper bluffs of the Missouri and its main tributaries. Farther west along the lesser streams, it forms the typical vegetation of the narrow valleys. It is more or less developed in the broken topography of the Bad Lands and pine ridges of western Nebraska and the Dakotas, and it reaches westward into the valleys of the foothills in Colorado and New Mexico. A similar subclimax occurs in central Texas, where the oak forest meets the prairies. On the Edwards Plateau the dwarf form of the live-oak, *Quercus virens*, mingles with the shin-oak, *Quercus undulata*, of the Rocky Mountains to form what is probably a climax community, closely related to the *Cercocarpus-Quercus* association, if not to be regarded as a part of it (plate 43).

The dominant species are typically shrubs for the most part, but several important ones are trees which become dwarfed in the more xerophytic conditions of the prairies and plains. This is the case with the bur-oak (*Quercus macrocarpa*), live-oak (*Q. virens*), ash (*Fraxinus viridis*), plum (*Prunus americana*), hawthorn (*Crataegus coccinea*), hackberry (*Celtis occidentalis*), box-elder (*Acer negundo*), elm (*Ulmus americana*), and linden (*Tilia americana*). A large number of the trees which reach the western edge of the deciduous forest exhibit the same tendency, but they extend little beyond the limits of the forest proper. The majority of the dominants are bushes or bushy shrubs from 3 to 10 feet high. They resemble those of the climax in producing root-sprouts readily and consequently in taking rapid and complete possession where forest is cleared or subclimax grassland is overgrazed.

**Extent and contacts.**—Subclimax chaparral appears along the western border of the deciduous forest and through valleys in the prairies from Manitoba and Saskatchewan to northern Mexico. It extends westward to the Rocky Mountains from Montana to Texas, and comes into repeated contact with mountain chaparral in the upper valleys of the North and South Platte, the Arkansas, Canadian, and Pecos Rivers. Throughout the eastern edge of this area, it marks the ecotone between the forest and grassland. It is naturally here that it finds its best expression, in accordance with the fact that the dominants are either trees of the forest, or shrubs and bushes which constitute a lower layer or play the rôle of seral dominants. The subclimax occurs generally throughout the grassland formation in valleys and sandhills where the water-content is above the normal. It is best developed in the eastern portion of the prairies and decreases steadily toward the west, persisting only in the larger valleys, on buttes, or in sandhills. It is everywhere surrounded by grassland, except where it comes in contact with mountain chaparral, or with the pine or aspen community in the Black Hills or other outlying montane regions.

DOMINANTS.

| Species. | Rank. | Species. | Rank. |
|---|---|---|---|
| Symphoricarpus occidentalis | 65 | Ribes cereum | 4 |
| Prunus demissa | 63 | Quercus undulata | 5 |
| Rhus trilobata | 61 | Amelanchier alnifolia | 28 |
| Elaeagnus argentea | 53 | Prunus americana | 24 |
| Rosa arkansana | 47 | Fraxinus viridis | 21 |
| Quercus macrocarpa | 29 | Ribes aureum | 16 |
| Shepherdia argentea | 15 | Xanthoxylum americanum | 8 |
| Quercus virens | 15 | Corylus americana | 8 |
| Cornus stolonifera | 12 | Celtis occidentalis | 3 |
| Rhus glabra | 11 | Prunus besseyi | 3 |

Subclimax Chaparral

A. *Rhus glabra* consocies, Peru, Nebraska.
B. *Quercus virens* and *undulata*, Edwards Plateau, Sonora, Texas.

The relative rank of the dominants is indicated by the figure placed after each one, indicating the observed frequence. These apply chiefly to the central and western portions of the area, and are less representative of the eastern and southeastern edge.

A number of other shrubs and bushes play some part, but most of these are secondary or incidental. A few will doubtless take their place finally as dominants. They are especially well represented in sandhill areas, such as those of Nebraska, Kansas, and Oklahoma. The most important of these are *Yucca glauca, Artemisia filifolia, Ceanothus ovatus, Salix humilis*, and *Rhus radicans. Sambucus canadensis* and *Cephalanthus occidentalis* are more or less hydrophytic shrubs which persist with the usual dominants for some time. *Cornus asperifolia, C. amomum*, and *Corylus rostrata* are layer dominants which sometimes occur outside the forest, while the shrubby forms of *Q. breviloba* and *Cercis canadensis*, which occur in Texas, are probably to be regarded as true dominants.

Groupings.—Owing to the fragmentary nature of the community, many of the dominants may occur in pure stands. This is most characteristic of the bushes, such as *Symphoricarpus, Rosa, Elaeagnus, Ceanothus*, etc., which make the closest approach to the grasses in their requirements. The shrubs and the shrub-forms of the trees demand a higher water-content, and this permits the mixing or intimate alternation of several dominants. Two dominants have been found associated in 35 cases, three in 26, four in 29, and five, six, or seven in 45 instances. As a result, the various groupings are too numerous to be indicated, but the composition of the most common is indicated by the relative sequence of the first 10 or 12 dominants. In the southern portion, *Quercus virens* is the chief species, often with *Q. undulata* or *Q. breviloba* and more or less *Celtis, Cercis, Rhus*, and *Berberis trifoliata.*

Relations of the dominants.—The general sequence and factor relations of many of the dominants have already been indicated. The subclimax chaparral possesses a peculiarly wide range of adjustment, as suggested by the great variation in the extent and complexity of the communities and the size of the plants. Moreover, while it finds fair expression as far west as the isohyete of 20 inches, this is usually possible only where the evaporation is low (as toward the north) or the water-content high (as in sandhills and broken plateaus). As would be expected from its relation to forest, its best development obtains between the lines of 30 and 40 inches of rainfall. The explanation of its constant recurrence throughout the grassland climax is found partly in the higher water-content of valleys, sandhills, and escarpments, and partly in the competition relations between shrubs and grasses. It is highly probable that shrubs and trees establish themselves in grassland during the wet phase of the climatic cycle and are then able to persist during the dry phase by virtue of their deeper root-systems. This appears to be the general explanation of both tree and scrub savannah (Chap. VI) and the fragments of subclimax scrub bear a similar relation to the dominance of the grasses. Once established, such clumps of shrubs are practically permanent, since they can be destroyed only by repeated fires or by the hand of man.

While the shrubs modify the air and soil conditions in each thicket, their growth is still controlled by the climatic factors, more or less affected by the competition of the grasses. This becomes controlling in the case of both propagation and reproduction and makes clear why the spread of a particular clump or the beginning of a new one depends upon the recurrence of wet phases, in which the upper layer of the soil contains more water than the grasses need. The size and continuity and the height of the shrubs reflect the water relations with much accuracy and are in close accord with the gradual decrease of rainfall to the west. This relation is naturally disturbed or obscured by fires and grazing, though it is rarely hidden by them. Repeated fires confine or destroy the shrubs, while grazing reduces the water requirements of the grasses and correspondingly increases the growth and spread of chaparral. This is obviously not true in the case of browsing animals, such as goats.

### SOCIETIES.

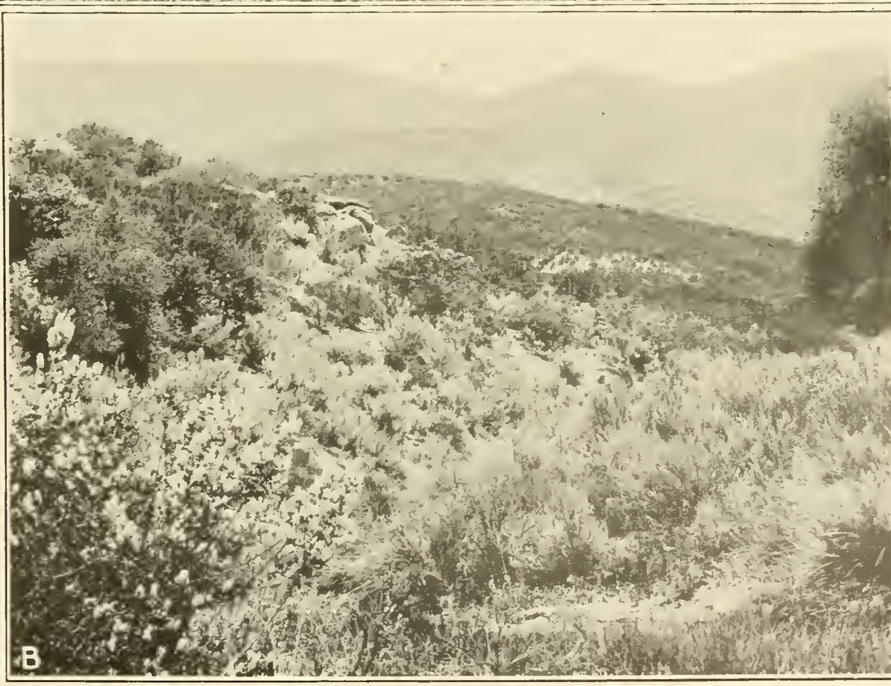
The societies of the subclimax chaparral are derived wholly from the forest or grassland. Practically none of these societies are peculiar to it, though some of those derived from the grassland are more or less characteristic, owing to their increased height or abundance in the shade. Among the important woodland species are *Fragaria virginiana*, *F. vesca*, *Viola cucullata*, *Galium aparine*, *G. boreale*, *Aralia nudicaulis*, *Smilacina stellata*, *Sanicula marilandica*, *Aster levis*, *Heliopsis scabra*, *Urtica gracilis*, and *Elymus virginicus*. From the grassland have entered *Poa pratensis*, *Monarda fistulosa*, *Vicia americana*, *Anemone canadensis*, *A. cylindrica*, *Oxalis stricta*, *Lithospermum hirtum*, *Potentilla arguta*, *Teucrium canadense*, *Lepachys columnaris*, *Artemisia gnaphalodes*, *Solidago canadensis*, *S. rigida*, and others.

## THE COASTAL CHAPARRAL.

### ADENOSTOMA-CEANOTHUS ASSOCIATION.

Nature and extent.—The Coastal or Pacific chaparral differs from the Petran in consisting chiefly of evergreen or sclerophyll dominants. One of the four major dominants, *Quercus dumosa*, is imperfectly evergreen, and about 20 per cent of the minor dominants are deciduous. This association is regularly much more massive and continuous than that of the Rocky Mountains. This is true, however, only of California, where the chaparral reaches its best expression, and toward the north and southeast the community is similarly interrupted. Apart from the fact that the one is typically deciduous and the other typically evergreen, the two associations resemble each other closely in the form, height, and general behavior of the dominants and the essential character of the community. The Coastal association has been more subject to fire and its responses to this agency are correspondingly emphasized. It is also unique in passing gradually into a very similar but distinct subclimax chaparral typical of the montane zone.

The Coastal association is best developed on the Coast and cross ranges of middle and southern California and in northern Lower California. Although reduced in species, it is still an important community in northern California and Oregon, but beyond this it is represented by a single species and is very fragmentary. It extends eastward to the lower slopes of the Sierra Nevada and thence to southeastern California and adjacent Nevada and Arizona. Here it is reduced to *Ceanothus cuneatus greggii* and *Arctostaphylus pungens*, Coastal Chaparral



A. Chaparral hills and sagebrush valley, Pine Valley, California.
B. *Adenostoma-Ceanothus* association, Descanso, California.

which range to southern Utah, western Colorado, southern New Mexico, trans-Pecos Texas, and Mexico, where they blend with the Petran association. The general altitudinal range of this chaparral is from sea-level to 5,000 to 7,000 feet, but the actual limits vary greatly with the region and the slope. The normal upper limit is rarely above 5,000 feet (plate 44).

DOMINANTS.

| | | |
|---|---|---|
| Adenostoma fasciculatum. | Arctostaphylus manzanita. | Heteromeles arbutifolia. |
| Ceanothus cuneatus. | Arctostaphylus pungens. | Dendromecum rigidum. |
| Arctostaphylus tomentosa. | Arctostaphylus bicolor. | Eriodictyum californicum. |
| Quercus dumosa. | Rhamnus crocea. | Adenostoma sparsifolium. |
| Ceanothus divaricatus. | Rhamnus californica. | Prunus ilicifolia. |
| Ceanothus sorediatus. | Rhus integrifolia. | Prunus demissa. |
| Ceanothus dentatus. | Rhus diversiloba. | Cercocarpus ledifolius. |
| Ceanothus hirsutus. | Rhus laurina. | Amelanchier alnifolia. |
| Ceanothus verrucosus. | Rhus ovata. | Holodiscus discolor. |
| Arctostaphylus glauca. | Cercocarpus parvifolius. | |

This list is in essential agreement with the more complete list of Cooper (1919) for the California chaparral. However, a number of species of limited range have been omitted. *Simmondsia californica* is thought to belong more properly to the desert scrub and the position of *Adolphia californica* is uncertain. *Eriodictyum californicum* is the typical dominant in burns and other disturbed areas, but is included because of its frequence.

More than two-thirds of the dominants listed are confined to California and Lower California. Of the four major dominants, *Ceanothus cuneatus* and *Arctostaphylus tomentosa* extend to Oregon and British Columbia, respectively, while of those of considerable importance, *Arctostaphylus pungens*, *Rhamnus californica*, *R. crocea*, *Cercocarpus parvifolius*, and *Amelanchier alnifolia* extend through Arizona into the Petran association, where the last two become major dominants.

Groupings.—The number of groupings is large and only a few of the most common can be indicated. The four major dominants frequently occur in pure stands of considerable size, and this is sometimes true of other important dominants as well. The general rule, however, is a mixture of several species, usually 5 or more. *Adenostoma* is the chief dominant from Lake County southward in California, usually associated with several of the following: *Arctostaphylus tomentosa*, *A. glauca*, *Ceanothus cuneatus*, *Quercus dumosa*, *Heteromeles arbutifolia*, *Cercocarpus parvifolius*, and *Rhamnus californica*, several of which may become more important locally than *Adenostoma*. The latter drops out beyond Trinity County, and *Ceanothus cuneatus* and *Arctostaphylus tomentosa* form the regular groupings as far as northern Oregon, where the former disappears. *Rhus diversiloba* occurs with them frequently and *Cercocarpus*, *Amelanchier*, *Purshia*, *Holodiscus*, and *Philadelphus* are increasingly associated with them to the northward. In the San Gabriel mountains of southern California, *Adenostoma*, *Quercus dumosa*, *Ceanothus divaricatus*, *Arctostaphylus*, and *Cercocarpus* are the most important dominants, while in the neighboring San Bernardino Range the grouping is practically the same, but with *Cercocarpus* much more important (Leiberg, 1900 : 419, 439). On San Jacinto Mountain, *Adenostoma fasciculatum* and *A. sparsifolium* constitute 50 to 75 per cent of the chaparral below 5,000 feet, with

*Ceanothus divaricatus*, *Quercus dumosa*, and *Cercocarpus parvifolius* as their most abundant associates, and a dozen or more of less importance (Leiberg, 1900 : 465; Hall, 1902 : 17). Practically the same grouping occurs through the Laguna and Cuyamaca Mountains to the coast about San Diego. The chaparral of Lower California is composed chiefly of both species of *Adenostoma*, *Arctostaphylus glauca* and *pringlei*, *Cercocarpus parvifolius*, and *Ceanothus divaricatus* (Goldman, 1916 : 330).

Throughout southern California generally, *Adenostoma fasciculatum* mixes and alternates at the lower levels and on drier areas with *Artemisia californica*, *Salvia mellifera*, *Salvia apiana*, or *Eriogonum fasciculatum*, the dominants of the Coastal sagebrush association. This is more xerophytic than the chaparral, and is subclimax to it, a relation which Cooper (1919) has emphasized.

**Factor and seral relations.**—In an intensive study of the habitats of subclimax oak forest and the chaparral, Cooper (1919) has reached the following conclusions:

"As to soil: Humus in the chaparral is very scanty, but in the forest is abundant—nearly 2 per cent by weight in the surface layer and considerable to the depth of 1 meter. In water-content there is large difference during the rainy season, the forest having the greater amount. At this time the surface layers are most important, since the major part of the absorbing roots are contained therein. It is here, too, that the water-content differences mainly show themselves; at the depth of 1 meter such being practically negligible. As the dry season advances, water-content values in both communities and at all depths converge, and at its culmination they are all very close together and the correspondence is rendered still more striking by comparison with the wilting coefficient in each case. In brief, there is notable difference in the actual amount of water available, but at the critical period conditions are about equally severe in both communities. In water-retaining capacity the only noteworthy feature is the relatively high value in the surface soil of the forest community, due to humus. As to soil temperature, the comparative march is the reverse of water-content; the values are closely similar in the wet season but widely divergent in the dry, the chaparral being much the higher.

"As to atmospheric factors: Rainfall, cloud, fog, and wind may be dismissed as immaterial to the present local problem. The light impinging upon a leaf of the foliage canopy is much greater in chaparral than in forest, because of the fewer obstacles to its transmission, and reflection and diffusion from the light-colored soil surface. The intensity in the shade is considerably less beneath the forest canopy, both absolutely and proportionally. The fact that the shade intensity beneath *Arctostaphylus* is practically the same as in the forest indicates that the leaf character is determinative—the sparse needle foliage versus the broad leaves of the other shrubs and the trees. Temperature and relative humidity data are unsatisfactory, but their effects relative to the present purpose are largely included in evaporation. The differences in this factor, though not strikingly great, are constant throughout the year, the *Adenostoma* chaparral being the highest and the *Arctostaphylus* chaparral intermediate. This conclusion is drawn from the values obtained at the top of the vegetation. The rate at the surface of the ground does not show differences of import to the problem in hand.

"Our conclusion, then, is that the fundamental distinguishing difference between the two broad-sclerophyll climaxes—their continuing cause, so to speak—is in the water balance and its variations, whatever the indirect factors influencing it; that its importance is equally divided between wet and dry seasons, the greater excess of supply over loss in the forest during the growing season explaining the size and luxuriance of the plants living there, and the higher evaporation rate in the chaparral during the dry season, with equally severe soil-moisture conditions, accounting for the absence of mesophytic species in that habitat."

### SOCIETIES.

The winter rainy season of the Coast region causes a corresponding early development of societies and necessitates a readjustment of the aspects. Because of favorable temperatures, societies appear in southern California as early as January and the first aspect attains its maximum in February or March. In order to maintain the usual seasonal relations, this is regarded as the prevernal aspect. It is followed by a late spring or vernal aspect, and this by one in which summer and autumn relations are more or less combined. With few exceptions, the societies listed are perennial. Some of them bloom through more than one aspect, but these are listed in the first one in which they appear. A large number of annuals occur, especially in southern California, but these are either members of subsere communities, or they are desert annuals, most of which have already been given under the desert scrub. It is practically certain that some of the societies listed below have been derived from the original *Stipa* grassland, but the exact determination of these must await further study.

*Prevernal Societies:*
- Brodiaea capitata.
- Brodiaea congesta.
- Brodiaea grandiflora.
- Brodiaea minor.
- Sisyrinchium bellum.
- Eriogonum compositum
- Eschscholtzia californica.
- Delphinium parryi.
- Sidalcea malviflora.
- Viola pedunculata.
- Sanicula bipinnata.
- Sanicula bipinnatifida.
- Dodecatheon clevelandii.
- Castilleia foliolosa.
- Wyethia glabra.
- Wyethia helenioides.

*Vernal Societies:*
- Calochortus luteus.
- Calochortus venustus.
- Calochortus splendens.

*Vernal Societies*—continued.
- Hosackia glabra.
- Pentstemon heterophyllus.
- Pentstemon azureus.
- Lupinus formosus.
- Lathyrus splendens.
- Lathyrus vestitus.
- Astragalus crotalariae.
- Astragalus leucopsis.
- Eriophyllum confertiflorum.
- Eriophyllum lanatum.
- Phacelia ramosissima.
- Castilleia affinis.
- Delphinium hesperium.
- Gnaphalium bicolor.
- Gnaphalium decurrens.
- Polygala californica.
- Haplopappus linearifolius.
- Eriogonum nudum.
- Oxalis corniculata.
- Agoseris retrorsa.
- Agoseris grandiflora.

*Vernal Societies*—continued.
- Hypericum concinnum.
- Scrophularia californica.
- Convolvulus occidentalis.
- Paeonia brownii.
- Wyethia angustifolia.
- Corethrogyne filaginifolia.
- Galium andrewsii.
- Lomatium tomentosum.

*Estival Societies:*
- Artemisia heterophylla.
- Achillea millefolium.
- Solidago californica.
- Gutierrezia sarothrae.
- Senecio douglasii.
- Zauschneria californica.
- Verbena prostrata.
- Verbena stricta.
- Opuntia engelmannii.
- Opuntia basilaris.

## THE WOODLAND CLIMAX.

### PINUS-JUNIPERUS FORMATION.

Nature.—The woodland formation consists of small trees capable of forming a canopy and hence of constituting a real though low forest. A number of reasons combine to make it the most difficult of all formations to delimit and to characterize. The first of these lies in the ability of practically all the dominants to vary from trees 30 to 50 feet high to shrubs of 10 to 20 feet, and in some cases to bushes of less than 10 feet. As trees they often give the appearance of being integral parts of the forest communities in which they occur, while in the form of shrubs and bushes they are equally at home in chaparral. The consequence is that the same species may appear as an important if not dominant constituent of chaparral, woodland, and forest, and its proper rôle becomes very difficult of determination. As a community, the woodland occupies fairly narrow limits of altitude, and hence becomes massive only on great upland plateaus, such as the Mesa Verde. In general, it occurs on hillsides and mountain slopes in regions of rough topography. As a consequence, it not only lacks mass and often continuity as well, but it is also more or less obscured by admixture with dominants from the zones above and below. This is emphasized by the character of the dominants. Where the oaks are abundant, they give the woodland the appearance of belonging to the chaparral, or of constituting an oak savannah, while the piñon and cedar aline it rather with the forests of yellow pine and fir. However, the chief source of confusion lies in the ability of all the dominants, but of the cedar[1] especially, to invade rocky areas, largely as a result of the readiness with which their fruits are distributed by rodents and birds. As a consequence, an open chaparral-like type occurs throughout the West from Texas to California and from Mexico to Montana. It agrees with the climax woodland only in the presence of one or two of the dominants, but differs from it in habitat, structure, and development. In some regions, it will pass into the climax, but as a rule it is an anomolous subclimax stage which yields to chaparral, sagebrush, or forest.

Typically, the woodland consists of small trees 20 to 40 feet high, belonging to the three genera, *Juniperus*, *Pinus*, and *Quercus*. While these vary widely in leaf character, they agree in being evergreen and xerophytic. They form fairly dense crowns and in favorable situations make a continuous canopy and a fairly uniform shade. The term woodland was apparently first applied by the Forest Service, and is used to include all areas in which piñon and cedar are characteristic. In the present case, woodland is used only for the climax proper, consisting of cedar, pines, or oaks variously mixed in forests of low stature. About such climax areas are often much wider ones in which one of the dominants constitutes a grassland or scrub savannah.

Range and extent.—The woodland formation is essentially southwestern in extent. It finds its best expression as a climax on the high plateaus of the Colorado Basin, but it occurs from the Davis and Guadalupe Mountains of western Texas through northern Mexico to Lower California. It extends northward along the foothills in New Mexico and Colorado to southwestern Wyoming, and then westward through Utah and Nevada to northern California. Over by far the greater part of this vast area it forms a more or less continuous belt along the mountain ranges, broadening out into extensive forests only where tablelands of median altitude permit. The piñon-cedar association is much the most extensive as well as the most typical, while the oak-cedar community is restricted to southwestern Texas, southern New Mexico and Arizona, and northern Mexico, and the pine-oak to California. The cedar ranges far beyond the climax region, forming characteristic communities on rocky slopes and escarpments from Scott's Bluff and Pine Ridge

[1]In view of the divergence in the botanical use of cedar and juniper for various species of *Juniperus*, cedar has been preferred as representing the common usage in the West.

in western Nebraska northward into Saskatchewan and westward to Oregon. It also occurs frequently with chaparral and scrub on the Edwards Plateau in Texas.

Unity of the formation.—As has already been indicated, the geographic unity of the woodland climax is less than in any other western formation. This is necessarily the case because of its regular occurrence on the lower levels of mountain ranges and plateaus. As a consequence, it is characteristically fragmentary, though consistent in being generally southern and at middle altitudes of 7,000 to 8,000 feet. Climatically, it is intermediate between chaparral and sagebrush on the one hand and the montane forest on the other. The average rainfall is 15 to 20 inches and the average evaporation about 20 to 25 inches. The summer temperatures are high and the winters moderate for the most part, though snow lies for some time over most of the climax regions (fig. 8).

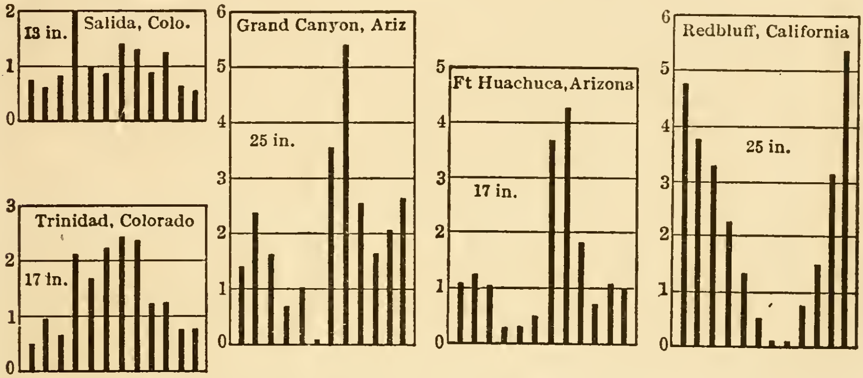



Fig. 8.—Monthly and total rainfall for representative localities in the associations of the woodland climax.

Floristically, the woodlands show a high degree of unity. The dominants all belong to three genera, *Pinus*, *Juniperus*, and *Quercus*. While the number of minor species or varieties is large, amounting to 19, the actual species are but 8. The most important of these are *Pinus edulis*, *Juniperus californica*, and *J. occidentalis*. These three with their varieties range throughout the region, and one or the other occurs more or less regularly in each association. The subdominants are relatively few, but it is significant that *Rhus*, *Ceanothus*, *Cercocarpus*, *Purshia*, etc., are found over the major portion of the formation.

Ecologically the formation is essentially uniform in its composition, consisting of small trees with evergreen leaves. While the latter are present in three forms, scale, needle, and broad leaf, it seems clear that these are ecologically equivalent or nearly so. The constant mixture of cedar and piñon in the central association leaves no doubt of their essential equivalence, though the scale-leaved cedar is clearly the more xerophytic. The same is true of the southern association of cedar, piñon, and oak, and apparently also of the California association of digger pine and oak. In all of these communities, the dominants have marked ability to adjust themselves to more xerophytic conditions by becoming shrubby or by growing in an open stand. A direct and characteristic consequence of this is the almost universal production of mixed communities, in which grassland, chaparral, or sagebrush play an important or controlling part. Practically all the dominants are intolerant of shade, and hence they never constitute a secondary layer in the montane forest of the zone above.

No special study of the successional relations of woodland has been made as yet. Throughout the climax area, as well as beyond it, open shrubby woodland appears relatively early on rocky slopes or hills, forming a subclimax to woodland proper or to montane forest, or being displaced by scrub or grass as the habitat develops. The climax woodland may replace grassland, sagebrush, or chaparral, and may in its turn be displaced by yellow pine or other dominants of the montane forest at the upper edge of its zone.

In origin, the woodland is uniformly southern and largely Mexican. *Pinus edulis* and *Juniperus monosperma* have their centers in Colorado, Utah, Arizona, and New Mexico, though they extend into Texas and Mexico. *Pinus monophylla* and *Juniperus utahensis* are confined almost wholly to Utah, Nevada, northeastern Arizona, and eastern California. *P. cembroides* and *J. pachyphloea* are chiefly Mexican, extending into Arizona, New Mexico, and western Texas. The oaks are all Mexican, with the exception of *Quercus douglasii* and *Q. wislizenii*, which are almost exclusively Californian. They range to central Arizona, New Mexico, and western Texas. *Juniperus scopulorum* is by far the most widespread of the dominants, as would be expected from its close relationship to the eastern *J. virginiana*. It occurs from central Nebraska to Washington and from British Columbia to the Mexican boundary, while *J. occidentalis* ranges from Washington to the border of southern California. The limits of *Pinus sabiniana* lie wholly in California, from near the northern boundary southward to the Tehachapi. Of the 19 species and varieties which comprise the dominants of the formation, practically all but *Juniperus scopulorum* and *J. occidentalis* find their northern limits below the forty-second parallel, 11 are predominantly Mexican, 4 have their center on the Colorado plateaus, and 2 are Californian.

The above account indicates clearly the differentiation which has occurred in the formation. The greatest number of dominants still occurs in the region of the Mexican boundary. The most uniform development of the formation is on the Colorado Plateau, while the most specialized area is found in California, as a natural consequence of the desert and mountain barriers.

Structure of the formation.—The dominants are as follows:

| | | |
|---|---|---|
| Juniperus californica. | Juniperus sabinoides. | Quercus emoryi. |
| Juniperus californica utahensis.[1] | Juniperus virginiana scopulorum. | Quercus reticulata. |
| Juniperus occidentalis. | Pinus edulis. | Quercus reticulata arizonica. |
| Juniperus occidentalis monosperma. | Pinus edulis monophylla. | Quercus reticulata oblongifolia. |
| Juniperus pachyphloea. | Pinus edulis quadrifolia. | Quercus douglasii. |
| Juniperus flaccida. | Pinus cembroides. | Quercus wislizenii. |
| | Pinus sabiniana. | |

These are grouped in three associations, namely, the *Quercus-Juniperus*, the *Pinus-Juniperus*, and the *Pinus-Quercus*. The first of these is southern and

[1]The specific relationship of the varieties as understood here is indicated by means of the trinomial, but the name of the species is omitted in the text for the sake of brevity.

southeastern in position, and is thought to represent the original mass of the formation. The second is central and typical, while the last is Californian and its relationship is less definite. The first two are in contact with each other for a long distance, but they are readily distinguished by the presence or absence of *Juniperus pachyphloea* and the evergreen oaks. The California association is separated from the other two by the Colorado and Mohave Deserts and the Sierra Nevada, and the dominants mix but slightly. *Pinus monophylla* and *Juniperus californica* are the two species which maintain the contact between the associations. This contact is in no wise as close or significant as that between the two eastern associations, but this seems adequately explained by the barriers mentioned. In other respects especially, the *Pinus-Quercus* community appears much more nearly related to the woodland than to any other climax.

**Contacts.**—The woodland climax occupies the position indicated by its vegetation-form, viz, the small evergreen tree. This is true both geographically and successionally, except where one or more dominants occur outside of the climax area. At its lower limit it is regularly in contact with scrub of some type, usually sagebrush or chaparral, rarely desert scrub. In the region of the latter, the contact is usually with *Prosopis* savannah or with the *Parkinsonia-Cereus* scrub, or the oak mass itself shades out into a savannah dominated by *Bouteloua* and *Andropogon*. Throughout its central area in the Great Basin, sagebrush is everywhere in touch with the woodland, though sometimes mixed with chaparral. Along the eastern ranges of the Rocky Mountains and in California, the contact is with chaparral. At the upper edge, woodland is almost universally in touch with the montane forest, and particularly the *Pinus ponderosa* consociation, which is the most xeroid. The contact may also be with a mixture of *Pinus* with *Pseudotsuga mucronata* or *Abies concolor*, or with either of the latter consociations alone. This last case is infrequent, however, and usually occurs where the yellow pine is absent or unimportant. Successionally, woodland yields to yellow pine forest in the ecotone between the two climaxes, especially during the wet phase of major sun-spot cycles. Outside of the climax region, where it is represented by cedar especially, it gives way to the chaparral, sagebrush, or grassland climax with which it is in contact.

## THE PIÑON-CEDAR WOODLAND.

### PINUS-JUNIPERUS ASSOCIATION.

**Nature and extent.**—This association is the most typical and definite of the three that constitute the woodland climax. It usually consists of two dominants, *Pinus* and *Juniperus*, which are regularly associated. They are similar in character and requirements, and hence give a much more uniform physiognomy than is found in the other two communities. This type of woodland occurs most frequently in narrow belts a mile or less to a few miles wide along the foothills of ranges from the Front Range of the Rocky Mountains to the eastern slopes of the Sierra Nevada. On the north it ranges from the southern edge of Idaho and Wyoming to Lower California, central Arizona, and New Mexico. Its most typical expression is found in the center of this great region on the high plateaus of the Colorado River. In such areas it forms more or less continuous forests many miles in extent. The trees are 20 to 40 feet high and stand sufficiently close to shade three-fourths or more of the ground. This results in a sparse though characteristic ground cover. Such extensive stretches of woodland are typical of the Grand Canyon plateau in northern Arizona and southern Utah and of the Mesa Verde and Uncompahgre plateaus in southwestern Colorado. It is on these that the climax association is to be seen at its best and its extent and importance fully appreciated (plate 45).

The woodland dominants also occur throughout the range of the association as a subclimax community in relatively new areas. They are the distinctive feature of rocky slopes and of cliffs and escarpments at elevations of 5,000 to 8,000 feet over most of the climax area. Single dominants may extend far beyond the latter as subclimax in sagebrush, chaparral, or grassland. This is especially true of *Juniperus*, but it holds for *Pinus* also in some measure. Such seral communities are mixed in varying degrees with the dominants of the climax in which they occur and frequently lead to the assumption that the woodland dominant is a member of the sagebrush or chaparral. All of the evidence contradicts this assumption, however, and supports the view that this is merely the normal response to developmental processes where two climaxes occupy a broad and greatly interrupted ecotone. The contacts of this association are essentially those already indicated for the formation, namely, sagebrush and chaparral below and montane forest above. At its own level, it touches the *Quercus-Juniperus* association broadly from Arizona to Texas, and comes into fragmentary contact with the *Pinus-Quercus* community in California.

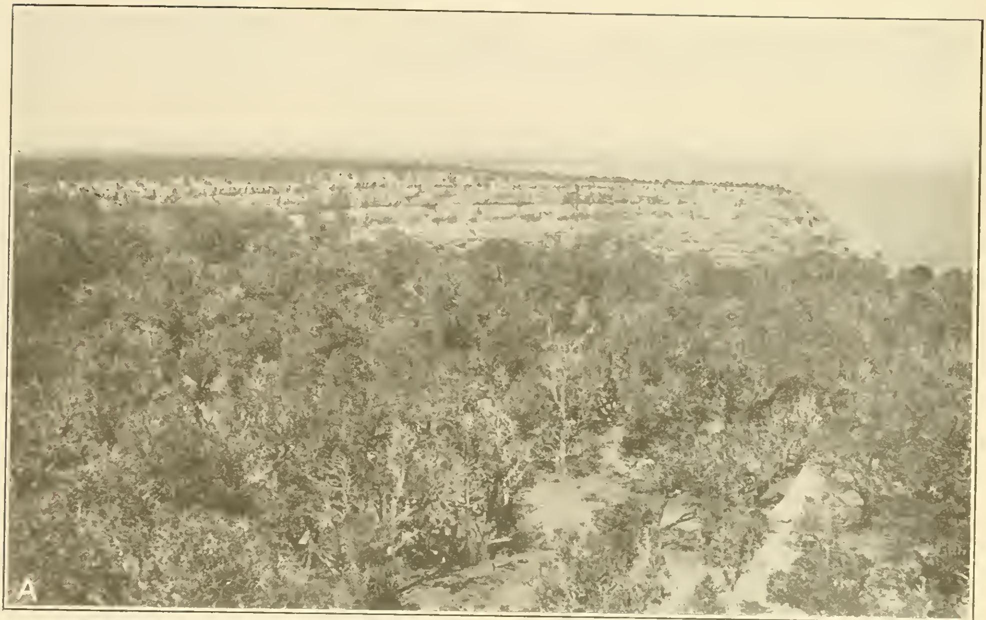
DOMINANTS.

Juniperus occidentalis monosperma.
Juniperus californica utahensis.
Juniperus virginiana scopulorum.
Pinus edulis.
Pinus edulis monophylla.

The most important of the dominants are *Pinus edulis* and *Juniperus monosperma*. They occupy by far the major portion of the climax area, and are regularly associated. *Juniperus scopulorum* has much the widest range, especially northward, but it is usually of secondary importance in the community. The other four dominants exhibit two interesting and novel correlations. *Pinus monophylla* and *Juniperus utahensis* are regular associates in the western half of the climax, as are *P. edulis* and *J. monosperma* in the eastern. Moreover, they are complementary forms, the latter dominating the association through Colorado and most of New Mexico, Arizona, and Utah, the former in Nevada and California. In western Utah and northwestern Arizona the ranges of these four dominants overlap.

In this common region, all five dominants may occur together, but this is rare. The association of the four just mentioned is less so, but it is infrequent at best. The general rule is that *Pinus edulis* and *J. monosperma*, or *P. monophylla* and *J. utahensis* occur together, or that either one of the piñons is found with both of the cedars. In Colorado and New Mexico at least, it is not uncommon to find *P. edulis* associated with both *J. monosperma* and *J. scopulorum*, though usually in the more open and less typical stands. With the exception of *J. scopulorum*, all of the dominants frequently occur in pure stands, but this is usually a consequence of differentiation by altitude.

Piñon-cedar Woodland



A. *Pinus-Juniperus* association, Grand Canyon, Arizona.
B. Detail of piñon-cedar woodland, Delta, Colorado.

The groupings of the piñon-cedar woodland have been noted in approximately a hundred localities throughout the climax area. In the majority of these, *Pinus edulis* and *Juniperus monosperma* are the dominants. The piñon occurs infrequently in pure stands, but this is regularly the case with cedar at lower altitudes, where the piñon drops out. In such instances, however, the climax woodland soon disappears and the cedar forms a savannah in sagebrush or grassland. In addition to the Colorado plateaus already mentioned, extensive climax areas of piñon-cedar have been studied in Colorado at Garland, Arboles, Mancos, Cortez, Dolores, on the San Miguel plateau, and on the plateau of Deadman's Cañon south of Cheyenne Mountain. In Utah similar areas occur at Moab, La Sal, and Bluff.

The piñons make greater demands than the cedars for water though not for light. In the general absence of quantitative studies, the sequence must be determined by the consideration of successional relations supplemented by evidence from growth-forms and distribution. Upon this basis, *Pinus edulis* is the least xerophytic, followed by *P. monophylla*, *J. monosperma*, and *J. utahensis*. *J. scopulorum* seems to approach *P. edulis* more nearly, judging from the fact that it usually makes its best growth in moist canyons. The habit of *P. monophylla* and *J. utahensis*, as well as the nature of the community, accords with the fact that the western portion of the climax receives several inches of rain less than the eastern in general. The reduction of the fascicle to a single leaf in the piñon also suggests the differentiation of this association into two very closely related communities.

## SOCIETIES.

Societies proper to the woodland are to be expected only where the climax is more or less extensive. In subclimax areas and especially where the community is fragmentary or becomes converted into savannah, the herbs and shrubs of the ground cover are derived from the adjacent or surrounding climax, sagebrush, chaparral, or grassland. Moreover, the shade of the typical woodland has reduced the scrub or grassland species which could adapt themselves to it, just as the more xerophytic habitat has discouraged invasion from the montane forest. As a consequence, the ground cover is composed of a sparse community of shade species in the denser woodland, while the more open areas are occupied by societies more or less common to the adjacent formations. Aspects are little if at all developed in the former, and no attempt has been made to distinguish them here. Several of the dominants of the chaparral, sagebrush, and grassland have the appearance of societies, as they are not only constant features, but also take on a habitat-form more or less peculiar to the shady woodland.

*Shade societies.*

| | | |
|---|---|---|
| Chenopodium fremontii. | Aster ericoides. | Gutierrezia sarothrae. |
| Draba caroliniana. | Malvastrum coccineum. | Senecio fendleri. |
| Pentstemon linarioides. | Gymnolomia multiflora. | Astragalus flexuosus. |
| Sisymbrium incisum. | Allium acuminatum. | Hymenopappus filifolius. |
| Gilia aggregata. | Grindelia squarrosa. | Eriogonum umbellatum. |
| Erysimum parviflorum. | Pedicularis centranthera. | Artemisia discolor. |
| Pentstemon barbatus. | Arabis drummondii. | Artemisia frigida. |
| Pentstemon coeruleus. | Chenopodium leptophyllum. | Actinella acaulis. |
| Opuntia mesacantha. | Cordylanthus wrightii. | Physaria didymocarpa. |
| Lesquerella argentea. | Aster bigelovii. | Yucca baccata. |
| Hedeoma drummondii. | Chrysopsis villosa. | |

## THE OAK-CEDAR WOODLAND.

### QUERCUS-JUNIPERUS ASSOCIATION.

**Nature and extent.**—The oak-cedar association is regarded as the basic or original community from which the related piñon-cedar and pine-oak woodland have been differentiated, one to the north and the other to the west. This is indicated by its position, but especially by its composition. It contains the three dominant genera and the largest number of species and varieties. It differs from the northern association in the predominance of oaks. The latter are important also in the western woodland, but to a less degree, and they belong to different species. The presence of oaks, pines, and cedars in these two associations shows the essential equivalence of the broad-leaved and needle-leaved evergreens as formational dominants. The variable nature of the deciduous habit is shown by the fact that *Quercus douglasii* loses its leaves in the fall or winter, while the other species drop them at different times in the spring. All of them agree in being essentially sclerophyll in habit (plate 46).

The oak-cedar woodland has its center in southern Arizona and New Mexico and in northern Mexico. It occurs commonly in the mountain ranges of trans-Pecos Texas and is found scattered in the canyons and escarpments of the Staked Plains and the Edwards Plateau. It extends north over the mountains of the eastern half of Arizona and the western half of New Mexico to the thirty-fifth parallel, where it yields rather abruptly to the piñon-cedar association. *Pinus cembroides* occurs also in Lower California, where it is associated with *P. edulis, P. monophylla, P. quadrifolia,* and *Juniperus californica,* and serves to emphasize the general unity of the formation.

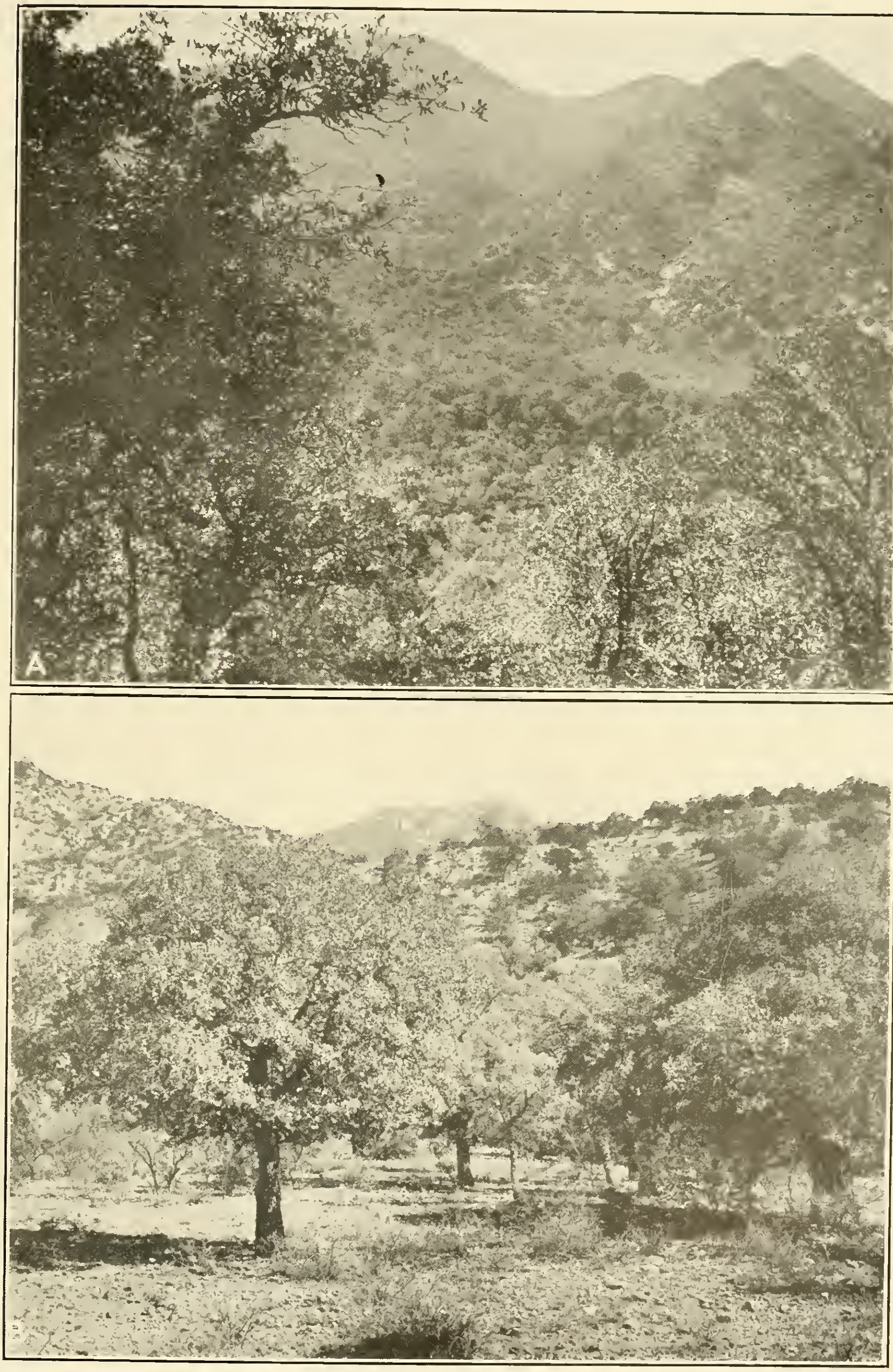
DOMINANTS.

| | | |
|---|---|---|
| Quercus emoryi. | Quercus reticulata. | Juniperus flaccida. |
| Quercus reticulata arizonica. | Juniperus pachyphloea. | Juniperus virginiana scopulorum. |
| Quercus reticulata oblongifolia. | Juniperus occidentalis monosperma. | Pinus edulis. |
| Quercus hypoleuca. | Juniperus sabinoides. | Pinus cembroides. |

An intermediate mixture of several dominants is characteristic of most of the associational area, especially the central portion in southern New Mexico and Arizona, and northern Mexico. The fundament of the latter is formed chiefly by the oaks, in which cedar and piñon occur in varying abundance. Pure stands are the exception, particularly in the central mass. They are more frequent as the areal or altitudinal limits of the association are approached, owing to the decrease in the number of dominants. At the edges, communities of single dominants are more or less typical, but they usually take the savannah form, as in the oaks, or they characterize seral areas, such as the escarpments covered with *Juniperus sabinoides.* Near the margin of the association, there is also a marked tendency for the dominants to become low and shrubby, and consequently to become confused with the elements of the chaparral. In the mountains of southern Arizona, the greatly broken topography produces innumerable fragmentary habitats and causes a confusing mixture of woodland with desert scrub, chaparral, and even montane forest (cf. Shreve, 1915 : 31).

The most typical grouping of the oak-cedar woodland is *Quercus emoryi, Q. arizonica,* and *Q. hypoleuca* with *Juniperus pachyphloea* and *Pinus cem-*

Oak-cedar Woodland




A. *Quercus-Juniperus* association, Santa Rita Mountains, Arizona.
B *Quercus arizonica* consociation, Santa Rita Mountains.

*broides.* This is nearly universal in the mountains of southeastern Arizona and adjacent New Mexico, and doubtless in those of northern Mexico as well. *Quercus oblongifolia* is regularly present in the lowest part of the zone, and a shrubby form of *Q. reticulata* in the uppermost portion. To the north and east *Pinus edulis* and *Juniperus monosperma* enter the mixture also. On the Guadalupe and Davis Mountains of trans-Pecos Texas the grouping is *Quercus arizonica, Q. emoryi, Pinus edulis, Juniperus pachyphloea, J. monosperma,* and *J. sabinoides.* In the Chisos Range to the south, *Pinus cembroides* and *Juniperus flaccida* occur as well. East of the Pecos River, the number of dominants decreases abruptly, and the rough areas of the Staked Plains and the Edwards Plateau show only *Juniperus sabinoides, J. monosperma, Pinus edulis,* and *Quercus arizonica,* single or in varying mixture. *Quercus arizonica* in particular becomes reduced to a shrub and mingles with the live-oak chaparral.

**Factor relations.**—The relative requirements of the dominants are shown by their altitudinal positions. In the mountains of southern Arizona, the lowest oak is *Q. oblongifolia,* followed by *Q. emoryi,* this by *Q. arizonica,* and then by *Q. hypoleuca.* They drop out in about the same order, except that *Q. arizonica* is represented at the highest elevations by the shrubby form of *Q. reticulata. Juniperus pachyphloea* begins above the lower oaks, while *Pinus cembroides* enters still later. Shreve (1915 : 24) places the lower limit of the woodland or "encinal" zone of the Santa Catalina Mountains at 4,300 feet and the upper at 6,000 to 6,500 feet. *Quercus oblongifolia* and *Q. arizonica* are the first to appear at the lower edge of this zone, followed by *Juniperus pachyphloea. Quercus emoryi* and *Pinus cembroides* enter at 5,000 feet, and *Q. hypoleuca* at 5,600 feet. The cedar and piñon reach their maximum abundance between 5,500 and 6,500 feet. *Quercus oblongifolia* disappears at about 5,200 feet and the typical form of *Q. arizonica* at 6,500 feet. *Quercus emoryi* reached its upper limit at 6,300, while *Pinus* and *Juniperus* cease to be dominants between 6,500 and 7,000 feet.

*Summer rainfall in inches.*

| Elevation. | 1911. | 1912. | 1913. | 1914. | Average. |
|---|---|---|---|---|---|
| 3,000 feet..... | 6.27 | 5.61 | 6.46 | 10.62 | 7.55 |
| 4,000 feet..... | 9.45 | 9.77 | 8.59 | 14.73 | 10.63 |
| 5,000 feet..... | 11.97 | 8.24 | 10.27 | 19.13 | 12.40 |
| 6,000 feet..... | 11.07 | 8.68 | 8.73 | 22.68 | 8.05 |
| 7,000 feet..... | 15.86 | 14.57 | ..... | 27.64 | 15.21 |

*Average daily evaporation in cubic centimeters for north and south exposures.*

| Elevation. | May-June. | | June. | | June-July. | | July-Aug. | | Aug.-Sept. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | S. | N. | S. | N. | S. | N. | S. | N. | S. | N. |
| 3,000 feet....... | 120.5 | .... | 85.7 | .... | 61.1 | .... | 49.8 | .... | 55.6 | .... |
| 4,000 feet....... | 84.8 | 91.2 | 81.3 | 88.4 | 67.6 | 76.5 | 54.7 | 53.5 | 42.8 | 56.9 |
| 5,000 feet....... | 74.2 | 83.1 | 60.8 | 88.8 | 50.9 | 46.1 | 44.2 | 37.2 | 50.8 | 33.4 |
| 6,000 feet....... | 67.7 | 68.6 | 52.8 | 47.4 | 50.4 | 43.3 | 34.2 | 33.6 | 39.5 | 28.3 |
| 7,000 feet....... | 72.5 | 57.5 | 55.2 | 44.3 | 46.8 | 43.3 | 37.3 | 34.1 | 39.3 | 24.0 |

*Decrease of temperature with altitude.*

| Elevation. | 1914. | Average. |
|---|---|---|
| 4,000 feet.. | 1.6 | 1.9 |
| 5,000 feet.. | 8.1 | 8.1 |
| 6,000 feet.. | 7.6 | 9.2 |
| 7,000 feet.. | 14.0 | 13.7 |

Shreve (*l. c.*, 46) has made a thorough study of the climatic relations of the Santa Catalina Mountains, and the three preceding tables for the woodland have been taken from his tables for rainfall (52), evaporation (64), and temperature (75).

### SOCIETIES.

The oak-cedar woodland has few distinctive societies. It is in constant or repeated contact with desert scrub, grassland, chaparral, and montane forest, and holds practically all its subdominants in common with one or more of these. Because of its savannah-like contact with the desert plains, the majority of the societies have been derived from the latter. It is desirable to consider here only those which occur in the partial or complete shade of the woodland as a dominant community. The societies vary with the season and altitude, but a detailed treatment of them is impossible at present.

*Shade Societies.*

Solidago speciosa.
Artemisia gnaphalodes.
Monarda citriodora.
Hymenothrix wrightii.
Gaura suffulta.
Desmodium batocaule.
Sporobolus confusus.
Crotolaria lupulina.
Gymnolomia multiflora.
Haplopappus gracilis.
Polygala alba.
Comandra umbellata.
Hymenopappus mexicanus.
Cordylanthus wrightii.
Andropogon scoparius.
Bouteloua racemosa.
Muhlenbergia affinis.
Rhus radicans.
Rhus trilobata mollis.
Pteris aquilina.
Pellaea wrightiana.
Cheilanthes fendleri.

## THE PINE-OAK WOODLAND.

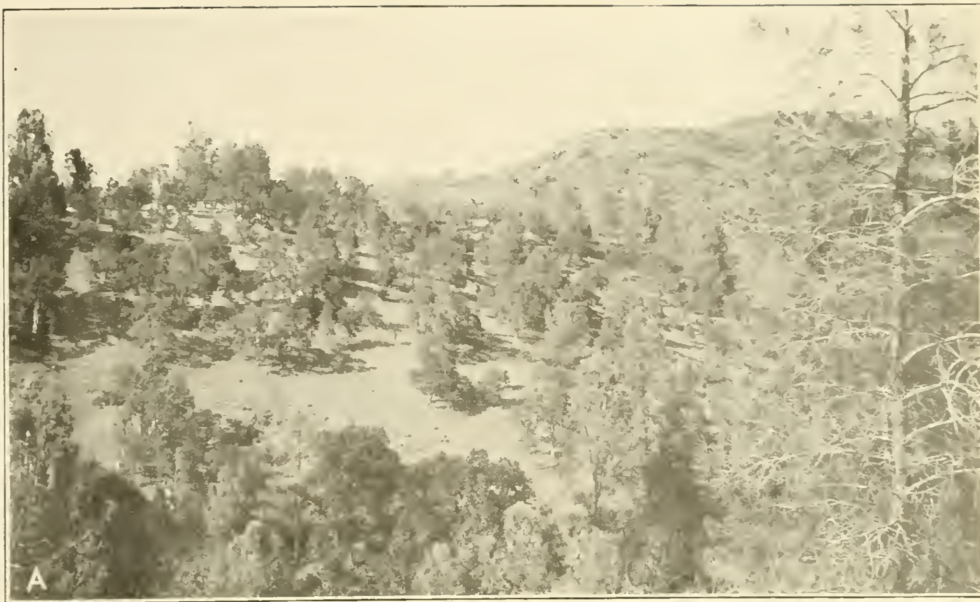
### PINUS-QUERCUS ASSOCIATION.

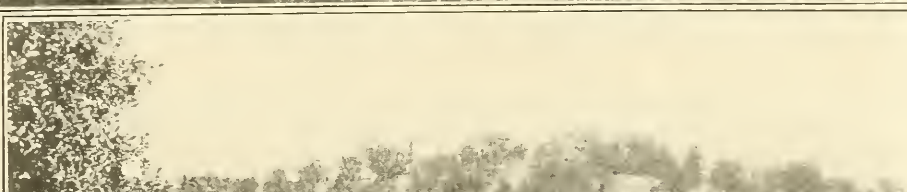
Nature and extent.—The first suggestion that the community of *Pinus sabiniana* and *Quercus douglasii*, so typical of dry foothill slopes in central California, constituted a third association of the woodland formation was due to its general likeness in appearance and position to the oak-cedar woodland. The probability of this relationship has been greatly increased by the discovery that these two characteristic dominants are associated with piñon and cedar where their ranges overlap. This is pointed out by Abrams (1910: 317):

"The Upper Sonoran area on the desert slopes of the mountains is commonly called the piñon and juniper belts, the two conifers, *Pinus monophylla* and *Juniperus californica*, being the most characteristic species. Several trees and shrubs which belong properly to the Intramontane district penetrate through Tejon Pass and extend in a narrow belt along the western slope of Antelope Valley. The normal flora of the desert slopes is modified in this section by the presence of such species as *Pinus sabiniana* and *Quercus douglasii*."

A further search for groupings of *Pinus sabiniana* or the associated oaks with piñon or cedar has disclosed the fact that Coville (1893) had noted these repeatedly in the southern Sierra Nevada:

Pine-oak Woodland





A. *Pinus-Quercus* association, Chico, California.
B. *Quercus douglasii* consociation, Red Bluff, California.

"At about 3,000 feet, the gray-leaf pine (*Pinus sabiniana*) begins, intermixed with a few Nevada nut pines (*P. monophylla*)." (8)

"The tree (*P. sabiniana*) did not form a forest at any point, but grew with nut pines scattered about in open places or chaparral slopes." (223)

"*Juniperus californica* was found to occur to some extent in both the chaparral belt and that of Douglas's oak." (225)

This correlation of the California woodland seems also to furnish the explanation of the anomaly described by Parish (1903 : 221):

"In the upper end of Antelope Valley, the orographical confusion which there exists has given rise to a curious phytogeographical anomaly. Here *Pinus sabiniana, Quercus douglasii*, and *Q. wislizenii*, trees characteristic of the western slope of the Sierra Nevada throughout central California, coming through Tejon Pass, find themselves on the eastern slope of that range, and the unusual sight is presented of desert foothills clothed with an almost unmixed growth of scrub-oaks."

The dominants of the pine-oak woodland correspond somewhat closely with those of the oak-cedar association. *Pinus sabiniana* is representative of the piñons, especially *P. cembroides. Juniperus californica* corresponds with *J. pachyphloea, J. monosperma*, or *J. sabinoides. Quercus douglasii* is the counterpart of *Q. reticulata* and its varieties, and *Q. wislizenii* is related to *Q. hypoleuca* and perhaps even more closely to *Q. emoryi*. The two associations occupy the same relative position with reference to montane forest, chaparral, desert scrub, and grassland. Both show a preference for rough topography and dry unstable slopes, and are in consequence much mixed with chaparral. The oaks of both associations likewise regularly give rise to savannah where they come in contact with grassland. In both cases the contact is with associations of the grassland climax, though in the California the original rôle of *Stipa* in the savannah is almost completely obscured by the dominance of the ruderal species of *Avena* and *Bromus* (plate 47).

This association is limited to California and Lower California. It extends from the general region of Mount Shasta southward along the foothills and mountain slopes to the San Pedro Martir Mountains of Lower California. In the central part of California, it ranges from the Sierra Nevada to the mountains along the coast, but toward the south it is restricted chiefly to the San Bernardino, San Jacinto, and Cuyamaca Mountains.

DOMINANTS.

| | | |
|---|---|---|
| Pinus sabiniana. | Juniperus californica utahensis. | Pinus edulis quadrifolia. |
| Quercus douglasii. | Juniperus occidentalis. | Pinus cembroides. |
| Quercus wislizenii. | Pinus edulis monophylla. | Yucca arborescens. |
| Juniperus californica. | | |

The two most typical dominants are *Pinus sabiniana* and *Quercus douglasii*, and these give the character from Mount Shasta southward to the foothills of Antelope Valley and the Mohave Desert. *Quercus wislizenii* and *Juniperus californica* are not infrequent associates, but they are less frequent as codominants. They extend southward into Lower California and hence are more often associated with the piñons. The latter seem to meet *Pinus sabiniana* and *Quercus douglasii* only in the neighborhood of Tejon Pass and Tehachapi Pass. South of these points it is often difficult if not impossible to draw a line between the pine-oak and piñon-cedar woodlands, since *Juniperus utahensis* extends well into California and *Pinus monophylla* to Lower California. However, the presence of *Quercus wislizenii*, *Juniperus californica*, and *Pinus quadrifolia* from the San Bernardino or Santa Rosa Mountains to Lower California, as well as that of *P. cembroides*, is regarded as indicating the pine-oak association.

The community relationship of *Yucca arborescens* is somewhat uncertain, but its constant association with *Juniperus californica* along the northern base of the San Bernardino Mountains from Cajon Pass to Neenach, and to Hesperia indicates that it is a dominant of the woodland. Like *Yucca radiosa* and *Y. macrocarpa*, it extends downward into the desert scrub, but its life-form, optimum growth and zone of dominance warrant its inclusion in the woodland. Merriam (1893 : 341, 354) has noted the occurrence of *Yucca arborescens* and *Juniperus californica* on the mountain ranges south and north of the Mohave Desert, where they form a distinct belt at 3,500 to 4,000 feet. Leiberg (1900 : 444–445, 471) has recorded the composition of several woodland communities in which *Yucca* occurs on the lower levels of the San Bernardino Mountains. It is associated with *Juniperus californica* and *Pinus monophylla*, with these and *Juniperus occidentalis*, with *Pinus monophylla* alone or with *P. monophylla* and *Q. wislizenii* also. Parish (1903 : 221) has found *Yucca* and *Juniperus californica* forming an open community along the San Bernardino and Chuckawalla Mountains and from Daggett to Pilot Knob, while Sudworth (1908 : 201) states that *Yucca* is also associated with juniper, piñon, and *Pinus sabiniana*. From the nature of its crown, the tree-yucca forms even more open communities than the other dominants of the woodland, and hence the consociation is constantly mixed along its lower portion with dominants from the desert scrub and sagebrush.

Little is known of the factor or successional relations of this community. The latter seem in general to correspond with those of the oak-cedar woodland. The oaks are the more xerophytic, and *Quercus douglasii* rather more than *Q. wislizenii*, if distribution be regarded as an indication. Their relative position seems definitely indicated by the frequency with which they form savannah with grassland at their lower limits. In spite of their occurrence in rocky subclimax areas, the cedars and piñons appear to be rather more mesophytic than *Pinus sabiniana*. This is suggested by the respective altitudes at which they reach their greatest dominance, and seems to be certainly true for *Pinus cembroides*.

In the rough topography of the foothills, woodland, chaparral, and montane forest are often much mixed and confused. In spite of this, they appear as distinct units when differences of slope and successional development are taken into account. The two oaks and the digger-pine are frequently mixed with *Quercus californica* or *Q. garryana*, which really constitute a subclimax leading to the montane forest of *Pinus ponderosa* and *Pseudotsuga mucronata*. Where any of the three dominants occur with chaparral, the grouping is usually successional in character, or it represents an ecotone. In some cases where the trees are scattered more or less uniformly through a chaparral cover, the community is to be regarded as a savannah in which the grasses are replaced by shrubs, and it is probably to be similarly related to the climatic cycle.

## THE MONTANE FOREST CLIMAX.

### PINUS-PSEUDOTSUGA FORMATION.

**Nature.**—This climax is an evergreen forest in which the dominants are exclusively conifers. Broad-leaved deciduous and evergreen species occur in it, such as *Populus tremuloides*, *Quercus californica*, and *Arbutus menziesii*, but they are typically subclimax in character. In contrast with the woodland, this is a true forest formation. The trees are tall, usually 75 to 150 feet or more in height at maturity, with massive trunks and dense crowns. In typical habitats, they grow more or less closely, forming a continuous canopy. The latter is less dense than in the other two forest formations and the forest normally exhibits a good development of layers. The number of societies of shrubs and herbs is large and the aspects are well-marked. The major dominants are few, but they have a wide range and the composition of the formation is exceptionally uniform. The number of more restricted and of local dominants is larger, and they serve to give character to the associations. The most typical as well as the most xeroid of its dominants, *Pinus ponderosa*, possesses a striking power of adjustment and often forms savannah, which extends far into the Great Plains as belts of woodland.

**Extent.**—The montane forest is the most extensive and important of all the western forest climaxes. In its broadest outlines it extends from the foothills of western Nebraska and South Dakota and the mountains of western Texas to the Pacific Coast. It reaches from the mountains of central British Columbia to those of northern Mexico and Lower California. It occurs throughout the mountain ranges of the Great Basin and on those of the southwestern deserts where the altitude permits. On the east, extensive forests of *Pinus ponderosa* cover the Black Hills of South Dakota and a narrow strip of the same forest follows the canyon of the Niobrara River as far east as the ninety-ninth meridian. The southeastern limits of the formation are found in the Guadalupe and Davis Mountains of trans-Pecos Texas. The southernmost limit is attained by *Pinus ponderosa*, *P. arizonica*, and *P. chihuahuana* in the ranges of Sinaloa and Durango.

**Unity of the formation.**—The occurrence of the three major dominants, *Pinus ponderosa*, *Pseudotsuga mucronata*, and *Abies concolor*, from Montana to Mexico and Colorado to California leaves no question of the unity of the formation. This is further emphasized by the more or less constant presence of *Pinus contorta*, *P. flexilis*, and *P. albicaulis* in both associations. In addition, *Pinus* is represented by three species peculiar to each of the two associations, *Picea* by one species, and *Cupressus* by one. There is also a marked agreement as to the genera of the societies, more than three-fourths of these being common to both associations. With the major dominants so universal and controlling, it follows that the ecologic and phylogenetic unity of the formation is equally clear.

Geographically, the formation is typical of the great Cordilleran system from which it extends out upon the interior plateaus, such as that of the Colorado, and along the minor ranges and escarpments which front the Rocky Mountains on the east. Its climatic range rivals that of the grassland in so far as latitude is concerned. Both formations extend several degrees northward into Canada, and even a greater distance southward into Mexico. But grassland has a wider extension vertically and hence probably occupies a broader climatic belt. The vertical range as a climax is often more than 6,000 feet in the Rocky Mountains, and it is usually somewhat more in the Sierras and Cascades. The corresponding range in rainfall and temperature is enormous, and in either physical or human terms the climax contains several climates. In the form of the pine consociation, the montane forest often occurs in a rainfall of 20 inches or less from Colorado to Arizona and the Great Basin. On the Pacific Coast, it is frequently found in a rainfall of 50 to 60 inches. Moreover, along the central axis of the Rocky Mountains, 50 per cent or more of the rainfall occurs in the summer, while along the Sierras and Cascades, 70 to 90 per cent of the precipitation falls during the winter. The figures for temperature are less striking, but still very divergent. There is a difference of more than 20 degrees in the mean temperatures of the formation in northern Montana and northern California, and of 60 degrees in the lowest recorded minimum. In spite of this, the regular association of the three major dominants throughout the formational area indicates that the climate is essentially a unit from the standpoint of the dominant vegetation (fig. 9).

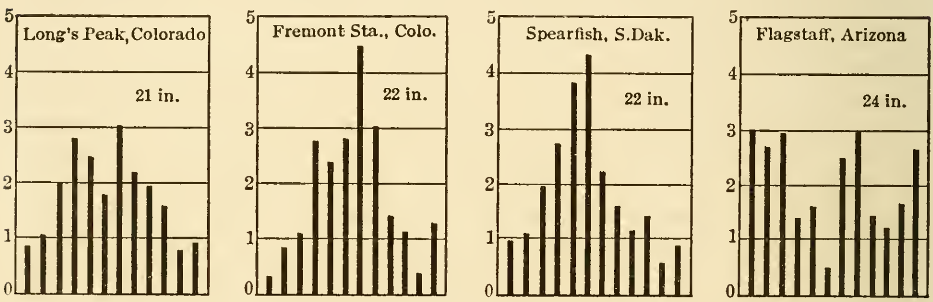



Fig. 9.—Monthly and total rainfall for representative localities in the association of the Petran montane forest.

**Relationship and contacts.**—The closest relationship of the montane climax is with the coast forest. This is best shown in northwestern Montana, northern Idaho, and adjacent British Columbia, where the two meet to form a broad transition. It is further indicated by the fact that *Pseudotsuga* is the typical subclimax species of the cedar-hemlock forest. The most important contact is with the subalpine forest. These touch each other for thousands of miles along the ranges of the Rocky Mountains and of the Sierra-Cascade system. They constitute a broad forest zone of fairly uniform physiognomy and have even been regarded as a single formation. Gray (1878) seems to have been the first to recognize their distinctness, and a similar view has been maintained by Merriam (1898) and his followers, obscured somewhat by the unsuccessful attempt to distinguish two zones, Canadian and Hudsonian, in the subalpine climax. While the two climaxes are similar in appearance, they differ fundamentally in composition, climatic and successional relations, and in origin. The difference between them is clear where they occur in massive zones, but is more or less hidden in regions of much topographic diversity.

The contacts along the lower edge of the formation are varied. The normal contact ecologically is with the woodland climax, and this is regularly found in the southern half of the formational area in which woodland is more or less

Petran Montane Forest

A. *Pinus ponderosa* consociation, Flagstaff, Arizona.
B. *Pinus ponderosa* consociation, Bend, Oregon.
C. *Pinus ponderosa* consociation, Black Hills, South Dakota.

constant. In the absence of the latter, the pine consociation meets chaparral in the coast regions and along the slopes of the central Rockies. On the desert slopes of the Great Basin it is often in touch with sagebrush, especially where represented by the subclimax lodgepole pine. It may also come in direct contact with the mixed prairie from Colorado northward, where it passes into extensive savannahs, characteristic of the isolated ranges and uplands of the Black Hills and adjacent regions.

Associations.—The general occurrence of *Pinus ponderosa, Pseudotsuga mucronata,* and *Abies concolor* through the montane climax was thought at first to indicate the presence of a single association. A scrutiny of the list of codominants reveals a fairly clear differentiation into a Rocky Mountain and a Sierra-Cascade community. These have three codominants in common, namely, *Pinus contorta, P. flexilis,* and *P. albicaulis.* The former differs much in habit and habitat between the two associations, while *Pinus flexilis* is more important in the Rocky Mountains and *P. albicaulis* in the Coastal region. Of the remaining 13 codominants, 5 are restricted wholly to the Rocky Mountain community and 8 to the Sierran. This differentiation is also emphasized by the variation in habit and size of *Pinus ponderosa* and *Pseudotsuga* in the two regions. This is so pronounced in the case of the pine that the common form of the Rocky Mountains has generally been treated as a variety or even as a species, while foresters have regarded the Douglas fir of the Pacific coast as a distinct variety. A similar differentiation is reflected in the societies of the forest. More than 75 per cent of the generic subdominants are the same for both associations, while they have less than 25 per cent of common species. Finally, the division of the montane climax has its causal justification in the striking climatic differences between the Rocky Mountain and the Pacific regions.

The task of finding concise descriptive names for the two associations has not been simple, owing to the all but universal presence of the major dominants. After much consideration, it seems best to refer to the eastern community as the pine-fir association, and to the western as the pine association. When it is desired to emphasize their geographical relation, the Rocky Mountain association is termed Petran, and the Sierra-Cascade one, Sierran.

## THE PETRAN MONTANE FOREST.

### PINUS-PSEUDOTSUGA ASSOCIATION.

Extent.—The montane forest of the Rocky Mountain region extends from central Alberta to the Guadalupe and Chisos Mountains of western Texas, and southward from the mountains of New Mexico and Arizona to Sinaloa and Durango. At the north its area is relatively narrow and it yields to the transition association of the Coast forest in the Selkirk Mountains of British Columbia and in the Kootenai and Coeur d'Alene ranges of northwestern Montana. It is broadest near the center where it ranges from the Black Hills of South Dakota and the Pine Ridge and Wild Cat Mountains of Nebraska to the eastern slopes of the Sierras in Nevada. It apparently finds its southwestern limit in the Charleston Mountains of Nevada and its southern in the Sierra Madre of Durango and Sinaloa. It is the characteristic forest of the mountain ranges of this vast region and is the most extensive of all the forest associations of the West (plate 48).

DOMINANTS.

| | | |
|---|---|---|
| Pinus ponderosa. | Picea pungens. | Pinus strobiformis. |
| Pseudotsuga mucronata. | Pinus flexilis. | Pinus chihuahuana. |
| Abies concolor. | Pinus flexilis albicaulis. | Pinus arizonica. |
| Pinus contorta. | | |

As already indicated, the first 3 species are to be regarded as the major dominants of the association by reason of their abundance and wide occurrence. The lodgepole pine (*Pinus contorta*) ranks next in importance. It is typically the subclimax dominant of the burn subsere in both the montane and subalpine forests. However, it is more or less exclusive over such large areas in the northern Rocky Mountains, and is so relatively permanent owing to repeated fires that it must be considered with the climax. *Picea pungens* is limited to the central Petran regions, and usually occurs in restricted stands along the lower edge of the zone. More rarely, it forms a mixed forest with yellow pine and Douglas fir, as in the Pike's Peak region, and in the Blue and White Mountains of Arizona (Greenamyre, 1913). *Pinus flexilis* and *P. albicaulis* are trees of wide range altitudinally, and hence are found in both the montane and subalpine climaxes. They are more abundant and relatively more important at upper elevations near timber-line, and hence are regarded as belonging primarily to the subalpine forest. *Pinus flexilis* occurs throughout the association, while *P. albicaulis* ranges from the northern edge to Yellowstone Park. *Pinus strobiformis* is a related pine which occurs only in southeastern Arizona and adjacent New Mexico, and thence southward into Sonora and Chihuahua. *Pinus chihuahuana* and *P. arizonica* are close relatives of *P. ponderosa.* They occur with the latter or represent it in southern Arizona or New Mexico at elevations of 6,000 to 8,000 feet, and extend southward into the Sierra Madre of Mexico.

Groupings.—The four most important dominants, *Pinus ponderosa, P. contorta, Pseudotsuga,* and *Abies,* regularly occur in pure stands as well as in mixed communities. This is especially true of the two pines. In the case of the lodgepole pine, this is a consequence of its ability to occupy burned areas completely, while with the yellow pine it results from its extension far beyond the mass of the association. With these two very important exceptions, the montane forest is largely a mixture or consists of small alternes of the different species. The minor dominants usually occur intimately mixed with the major ones, though they too may form pure communities of small size.

In general, *Pinus ponderosa, Pseudotsuga,* and *Abies* occur together throughout the mass of the association. To the northwest, *Abies* becomes secondary or is lacking, and the forest consists primarily of yellow pine and Douglas fir, or of lodgepole pine. Since these are related successionally, one often contains relicts of the other. In the Wasatch Mountains, *Pinus ponderosa* is mostly absent and the forest consists of *Pseudotsuga* and *Abies,* while in the desert ranges, farther west, *Pseudotsuga* is usually the missing one of the three. *Picea pungens* is practically limited to the central area of the association, represented by Colorado, Utah, northern Arizona, and New Mexico. It is often in open woodland along streams, but it may be an important member of the lower portion of the montane zone, mixed with Douglas fir and yellow pine, or more rarely with *Abies concolor. Pinus flexilis* occurs with yellow pine or Douglas fir, or with both on xerophytic ridges and slopes at lower levels. *P. albicaulis* has a similar habit, but is much less common in this association. As already indicated, *Pinus strobiformis, P. chihuahuana,* and

*P. arizonica* either occur scattered in the pine consociation or codominant with it from Arizona southward into Mexico.

Both the yellow pine and the lodgepole pine form pure stands which may stretch hundreds of miles beyond the main body of the association. The finest body of yellow pine on the continent is found on the Colorado plateau of northern Arizona far from the central mass. Similar pure communities but of less importance occur on the ranges of eastern Wyoming and the Black Hills. On the mesas of western Colorado and the foothills of central Wyoming, the *Pinus contorta* consociation breaks up into masses of varying size, surrounded by sagebrush or grassland in the respective regions. These are outposts of the lodgepole forest and are quite different from the savannah type assumed by yellow pine where conditions favor grassland. Both represent the same climatic tendency, however, as is shown also by the fact that aspen, *Populus tremuloides*, often accompanies them.

**Factor relations.**—The montane forest of the Rocky Mountains has received more quantitative study than any other community, with the possible exception of the prairie. This is due to the location in it of the Alpine Laboratory and the Fremont Forest Experiment Station at Pike's Peak, where factor studies have been carried on more or less continuously since 1900 and 1910 respectively, and of the Fort Valley Forest Experiment Station near Flagstaff, Arizona, where observations have been made since 1909. In addition, the Desert Laboratory has maintained stations in the montane zone of the Santa Catalina Mountains since 1908. As a consequence, a large mass of factor data is available, of which but a few general results can be given here.

The rainfall limits for the montane forest are approximately 18 to 20 inches for the lower margin and 22 to 23 inches for the upper. The great majority of the records are for the eastern slope, but they agree closely with those for western Colorado and northern Arizona. The rainfall is somewhat higher in New Mexico and lower in Montana, but this is obviously compensated by the evaporation. The savannah form of the pine consociation is found where precipitation is as low as 15 inches, and lodgepole outposts occur at even lower limits in western Colorado. The total evaporation for the growing season is not known, but the relative evaporation is a third greater in the *Pseudotsuga* consociation than in that of *Picea engelmanni* in the lower part of the subalpine forest. The measurement of light values through several summers has shown that there is no difference in the intensity of the light which falls upon the two forest zones in the Rocky Mountains. There is a constant difference in air and soil temperature, and in water relations, especially water-content, the montane forest naturally showing the higher temperatures and lower rainfall, humidity, and water-content.

**Seral relations.**—Factor measurements show that *Pinus ponderosa* is the most xerophytic of the three major dominants, *Pseudotsuga* less so, and *Abies* somewhat less still. The most mesophytic is *Picea pungens*. *Pinus contorta* is practically as xerophytic as the yellow pine, but it has a wider range of adaptation. Much the same is true for *P. flexilis* and *P. albicaulis*. The three southern pines resemble *Pinus ponderosa* in their water requirements. As to light requirements, the pines are all intolerant. *Picea pungens* is somewhat more tolerant, *Pseudotsuga* is moderately tolerant, and *Abies* endures still deeper shade. In Colorado the normal light intensity for the mature lodgepole consociation was found to be 0.08 to 0.07, while germination was only fairly good at 0.2 to 0.14 (Clements, 1910 : 40). The values of yellow pine and limber pine (*Pinus flexilis*) are not very different, though such forests are usually more open. Douglas fir is much more tolerant, reproducing readily in values as low as 0.04, while the mature forest may show intensities below 0.01.

As would be expected, the seral sequence conforms to the water and light demands. *Pinus ponderosa* is everywhere the earliest of the three major dominants, and is followed by *Pseudotsuga*, and this a little later by *Abies* as a rule (Clements, 1905 : 270). *Pinus contorta* is the universal subclimax dominant of burns everywhere from central Colorado northward into Alberta and British Columbia. In the Rampart Range, about Pike's Peak and southward, its rôle is taken chiefly by aspen. *Picea pungens* is generally somewhat subclimax in moist valleys and cañons, while the remaining pines resemble *Pinus ponderosa* in their general successional relations (plate 49).

## SOCIETIES AND CLANS.

The following lists are for the central Rocky Mountains and are based chiefly upon studies made in Colorado (Clements, 1904 : 8). Rydberg (1915) has given comparative lists of the herbaceous flora of the different regions, and Shreve (1915 : 32, 35) has noted the characteristic species of the pine and fir forests of the Santa Catalina Mountains of Arizona. The majority of the genera in the latter are those of the central region, though the species are largely different. The central and northern areas are seen to resemble each other closely in the important species, when it is recognized that the transition region of northwestern Montana and northern Idaho belongs rather to the Coast forest. Because of the shortness of the season, it is convenient to distinguish but two aspects, a vernal and an estival.

### *Vernal Aspect.*

*Societies:*

Shrubs—

| | | |
|---|---|---|
| Acer glabrum. | Opulaster opulifolius. | Jamesia americana. |
| Betula occidentalis. | Ribes lacustre. | Rosa acicularis. |
| Prunus pennsylvanica. | Arctostaphylus uva-ursi. | Viburnum pauciflorum. |
| Cornus amomum. | | |

Herbs—

| | | |
|---|---|---|
| Fragaria vesca. | Heuchera parvifolia. | Washingtonia obtusa. |
| Viola biflora. | Pseudocymopterus montanus. | Aralia nudicaulis. |
| Mertensia pratensis. | Pentstemon gracilis. | Atragene alpina. |
| Besseya plantaginea. | Pentstemon secundiflorus. | |

*Clans:*

| | | |
|---|---|---|
| Actaea rubra. | Pirola chlorantha. | Viola blanda. |
| Habenaria stricta. | Smilacina stellata. | Calypso borealis. |
| Erigeron glandulosus. | | |

### *Estival Aspect.*

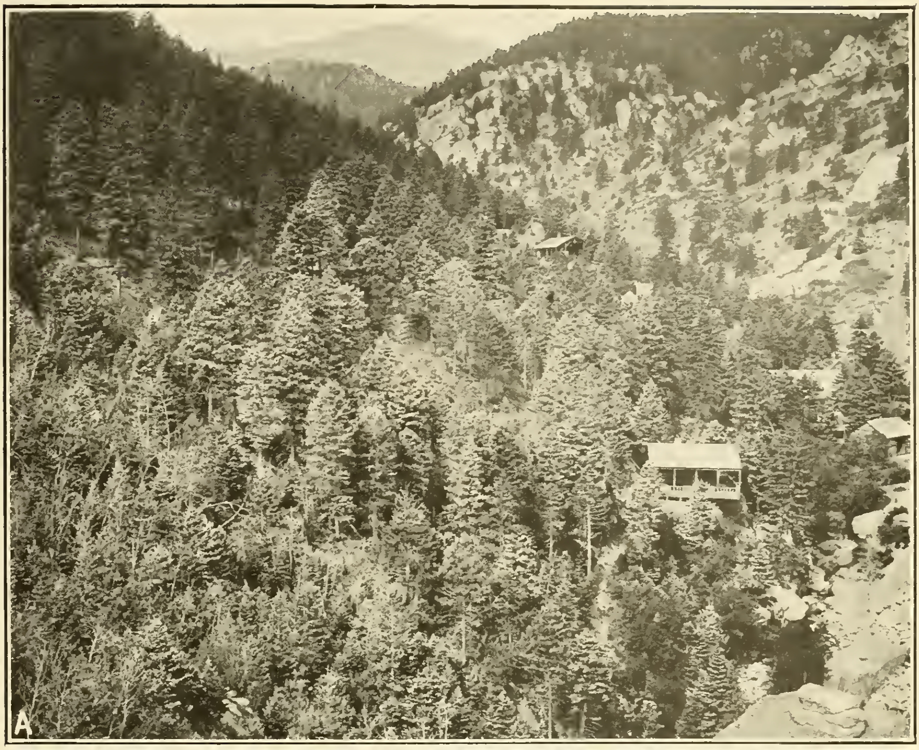
*Societies:*

| | | |
|---|---|---|
| Thalictrum fendleri. | Arnica cordifolia. | Valeriana silvatica. |
| Galium boreale. | Gentiana amarella. | Senecio cernuus. |
| Geranium caespitosum. | Potentilla glandulosa. | Haplopappus parryi. |
| Geranium richardsonii. | Pirola uliginosa. | Gentiana affinis. |
| Castilleia miniata. | Saxifraga bronchialis. | Streptopus amplexifolius. |
| Erigeron asper. | Heracleum lanatum. | Aquilegia coerulea. |

*Clans:*

| | | |
|---|---|---|
| Allium cernuum. | Pirola secunda. | Galium triflorum. |
| Solidago oreophila. | Androsace septentrionalis. | Peramium ophioides. |

Petran Montane Forest





A. *Pseudotsuga mucronata* consociation, Alpine Laboratory, Pike's Peak.
B. Detail of *Pseudotsuga-Abies* forest, Cameron's Cone, Pike's Peak.

## THE SIERRAN MONTANE FOREST

### PINUS ASSOCIATION.

**Extent.**—The northern limits of the montane forest of the Pacific coast are extremely difficult to draw, owing to the fact that *Pseudotsuga* continues into the Coast forest as an important dominant and also occurs with *Pinus ponderosa* in both the transition and the Petran montane forest. In general, its northern limit is regarded as determined by the disappearance of *Pinus lambertiana, Libocedrus decurrens,* and *Abies concolor.* This forest extends well into southern Oregon on the Siskiyou and Coast ranges and to central Oregon along the Cascade Mountains. It is found on the eastern slope of the Cascades and reaches its eastern limit in the lake region. In northeastern California it is present on both slopes of the Sierras, but southward from Lake Tahoe it is almost confined to the western one. The northern Coast ranges exhibit this community as far south as Lake County, but it yields to the redwood forest along the coast. It is fragmentary in the southern Coast ranges, but becomes the typical forest at the proper levels in the San Rafael, Sierra Madre, San Bernardino, San Jacinto, and Cuyamaca Mountains. It reaches the southern limit in the San Pedro Martir Mountains of Lower California.

The range in altitude is exceptionally great. In the Coast ranges of northern California and Oregon the montane forest occurs at altitudes of 1,000 to 3,000 feet, while in the Cascades it is found at 2,000 to 6,000. In the central Sierras the general elevation is 3,000 to 6,000, but this increases steadily toward the south and the upper limit reaches 7,000 to 8,000 feet in southern California and 8,000 to 10,000 feet in Lower California.

DOMINANTS.

Pinus lambertiana.
Pinus ponderosa.
Pseudotsuga mucronata.
Abies concolor.
Libocedrus decurrens.
Pinus ponderosa jeffreyi.
Pseudotsuga mucronata macrocarpa.
Pinus attenuata.
Pinus coulteri.
Sequoia gigantea.
Cupressus goveniana.
Picea breweriana.

The major dominants of the association are *Pinus lambertiana, P. ponderosa, Pseudotsuga mucronata, Abies concolor,* and *Libocedrus decurrens.* All of these occur from the northern limit of the area in central or southern Oregon to the San Pedro Martir mountains in Lower California, though the Douglas fir is represented in southern and Lower California by its variety, *Pseudotsuga m. macrocarpa.* In somewhat similar fashion, *Pinus ponderosa* is replaced at higher levels by *P. p. jeffreyi.* The remaining species are all of secondary importance. *Pinus attenuata* ranges from central Oregon to southern California, and *P. coulteri* extends from central to Lower California. Both are relatively xeroid and subclimax in character. *Sequoia gigantea* is the most interesting of the dominants, but it is restricted to scattered groves on the west slopes of the Sierra Nevada from Placer County to Tulare County. These are the survivors of what must have been an extensive consociation in later Tertiary times. *Cupressus goveniana* occurs sparsely through the Coast region from Ukiah to Dulzura near San Diego. *Picea breweriana* is localized in northwestern California and adjacent Oregon.

Three species of broad-leaved trees occur so frequently in the montane forest that they require mention. These are *Quercus californica, Q. garryana,* and *Arbutus menziesii.* They are all subclimax in character and occur commonly in the edges of the forest or in the more open stands or outposts of Douglas fir or yellow pine. *Quercus californica* and *Arbutus* extend through the association to southern California, while *Q. garryana* has its southern limit in the Santa Cruz Mountains.

Groupings.—The great mass of the association is constituted by the five major dominants in the most variable proportions. In 50 localities from Crater Lake to southern California, 4 or usually all 5 of these were found in more than half the cases. While mixed forest is the rule, *Pinus ponderosa* and *Pseudotsuga mucronata* often occur in extensive pure stands, or they may be mixed in more or less equal numbers. *Abies concolor* also occurs pure, but to a less degree. On the other hand, *Pinus lambertiana* and *Libocedrus* practically always occur in mixture, in which they rarely make more than 15 per cent of the stand. *Sequoia gigantea* occasionally is found in pure stands, but it is usually associated with *Pinus lambertiana* and *Abies concolor*, and with the latter alone at the higher elevations. It is less commonly mixed with yellow pine and incense cedar, and still less with Douglas fir. Toward the Coast forest on the north and west, and the Petran montane forest in central Oregon, the typical members of the community drop out, leaving only the yellow pine and Douglas fir, in mixture or in pure forests. At the highest altitudes reached by the montane forest, *Abies concolor* and *Pinus jeffreyi* are the chief dominants, extending more or less into the subalpine forest above. The exceptional solidarity of the association is shown by its composition in the desert ranges near its southern limit. *Pinus ponderosa, P. lambertiana, Libocedrus decurrens, Abies concolor, Pseudotsuga macrocarpa*, and *Pinus coulteri* form the montane forest on the San Jacinto Mountains (Hall, 1902 : 19) and in the San Pedro Martir Mountains of Lower California (Goldman, 1916: 313).

Of the minor dominants, *Pinus attenuata* is the only one which forms extensive pure forests. It resembles lodgepole pine in making dense growth in burned areas, and hence is properly subclimax. In the southern half of California, it occurs frequently with *Pinus coulteri* in the lower portion of the forest, where they are associated with *P. ponderosa, Pseudotsuga macrocarpa*, and *Libocedrus*. *Pseudotsuga macrocarpa* is thought by Sudworth (1908 : 105) to have occurred formerly in larger pure stands in southern California, but to-day it ranges widely through the montane zone in small groups or scattered singly, and extends down into the chaparral formation (plate 50).

Factor and seral relations.—The montane association grows in a rainfall of 80 inches in the Coast ranges of northern California. The rainfall decreases regularly toward the south, until it reaches 20 inches in the montane zone of the San Jacinto and San Pedro Martir Mountains. No figures are available for evaporation, but it must be much greater to the southward also. It is surprising that such great changes in the water relations do not have a marked effect upon the composition, but the latter is modified chiefly by the substitution of *Pseudotsuga macrocarpa* for *P. mucronata*. The height of the dominants and the density of the stand, however, are greatly reduced in the southern ranges. Even a more striking adjustment to water and temperature is seen in the upward movement of the zone, from a lower limit of 1,000 feet or less in the north to 8,000 or 9,000 feet in Lower California.

Sierran Montane Forest


A. *Pinus ponderosa-lambertiana* association, Prospect, Oregon.
B. *Pinus, Libocedrus, Abies,* and *Pseudotsuga,* Yosemite National Park, California.

While no factor studies have been recorded for the Sierran montane forest, the experience of foresters has enabled them to indicate the comparative relations of the dominants to both water and light. Larsen and Woodbury (1916 : 7) have shown the soil and water requirements of the major dominants in the following, in which the order is from more exacting to less exacting. As to light requirements, the dominants are ranked from the least tolerant to those most tolerant of shade.

| Soil. | Water. | Light. |
|---|---|---|
| Pseudotsuga mucronata. | Pinus lambertiana. | Pinus attenuata. |
| Abies concolor. | Pseudotsuga mucronata. | Pinus ponderosa. |
| Pinus lambertiana. | Abies concolor. | Pinus jeffreyi. |
| Libocedrus decurrens. | Libocedrus decurrens. | Pseudotsuga mucronata. |
| Pinus ponderosa. | Pinus ponderosa. | Pinus lambertiana. |
| Pinus jeffreyi. | Pinus jeffreyi. | Abies concolor. |
| | | Libocedrus decurrens. |

The general relation of the dominants to the combined influence of water and temperature is shown by the order in which they occur with increasing altitude. The lowermost species are *Pinus attenuata*, *P. coulteri*, and *Pseudotsuga macrocarpa*, followed by *Pinus ponderosa*, *Pseudotsuga mucronata*, *Libocedrus decurrens*, *P. lambertiana*, *Abies concolor*, and *P. jeffreyi*. This is the order of the potential succession (Clements, 1916 : 108). It corresponds closely with the actual seral sequence of the dominants, when the difference in the tolerance and zonal position of *Libocedrus* and *Pinus jeffreyi* is taken into account. The first three species are essentially subclimax, *Pinus ponderosa* is the first and most xerophytic of the true dominants in the lower half or more of the forest and *P. jeffreyi* in the upper, and *Pseudotsuga* is next. The remaining three differ but little, since the greater tolerance of *Libocedrus* is offset by a smaller water requirement.

## SOCIETIES.

Shrubs are well developed in the montane zone, but they reach their best expression in open woodland and in clearings where fire has been active. They disappear largely or completely in the closed forest stands, in which herbaceous societies are more or less prominent. Many of the shrubs belong to the same genera as the dominants of the chaparral and hence form communities with a striking resemblance to the latter. While they ultimately yield to the montane forest in undisturbed areas, recurrent fires enable them to occupy the ground as a more or less permanent subclimax. The latter has usually been included in the general term chaparral, but this view is ecologically incorrect, as Cooper (1919) has emphasized.

*Shrubs:*

Ceanothus cordulatus.
Ceanothus velutinus.
Ceanothus integerrimus.
Ceanothus parviflorus.
Ceanothus prostratus.
Arctostaphylus patula.
Arctostaphylus drupacea.
Castanopsis sempervirens.
Castanopsis chrysophylla minor.
Quercus breweri.
Quercus sadleriana.
Quercus chrysolepsis vaccinifolia.
Pasania densiflora echinoides.
Corylus rostrata.
Prunus demissa.
Prunus emarginata.
Rhamnus californica.
Rhamnus purshiana.
Holodiscus discolor.
Amelanchier alnifolia.
Symphoricarpus oreophilus.
Symphoricarpus mollis.
Ribes nevadense.
Rubus parviflorus.
Chamaebatia foliolosa.
Rhus diversiloba.

*Herbs:*

Pteris aquilina.
Polystichum munitum.
Aspidium rigidum.
Pentstemon gracilentus.
Pentstemon deustus.
Pentstemon bridgesii.
Pentstemon labrosus.
Fragaria virginiana.
Washingtonia nuda.
Monardella odoratissima.
Adenocaulum bicolor.
Lupinus grayi.
Lupinus ornatus.
Hosackia decumbens nevadensis.
Hydrophyllum occidentale.
Lathyrus sulphureus.
Trifolium breweri.
Castilleia parviflora.
Pedicularis semibarbata.
Achillea millefolium.
Erigeron breweri.
Microseris nutans.
Hieracium albiflorum.
Senecio lugens.
Crepis occidentalis.
Crepis intermedia.
Chaenactis douglasii.
Antennaria argentea.
Kelloggia galioides.
Phacelia ramosissima.
Draperia systyla.
Viola lobata.
Pirola picta.
Delphinium decorum.
Silene californica.
Silene lemmonii.
Erysimum asperum.
Eriogonum umbellatum.
Iris hartwegii.
Corallorhiza multiflora.
Sarcodes sanguinea.

## THE COAST FOREST CLIMAX.

### THUJA-TSUGA FORMATION.

Nature.—The Coast climax of the Northwest is a coniferous forest of unrivaled magnificence. The mature trees are very tall, 125 to 200 feet high and 5 to 15 feet in diameter; or, in the case of *Sequoia sempervirens*, 300 feet or more high and 10 to 20 feet in diameter. They form a dense canopy which makes a deep shade, in which secondary trees find growth all but impossible. In the mature forest, layers of shrubs and herbs are poorly developed or consist of relatively few species. The layer of duff and organic soil is deep, and the conditions within the forest are almost ideal for germination and growth, except for the low light intensity. The number of major dominants is practically the same as in the montane forest, with which the Coast climax shows a close relationship. The dominants are much more restricted in range, however, especially from east to west. As a consequence, the cedar-hemlock forest shows less differentiation, and it might well be regarded as composed of a single association. The breadth and importance of the transition zone between it and the montane forest, together with other reasons discussed later, seem such as to warrant the recognition of two associations.

Extent.—As the name implies, the Coastal climax has its greatest development along the Pacific coast. The main body of the formation stretches from southern British Columbia to northern California, but several of the major dominants extend much farther northward as well as southward. The northernmost in range is *Picea sitchensis*, which finds its boreal limit at Cook Inlet and Kodiak Island, Alaska. *Tsuga heterophylla* and *Chamaecyparis nootkatensis* extend nearly as far, reaching Prince William Sound, while *Thuja plicata* is found in southern Alaska and *Abies amabilis* at the extreme southern end. The most southerly range is that of *Sequoia sempervirens*, the last outposts of which are found in the Santa Cruz and Santa Lucia Mountains of California. This striking species is practically confined to this State, occurring elsewhere in but few groves just across the Oregon line. Four other major dominants are found with the redwood to Mendocino, Sonoma, and Marin Counties. These are *Tsuga heterophylla*, *Thuja plicata*, *Picea sitchensis*, and *Abies grandis*. While *Pinus monticola*, *Pseudotsuga mucronata*, and other members of the transition association extend farther south, especially in the Sierra Nevada, it is as dominants of the subalpine or of the montane forest.

While the best expression of this formation is along the coast, it extends to the Cascades and covers their western slopes in typical form. East of the Cascade Mountains, it passes into a broad transition forest which reaches to the western slopes of the main range of the Rocky Mountains in northern Montana and southeastern British Columbia. In the Cascade Mountains of central Oregon, it is replaced by the montane forest, and becomes more and more restricted to the coastal belt from this point southward. In similar manner, it is replaced in central British Columbia by the montane forest, though the coastal belt remains somewhat broad as a result of the numerous islands and inlets.

In altitude, the Coast forest extends from the sea-level as far as 3,000 to 6,000 feet in the Coast ranges and the Cascades. On the interior ranges, it reaches its upper limit at 5,000 feet or lower.

Unity.—The treatment of the Coast climax as a distinct formation is abundantly justified by the regular association of the major dominants from Alaska to California and from Washington to Montana. As already indicated, five of these occur in Alaska, and five also in California, three of these, *Tsuga*, *Thuja*, and *Picea*, being common to both extremes. The number of dominants with a wide lateral range is even greater. Those which range from the Coast to Montana are *Tsuga heterophylla*, *Thuja plicata*, *Abies grandis*, *Larix occidentalis*, *Pinus monticola*, *Pseudotsuga mucronata*, and *Pinus contorta*, while *Picea engelmanni* and *Pinus ponderosa* extend as dominants from the Cascades to Montana. While there is a marked change in the rank of the dominants as the Cascade Mountains are passed, this is clearly connected with the differentiation of associations. The ecological character of the forest remains essentially the same toward the limits at the east, except where more or less subclimax dominants, such as *Pinus ponderosa* and *P. contorta*, become controlling.

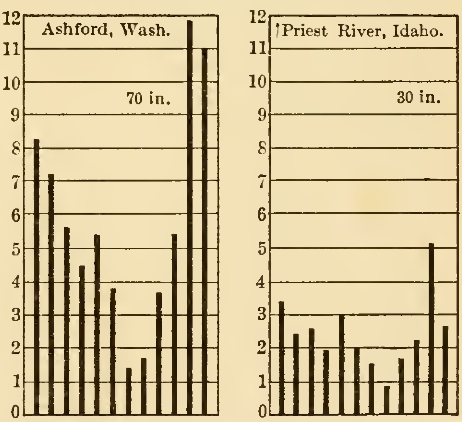


Fig. 10.—Monthly and total rainfall for representative localities in the associations of the Coastal forest.

Geographically, the ferest belongs to the Coast and tho Columbia Basin. At the higher levels, the latter, like the former, is a region of relatively high rainfall and low evaporation. The temperature relations are less uniform from east to west at least, but this is reflected in the mixing of the two climaxes and the differentiation of a transition community (fig. 10).

Relationship and contacts.—As the last statement indicates, the closest relationship of the Coast forest is with the montane climax. They resemble each other much in the size and vigor of the dominants and in the luxuriance of the forest itself. This is reflected by the important role of *Pseudotsuga mucronata* in both and the significant occurrence of closely related *Sequoia* consociations in each. Other important species which they have in common are *Pinus monticola*, *P. ponderosa*, and *P. contorta*, while such subclimax species as *Arbutus menziesii* and *Quercus californica* occur in both. By far the most significant fact, however, is the association of 5 coastal dominants with 4 from the montane forest to constitute the transition community.

The chief contact of the Coast climax is with the montane forest. They are in touch with each other from northern California to central Oregon, and then as outposts through northeastern Oregon to Idaho and Montana. This contact continues through British Columbia to the sixtieth parallel. Here the montane and subalpine forests give way to the boreal forest of *Picea mariana*, *P. alba*, and *Pinus divaricata*, which covers the interior of Yukon and Alaska behind the coastal strip of *Picea sitchensis* and *Tsuga heterophylla*. On the mountain ranges of the central area the Coast forest meets the subalpine climax at altitudes of 5,000 to 7,000 feet. They mingle over a wide mountain ecotone, and in the transition association, *Picea engelmanni* and *Abies lasiocarpa* form subclimax communities at exceptionally low levels.

Associations.—The chief reasons for recognizing two associations in the Coast formation have already been touched upon. It may be well to state them explicitly here, as this involves a readjustment of the current views. The first and most important of these reasons is the change of dominance from the western to the eastern portion. *Picea sitchensis* drops out before the Cascade Mountains are crossed, while *Tsuga* and *Thuja* change from primary to secondary rank. *Pseudotsuga* continues to be of the first importance, but shares this with several other dominants. A second reason of almost equal significance is that *Pinus monticola* and *Larix occidentalis* reach their best development and maximum dominance in the mountains of northern Idaho and the adjacent region. The behavior of *Picea engelmanni* and, to a less extent, of *Abies lasiocarpa* in descending from the subalpine forest to play an important rôle in valleys and on north slopes, is also significant. Furthermore, the subdominants of the transition forest and its subclimax stages are largely Rocky Mountain in relationship, especially in Idaho and Montana. Finally the differences in the vegetation are correlated with a similar differentiation of the climate. Over the region of the coastal community, the rainfall ranges generally from 50 to 80 inches, with a maximum in the Olympic peninsula of more than 100 inches. Over most of the transition forest the rainfall is only 20 to 35 inches, with a maximum of 40 inches only in the Bitter Root range. There is likewise a marked difference in the annual distribution for the two regions. In the case of the eastern area, 30 to 60 per cent of the precipitation occurs between April 1 and September 30, while in the western but 10 to 30 per cent—*i. e.*, 70 to 90 per cent of the rainfall takes place during the winter months. The significant difference in temperature relations is indicated by a mean temperature of 45° to 52° and a minimum one of 14° to −4° for western Washington, and of 38° to 45° and −25° to −49° for western Montana.

The two associations may be almost equally well designated on the basis of location and composition. The latter seems to afford the more clear-cut and convenient distinction. The western or coastal portion is hence termed the cedar-hemlock forest or *Thuja-Tsuga* association and the eastern is called the larch-pine or *Larix-Pinus* association.

Coast Forest

A. *Pseudotsuga*, *Thuja*, and *Tsuga*, Rainier National Park, Washington.

B. *Sequoia sempervirens* consociation, Muir Woods, Mt. Tamalpais, California.

## THE CEDAR-HEMLOCK FOREST.

### THUJA-TSUGA ASSOCIATION.

**Nature and extent.**—This is much the more massive and continuous of the two associations. The dominants are fewer and the composition less varied, though the northern and southern extremes show striking differences from the central portion. The trees are taller, the canopy denser, and the shrubby undergrowth often developed to form almost impenetrable thickets. The most typical expression of the forest is found between the coast and the upper slopes of the Cascade Mountains from southern British Columbia to northern Oregon. The long extension to the northward in Alaska shows a more or less similar ecological character, but becomes reduced practically to two dominants, *Picea sitchensis* and *Tsuga heterophylla.* The southward prolongation into California resembles the main portion in the presence of practically all its dominants, but this narrow coastal strip is differentiated by the paramount rôle of *Sequoia sempervirens* (plate 51).

DOMINANTS.

| | | |
|---|---|---|
| Tsuga heterophylla. | Abies grandis. | Abies nobilis. |
| Thuja plicata. | Sequoia sempervirens. | Chamaecyparis nootkatensis. |
| Picea sitchensis. | Abies amabilis. | Chamaecyparis lawsoniana. |
| Pseudotsuga mucronata. | | |

*Pseudotsuga mucronata* is much the most important dominant with respect to abundance. It is the typical species of burned areas, and hence has more or less of the nature of a subclimax, particularly in view of its relatively low tolerance. In addition, it is a major dominant of the montane forest, and for these reasons it is less characteristic of the association than *Tsuga* and *Thuja.* The essential character is given by *Tsuga, Thuja, Picea,* and *Sequoia,* practically all of which attain their best development along the coast or in lowlands. *Abies grandis* is almost equally important in the larch-pine association and *A. amabilis* in the subalpine forest. *Abies nobilis* and *Chamaecyparis nootkatensis* also occur to some extent in the subalpine forest. While the latter ranges to the northern limits of the formation in Alaska, it drops out in northern Oregon. *Abies nobilis* is restricted to western Washington and Oregon and *Chamaecyparis lawsoniana* practically to the fog belt from Coos Bay, Oregon, to Humboldt Bay, California.

**Groupings.**—The typical grouping of the cedar-hemlock forest is *Pseudotsuga, Tsuga, Thuja,* and *Picea.* According to Gannett (1900 : 14) *Pseudotsuga* forms 64 per cent of the standing timber in western Washington, *Tsuga* 16 per cent, *Thuja* 14 per cent, and *Picea* 6 per cent. In western Oregon, the figures are *Pseudotsuga* 81 to 85 per cent, *Tsuga* 6 to 7 per cent, and *Thuja* 1 to 2 per cent (1899 : 43), excluding the coast region where *Picea* occurs. All of the four major dominants may form pure stands, but this is exceptional for *Thuja* and frequent for *Tsuga* and *Picea* only in the north. It is more or less common in the case of *Pseudotsuga,* though as a rule the other dominants are scattered through this consociation. Near the coast from British Columbia to California, Douglas fir and Sitka spruce are the chief associates, while in California *Pseudotsuga* and *Sequoia* are most important. According to Sudworth (1908 : 147), the redwood is rarely pure, but usually forms 50 to 75 per cent of the stand, with Douglas fir most abundant except in damp places, and more or less *Abies grandis, Tsuga,* and *Thuja.* On river flats along the coast, scattered *Picea, Chamaecyparis lawsoniana, Tsuga,* and *Abies* occur in it. *Abies amabilis* and *A. nobilis* occur more or less commonly through the groupings of the four major dominants, but usually form only a small fraction of the stand, as is true also of *Chamaecyparis nootkatensis.*

*Tsuga heterophylla* and *Picea sitchensis* constitute the coastal forest of Alaska. Sometimes they form pure stands, but they usually occur in mixture, one or the other being dominant, *Picea* preferring the vicinity of the coast. In southern Alaska they are more or less mixed with *Thuja plicata, Abies grandis* and *A. amabilis,* and *Chamaecyparis nootkatensis.*

**Factor and seral relations.**—The cedar-hemlock forest occupies a region of excessive rainfall and frequent or constant fog, with consequent low evaporation. Over much of it the annual rainfall is in excess of 80 inches, the range being 50 to 120 inches. In the United States 10 to 30 per cent of this falls during the six winter months, and much the same conditions obtain to Sitka and beyond. The temperatures are generally equable except at the higher altitudes. The absolute minimum as far north as Sitka is but $-4°$.

Quantitative studies of the water and light relations of the dominants are still few (cf. Cooper, 1917 : 179), but they are in general agreement with the topographic and seral relations. The following table of tolerance, based upon successional relations, agrees fairly well with the conclusions of foresters. The sequence is from the least to the most tolerant.

*Tolerance of Dominants.*

| | | |
|---|---|---|
| Pseudotsuga mucronata. | Abies amabilis. | Picea sitchensis. |
| Abies nobilis. | Sequoia sempervirens. | Thuja plicata. |
| Abies grandis. | Chamaecyparis nootkatensis. | Tsuga heterophylla. |

The last five are unusually close in their tolerance, and the order given here is not infrequently changed by soil, water, or temperature relations. In a region of such excessive precipitation, the water relations are less clear and are much influenced by temperature. The general relation to these combined factors is indicated by the altitudinal range, though this is not in full accord with that in latitude. The typical fog-belt trees are *Picea sitchensis, Sequoia sempervirens,* and *Chamaecyparis lawsoniana.* These represent the maximum conditions as to water-content and humidity. They are followed closely by *Thuja plicata,* and this by *Tsuga heterophylla* and *Abies grandis.* The ability of *Abies amabilis, A. nobilis,* and *Chamaecyparis nootkatensis* to endure more xeroid conditions is indicated by the fact that they occur in the subalpine zone, where the first is frequent at timber-line. *Pseudotsuga* is the most xeroid of all the dominants, a fact in complete accord with its dominance in burns and its importance in the montane forest.

## SOCIETIES.

The development of shrubby societies often reaches a maximum in the cedar-hemlock forest, though the actual number of species is few. As a consequence, the light at the ground level is greatly reduced, and the herbaceous societies as a result are poorly developed.

*Shrubs:*

Gaultheria shallon.
Berberis nervosa.
Berberis aquifolium.
Vaccinium parvifolium.
Vaccinium macrophyllum
Vaccinium ovatum.
Salix scouleriana.
Acer circinatum.
Acer glabrum.
Cornus nuttallii.
Echinopanax horridum.
Sambucus callicarpa.
Sambucus glauca.
Rubus parviflorus.
Rubus spectabilis
Ribes sanguineum.
Ribes bracteosum.
Ribes laxiflorum.
Ribes lacustre.
Pirus diversifolia.
Menziesia ferruginea.
Pachystigma myrsinites.
Chimaphila umbellata.
Linnaea borealis.
Spiraea menziesii
Symphoricarpus mollis.
Viburnum ellipticum.
Prunus emarginata.
Rhododendrum ellipticum.

*Herbs:*

Pteris aquilina.
Epilobium spicatum.
Blechnum spicant.
Polystichum munitum.
Anaphalis margaritacea.
Adenocaulum bicolor.
Oxalis oregana.
Oxalis pumila.
Fragaria vesca.
Cornus canadensis.
Trientalis latifolia.
Clintonia uniflora.
Asarum caudatum.
Actaea spicata arguta.
Tiarella trifoliata.
Tellima grandiflora.
Mitella trifida.
Pirola picta.
Aquilegia formosa.
Anemone oregana.
Anemone quinquefolia.
Antennaria racemosa.
Disporum smithii.
Streptopus roseus.
Washingtonia divaricata.
Vancouveria hexandra.
Viola sempervirens.
Viola howellii.
Lilium parviflorum.
Lathyrus polyphyllus.
Trillium ovatum.
Smilacina amplexicaulis.
Apocynum androsaemifolium.
Lupinus lepidus.
Lupinus rivularis.
Ranunculus occidentalis.
Ranunculus oreganus.
Calypso borealis.
Moneses uniflora.
Dicentra formosa.

## THE LARCH-PINE FOREST.

### LARIX-PINUS ASSOCIATION.

**Nature and extent.**—The transition forest shows much of the general character of the coastal association, but in a smaller way. The trees are not so vigorous and the association is less dense and exclusive. Of the four major dominants of the cedar-hemlock forest, *Picea sitchensis* has disappeared, *Tsuga* and *Thuja* are greatly reduced in importance as a rule, and *Pseudotsuga* shares the control with several equally important species. The canopy is more open and the undergrowth richer in both species and individuals. There is a wider range of habitat conditions with the result that the major dominants are more equal in rank and occur in more clearly differentiated groupings.

This association occupies the eastern slopes of the Cascade Mountains of Washington and Oregon, below the subalpine zone. It stretches across the mountains of northern Washington into northern Idaho and northwestern Montana, reaching its eastern limit on the western slopes of the Continental Divide. It is found on the Gold and Selkirk Ranges of southeastern British Columbia and in the Blue and Wallowa Mountains of Oregon and adjacent Washington. From here it extends eastward through the ranges of Idaho to the southern portion of the Bitterroot Mountains. To the southeast, as well as in the interior ranges of British Columbia and northern Washington, it is often reduced to one or two of the dominants found in the Petran montane forest, and it then becomes impossible to draw a clear line between the two formations (plate 52).

DOMINANTS.

Larix occidentalis.
Pinus monticola.
Abies grandis.
Thuja plicata.
Tsuga heterophylla.
Pseudotsuga mucronata.
Pinus ponderosa.
Pinus contorta.
Picea engelmanni.

The first five species represent the coastal association, the others the montane forest. *Pseudotsuga*, however, belongs to both, and *Picea engelmanni* is normally a dominant of the subalpine zone. *Pinus monticola* is also more or less montane in character, ranging far south into the Sierra Nevada. Like *Larix occidentalis*, it reaches its optimum development in northern Idaho and the adjacent regions, and these two may well be regarded as the most typical dominants of the transition forest. While *Abies grandis* ranges from the Coast to northwestern Wyoming, it too is more characteristic of the transition forest, largely perhaps because of the absence of the more tolerant species. *Tsuga* and *Thuja* occur generally throughout the region, but are usually of minor importance. *Tsuga* drops out first toward the boundaries of the forest, leaving *Abies* and *Thuja* to represent the final stage of the climax. *Pinus ponderosa*, *P. contorta*, and *Picea engelmanni* are all of the widest range and play a part in at least two formations.

Groupings.—The groupings of the dominants of the larch-pine forest are numerous and complex. The drier areas are generally controlled by *Pinus ponderosa* and *Pseudotsuga*, with more or less *P. contorta*, *Abies grandis*, and *Larix*. The moister ones are dominated by *Pinus monticola* and *Larix*, with varying amounts of *Thuja*, *Tsuga*, and *Picea engelmanni*. In the Priest River region Leiberg (1899: 246) gives the abundance of the dominants as follows: yellow pine zone *Pseudotsuga* 70 per cent, *Pinus* 10 per cent, *Abies* 15 per cent; white pine zone *Pinus monticola* 42 per cent, *Larix* 35 per cent, *Thuja* 8 per cent, *Picea engelmanni* 6 per cent, *Tsuga* 3 per cent, *Abies* 2 per cent. In the Bitterroot Mountains where the western species are important, the percentages are: *Pinus contorta* 25, *Picea engelmanni* 19, *Pseudotsuga* 14, *Pinus monticola* 12, *Abies grandis* 9, *Larix* 6, and *Thuja* 4. Where the montane element predominates the values are: *Pseudotsuga* 34, *Pinus ponderosa* 21, *P. contorta* 17, *Picea engelmanni* 11, *Thuja* 5, *Abies* 4. In the Flathead region of Montana *Larix* and *Pseudotsuga* are often the most important, with all the other dominants present here and there in some degree. In the Selkirks *Thuja* and *Picea* usually occupy the valleys and *Pseudotsuga* and *Tsuga* the slopes, while *Pinus monticola*, *Larix*, *Pinus contorta*, and *P. ponderosa* also occur. In eastern Washington *Pinus* and *Pseudotsuga* are controlling, with considerable *Larix*, *Pinus contorta*, *P. monticola*, and a small amount of *Tsuga* and *Thuja*. The dominants of the Blue Mountains are *Pinus ponderosa*, *Pseudotsuga*, *Abies grandis*, *Larix*, and *Pinus contorta*.

Factor and seral relations.—The general climatic relations of the larch-pine forest have already been pointed out (p. 216). Larsen (1916: 437) has indicated the general water and light relations of the dominants in the following lists:

Water-content, on wet ground: *Picea engelmanni*, *Tsuga heterophylla*, *Thuja plicata*.

Water-content, moist or intermediate ground: *Pinus monticola*, *Abies grandis*, *Larix occidentalis*.

Water-content, dry ground: *Pinus contorta*, *Pseudotsuga mucronata*, *Pinus ponderosa*.

Tolerance: *Pinus ponderosa*, *Larix occidentalis*, *Pinus contorta*, *Pseudotsuga mucronata*, *Pinus monticola*, *Picea engelmanni*, *Abies grandis*, *Tsuga heterophylla*, *Thuja plicata*.

Transition Forest

A. *Pseudotsuga*, *Tsuga*, and *Pinus monticola*, Carson, Washington.
B. *Pseudotsuga*, *Pinus monticola*, *Larix*, and *Thuja*, Priest River, Idaho.

The range in altitude is shown by the following list, in which the order is descending. The first two belong primarily in the subalpine forest.

| | | |
|---|---|---|
| Abies lasiocarpa. | Abies grandis | Pinus monticola. |
| Picea engelmanni. | Larix occidentalis. | Tsuga heterophylla. |
| Pinus contorta. | Thuja plicata. | Pinus ponderosa. |
| Pseudotsuga mucronata. | | |

Weaver (1917: 19) has studied succession in the transition forest near Moscow, Idaho, and has determined its relation to water-content, evaporation, and soil temperature. *Thuja* is the final dominant in this region, *Tsuga* being absent. The sequence is as follows: *Symphoricarpus-Opulaster*, *Pinus-Pseudotsuga*, *Pinus*, *Pseudotsuga*, *Larix-Abies*, *Larix*, *Abies*, *Thuja* (*Tsuga*).

The water-content of the yellow pine community ranged from 5 to 15 per cent lower than in the Douglas fir-larch, and 20 to 30 per cent below that in the grand fir-larch, while in the latter it was 10 to 40 per cent lower than in the final cedar forest. Evaporation in the latter was 2 to 5 c.c. less daily than in the *Pseudotsuga-Larix* mictium and 5 to 15 c.c. less in this than in the yellow pine forest. The soil temperatures decreased with much uniformity from the pine to the cedar community. The minimum light value for the *Pseudotsuga* forest is about 0.02, for the *Larix-Abies* mictium 0.01 to 0.007, and for the *Thuja* forest 0.005 to 0.003.

### SOCIETIES.

The number of these depends primarily upon the light intensity. In the less shady *Larix-Abies* forest, the number is fairly large and the shrub layer is well-developed, while the deep shade of the *Thuja* forest permits but a small number to persist (Weaver, 1917: 86, 88).

#### LARIX-ABIES COMMUNITY.

*Shrubs:*

| | | |
|---|---|---|
| Chimaphila umbellata. | Pirus sitchensis. | Rubus parviflorus. |
| Lonicera utahensis. | Ribes viscosissimum. | Sambucus melanocarpa. |
| Menziesia ferruginea. | Ribes lacustre. | Vaccinium macrophyllum. |
| Pachystigma myrsinites. | Rosa pisocarpa. | |

*Herbs:*

| | | |
|---|---|---|
| Actea spicata arguta. | Coptis occidentalis. | Streptopus majus. |
| Adenocaulum bicolor. | Disporum majus. | Thalictrum occidentale. |
| Anemone quinquefolia. | Fragaria vesca. | Tiarella unifoliata. |
| Arnica cordifolia. | Linnaea borealis longiflora. | Smilacina amplexicaulis. |
| Asarum caudatum. | Mitella trifida. | Trillium ovatum. |
| Clintonia uniflora. | Pirola picta. | Washingtonia divaricata. |

#### THUJA COMMUNITY.

*Shrubs:*

| | |
|---|---|
| Ribes lacustre. | Rubus parviflorus. |

*Herbs:*

| | | |
|---|---|---|
| Aconitum columbianum. | Claytonia asarifolia. | Tiarella unifoliata. |
| Anemone quinquefolia. | Clintonia uniflora. | Trillium ovatum. |
| Asarum caudatum. | Coptis occidentalis. | Viola glabella. |
| Athyrium cyclosorum. | Smilacina amplexicaulis. | Viola orbiculata. |
| Circaea pacifica. | Streptopus majus. | |

## THE SUBALPINE FOREST CLIMAX.

### PICEA-ABIES FORMATION.

Nature.—The subalpine climax is the most variable of all the forests in its ecological character. At its contact with the montane forest, the trees are often 100 feet high, the canopy is closed, and a typical undergrowth is present. In the ecotone between the two, the respective dominants meet on nearly equal terms to form an apparently homogeneous forest. At higher altitudes the forest mass becomes more and more open or fragmented and nearer timber-line is broken up into isolated groves and clumps. The individuals decrease steadily in stature as the altitude increases and at timber-line they are either greatly dwarfed or much deformed by the action of wind or snow. It is exceptional that an actual forest community exists at timber-line when the latter is due to climatic rather than local causes. The subalpine forest may be bordered by a more or less complete zone of scrub, consisting of willows, birches, or heaths, at its upper edge, or it may yield directly to alpine sedgeland. The latter may extend down into the forest for considerable distances along valleys or on rock or gravel slides, and as a consequence often furnishes a large part of the undergrowth at the higher altitudes. There is generally a marked tendency to form pure stands, as a result of the rigorous climatic selection of species. The number of the latter is especially reduced toward timber-line, which is often formed for long distances by one or two species.

Extent.—The subalpine forest is found from Alaska and Yukon to Mexico and Lower California, wherever the altitude is sufficiently great. At the north it extends somewhat into the plains east of the Rocky Mountains where it meets the boreal *Picea-Abies* climax. South of the northern portion of New Mexico and Arizona, and of the Sierra Nevadas, it is fragmentary and usually represented by but one or two species. Its eastern limit lies along the crests of the Front ranges in Colorado, and the western is found on the San Jacinto, San Bernardino, and Sierra Nevada ranges north to the Siskiyous. In Oregon and Washington, the western limit runs along the Cascades to the Olympics and the peaks of Vancouver Island, from which it follows the Coast ranges as far as Cook Inlet in Alaska. The northernmost dominant is *Pinus contorta*, which reaches latitude 64° in Yukon. Between the two great mountain axes on which the subalpine formation attains its major expression, it is found in reduced form on the higher ranges of the interior, such as the Blue and Powder River Mountains of Oregon, the Charleston Mountains of Nevada, and the Panamint and Inyo Ranges of southeastern California.

Unity.—The floristic unity of the subalpine climax is necessarily somewhat less than that of the montane and coast formation, owing to the many barriers offered by climate, topography, and vegetation to the species of high altitudes. In spite of this fact, however, the formation exhibits a high degree of unity. The two chief dominants, *Picea engelmanni* and *Abies lasiocarpa*, occur throughout the formation, except in California. As a subalpine dominant, *Pinus contorta* extends from the mountains of Yukon to the San Pedro Martir of Lower California, and from the Front Range of Colorado to the Cascades and the northern Coast ranges. *Pinus flexilis* and *P. aristata* also occur practically throughout the entire formation, though each develops two distinct forms which replace each other. The two other most typical dominants are *Tsuga mertensiana* and *Larix lyallii.* These are essentially Coastal in character, but both occur in the transition area of northern Montana and Idaho and *Larix* reaches the Rocky Mountains in southern Alberta. The other characteristic dominant is *Abies magnifica,* which is found only in California and southern Oregon, and may well be regarded as the ecological representative of *A. lasiocarpa.*

The ecological unity of the formation is well shown by the behavior of the individuals as well as of the community in the upper part of the zone and at timber-line, as already noted. This is emphasized by its constant relation to the montane forest below it and the alpine climax above. Geographically, the formation is consistently one of high mountain ranges and peaks or of northern ones. The geographic and topographic relations serve to explain the uniformly boreal climate in which it flourishes. This is characterized by a short growing season, high precipitation, largely in the form of snow, and wide diurnal and seasonal range of temperatures. The long winter is often marked by high winds and excessive transpiration in relation to the chresard, and these have a controlling influence in determining the timber-line (fig. 11).

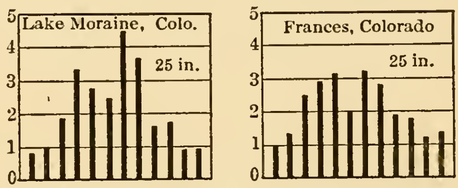


Fig. 11.—Monthly and total rainfall for representative localities in the Petran subalpine forest.

**Relationship and contacts.**—The subalpine climax shows some relationship to three different formations, viz, the boreal forest, the Coast forest, and the montane forest. Its closest relationship appears to be with the first, since the chief dominants in both belong to the two genera, *Picea* and *Abies,* and the species are also more or less related. It seems probable that the boreal forest represents a Tertiary spruce-balsam climax from which the subalpine formation was differentiated. The relationship to the Coast forest is shown by the species of *Abies* in the latter, and by the presence of *Tsuga* and *Larix* in each, though represented by different species. An additional relation is found in the fact that *Picea engelmanni* is common and *Abies lasiocarpa* not infrequent in the lower levels of the transition association of the Coast forest. Finally, several dominants of the latter, such as *Abies amabilis, A. nobilis,* and *Chamaecyparis nootkatensis* occur frequently in the subalpine zone, and the former especially may often form the timber-line. The relationship to the montane forest is shown chiefly by the presence in each of closely related species of *Picea* and *Abies,* though the two genera play a much less important rôle in the montane zone. *Pinus contorta* and *Populus tremuloides* are common to the two zones, and *Abies concolor, Pinus jeffreyi,* and *Pinus monticola* form a broad ecotone with the subalpine dominants.

The lower contact of the subalpine formation is with the montane forest in the Rocky Mountains from New Mexico to Alberta and in the ranges of the interior. This is the case also in the mountains of southern California, the Sierra Nevada, and the Cascades to northern Oregon. From here to the Kenai Peninsula in Alaska, and to Idaho and northwestern Montana, the subalpine forest touches the Coast climax. In northern British Columbia and Alberta, and in the Yukon, it lies in contact with the boreal forest. The upper contact is everywhere with the alpine climax when this is present. In many places the forest becomes so dwarfed and open as to form what is essentially an alpine savannah.

Associations.—The subalpine climax resembles the montane one in its differentiation. This is obviously due to the practically complete separation of the Petran and Sierran axes, except in the north. As a result, the formation has developed a distinct association along each axis where they are widely separated and exhibits a transition area in the north, where they are contiguous. Since the transition results from the mingling of two associations of the same formation, it is undesirable to give a distinct value to it, as was done with the broad ecotone between the Coast and montane climaxes.

There are three chief reasons for recognizing two associations. The first is that *Picea engelmanni* and *Abies lasiocarpa* are the two major dominants in the Rocky Mountains, while they have several codominants from Oregon and Idaho to Alaska and are lacking in California. The second reason is that *Pinus flexilis* and *P. aristata* are typical of the Petran axis, but the former is replaced in the Northwest and the Sierras by *P. albicaulis*, and the latter by *P. balfouriana* in California. The third lies in the fact that *Tsuga mertensiana, Larix lyallii*, and *Abies magnifica* are confined to the western association. Furthermore, the societies of the two associations are composed for the most part of different species, though the genera are largely identical.

The two associations may be designated as eastern and western simply, as Petran and Sierran, or by using the names of typical dominants, as the spruce-balsam and pine-hemlock associations. It seems preferable to use the terms Petran and Sierran as a rule, since the division is similar to that of the montane forest. In both cases the word Sierran is used to include the mountain axis from California to British Columbia.

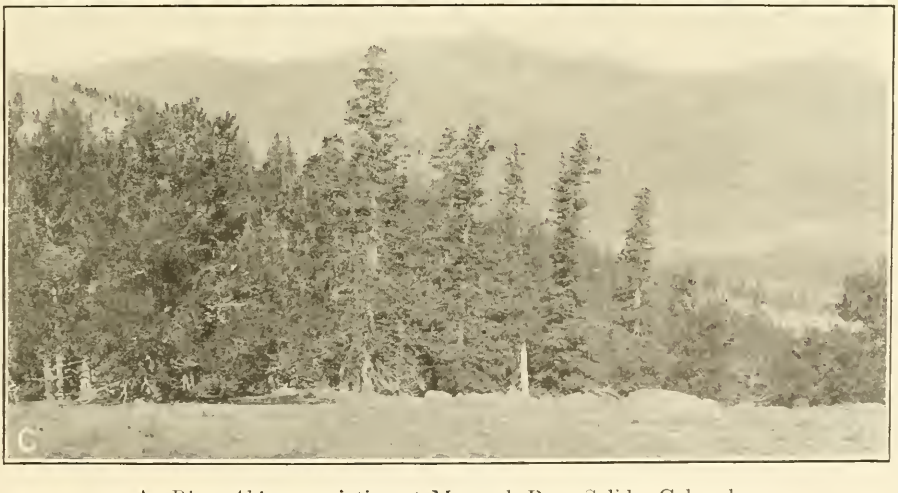
## THE PETRAN SUBALPINE FOREST.

### PICEA-ABIES ASSOCIATION.

Extent.—The northern limit of the spruce-balsam forest seems to be in the inland ranges of southern Yukon, but the contiguity of the two associations and the boreal forest is such that it is impossible to distinguish their proper limits with our present knowledge. This association is well-developed in the Rocky Mountains of British Columbia and Alberta and extends eastward toward the Lesser Slave Lake. It occurs throughout the main ranges of the Petran axis from Montana to northern New Mexico and Arizona. It is found in reduced form on the Charleston Mountains of southern Nevada and the Panamint Range of southeastern California. It should probably be assigned to the Blue Mountains of Washington and Oregon also, though *Tsuga mertensiana* occurs on one peak. This illustrates the difficulty in drawing a limit between the two associations in the Northwest, and at present it must suffice to assign the spruce-balsam community to the ranges of central Idaho and southwestern Montana (plate 53).

In altitude, the community ranges from 3,000 to 7,000 feet in the north to 8,000 to 12,000 feet in Colorado and New Mexico.

Petran Subalpine Forest



A. *Picea-Abies* association at Monarch Pass, Salida, Colorado.
B. *Picea-Abies* association on Uncompahgre Plateau, Colorado.
C. *Picea-Pinus aristata* at timber-line, King's Cone, Pike's Peak.

DOMINANTS.

| | | |
|---|---|---|
| PICEA ENGELMANNI. | PINUS ARISTATA. | PINUS FLEXILIS ALBICAULIS. |
| ABIES LASIOCARPA. | PINUS FLEXILIS. | PINUS CONTORTA. |

*Picea engelmanni* and *Abies lasiocarpa* are the two major dominants through practically the entire area of the association, except for the ranges of the Great Basin. *Pinus contorta* has a similar extensive range, but it drops out in southern Colorado. *Pinus flexilis* is much less important, though it has the widest range of all, extending from Alberta to New Mexico, Arizona, and southeastern California. *Pinus albicaulis* belongs chiefly to the Sierran association, but is found in the Rocky Mountains from Alberta to northwestern Wyoming. *Pinus aristata* is essentially southern in distribution, occurring from northern Colorado to northern New Mexico and Arizona and westward to the Panamint and Inyo Ranges of southeastern California.

Groupings.—The basic grouping throughout is that of *Picea* and *Abies* This is varied in the north chiefly by the inclusion of *Pinus contorta. Pinus flexilis* and *P. albicaulis* may occur in the community here also, and even *Larix lyallii* enters it in Alberta. In northern Colorado the usual grouping is *Picea, Abies, Pinus contorta,* and *P. flexilis,* while in central Colorado and southward the lodgepole pine drops out and *Pinus aristata* appears. In the Pike's Peak region both *Pinus contorta* and *Abies lasiocarpa* are absent and the forest consists of *Picea engelmanni* for the most part, while *Pinus aristata* and *P. flexilis* become associated with it toward timber-line. On the desert ranges of the Southwest, *Pinus flexilis* and *P. aristata* alone remain to represent the subalpine forest. Extensive pure stands are frequent for *Picea, Abies,* and *Pinus contorta,* while the mixed forest of *Picea* and *Abies* often covers great areas without any other dominant except the subclimax *Populus tremuloides.* The last is an important tree throughout the subalpine zone, covering burned areas everywhere, in the absence of the lodgepole pine especially. It also resembles the latter in occurring in both zones.

Factor and seral relations.—The precipitation in the central part of the area ranges from 22 to 40 inches a year, of which the snowfall is 8 to 14 feet. On interior ranges the rainfall may be somewhat less. The evaporation is much less than in the montane zone, the reduction often exceeding 25 to 50 per cent. At the lower limit the growing season is 3 to 4 months long, at the upper barely 2 months. The mean temperatures are 5 to 10 degrees lower than in the montane forest, and near timber-line frost occurs frequently or regularly during the summer.

*Picea engelmanni* is the most mesophytic of the dominants, often growing at the edges of streams and in bogs. It is followed more or less closely by *Abies lasiocarpa,* while all the pines are much more xeroid. *Pinus contorta* is the most mesophytic of these, while the remaining species are more or less similar, *P. flexilis* usually growing in the driest situations. As to light relations, *Picea* is the most tolerant, though *Abies* often equals it. The pines are all much less tolerant and do not differ markedly from each other in this respect. *Pinus contorta* is the most tolerant, and *P. flexilis* and *P. aristata* the least, though all must be regarded as intolerant.

The water and light relations furnish a clear explanation of the successional sequence (Clements, 1910: 54). The main body of the forest is composed of

*Picea* and *Abies*, the slight handicap of the latter in competition with *Picea* being offset by its ability to produce new plants by layering. Burn areas are dominated by lodgepole pine or aspen, or by the two in varying mixture. The aspen yields to the pine, and this in turn to the spruce and balsam. This is likewise true of *Pinus flexilis* or *P. aristata*, where they occur on rocky ridges or dry slopes in the heart of the association. When the forest becomes more open or breaks up into groups toward timber-line, the tolerance of the spruce and balsam loses most of its advantage and the pines persist as permanent constituents of the community.

### SOCIETIES.

Owing to its position, the subalpine forest has many societies in common with the montane forest in its lower half and with the alpine meadow in the upper. The societies are best developed in the central area, and decrease in number and importance toward both extremes, but especially to the north. The following list for the Colorado region is fairly representative:

| | | |
|---|---|---|
| *Shrub layer:* | | |
| Linnaea borealis. | Ribes lacustre. | Vaccinium caespitosum. |
| Lonicera involucrata. | Shepherdia canadensis. | Vaccinium myrtillus. |
| Pachystigma myrsinites. | Salix nuttallii. | |
| *Herbs, Vernal Societies:* | | |
| Thalictrum fendleri. | Arabis drummondii. | Mitella pentandra. |
| Polemonium pulchellum. | Alsine baicalensis. | Mitella trifida. |
| Mertensia polyphylla. | Adoxa moschatellina. | Parnassia fimbriata. |
| Aquilegia coerulea. | Zygadenus elegans. | Androsace septentrionalis. |
| Fragaria vesca. | Aragallus deflexus. | Pentstemon glaucus. |
| Draba aurea. | Ligusticum porteri. | Pseudocymopterus montanus. |
| Draba streptocarpa. | Pirola minor. | |
| *Herbs, Estival Societies:* | | |
| Sedum stenopetalum. | Carduus hookerianus. | Gentiana frigida. |
| Solidago humilis. | Castilleia miniata. | Gentiana amarella. |
| Arnica cordifolia. | Erigeron elatior. | Poa pratensis. |
| Pedicularis racemosa. | Erigeron salsuginosus. | Festuca ovina. |

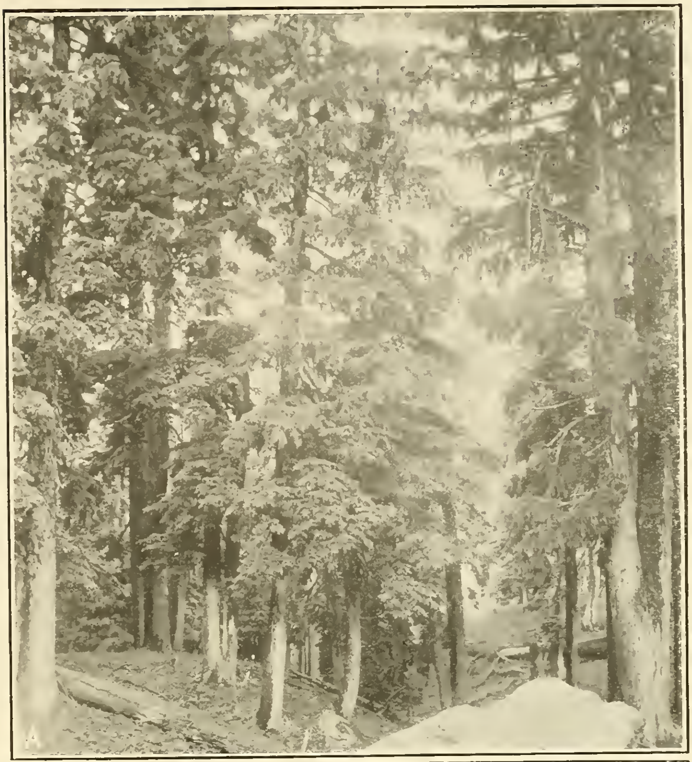
## THE SIERRAN SUBALPINE FOREST.

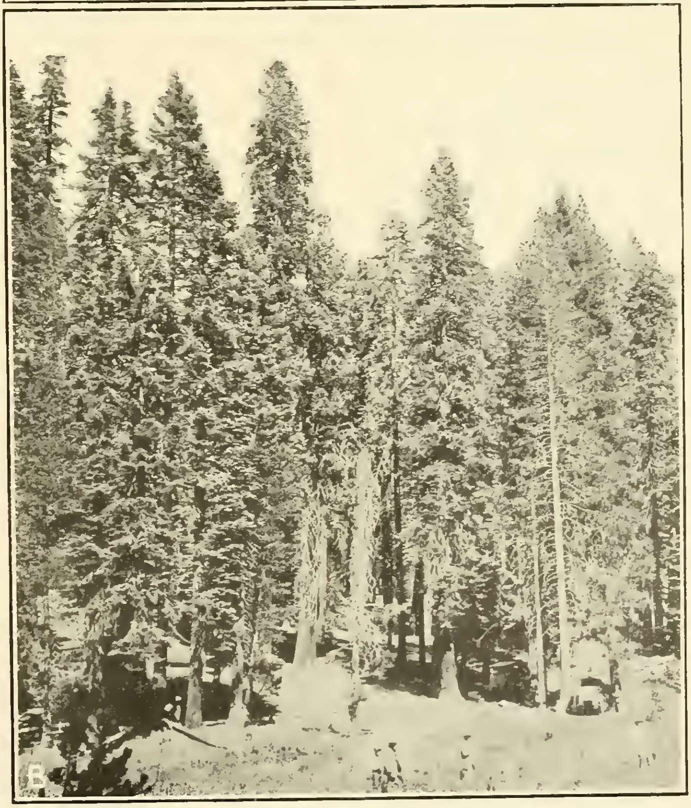
### PINUS-TSUGA ASSOCIATION.

Extent.—The subalpine forest reaches its northern limit along the Pacific in the neighborhood of the sixtieth parallel, stretching west in Alaska from Lynn Canal to Cook Inlet. It follows the summits of the Coast ranges southward to southern British Columbia, where it broadens out to the eastward and comes into contact with the Petran association in Alberta and Montana. It occurs throughout the mountains of Washington from the Olympics to those of the northeastern part of the State, but is only slightly developed in the Blue Mountains. It follows the Cascade Range throughout Oregon into the Siskiyou and the Sierra Nevada of California. It maintains its characteristic expression throughout the latter, though *Picea* and *Abies lasiocarpa* have disappeared. On the eastern slopes, it sometimes comes into contact with the Petran association. The subalpine forest is much reduced in the San Bernardino and San Jacinto Mountains; its most southern outpost is probably in the San Pedro Martir Range of Lower California (plate 54).

The altitude of the subalpine zone changes greatly from Alaska to southern California. In Alaska it is chiefly at 2,000 to 4,000 feet, in southern British Columbia at 3,000 to 6,000 feet, and in the Cascades at 5,000 to 8,000; while in the Sierra Nevada it lies at 7,000 to 10,000, or rarely 12,000 feet.

Sierran Subalpine Forest




A. *Tsuga lyallii* consociation, Crater Lake, Oregon.
B. *Abies magnifica* consociation, Glacier Point, Yosemite National Park, California.

DOMINANTS.

| | | |
|---|---|---|
| TSUGA MERTENSIANA. | PINUS ARISTATA BALFOURIANA. | ABIES AMABILIS. |
| PINUS CONTORTA. | PICEA ENGELMANNI. | ABIES NOBILIS. |
| PINUS FLEXILIS ALBICAULIS. | ABIES LASIOCARPA. | CHAMAECYPARIS NOOTKATENSIS. |
| LARIX LYALLII. | PINUS FLEXILIS. | PINUS MONTICOLA. |
| ABIES MAGNIFICA. | | |

The characteristic dominants of this association are the first six. The next three are more typical of the Petran subalpine forest, and the last four of the Coast forest climax. These differences seem to forehadow a further differentiation of the community, but they may be due largely to the uncompleted migration of certain species. The two dominants of the greatest extension are *Tsuga* and *Pinus contorta*, the latter more truly climax in nature than in the related association. *Tsuga* ranges from Cook Inlet to the southern Sierras and from the Coast to the Bitterroot Range between Idaho and Montana. *Pinus contorta* extends from Skagway in Alaska to Lower California and throughout the greatest width of the association from the coast to Montana. *Pinus albicaulis* occurs from southern British Columbia and adjacent Montana to the Cascades of Washington and Oregon and thence southward along the Sierra Nevada to the thirty-sixth parallel. *Larix lyallii* has a much more restricted distribution; it is found in Canada only in southeastern British Columbia and adjacent Alberta. It is frequent in northwestern Montana and northern Idaho and occurs throughout the Cascade Mountains of Washington as well as in those of the northeast, but is found only rarely in the Cascades of northern Oregon. *Abies magnifica*, with its variety *shastensis*, is confined to California and Oregon, extending from Crater Lake southward in the Sierra Nevada to Kern River, and in the Coast ranges to Lake county. *Pinus balfouriana* is found only in California.

*Abies lasiocarpa* and *Picea engelmanni* extend from Alaska to southern Oregon, while *Pinus flexilis* appears to enter this association only in Alberta and Montana, the southern Sierras, and the cross ranges from Mount Pinos to the San Jacinto Mountains. *Abies amabilis*, *A. nobilis*, and *Chamaecyparis* do not occur south of Oregon, while *Pinus monticola* is important in the subalpine forest chiefly in the Sierra Nevada.

Groupings.—The large number of dominants and the extensive range make the groupings exceedingly varied. There is a marked tendency for the dominants to appear in pure consociations near timber-line, while in the lower part of the zone several usually occur in mixture. In the ranges of the upper Columbia Basin, *Abies lasiocarpa* and *Picea engelmanni* are regularly present and usually are associated with one or more of the following: *Pinus contorta*, *Pinus albicaulis*, *Larix lyallii*, and *Tsuga mertensiana*. *Tsuga* and *Abies lasiocarpa* are found together in Alaska, while farther south *Picea engelmanni*, *Pinus albicaulis*, *Larix lyallii*, and *Abies amabilis* are commonly associated with them, and *Abies nobilis* and *Chamaecyparis* less frequently. In the Sierra Nevada, *Tsuga* occurs with *Abies magnifica*, *Pinus contorta* and *P. monticola* through most of the zone and with *P. albicaulis* in the upper portion. *Pinus balfouriana* replaces or mixes with *P. albicaulis* in much the way that *P. aristata* does with *P. flexilis* in the Rocky Mountains. It occurs with *Pinus contorta*, *Abies magnifica*, and *Tsuga* in the lower part of the forest, with *P. monticola* higher up, and with *P. albicaulis* at timber-line. In the southern Sierras and in the cross ranges of southern California *Pinus flexilis* is associated with *P. contorta* and *Tsuga*, or with either alone.

Factor and seral relations.—Climatic data for the pine-larch association are almost completely lacking. In the Sierras, the precipitation ranges above 50 to 75 inches, and the snowfall may be as great as 300 to 900 inches, or 50 to nearly 100 per cent of the total. The general climatic relations are as already indicated for the formation.

The water relations of the dominants are imperfectly known. *Picea*, *Tsuga*, and *Abies lasiocarpa* grow generally in the moister areas, *Pinus monticola*, *P. contorta*, *Larix*, and *Abies magnifica* in intermediate ones, and *Pinus albicaulis*, *flexilis*, and *balfouriana* in the drier. The general light relations may be indicated by the following table of tolerance in which the order is from the intolerant to the tolerant. The order of the dominants likewise indicates the seral sequence in so far as it is known.

1. Pinus balfouriana.
2. Pinus flexilis.
3. Pinus albicaulis.
4. Larix lyallii.
5. Pinus contorta.
6. Abies magnifica.
7. Pinus monticola.
8. Abies lasiocarpa.
9. Picea engelmanni.
10. Tsuga mertensiana.

### SOCIETIES.

The Sierran subalpine forest does not have a large number of societies peculiar to it. The majority of those which occur in it have been derived from the montane forest or the alpine meadow. This is especially true of the shrubs, many of which extend up from the subclimax chaparral (p. 213). The following list applies particularly to California:

*Shrubs:*

Arctostaphylus nevadensis.
Ribes viscosissimum.
Ribes montigenum.
Potentilla fruticosa.
Haplopappus suffruticosus.
Lonicera conjugialis.
Juniperus communis.
Vaccinium occidentale.
Vaccinium caespitosum.
Ceanothus cordulatus.
Acer glabrum.

*Herbs:*

Artemisia norvegica.
Hieracium gracile detonsum.
Sibbaldia procumbens.
Haplopappus macronema.
Potentilla breweri.
Ranunculus alismifolius.
Phacelia hydrophylloides.
Whitneya dealbata.
Orthocarpus pilosus.
Erysimum asperum.
Eriogonum marifolium.
Eriogonum ursinum.
Polygonum davisiae.

## THE ALPINE MEADOW CLIMAX.

### CAREX-POA FORMATION.

Nature.—The alpine climax is essentially a grassland in appearance, though it is chiefly composed of sedges. The dominants are all grasslike in character and the most typical regularly form a turf which rivals that of the buffalo-grass in compactness. They are 2 to 6 inches high for the most part, though some exceed this in subclimax situations or in the lower part of the zone. The total number of dominants is greater than for any other formation, but the number in a particular community is rarely excessive. A characteristic feature of the dominants is their remarkable range, nearly half of them occurring from Greenland to Colorado, California, and Alaska, wherever alpine or arctic habitats are found. A large number of these grow in similar situations

Petran Alpine Meadow.

A. *Carex-Poa* association, King's Cone, Pike's Peak.
B. *Carex* consociation, *Campanula* society, Pike's Peak.

in Eurasia. This unique extension of arctalpine plants has a definite historical as well as physical basis.

The total number of subdominants which form important societies is probably greater than for any other formation. The grassland climax approaches it in this respect, while the prairie and the alpine meadow have much in common in so far as the number and luxuriance of the societies are concerned. These are often so dense and continuous that the grass-like character of the climax is completely hidden. The subdominants are even more strikingly dwarfed than the dominants, chiefly because of a relatively greater emphasis on the flower. In many the inflorescence is reduced to a single flower of unusual size, while the stem is often less than an inch in height. A considerable number have assumed the mat or rosette habit and are essentially stemless, though this is more frequently the case in seral habitats.

The true character of the alpine climax is often difficult of recognition, owing to the wide variation in conditions over what appears to be fairly uniform terrain. Rock fields of all degrees, gravel-slides, bogs, wet meadows, and temporary snow-seeps in all stages of succession frequently blur the outlines of the climax or break it up into many fragments. The real nature of the climax is best seen in the Rocky Mountains of Colorado, where the alpine areas are unusually extensive as well as free from snow during the summer. In such places the general resemblance to a short-grass plain is striking. While the alpine climax is ecologically a grassland, the predominance of sedges makes it more accurate to refer to it as sedgeland. The term alpine meadow is perhaps even more descriptive and is to be preferred to alpine heath, since the latter is usually subclimax in character (plate 55).

Extent.—In the view advanced here, the alpine and arctic sedgelands of North America are regarded as constituting one formation. This seems to accord with the general opinion that the arctalpine region is a unit life-zone (Merriam, 1898). As such, the arctalpine climax extends across Arctic America from Greenland to Alaska. The southern limit of it as a continental zone runs from central Labrador northwest to the lower Mackenzie River, and then westward through Alaska. As is well known, the arctalpine climax extends south over the isolated alpine summits of New England, but sweeps much farther southward in the Rocky Mountains and the Sierra Nevada. An alpine zone is found on the volcanoes of Mexico, but its relationship to the present climax is uncertain. Along the Rocky Mountain axis the last outposts of the climax are found in the Sangre de Cristo Mountains of northern New Mexico and the San Francisco peaks of northern Arizona. In California, the single locality south of the Sierra Nevada is in the San Jacinto Range (Hall, 1902: 16), where it is reduced to a mere fragment. By far the most extensive development of the formation is found in the central Rockies of Colorado and Wyoming and adjacent Utah, while the most complete and continuous is in Colorado.

Unity.—The ecologic and climatic unity of the arctalpine climax is so striking as to need little comment. The topographic and geographic unity appears to be slight, but an adequate explanation is found in the correlating influence of latitude and altitude. The general ecological unity appears to be fully confirmed by the distribution and occurrence of the dominants as shown by the table on the following page.

*Distribution of dominants*

| Genera. | No. of species. | Eastern Arctica. | Western Arctica. | Petran. | Sierran. | Eurasia. |
|---|---|---|---|---|---|---|
| Carex | 32 | 12 | 17 | 28 | 21 | 14 |
| Kobresia | 1 | 1 | | 1 | 1 | 1? |
| Elyna | 1 | 1 | 1 | 1 | 1 | 1 |
| Cyperaceae | 34 | 14 | 18 | 30 | 23 | 16 |
| Poa | 15 | 4 | 5 | 11 | 7 | 1 |
| Agrostis | 3 | 1 | 1 | 3 | 3 | |
| Festuca | 2 | 2 | 2 | 2 | 2 | 1 |
| Calamagrostis | 2 | 2 | 2 | 2 | 2 | |
| Deschampsia | 2 | 2 | 2 | 2 | 2 | 2? |
| Trisetum | 1 | 1 | 1 | 1 | 1 | |
| Danthonia | 1 | 1 | | 1 | 1 | |
| Phippsia | 1 | 1 | 1 | 1 | | 1 |
| Poaceae | 27 | 14 | 14 | 23 | 18 | 5 |
| Juncodes | 4 | 4 | 4 | 4 | 2 | 4 |
| Juncus | 6 | 3 | 5 | 5 | 3 | 3 |
| Juncaceae | 10 | 7 | 9 | 9 | 5 | 7 |
| Grand total | 71 | 35 | 41 | 62 | 46 | 28 |

The occurrence of the 13 dominant genera practically throughout the four regions seems conclusive evidence of their formational unity. This is emphasized by the distribution of the genera of subdominants as well. The preeminence of *Carex* is obvious, as well as the importance of *Poa*. *Juncus* probably has a higher value than it deserves, owing to the fact that some subclimax species persist into the climax. The typical character of the Petran region is shown by the fact that nearly 90 per cent of the dominants are found in it. The number of endemic dominants in any one of the regions is so small as to be negligible. The close relationship to the Eurasian arctalpine climax is evident, as well as the fact that this is largely due to *Carex, Juncodes,* and *Juncus.*

**Relationship and contacts.**—The primary relationship of the arctalpine climax is with the corresponding Eurasian formation. The number of dominants and subdominants common to both is sufficiently large to suggest that they should be regarded as associations of the same formation. In this respect, however, their difference is greater than their similarity, as one who has seen both must readily recognize. There can be little question that the two climaxes have originated from a common ancestral community. The arctalpine climax is also related to a similar community on the high peaks of Mexico. The two have many genera in common, but the species are nearly all different and the rôle of the grasses is emphasized at the expense of *Carex*. In the present state of our knowledge, it seems best to regard the alpine meadows of northern Mexico as a transition between the arctalpine climax and an Andean alpine climax. Finally, there are certain resemblances between the alpine meadow and the short-grass plains which suggest a broader contact than exists at present, if not an actual though more remote relationship. These are largely in the life-form, habits, and size of the dominants and in the genera of many of the subdominants. A more definite relationship is seen in the presence of *Carex filifolia* as a dominant in both, in the contact maintained by such closely related species as *Carex rupestris* and *C. obtusata*, and by the important part which *Selaginella rupestris* may take in both. A similar suggestion is contained in the presence of *Festuca* and *Agropyrum* in both communities also.

At present the chief contact of the arctalpine climax is with the subalpine forest in the Rocky Mountains and the Sierra Nevada-Cascade axis and with the boreal forest in northern Canada and Alaska. The ecotone is very irregular, and tongues and outposts of the one may extend far into the other. In the mountains the two are sometimes separated by a narrow belt of scrub, and this is often, if not regularly, the case in the Barren Grounds of the north. The lower temperatures and higher water-content of the broader mountain valleys have afforded a ready pathway for the downward movement of alpine species and also perhaps for the upward migration of lowland hydrophytes. In any event, the wet meadows and grasslands of the subalpine and montane zones furnish a meeting-place for the more mobile species of two floras.

Associations.—The arctalpine climax has received almost no ecological study outside of the central Rocky Mountains. Much attention has been given to the floristic differences of various portions of it, but this has taken no account of dominance and succession, which are vital to an understanding of the vegetation. As a consequence, it is more than usually difficult to delimit the associations and determine their relationship. This is particularly true of the vast Arctic portion, owing to the inherent difficulties of travel and investigation in such a region. The table of dominants on page 230 indicates a close relationship between the eastern and western portion of the Arctic region, and one closer than with either the Petran or Sierran. On the basis of dominants the latter are less closely related to each other, and the subdominants confirm the view that they should be regarded as two associations. In a table of the characteristic alpine species of Washington, Piper (1906: 63) has indicated their occurrence in the Arctic region, in the mountains of California, and in the Rocky Mountains. Of 156 species found on the high peaks of Washington, 72 occur in California, 56 in the Arctic region, and 49 in the Rocky Mountains.

For the above reasons, it proves necessary to recognize a Petran and a Pacific or Sierran association. The best evidence at present indicates the presence of a single Arctic association from Greenland and Labrador to Alaska. This is very little known, and it may prove desirable to recognize an eastern and western association with fuller knowledge. It has not been seen by the writer, and the general absence of ecological information in regard to it makes it undesirable to touch it more than incidentally. Hence, the discussion below deals only with the alpine portion of the formation and the corresponding Petran and Pacific or Sierran associations.

## THE PETRAN ALPINE MEADOW.

### CAREX-POA ASSOCIATION.

Extent.—The alpine meadow of the Rocky Mountains reaches its typical development between 12,000 and 14,500 feet, though it descends to lower altitudes in Montana and Alberta. In Colorado it is found in more or less characteristic form in lake basins at 11,000 feet, but this is apparently due to cold-air drainage and the influence of water. A number of dominants and subdominants may be found still lower, but these are chiefly subalpine in nature, or occur merely as fragmentary outposts. The northern limit of the association is thought to be in southern Alberta, since the alpine plants of Mount Robson (Standley, 1913: 77) are largely those of the Pacific association. The southeastern outposts are in the Sangre de Cristo Range of northern New Mexico, and the southwestern on the San Francisco peaks of northern Arizona. The general western limit is thence northward along the Wasatch Mountains of Utah into eastern Idaho and southwestern Montana. The association occurs in reduced form in some of the ranges of Nevada. The central portion is most typical and extensive. It occupies Colorado and Wyoming and includes the Uinta Mountains of Utah and the San Juan and Sangre de Cristo ranges of New Mexico (plate 56).

### DOMINANTS.

The Petran association exhibits 62 dominants which play a rôle of more or less importance in the climax. Of these, 30 are sedges, 23 are grasses, and 8 are rushes. The majority of them occur also in the Pacific association, but 18 or nearly a third are lacking there. For the sake of brevity, only the most typically alpine or the most abundant dominants are included in the following list. In *Carex* and *Poa* the order is that of relative importance on the alpine peaks of Colorado.

Carex rupestris.
Carex filifolia.
Carex pyrenaica.
Carex nigricans.
Carex festiva.
Carex atrata.
Carex nova.
Carex capillaris.
Carex tolmiei.
Carex alpina.
Carex petasata.
Carex engelmanni.
Carex nardina.
Carex illota.
Carex concolor.
Elyna bellardi.
Poa alpina.
Poa arctica.
Poa alpicola.
Poa epilis.
Poa crocata.
Poa rupicola.
Poa pattersoni.
Poa grayana.
Poa lettermani.
Trisetum subspicatum.
Festuca brachyphylla.
Deschampsia caespitosa.
Juncodes spicatum.
Juncus triglumis.
Juncus castaneus.

Groupings.—As a result of the large number of dominants and the consequent equivalence, the number of groupings is exceptional. Pure consociations are extremely rare, except in areas of a few square meters, and mixed communities are universal. The number of dominants in each mixture is large, and the groupings consequently merge into a more or less indefinite pattern. *Carex rupestris* and *C. filifolia* are the most important dominants on a score of Colorado peaks, as well as on the San Francisco Mountains of Arizona, though apparently absent on those of New Mexico. *Poa, Elyna, Trisetum,* and *Juncodes* are commonly associated with them. *Carex pyrenaica* and *C. nigricans* are found on a number of alpine summits in Colorado, but they are much less important. They nowhere seem to have the dominance characteristic of them in the Pacific association.

Petran Alpine Meadow

A. *Polygonum bistorta* society, Pike's Peak.
B. *Campanula rotundifolia* society, Pike's Peak.
C. *Mertensia alpina* society, Pike's Peak.

**Factor and seral relations.**—From 1900 to 1906 quantitative studies were made of alpine habitats and communities on Pike's Peak and the neighboring Mount Garfield or King's Cone. These confirmed the general opinion as to temperature and water relations, but not as to the light intensity. The annual precipitation on the summit of Pike's Peak (14,100 feet) is 30 inches; at Lake Moraine (10,200 feet), which lies at the base of the Peak proper and in the subalpine forest, it is 25 inches; at the Alpine Laboratory (8,500 feet) in the montane forest it is 22 inches; and on the short-grass plains at the base (6,000 feet) it is 15 inches. The relative humidity on Mount Garfield (12,500 feet) averaged 5 per cent higher than at the Alpine Laboratory, but in spite of this the transpiration was 25 per cent higher at the former. The mean temperature is 19° on Pike's Peak, 36° at Lake Moraine, and 47° at Colorado Springs on the plains. During the growing season, temperatures averaged 15° higher at the Alpine Laboratory and 25° higher at Manitou (6,500 feet) than on Mount Garfield. Comparative light readings have been made for several summers at Pike's Peak and Mount Garfield and at the Alpine Laboratory, Manitou, and Colorado Springs. For the most part, these have given identical results at the different altitudes in spite of a range of 8,000 feet. This is probably to be explained by the low humidity (fig. 12).

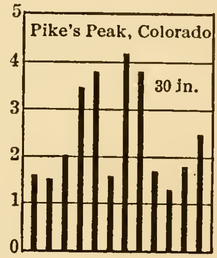


FIG. 12.—Monthly and total rainfall for the alpine meadow climax, summit of Pike's Peak, 14,100 feet.

The typically climax condition of the association is marked by the sod-forming or densely cespitose sedges, such as *Carex rupestris, filifolia, pyrenaica, nigricans, nardina, engelmanni,* etc. These are also of low stature, usually 2 to 5 inches, and rarely as much as 6 to 8 inches. *Juncodes spicatum* and *Elyna bellardi* are nearly equivalent to the low sod-forming sedges, but they have a wider range of adjustment. In the direction of the xerosere subclimax lie most of the grasses, some of which, such as *Festuca brachyphylla* and *Poa lettermanni,* are often if not usually seral in character. Most of them are bunch-grasses and are 6 to 12 inches tall. The taller sedges, such as *Carex festiva* and *C. atrata,* which range from 1 to 2 feet high, are more or less similar in nature. Toward the hydrosere occur such species as *Carex tolmiei, nova,* and *bella,* which are tall and more or less sod-forming, and the rushes. These lead to species of *Carex* and *Juncus* that are distinctly hydrophytic and seral.

## SOCIETIES.

The number of societies is very large, and no endeavor has been made to include them all. The following list is based primarily upon studies in Colorado, but it is representative of the entire central portion and even of such outlying areas as the San Francisco peaks. The endemic species drop out for the most part in Montana and Alberta, and there is an increasing number of species from the Arctic and Pacific associations. Of the 80 societies given, 29 are endemic, 32 occur in the Pacific alpine meadows, 32 in Arctic America, and the same number in Eurasia. The identity in number in the last three is merely a coincidence, for the species are not the same throughout.

The great majority of the societies listed belong typically to the climax, but some are normally seral or subclimax dominants which persist into the final stage more or less frequently. These relations have been indicated for Colorado (Clements, 1904: 329) and have been suggested for the entire region by Rydberg, who has also given a detailed account of the comparative distribution of the various species (1914: 459, 89; cf. also Cockerell, 1906: 861). The aspects are less marked than in the prairie on account of the short season, but there is a distinct difference between the earlier and later portions of the growing period, in spite of the fact that a considerable number occupy the mid-season. The distinction below is based upon the time when the species begins to bloom, as well as the maximum of the flowering period. By far the greater number of societies are mixed, and the order below is primarily that of importance.

*Vernal Societies.*

| | | |
|---|---|---|
| Sieversia turbinata. | Lloydi serotina. | Erigeron compositus. |
| Mertensia alpina. | Cerastium arvense. | Erigeron radicatus. |
| Rydbergia grandiflora. | Allium reticulatum. | Besseya alpina. |
| Primula angustifolia. | Salix reticulata. | Ranunculus macauleyi. |
| Silene acaulis. | Saxifraga nivalis. | Ranunculus nivalis. |
| Achillea millefolium. | Saxifraga flagellaris. | Ranunculus eschscholtzii. |
| Castilleia pallida occidentalis. | Saxifraga chrysantha. | Thalictrum alpinum. |
| Sibbaldia procumbens. | Polemonium confertum. | Phacelia alpina. |
| Androsace chamaejasme. | Pseudocymopterus montanus. | Phlox condensata. |
| Artemisia scopulorum. | Sedum roseum. | Polemonium viscosum. |
| Arenaria biflora. | Erigeron uniflorus. | Primula parryi. |
| Oreoxis humilis. | Draba aurea. | Douglasia nivalis. |
| Polygonum bistorta. | Draba streptocarpa. | Pedicularis lanata. |
| Pedicularis parryi. | Chionophila jamesii. | Pedicularis flammea. |
| Trifolium nanum. | Androsace septentrionalis. | Smelowskia calycina. |
| Eritrichium argenteum. | Dryas octopetala. | Trollius laxus. |
| Potentilla saximontana. | Phacelia sericea. | Astragalus alpinus. |
| Campanula uniflora. | Zygadenus elegans. | Myosotis alpestris. |
| | | Draba nivalis. |

*Estival Societies.*

| | | |
|---|---|---|
| Polygonum viviparum. | Haplopappus pygmaeus. | Ranunculus adoneus. |
| Campanula rotundifolia alpina. | Antennaria alpina. | Ranunculus pygmaeus. |
| Gentiana frigida. | Antennaria dioeca. | Ranunculus hyperboreus. |
| Gentiana amarella. | Salix nivalis. | Pedicularis scopulorum. |
| Solidago humilis nana. | Salix arctica. | Pedicularis oederi. |
| Agoseris aurantiaca. | Angelica grayi. | Swertia perennis. |
| Oreoxis alpina. | Arnica parryi. | Pentstemon hallii. |
| Saxifraga bronchialis. | Aster alpinus. | Pentstemon glaucus. |
| Potentilla nivea. | Erigeron leiomerus. | Claytonia megarhiza. |
| Trifolium dasyphyllum. | Phacelia lyallii. | Selaginella rupestris. |
| Trifolium parryi. | Anemone narcissiflora. | |

## THE SIERRAN ALPINE MEADOW.

### CAREX-AGROSTIS ASSOCIATION.

Extent.—While the highest alpine peaks of the Pacific Coast are a little higher than those of the Rockies, they are covered with permanent snow-caps of great size, and the alpine zone is consequently much lower. In Washington its best expression is found at 8,000 to 10,000 feet, and on Mount Shasta at 9,000 to 11,000 feet, though two species, *Draba breweri* and *Polemonium pulchellum*, reach 13,000 feet. In the central and southern Sierra Nevada the alpine meadows are best developed between 10,500 and 13,000 feet. The lowest limit for the zone is found in the mountains of the upper Columbia Basin, where it descends to 6,000 feet.

Sierran Alpine Meadow

A. *Carex-Agrostis* association, Mount Rainier, Washington.
B. *Lupinus volcanicus-Valeriana sitchensis* society, Mount Rainier, Washington.

The northern limit of the association is probably in northern British Columbia, though it is uncertain where it passes over into the Arctic association. Similar uncertainty exists as to the limits in northwestern Montana, where it meets the Petran community. Piper (1906: 63) states that the flora of the Blue Mountains of Washington and Oregon is as near that of the Rocky Mountains as of the Cascades, but this is not true for the typical central mass of the Petran association. The Sierran association occupies all the alpine summits of the Cascades, Olympics, Blue, and other mountains of Washington and of the Cascades of Oregon. It extends from Mount Shasta southward through the Sierra Nevada and reaches its southernmost limit on San Jacinto Mountain, where it is reduced to less than a half-dozen of true alpine species (plate 57).

### DOMINANTS.

The genera of the dominants are the same as for the Petran association. The small amount of ecological study which this community has received makes it impossible to distinguish climax from seral species with certainty, and the following list is necessarily provisional:

| | | |
|---|---|---|
| Carex nigricans. | Carex festiva. | Agrostis rossae. |
| Carex pyrenaica. | Carex scirpoidea. | Agrostis humilis. |
| Carex breweri. | Elyna bellardi. | Agrostis hiemalis geminata. |
| Carex nardina. | Kobresia bipartita. | Calamagrostis vaseyi. |
| Carex spectabilis. | Poa paddensis. | Calamagrostis langsdorffi. |
| Carex illota. | Poa suksdorfii. | Trisetum subspicatum. |
| Carex vernacula. | Poa rupicola. | Festuca ovina supina. |
| Carex ablata. | Poa alpina. | Juncodes spicatum. |
| Carex filifolia. | Poa arctica. | Juncodes divaricatum. |
| Carex phaeocephala. | Poa saxatilis. | Juncus parryi. |
| Carex atrata. | | |

Groupings.—The general grouping of the dominants is indicated by their respective ranges. *Carex* is represented by 8 species, which occur throughout the association from British Columbia or Washington to the Sierra Nevada. These are *Carex nigricans, breweri, spectabilis, illota, vernacula, ablata, filifolia,* and *atrata.* Among the grasses and rushes, those found throughout are *Poa saxatilis, Agrostis rossae, Calamagrostis langsdorffi, Trisetum subspicatum, Festuca supina, Juncodes spicatum, J. divaricatum,* and *Juncus parryi.* The intimate grouping is known only for Mount Rainier, where the climax stage is constituted typically by *Carex nigricans, pyrenaica, nardina,* and *illota,* while the taller *C. festiva, atrata, spectabilis,* and *ablata* occur in areas more or less seral in character. The chief grasses are *Poa saxatilis, arctica, paddensis,* and *suksdorfi,* and *Agrostis rossae.* Practically the same grouping is found in the northern Cascades, the Olympic Mountains, and on Mount Adams (Piper, 1906: 63). The alpine meadows of the Selkirk Mountains consist of *Carex nigricans, spectabilis,* and *festiva,* and *Poa alpina, arctica,* and *cusickii* (Shaw, 1916: 491).

Factor and seral relations.—There is practically no direct information upon the physical factors and succession, and these can only be inferred from the climatic conditions in the Petran association and the Sierran subalpine forest, and from the seral relations in the Rocky Mountains. The precipitation is apparently much higher in the Sierran association, often exceeding 75 inches.

Most of this occurs as snow, and results in much more extensive snow-caps and snow-fields than occur in the Rocky Mountains at corresponding latitudes.

For the present, the seral relations must be assumed from those in the Petran association (p. 233). This doubtless affords a fairly accurate idea of the processes, since the two associations have so many dominants in common.

SOCIETIES.

*Northern* (*Cascades, etc.*):

Pulsatilla occidentalis.
Lupinus lyallii.
Lupinus subalpinus.
Lupinus volcanicus.
Castilleia oreopola.
Castilleia pallida.
Potentilla flabellifolia.
Valeriana sitchensis.
Erigeron salsuginosus.
Erigeron radicatus.
Erigeron uniflorus.
Gentiana calycosa.
Arnica parryi.
Sieversia turbinata.
Silene acaulis.
Veronica alpina.
Sedum roseum.
Polygonum viviparum.
Epilobium alpinum.
Epilobium hornemannii.
Epilobium anagallidifolium.
Salix arctica.
Salix nivalis.
Salix reticulata.
Draba aurea.
Draba nivalis.
Arenaria biflora.
Dryas octopetala.
Sibbaldia procumbens.
Agoseris aurantiaca.
Phacelia sericea.
Phlox condensata.
Trollius laxus.
Erythronium grandiflorum.
Ranunculus eschscholtzii.
Douglasia nivalis.

*Southern* (*Sierra Nevada*):

Trifolium monanthum.
Sibbaldia procumbens.
Salix arctica.
Lupinus lyallii.
Senecio aureus borealis.
Mimulus primuloides.
Gentiana newberryi.
Castilleia culbertsonii.
Pentstemon confertus.
Antennaria alpina.
Dodecatheon alpinus.
Sedum roseum.
Horkelia gordonii.
Solidago multiradiata.
Agoseris aurantiaca.
Thalictrum alpinum.
Ranunculus eschscholtzii.
Erigeron salsuginosus.
Erigeron uniflorus.
Gentiana amarella.
Cerastium arvense.
Antennaria dioeca.
Campanula rotundifolia alpina.

# V. AGRICULTURAL INDICATORS.

General relations.—As the basic economic practice of plant and animal production, agriculture furnishes the standard for measuring the possibilities of soils, climates, and regions. There are many reasons for this, chief among them the fact that it gives relatively large and immediate returns upon a small capital. In addition, its operations are within the scope of the individual or family, and farming has inevitably become the traditional basis of the American homestead. The latter has played such a wonderful rôle in the development of the West that it has come to be regarded as a fetich, able to reclaim the most arid desert or to enrich the most sterile soil. During the last two decades the large majority of the homesteads filed upon have proved failures and the percentage of failures will steadily increase as still less promising regions are entered, unless the method of settlement is radically changed. The time when individual initiative would suffice to convert a tract of virgin land into a prosperous farm has gone. While millions of acres of public lands still remain for settlement, these are of such a nature that land classification, reclamation, demonstration, and cooperation are indispensable to their conversion into successful farms and ranches (plate 58).

## LAND CLASSIFICATION.

Nature.—The classification of land is an endeavor to forecast the type of utilization that will yield adequate or maximum returns. Properly, it should determine the optimum use as accurately as possible, and should insure the conditions under which development and utilization take place. In actual practice, classification has been conspicuously absent as a preliminary to the settlement of the arid regions of the West. Hurried and incomplete classifications have been made for special purposes, but these have covered only certain portions of the vast public domain and have usually suffered from inadequate and hasty methods. Perhaps their greatest fault has been that they were made with a particular end in view, and the primary object was to include or exclude as much land as possible without reference to its optimum utilization. In this respect the recent classification under the Ferris Act has been an improvement, but it has been handicapped by legislative restrictions and by the lack of an adequately trained field personnel. It has been especially unfortunate that only those lands were examined which had been filed upon, with the result that the examiner's judgment or decision was often influenced by local pressure. To the one who is interested solely in seeing the public domain developed in such a way as to secure the best economic and social conditions, it is incomprehensible that the prerequisite of an accurate and unbiased classification of the land should have been so long ignored.

Such a land classification would necessarily take account of the enormous amount of scientific reconnaissance and investigation done in the West, during the last thirty years especially. It would rest upon a rapidly increasing fund of practical experience and experimental study of crops and methods, and upon the paramount importance of drought periods and their recurrence in climatic cycles. In method, it would be complete, detailed, accurate, and unprejudiced, availing itself of all sources of information, but based primarily upon the relation of indicator vegetation to existing practice. The most difficult problem would be that of a large, adequately trained, and high-minded field force, but the rapid development of the Forest Service has shown how this can be accomplished.

Relation to practices.—While land classification is based primarily upon the division into agriculture, grazing, and forestry, other considerations must also be taken into account. At the outset, it is particularly important that the future as well as the immediate present be considered. Many areas which are non-agricultural at present can be made available for crop production by the development of a supply of irrigation water or by the draining of the soil to remove the excess of alkali. On the other hand, the extension of agriculture into mountain regions on a considerable scale would threaten the water-supply of existing irrigation projects. The maintenance of forests on a scientific basis is more than a matter of the present demand for lumber and fuel. It has a definite and often a decisive bearing upon the agricultural possibilities of the land in the adjacent valleys and plains. Moreover, questions of reforestation and afforestation enter in relation to agriculture and grazing, and perhaps to climate also. While the use of land primarily for agriculture excludes forestry or grazing on any considerable scale, this is not true of the latter. Under proper safeguards, forestry and grazing can be combined in practically all forest and woodland areas, as is the case on the national forests. It is not improbable that the extensive sandhill areas of the Great Plains region will some day be covered with forests of pine without seriously reducing the amount of grazing, and in some cases with an actual increase in the permanent carrying capacity.

The greater returns from agricultural land and the consequent possibility of supporting a larger population will always constitute a temptation to classify too much land as agricultural. If classification could be carried out only during drought periods, this tendency would be corrected. On the other hand, it would be emphasized during wet years, such as 1915, when many regions received 50 to 100 per cent more than their normal rainfall. As a consequence, the classification of land as agricultural must be made with a definite knowledge of the existing conditions of rainfall and temperature and their relation to the usual variations of the climatic cycle. Moreover, it must be recognized that it is much less serious to classify a potential agricultural area as grazing or forest land than to classify the latter as agricultural. The former merely involves an insignificant economic waste until the real possibilities of the land become recognized, while the latter often results in recurring tragedies due to the attempt to make a livelihood where it is impossible. Hence, it should become a cardinal principle of land classification to rate as grazing or forest land all areas in which it is impossible to produce an average crop three years out of four. This would insure an adequate and permanent development of agriculture wherever possible and would warrant the introduction of scientific and economic systems of grazing, which would change it from a game of chance into an industry.

Proposed bases of classification.—While soil and climate have been employed in connection with various desultory attempts at classification, the

A. Abandoned farm, Wood, South Dakota.
B. Field of corn and sudan grass during the drought of 1917, Glendive, Montana.

only proposals which need to be considered here are those which deal with indicator vegetation. The latter necessarily takes account of both soil and climate and furnishes the only basis for an adequate system. The first serious proposals of such a system were made by Hilgard, as already shown in the first chapter. As a student of soils, he was concerned primarily with the indicators of soils (1906: 487), and especially those which were regarded as significant of lime or alkali. He paid almost no attention to indicators of climate, and was concerned only with those which denoted agricultural land. Because of his primary interest in the distribution of animals, Merriam (1898) emphasized the importance of climate in agriculture, and ignored that of soil. His central idea was to enable the farmer "to tell in advance whether the climatic conditions on his own farm are fit or unfit for the particular crop he has in view, and what crops he can raise with reasonable certainty." Hence, he was concerned with a use survey rather than with land classification, though his "life zones and crop zones" possess certain values in connection with the latter.

Clements (1910:52) pointed out the difference between a classification survey and a use survey of occupied lands, and emphasized the necessity of employing soil and climate, native vegetation, and practical experience to constitute a complete system for classifying the lands of a region as agricultural, grazing, and forest. Several unoccupied townships of northern Minnesota were classified on this basis and several farming townships of the southern half were mapped in accordance with a use survey. The investigations of Shantz (1911) in eastern Colorado dealt chiefly with the indicator value of the different associations with reference to crop production and furnished a new basis for the classification of agricultural land with respect to probable yield. A similarly detailed and accurate study of the saline vegetation of Tooele Valley was made by Kearney and his associates (1914), in which the primary object was to provide a definite method of distinguishing agricultural from non-agricultural lands and of determining the relative values of the former.

The rapid establishment of national forests from 1902 to 1908 necessitated the use of a ready method of distinguishing between forest and agricultural land. The indicator method had not yet been definitized to a point where it was available, and studies of soil and climate were barely begun. In spite of this, forest and woodland constitute such obvious indicators that their use afforded fairly satisfactory results, particularly when water regulation was taken into account. The limits of the forests thus drawn necessarily included some agricultural land as well as great areas of grazing land. Much of the former has later been eliminated by reclassification, while the latter has been classified into various types (Jardine, 1911, 1913). Within the forests proper, the problem of classification has naturally revolved about the question of forest types. This has given rise to an extensive literature (Graves, 1899; Zon, 1906; Clements, 1909; cf. Proc. Soc. Am. For., 1913: 73) and is discussed in some detail in Chapter VII. Pearson (1913: 79; 1919) has emphasized the importance of ascertaining the agricultural possibilities of forested land in order to determine with certainty whether it should be classified as one or the other. He proposes a definite program of investigation to make the principles and methods of land classification more accurate. This is based upon actual tests of agricultural possibilities, the study of physical factors, and the correlation of crop production and plant associations, the last being regarded as the most important feature of the whole plan.

The most extensive and adequate application of the proper principles of and classification to the lands of the West has been made in connection with the stock-raising homestead act of 1916. This is based primarily upon the indicator method, and the details have been outlined by Shantz and Aldous (1917). While the primary object is to classify the areas filed upon for grazing homesteads, it has proved necessary to deal with the classification of agricultural and forest lands as well. In this connection the latter are relatively unimportant, but the recognition of lands for dry-farming is an essential part of the plan. This arises from the fortunate provision that a grazing homestead must contain areas on which it is possible to produce crops of forage. As already indicated, the only drawbacks to the method arise from an untrained personnel and the lack of sufficient time for adequate survey. The correlation of the indicator types upon the basis of structure and development would have revealed additional values, but the plan marks a great advance in land classification and it is unfortunate that its application is restricted to lands filed upon under the act.

**The indicator method of land classification.**—As the above discussion makes clear, practically all the effective proposals for classifying land into the three main types, or for subdividing these upon the basis of crops or values, rest upon the fundamental significance of indicator plants and communities. The systems proposed by Clements, Pearson, and Shantz and Aldous, though arrived at from three different angles, are practically identical so far as essentials are concerned. They recognize the importance of actual practice and experiment as well as of quantitative studies of soil and climate in definitizing the correlations of the indicator communities. The latter, however, constitute the indispensable tool of the land classifier, since its use is as ready as it is extensive and is limited only by its accuracy and sharpness. In the hands of a well-trained field force, it would permit the proper classification of all the unoccupied lands of the West within a period of five years. The essentials of such a classification are further discussed in a later section.

**Use of climax indicators.**—It is clear that the climaxes themselves furnish direct indications of great value for land classification. Thus, grassland, chaparral, and scrub are obviously indicators of grazing land, while forest and woodland are indicators of forest land. However, these comprise all the types, and a different method is necessary for the determination of agricultural land. This may be furnished by actual test, by the measurement of factors, or by the use of indicator correlations already established in other regions. As a matter of fact, some kind of farming test can be found almost anywhere in the West, in the driest deserts as well as at almost any altitude. The studies of the last decade have made the application of indicator correlations almost universal, and the measurement of soil and climatic factors has at least been begun in practically every climax. As a consequence, it becomes a relatively simple matter to use climax communities to indicate those grazing and forest lands which are also agricultural, in that they yield a larger return from crop production than from grazing or forestry (plate 59).

A. True prairie indicating agricultural land, Lincoln, Nebraska.
B. Oak chaparral indicating grazing land, Sonora, Texas.
C. Aspen, spruce, and pine indicating forest land, Minnehaha, Colorado.

In the West, the climax which serves as the best indicator of crop production is naturally grassland. As the most extensive of all the formations concerned, its various associations serve also to indicate all the types of farming from humid and semi-arid on the east to dry-farming and irrigation farming in the west. While the alpine meadow climax has many points of resemblance to the grassland, it is a clear-cut indicator of grazing land, since neither trees nor crops can thrive in it. The various scrub climaxes, sagebrush, desert scrub, and chaparral, as well as tree and scrub savannah, are primarily indicators of grazing land, unless irrigation is resorted to. Dry-farming is possible in certain areas in them, but these are usually in the transition to other formations or in the seral habitats. A notable exception occurs in the Coastal chaparral, in which the winter rainfall makes certain crops possible by evasion of the drought period of summer. The woodland climax is primarily an indicator of combined forest and grazing land. It has some agricultural possibilities, but these are rarely to be realized except under irrigation. Of the three forest climaxes, the Coast forest is a distinct indicator of crop production, and the subalpine forest is just as distinctly an indicator of non-agricultural land. The montane forest in general is like the subalpine in indicating forest-grazing land, but this depends upon the consociation and topography. The yellow pine consociation often indicates agricultural land, but the indication of the community must be checked by the nature of the topography and soil.

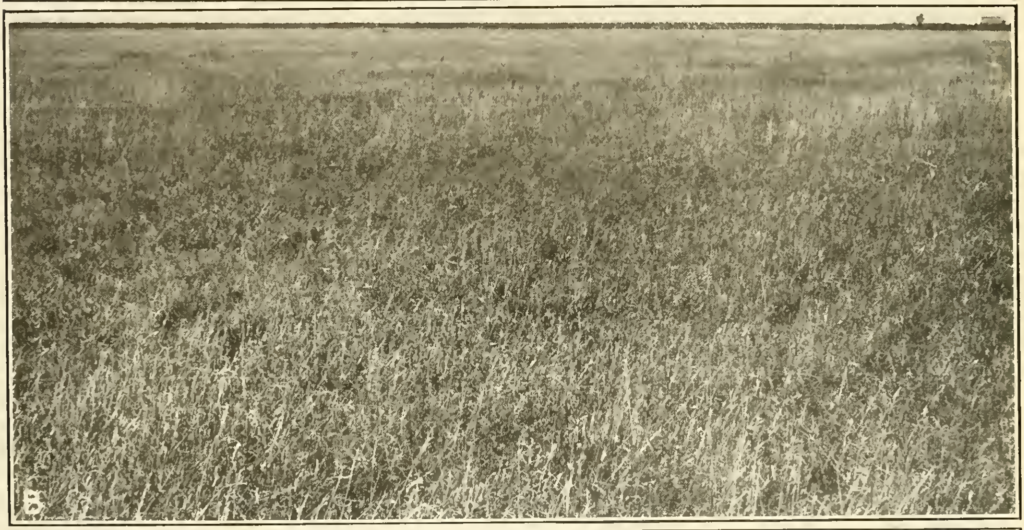
In the case of all climaxes, the relations of formation, association, consociation, and society to each other lie at the basis of the indicator correlations of the various communities. The indicator value of an association must be understood with reference to its formation, and that of the consociation with reference to its association. In general, these will be consistent with each other and hence they serve to denote smaller and smaller areas, and particular crops and methods rather than types of practice. This is especially true of the many local groupings of dominants and subdominants. The societies formed by the latter are particularly sensitive indicators of local variations in climax conditions (Shantz, 1911).

**Soil indicators.**—The significance of soil indicators is local, as well as subordinate to that of climax or climatic indicators. The soil is especially important in the actual practice of land classification, since it is more tangible than climate and is subject to much greater local variations. Consequently, in any particular region climax indicators should be employed for general climatic values, while soil indicators should be used for the special values which will determine the proper classification of a particular area. In view of the paramount importance of water-content in arid and semi-arid regions, the general correspondence between rainfall and water-content from east to west becomes especially helpful. While texture and topography will cause soils to vary much locally in their water-content, the water-content of tillable soils decreases more or less steadily to the westward or southwestward. This relation of climate and soil is readily seen in the soil regions of the West as recognized by the Bureau of Soils, namely, Great Plains, Rocky Mountain, Southwest Arid, Great Basin, Northwest Intermountain, and Pacific Coast. As would be expected, these regions also show more or less correlation with the climax formations.

The loess and glacial soils of the prairies are so completely cultivated that they hardly need consideration as to their indicators. The luxuriance of the three prairie associations and the large number of societies, especially of legumes, denote an agricultural region of the first importance. To the westward, the most extensive and important soils are gumbo or "hard land," saline soils, and sandy soils, usually of the sandhill or dune type. Where it is derived from the weathering of shales, as is frequently the case, the soil is usually both gumbo and saline. As Shantz (1911) has shown, "hard land" is primarily agricultural in the Great Plains, though its high echard is a serious disadvantage during drought periods. Soils recently derived from shales, such as the Pierre and the Graneros, however, bear a vegetation which suggests that their greatest value is for grazing. The work of Hilgard (1906) and of Kearney and his associates (1914) has shown that, in the Great Basin and similar saline regions, sagebrush is the one reliable indicator of agricultural land. While crops may be produced on land covered with *Atriplex confertifolia* or *Kochia,* it is only during years of exceptionally favorable rainfall, which are too rare for successful farming. Hence, practically all saline communities are indicators of grazing land, though such land may be converted to agricultural use when the removal of alkali is economically feasible.

The numerous sandhill and dune areas of the West bear distinctive indicators which denote the varying degrees of fixation of the sand. Typically, they are grazing areas, though they are usually interrupted or surrounded by more stable areas, such as the wet valleys of the sandhills of central Nebraska or the wire-grass lands of eastern Colorado, in which farming is possible. Even for grazing, their value is much less than it should be, and in addition there is a rapid deterioration of the cover where overgrazing is practiced. There is no question that the carrying capacity could be greatly increased and the tendency to "blow" correspondingly decreased by protection and seeding or planting. The Bad Lands, which occur throughout the West, but especially in the Rocky Mountain regions, likewise offer attractive regions for reclamation. Although the soil is a hard clay instead of blow-sand and the erosion is due to water in place of wind, sandhills and bad lands have much in common. The destruction due to erosion is often rapid and complete, as well as recurrent. They occur almost wholly in grazing communities, and the study of succession in both has reached a point where it is possible to make use of it as the chief method of reclamation, as is shown in Chapter VI. The extremely dissected topography of bad lands practically excludes agriculture, and in general the communities of rugged and rocky areas indicate their classification as grazing lands, even when climatic conditions might permit agriculture. In the case of swamp and bog communities, the direct indication is for grazing, but since they need drainage in order to be put into adequate commission, their classification should take this into account. When they are not too high or too far north, the drained areas will permit farming, but when they occur in the montane zone, or above, their chief value is for grazing (plate 60).

Shantz's results.—Shantz's studies of indicators in eastern Colorado are still the most complete and detailed account of the correlation of indicator communities and soil. His conclusions apply with slight modification to the entire short-grass association, and they also have much value for mixed prairies:



A. *Artemisia filifolia* indicating sandy soil, Canadian river, Texas.
B Grama and buffalo-grass on hard land, Goodwell, Oklahoma.
C. *Atriplex nuttallii* indicating non-agricultural saline land, Thompson, Utah.

"The chief plant associations of eastern Colorado which indicate land of agricultural value are the grama-buffalo-grass association and the wire-grass association (both of which belong to the short-grass formation) and the bunch-grass association and the sand-hills mixed association (both of which belong to the prairie-grass formation).

"The chief vegetation types of eastern Colorado which indicate nonagricultural land are the lichen formation, the *Gutierrezia-Artemisia* association of the short-grass formation, and the blow-out association of the prairie-grass formation.

"Of the associations indicating land of agricultural value in eastern Colorado, the grama-buffalo-grass association is most extensive, occupying the greater part of the hard land. The bunch-grass and the sand-hills mixed associations occur only in the sand-hill regions, while the wire-grass association occurs on land of intermediate character.

"In eastern Colorado the rainfall records show that the average monthly rainfall is greatest during the period April to August. The increased heat in July and August makes it almost certain that drought will occur in these months. September and the later fall months have normally very little rainfall, and fall-sown grain often fails to germinate unless planted on land in which water from rains earlier in the season has been conserved by summer tillage.

"Measurements show that from grama-buffalo-grass land a great amount of water runs off and does not enter the soil.

"Soil-moisture determinations in this type of land show that even during periods of more than normal rainfall available soil moisture is limited to a few inches of the surface soil.

"On this account the vegetation is composed largely of short grasses which have a great number of roots limited to the surface foot or two of the soil.

"M sture, even in the surface few inches of the soil, is often lacking except d ing a few weeks in spring and early summer. The short grasses have a comp ratively short growing season.

"Dee -rooted species are shut out by the lack of soil moisture in the deeper layers of the soil and later-season plants are excluded because available moisture is usually lacking, even in the surface layers, during late summer and autumn.

"An open cover of the short grasses indicates conditions less favorable for p production than a close cover.

'The presence of deeper-rooted plants mingled with the short-grass vegeta- on indicates better conditions for crop production than those found where ne cover is purely of the short grasses.

"The occurrence among the short grasses of plants characteristic of the associations which indicate land without agricultural value suggests a less favorable condition for crop production than where short grasses only are found.

"The presence of the wire-grass association indicates that there is a considerable amount of water in the deeper layers of the soil, owing to the lesser run-off and to the fact that the lighter soil permits deeper penetration.

"Conditions indicated by the wire-grass association are favorable for both shallow-rooted and deep-rooted plants and for a considerably longer period of growth than those indicated by the grama-buffalo-grass association.

"The bunch-grass association indicates a soil that is moist to a considerable depth. Here conditions are more favorable for deep-rooted and late-season plants than in land characterized by either the short-grass or the wire-grass vegetation.

"The sand-hills mixed association indicates conditions very similar to those of the bunch-grass association, but rather less favorable, as shown by the smaller amount of plant growth.

"The short-grass vegetation represents the final stage in a succession which may begin with the lichen formation and pass through the *Gutierrezia-Artemisia* association. Or the succession may begin with the blow-out association and pass through the sand-hills mixed and the bunch-grass associations and (by the aid of fires and grazing) through the wire-grass association to a pure short-grass vegetation.

"When short-grass land is left without cultivation after breaking it will be revegetated by either the wire-grass or the *Gutierrezia-Artemisia* association, depending upon the physical conditions.

"The vegetation which establishes itself after wire-grass is turned under is that which is naturally characteristic of a lighter soil.

"When the native sod of the bunch-grass or the sand-hills mixed associations is broken, a blow-out may result. Usually, however, the original vegetation is soon reestablished.

"When the vegetation of any of the plant associations is destroyed by breaking and the land is then abandoned the land will be reoccupied (after a weed stage) by vegetation that is characteristic both of a lighter type of soil and of an earlier stage in the natural succession. These successions are the result of changes in the physical conditions brought about largely as a result of the destruction and reestablishment of the plant cover itself.

"The taller, deeper-rooted plants are easily shut out by the shallow-rooted short grasses when the water that falls as rain is not sufficient to penetrate beyond the layer of soil occupied by the roots of the short grasses before it can be absorbed by them.

"Where water can readily penetrate below the depth ordinarily reached by the roots of the short grasses the conditions are favorable to the growth of deeper-rooted and taller species, which shut out the short grasses by overshading them. This increased penetration of water may be due either to greater rainfall or to lighter soil texture.

"When well supplied with water short-grass land is the most productive under cultivation of any in eastern Colorado. During drought, however, crops suffer on this land sooner than on any other type.

"During exceptionally dry years bunch-grass land produces the best crops of any in eastern Colorado, but during wet years its production is surpassed by that of all others except the land characterized by the sand-hills mixed association. The soil under both of these types of vegetation is likely to blow badly.

"Wire-grass land represents a safe intermediate condition where in years of ample rainfall crop production compares not unfavorably with that on short-grass land and where, even during dry years, a fair crop can often be produced.

"One of the chief reasons for the superiority of light land over heavy land in eastern Colorado is that crop growth is rapid on the latter and that the total available supply of soil water lies near the plant roots, the crops, therefore, being in somewhat the same condition as potted plants. These conditions favor a rapid exhaustion of soil moisture and, consequently, bring about sudden drought. On the lighter land water is distributed to greater depths, the plant growth is slower, and plants, by gradually increasing their root area, can resist much longer periods of drought.

"Investigations of soil conditions, as well as actual observations of crops in the field and studies of the native plant cover, show that as we pass from the prairie westward to the more arid portion of the Great Plains, the lighter soils present relatively more favorable moisture conditions and, therefore, conditions more favorable to plant growth than do the heavier types of land."

## A SYSTEM OF LAND CLASSIFICATION.

Bases.—As has been repeatedly emphasized, a system of land classification which is both practically and scientifically adequate must ignore no source of evidence. While indicator vegetation must be regarded as the chief tool, the latter is valueless unless it is correlated with practical experience and experiment on the one hand and with factor measurements on the other. Some indicator values can be disclosed by the use of a single one of these correlations, but all of them are necessary for complete certainty and accuracy. They not only serve to check each other, but also to reveal additional and final values. Furthermore, it must be recognized that all the climatic and hence many of the soil factors vary considerably and sometimes critically from year to year, and that this means a corresponding difference in crop production, and often in tillage methods. As a consequence, the annual variations in factors, indicators, and production must always be taken into account and related, as far as possible, to an average or norm. The normal rainfall or mean temperature is insufficient for this purpose, especially since it fails to disclose the number and occurrence of the critical dry years. For this purpose the use of climatic cycles is necessary, and in consequence they must be assigned an important part in the classification of lands in arid and semi-arid regions. The existence and effect of such cycles are established beyond a doubt, and the chief task at present is to learn how to make the fullest possible use of them. This naturally depends upon the certainty and accuracy with which the dry and wet phases of the cycle can be predicted (Clements, 1917: 304, 1918: 295). The nature and utilization of climatic cycles are discussed in the following section.

Classification and use.—The close relationship between classification and use surveys and the importance of developing the one into the other can hardly be emphasized too strongly. The vital connection between the two in the proper development of the possibilities of the land may be seen from the following (Clements, 1910: 52):

"The first step in determining the final possibilities of plant production is to ascertain just what the conditions of soil and climate are from the standpoint of the plant. This must be determined separately for the two great groups of lands, those still unoccupied and those now in use. For the former, a knowledge of soil and climate, and of the plant's relation to them, is necessary to decide what primary crop, grain, forage, or forest, is best. For the farms of the State, the best use is a matter of knowing the soil and climatic differences of regions and fields, and of taking advantage of this in crop production. For the unoccupied lands of Minnesota, we need a classification survey to determine the best use of different areas; to prevent the waste of human effort and happiness involved in trying to secure from the land what it can not give, and yet to insure that the land will reach as quickly as possible its maximum permanent return. For occupied lands, the study and mapping of soil and climatic conditions would constitute a use survey of the greatest value in adjusting plant production to the conditions which control it.

"A use survey is the logical outcome of the classification of land. Its greatest importance is with agricultural lands, since grassland and forest permit less specialization in crop production. The period of the one-crop farm seems nearly closed; that of the special-crop farm is barely begun in this country. As a method of conservation, diversified farming is a permanent step in advance. It is the foundation upon which a distinctively successful country life is possible. But intensive cultivation is the open secret of scientific farming, and it demands the closest possible harmony between the plant machine, the raw materials which it uses, and the conditions under which it works. This makes possible the successful specialization of a region in the crop best adapted to the soil or climate more or less peculiar to it. The task of a use survey in this connection is to determine the special advantage of soil or climate, and to suggest the particular kind of plant machine and the method of production adapted to it. The same careful method of survey, which makes possible the best use of the different agricultural lands of the State, is likewise of great value on the individual farm, whenever differences of soil or exposure exist. The general nature of the soil and climate of a farm must determine its special crop, and in a degree the secondary crops as well. But the complete success of the farm will rest upon a thorough knowledge of its differences of soil and climate, as well as upon a knowledge of the best varieties to grow or the best way to improve them."

Methods.—While it is undesirable to discuss in detail the actual methods of classification and use surveys, it must be pointed out that they depend in the first instance upon accuracy and thoroughness. This is exemplified in the work of the Botanical Survey of Minnesota ("Plant Succession," 436), in which the natural and cultural vegetation was mapped for every "forty" of the townships concerned, and quadrats, instruments, and photographs were employed throughout. Similar though less detailed methods have been used in the grazing reconnaissance of all the national forests (Jardine, 1911) and in the classification of grazing homesteads under the Ferris Act (Shantz and Aldous, 1917). The essential features of these are touched upon in the discussion of the methods of range survey in Chapter VI.

A logical and desirable outcome of a classification survey is a valuation of the various parcels of land, with respect to both leasing and purchase. It has been a natural assumption that the nation could well afford to dispose of the public domain at merely nominal prices, and such a policy was warranted in the Middle West. In the arid regions, however, values vary so greatly that it constitutes a serious mistake. This is readily seen when it is recognized that the best grazing lands will support more than 100 cattle to the section, while the poorest will support scarcely one. This is particularly true in the case of leasing, where proper valuation based upon actual carrying capacity will determine whether lands are to constitute a public asset or to be the usufruct of politicians. While the nation or State can afford to be generous to bona fide settlers, it can treat them all alike in fact only by fitting prices to the production value of the land and by making the operations of the speculator difficult if not impossible. Moreover, it should insure the success of each settler by means of use or management surveys which will give him a detailed and adequate knowledge of his particular farm and of the crops and methods to be used upon it. Since such surveys are of the greatest importance in connection with the combined grazing and dry farming which it seems must become typical of the West, their further discussion is deferred to the next chapter.

## CLIMATIC CYCLES.

**Nature.**—The general nature of climatic cycles as well as their universal occurrence and fundamental importance is summed up in the following statement (Plant Succession, 329):

"It is here assumed that all climatic changes recur in cycles of the most various intensity and duration. In fact, this seems to be established for historic times by Huntington and for geologic times by the studies of glacial periods which have made possible the table compiled by Schuchert. The cyclic nature of climatic changes has been strongly insisted upon by Huntington: 'The considerations which have just been set forth have led to a third hypothesis, that of pulsatory climatic changes. According to this, the earth's climate is not stable, nor does it change uniformly in one direction. It appears to fluctuate back and forth not only in the little waves that we see from year to year and decade to decade, but also in much larger ones, which take hundreds of years or even thousands. These in turn seem to merge into and be imposed upon the greater waves which form glacial stages, glacial epochs, and glacial periods.'

"Climatic changes, then, are assumed to be always related in cycles. No change stands out as a separate event; it is correlated with a similar event which has preceded it, and one that has followed or will follow it, from which it is separated by a dissimilar interval. Climate may thus be likened to a flowing stream which rises and falls in response to certain causes. It is not a series of detached events, but an organic whole in which each part bears some relation to the other parts. Considering climate as a continuous process, it follows that we must recognize changes or variations of climate only as phases or points of a particular climatic cycle, which lose their meaning and value unless they are considered in connection with the cycle itself. It is in this sense that changes and variations are spoken of in the following pages, where the cycle is regarded as the climatic unit."

Ignoring the familiar cycle of the year, there is more or less conclusive evidence of cycles of 2.5, 11, 22, 35, 50, 100, 400, and 1,000 years, approximately. In addition, there are the great geological cycles of unknown duration, which are discussed at some length in "Plant Succession" (337).

**The 11-year cycle.**—The best-known and most significant of climatic cycles for the present day is the 11-year cycle and its multiples. So far as its relation to tree growth, and hence to vegetation, is concerned, our knowledge of this cycle is due chiefly to Douglass (1909, 1914, 1919), though Huntington (1914) and Kapteyn (1914) have had a share in establishing the certainty of this relation. The effect of cycles upon succession, and consequently upon indicator communities and crop production, has been pointed out by Clements (1916: 342; 1917: 304; 1918: 295). The relation of the 11-year cycle to changes in native vegetation and to variations in plant production has received constant study since 1914. It has proved so universal and fundamental as to warrant its being made the basic feature of production systems in the arid West (fig. 13).

The 11-year cycle is known also as the sun-spot climatic cycle, owing to the striking correspondence with the sun-spot period. The correlation of the dry and wet phases of climate and of the variations of tree growth with the sun-spot cycle is often so exact as to warrant the assumption of a causal relation between the two. Such a relation has not yet been established, however, and investigation at present is chiefly confined to the nature and extent of the coincidence between them. The outstanding fact is that our knowledge has reached a point where it seems increasingly possible to employ the sun-spot cycle as a method of anticipating the coincident or related changes in climate and vegetation.

Evidences.—The evidence of the cycle of sun-spots has all the certainty of astronomical data. The number of sun-spots has been recorded for every year since 1750, and the dates of the maxima and minima are definitely known as well as their intensity. Cycles in the annual growth of trees have been found by Douglass in a number of diverse regions, in Europe as well as in America. It is obvious that trees growing in the most favorable conditions will not exhibit cycles, since there is no limiting factor to produce variations in the width of the rings. Moreover, the same tree sometimes fails to show cycles throughout its life, or does not show them with equal clearness. This is not difficult to understand when the complex relations of factors, of competition and reaction, parasites, fire, lumbering, and other disturbances are taken into account. By far the greater part of the evidence of existing cycles has been furnished by Douglass (1919). In his study of Arizona trees, he has found that, during the last 160 years, 10 of the 14 sun-spot maxima and minima have been followed about four years later by pronounced maxima and minima in tree-growth, and that the same trees show a strongly marked double-crested 11-year cycle during some 250 years of their early growth.

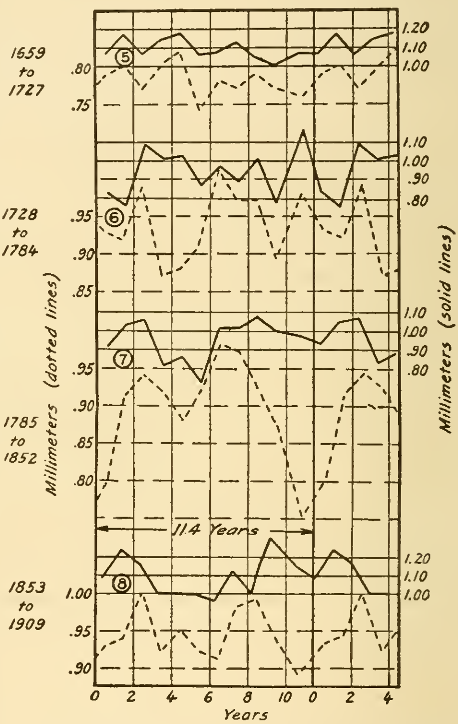


FIG. 13.—The 11-year cycle during the last 250 years, as shown by the yellow pine and *Sequoia*. After Douglass.

They likewise exhibited a relation to the temperature curve for southern California, and this curve in turn resembled in form and phase the inverted curve of the sun-spot cycle.

In the investigation of trees growing in wet climates, Douglass has also found conclusive evidence of cycles. The trees of Eberswalde near Berlin showed the 11-year sun-spot cycle since 1830 with accuracy. In the group as a whole, the agreement is marked, the maximum growth falling within 0.6 year of the sun-spot maximum. In six groups of trees from England, northern Germany, and the lower Scandinavian peninsula the growth since 1820 shows pronounced agreement with the sun-spot cycle, every maximum and minimum since that date appearing in the trees with an average variation of 20 per cent.

Kapteyn (1914: 70) has studied the growth of oak trees in Holland and Germany and reaches the conclusion that during fairly long intervals of time they exhibit not only a regularity, but also an actual and fairly constant periodicity in growth. From 1659 to 1784, or for a stretch of 125 years, a period of about 12.4 years is clearly indicated. While this period disappears in certain groups, it persists in others, so that its recurrence for two centuries is demonstrated, with only one minimum missing. Huntington (1914: 135) has devoted his attention chiefly to the major sun-spot cycles indicated in the rings of trees and has secured some exceedingly suggestive evidence of cycles of 100 years and more. Douglass (1919: 111) has examined the trees studied by Huntington, in order to obtain evidence from them as to the shorter cycles, especially that of 11 years, and to carry the existence of such cycles back for a period of 3,200 years:

"The variations in the annual rings of individual trees over considerable areas exhibit such uniformity that the same rings can be identified in nearly every tree and the dates of their formation established with practical certainty.

"In dry climates the ring thicknesses are proportional to the rainfall with an accuracy of 70 per cent in recent years, and this accuracy presumably extends over centuries; an empirical formula can be made to express still more closely this relationship between tree growth and rainfall; the tree records therefore give us reliable indications of climatic cycles and of past climatic conditions.

"Certain areas of wet-climate trees in northern Europe give an admirable record of the sun-spot numbers and some American wet-climate trees give a similar record but with their maxima 1 to 3 years in advance of the solar maxima. It is possible to identify living trees giving this remarkable record and to ascertain the exact conditions under which they grow.

"Practically all the groups of trees investigated show the sun-spot cycle or its multiples; the solar cycle becomes more certain and accurate as the area of homogeneous region increases or the time of a tree record extends farther back; this suggests the possibility of determining the climatic and vegetational reaction to the solar cycle in different parts of the world.

"A most suggestive correlation exists in the dates of maxima and minima found in tree growth, rainfall, temperature, and solar phenomena. The prevalence of the solar cycle or its multiples, the greater accuracy as area or time are extended, and this correlation in dates point toward a physical connection between solar activity and terrestrial weather.

"The tree curves indicate a complex combination of short periods including a prominent cycle of about 2 years."

In addition, Douglass has made a preliminary study of sections of fossil trees, which show a similar cycle for some of the more recent geological periods

Considerable preliminary work has been done in tracing the effects of the 11-year cycle in plants other than trees and in plant communities. It has been discovered that the dominant shrubs of sagebrush, chaparral, and desert scrub often show this cycle in the growth-rings and that, in some cases at least, the age of the shrub suggests that establishment takes place largely and sometimes only during the wet phase of the cycle. Studies of the extension of forest and woodland into grassland or other arid communities has shown that the entrance of the young trees occurred during the wet phase. Henry (1895: 49) has shown that the height-growth of trees varies greatly from wet to dry periods, and it seems certain that a similar relation exists for seed-production. In the special study of grazing during the past five years a large amount of material has been collected which shows the critical effect of the wet and dry phases upon growth and reproduction. As is well known, field crops also exhibit a striking response to years of abundant rainfall as well as to those of drought. While methods of tillage influence crop production profoundly, the latter clearly reflects the wet and dry phases of the climatic cycle at those stations in the arid regions where the record is sufficiently long. The effect of the 11-year cycle upon animals is most strikingly seen in the case of range cattle, which live under semi-natural conditions, but it is also readily discovered in all animal populations which are directly dependent upon the natural vegetation of arid regions for their food-supply.

Periods of drought.—While both wet and dry phases have a marked effect upon the annual production of natural and cultural crops, the periods of drought stand out with especial vividness. While this is particularly true of arid regions, it holds likewise for semi-arid ones during the period of early settlement, when economic resources are at a minimum. The consequences are sufficiently disastrous even in such cases, as the history of settlement in the Middle West proves. In the case of a native agricultural population held more or less rigidly within its own boundaries by the pressure of other tribes, they led to famine with attendant wars and revolts. As a result, there is much historical evidence of the periods of drought and famine in the Southwest, and this makes it possible to discover how closely these correspond with the phases of the 11-year cycle. As would be expected, there is frequent mention of droughts in the chronicles of Mexico and the Southwest from 1600 to 1850. A much smaller number of these were accompanied by famine, and appear to represent drought periods. Of more than a dozen such periods, all but two occurred at the sun-spot maximum, or within a year or two of it, and furnish a record of agreement comparable to that of the last half-century (fig. 14).

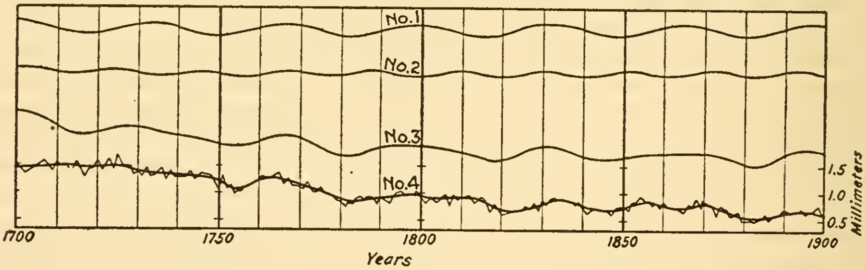



Fig. 14.—Double and triple sun-spot cycle in yellow pine from 1700 to 1900 A. D. After Douglass.

The agricultural development of the West began with the passage of the homestead act in 1862, and the consequent inrush of settlers. Since that time the drought periods are known with certainty, and their correlation can be made without question. In this connection it is essential to distinguish between drought periods and drought years. The former consist of two to three or even four years and are felt generally throughout the West. In the Great Basin, as well as in the Southwest, a single year of drought for a particular region or locality may occur at almost any time, since the normal rainfall is so low that almost any deficit is equivalent to a drought of some degree. However, while a dought year involves inconvenience and loss, it rarely causes disaster and the general abandonment of recently settled regions. Hence, in the discussion of climatic cycles and drought, the latter is understood to be a drought period several years in length and extending over all or nearly all of the West.

Recurrence of drought periods.—The assumption that the 11-year cycle could be traced in the present and future as well as in the past (Clements 1916: 330; 1917: 304; 1918: 295) led to a study of the coincidence of drought periods and sun-spot maxima from 1860 to 1915. The sun-spot maxima for this interval of 55 years occurred in 1860, 1870-72, 1883, 1893, and 1907. The maxima of 1870–72 and 1893 were known to coincide with times of general and critical drought in the West, and it was found that similar conditions had prevailed in 1859–60. In the case of the maximum for 1907, the deficit fell in 1908–09 for most regions and was less marked, while for the maximum of 1883 the record showed an excess of rainfall quite as often as a deficit. The close correspondence of sun-spot maxima and drought in 1870–72 and 1893–95, and the decrease or absence of agreement in 1883 and 1907, suggested that the maximum effects occurred in multiples of the 11-year period (Plant Succession, 336). The period involved in the two major droughts was 21 to 23 years, and this appeared to warrant the suggestion that a similar critical drought would recur in connection with the sun-spot maximum of 1917. The year 1915 proved to be exceptionally rainy, perhaps due to a lag of the effects expected at the sun-spot minimum in 1913, with the result that the ensuing drought period of 1916–18 appears to have been the most general and severe ever known in the West.

Drought periods not only bear a relation to the maximum of the sun-spot cycle, but also to periods of increased rainfall, with which they show a definite alternation. This alternation of dry and wet phases constitutes the climatic cycle which corresponds with the 11-year sun-spot cycle. As Douglass has found in the case of tree growth (1919), the drought period is much more marked, at least in its effects, and its rings are consequently used as basing points. The wet phase is related to the dry one in a cause-and-effect sequence, in accordance with which a deficit is followed within a year or two by an excess, or an excess by a deficit. While a preliminary investigation of this point indicates that it is the general rule, it is often obscured by local variations in the spatial distribution of rainfall. The wet phase likewise shows a correlation with the minimum of the sun-spot cycle, but it is usually less definite and striking than that of the dry phase. However, in a large number of localities representing different regions of the West, the rainfall at the sun-spot minimum is usually above the normal. It seems more or less probable that periods of excessive rainfall for 1 to 3 years occur on the second or third multiple of the 11-year cycle, and that they precede or follow a drought period as a rule.

The evidence that drought has occurred at frequent intervals during the past 300 years is conclusive. It is equally certain that drought periods have regularly alternated with wet ones, though these are naturally less frequently noted in the human record. Moreover, it must be recognized that the alternation of dry and wet phases will be seen most clearly in the grassland climax of the prairies and plains, where the rainfall ranges between 15 and 30 inches.

East of this, only the most intense droughts will be noted as such, and the minimum crop production is apt to occur in years of excessive rainfall. In the Southwest, where the rainfall is always low, the economic effects of drought may occur in almost any year when the distribution or timeliness of the rain is at fault. The existence of a climatic cycle coinciding with the sun-spot cycle, and consisting of a dry and a wet phase which falls respectively at the sun-spot maximum and minimum, appears to be established beyond a doubt by the work of Douglass, Huntington, and Kapteyn, as well as by the study of vegetation. Much more work is required to explain certain apparent exceptions and contradictions in widely divergent climates, but none of these seem to invalidate the general principle.

Significance of the sun-spot cycle.—The establishment of a cycle of relatively dry and wet periods with a usual length of 10 to 12 years is of paramount importance to the practice of agriculture, forestry, and grazing in the West. Since rainfall is the limiting factor over most of the region, a knowledge of what can be expected in the way of variation in rainfall and changes of climate will be of the greatest help. The most serious handicap to the proper agricultural development of the West lies in the almost universal misconception of climate and the nature of its changes. Much of this arises from the mistake of the earlier geographers in regarding the Missouri Valley as a part of the "Great American Desert." The rapid development of this region was sufficient proof that it had never been desert, but the persistence of the old idea could be reconciled with the facts only by the assumption that the rainfall had greatly increased as a result of cultivation. This impression that the rainfall was increasing was further strengthened by the luxuriant development of the tall-grasses as a consequence of the disappearance of the buffalo. This mistaken idea still persists over much of the West, where a marked and permanent increase in rainfall is confidently expected to follow settlement. This error has further serious consequences in that it leads to each drought period being regarded as the last, and consequently prevents the adoption of systems of settlement and management which will reckon with drought periods as certain to recur. Even where experience made it clear that droughts still occurred, the prejudice in favor of a changing climate, together with the general optimism and inertia of the pioneer, prevented the recognition of the patent fact. Moreover, during the disastrous drought of 1916–18, stockmen were often found who admitted that drought had occurred before and probably would again, but stated that this fact would be readily forgotten when the rains came.

The meteorologists have proved repeatedly, from the weather records, that there has been no progressive change in the climate of the West during the settlement of the latter. This has been conclusively shown by Swezey and Loveland (1896: 137) for Nebraska, the central position of which makes it typically representative of the climate and vegetation of the grassland climax:

"If we examine the precipitation for the series of years from 1849 to 1895 inclusive given in Appendix II, we shall find that, although the rainfall of the past few years has been less than that of the earlier years of the series, so far as we can judge from the rather meager records of those earlier years, yet there is afforded no evidence of any considerable progressive change in the climate of the State, either toward wetter or drier conditions. There have been excessively wet and excessively dry years, the annual rainfall having ranged from 13.30 inches to 47.53 inches; there have been groups of wet years and groups of dry years succeeding one another in a rather irregular manner. Thus the 47 years may be grouped into five periods as follows: The first 10 years were mostly wet years, only one of them, viz, 1852, having a rainfall less than normal; the next 9 years, 1859 to 1867 inclusive, constituted a period of scant rainfall, including particularly the exceedingly dry years of 1863 and 1864 and the scarcely less dry years of 1859 and 1860; the 9 years from 1868 to 1876 inclusive included years of plenteous and years of scant rainfall succeeding each other in a quite irregular manner; then followed 10 years, 1877 to 1886 inclusive, of rainfall generally above the normal; and finally the last 5 years have been, with the exception of 1891 and 1892, years of deficient rainfall, with the year 1894 the driest of the whole 47.

"But if we divide the entire series of 47 years into two periods of 24 and 23 years respectively, the average rainfall of the first period will exceed that of the last by only about an inch. The first year of the series, 1849, was one of excessive rainfall, not only as shown by the record made at Fort Kearney, the only station in Nebraska at which records were kept, but also as confirmed by records in the adjacent Territories. This difference of a little more than an inch between the mean rainfall of the first 24 years and that of the last 23 years of the 47 would almost disappear if this year of 1849 were omitted from the series; the mean precipitation for the 23 years from 1850 to 1872 is 23.55 inches, while that of the 23 years since is 23.46 inches.

"The conclusion, therefore, seems to be a safe one that the average rainfall of Nebraska, although subject to great fluctuations from year to year, yet in the long run remains substantially unchanged, so far as we can discover from the records of nearly half a century."

**Prediction of drought periods.**—The sun-spot cycle furnishes a ready method of predicting the occurrence of dry and wet periods. The sun-spot numbers are recorded with the greatest accuracy and detail, and the number for each month and year is readily obtainable. These numbers, taken in conjunction with the length of the recent cycles, make it possible to forecast the date on which the next maximum and minimum will fall, as well as something of their intensity. During the past century the average of 11.4 years for the cycle has been strikingly evident, practically all the cycles being from 10 to 12 years long. The accuracy of the correlation between the sun-spot cycle and the climatic cycle as recorded in the growth of trees is 85 per cent, according to Douglass's results (1919). This compares favorably with the accuracy of the daily forecasts of the Weather Bureau, and still more favorably with that of the weekly forecasts. However, there is one essential difference, in that the latter are actual forecasts, while the prediction of dry and wet phases has been attempted as yet only for the dry and wet phases of the current cycle (Clements, 1917, 1918). The close correspondence between the sun-spot cycle and the curve of tree growth strongly suggests a similar degree of accuracy in actual prediction, but repeated trial can alone determine this, as well as disclose the reasons for failure.

While it is thought and expected that the use of the sun-spot cycle will permit the prediction of drought periods for the West in general, as well as the occurrence of intervening but more diffuse wet periods, the prediction for a particular locality is subject to more uncertainty. In this respect, cycle predictions resemble the daily and weekly weather forecasts. The failure of a relatively small number of these to be verified is due chiefly to changes of intensity or of pathway in the cyclonic area. In addition, there are more obscure local differences in evidence in almost every storm by which the amount of rain may vary greatly at two neighboring points. As Kullmer and Huntington have pointed out (1914), the shifting of the storm-belt seems to afford a causal explanation of climatic differences at the sun-spot maximum and minimum, as well as of variations from one locality or region to another. Thus, while drought periods are general for the West at the double sun-spot cycle, as in 1870–72, 1893–95, and 1916–18, not all regions showed 3 years of drought, and during any one year a few regions recorded a rainfall approaching normal. Naturally, the drought was most intense and prolonged in the areas of normally scanty rainfall, and it decreased more or less regularly in the direction of regions of medium precipitation. During such periods, it is even possible that high mountain regions may receive an excessive amount of rain. This seems to result from the principle of compensation, in accordance with which deficit and excess are regularly linked together in time or in space. For the present, this is regarded as the most plausible explanation of variations and inconsistencies in the behavior of the climatic cycle, but it is probable that further knowledge will show that these are connected with the differentiation of contiguous climates. Hence, while the method of cycles can not assume to forecast the number of inches of rain for any locality during a certain year, it can predict the recurrence of drought periods and of succeeding wetter years for the West in general. The drought period will concern three regions out of four during most of its duration, and it will affect practically every locality at some time during its phase.

Utilization of cycles.—A study of settlement in the West since 1865 reveals the fact that it corresponds more or less closely to the climatic cycle. The exceptions are afforded by the rapid inrush after the homestead act, the Kinkaid act, etc., or after the opening of new regions. The general movement of settlers has advanced and receded in almost perfect agreement with the wet phases and drought periods of the climatic cycle (cf. Brückner, Huntington 1914: 89). A few years of unusual rainfall have afforded unscrupulous real-estate dealers and immigration commissioners an opportunity to dispose of even the most worthless land. The ensuing drought period then led to crop failure and the wholesale abandonment of the region, to be followed by another influx of settlers during the next wet phase. In more than one region of the West this process has been repeated three or four times, and its disastrous operation will continue until the States and the National Government recognize the necessity of proper land classification and of adequate regulation of settlement.

The knowledge that drought periods will recur is indispensable to any accurate and successful classification of land and to the economic management of dry-farm, grazing range, or forest. These results, which are of the first importance for the West, do not depend necessarily upon the accuracy of predictions based upon the sun-spot cycle. They are clearly indicated by the actual experience of the last 60 years, which not only confirms the recurrence of drought periods, but also suggests the interval. However, it is clear that it would be of the greatest value to be able to forecast the date, duration, and intensity of each drought period with some accuracy, as well as to anticipate the increasing rainfall of the wet phase. This would not only permit the taking of the necessary precautions against the disasters due to drought, but it would also make possible the development of an optimum system of management. This would enable the farmer to fit his crops and methods of tillage to the variations in rainfall and would permit the stockman to increase or decrease his herds or to vary his supplies of forage with the wet and dry phases of the cycle. In short, the cycle management of all the basic practices of the West would provide the maximum insurance against loss or disaster and would afford the greatest possible annual returns. It is further discussed in connection with agricultural and forest indicators, but its value is especially emphasized under grazing, since the latter and the related dry-farming are most dependent upon climatic conditions.

## FARMING INDICATORS.

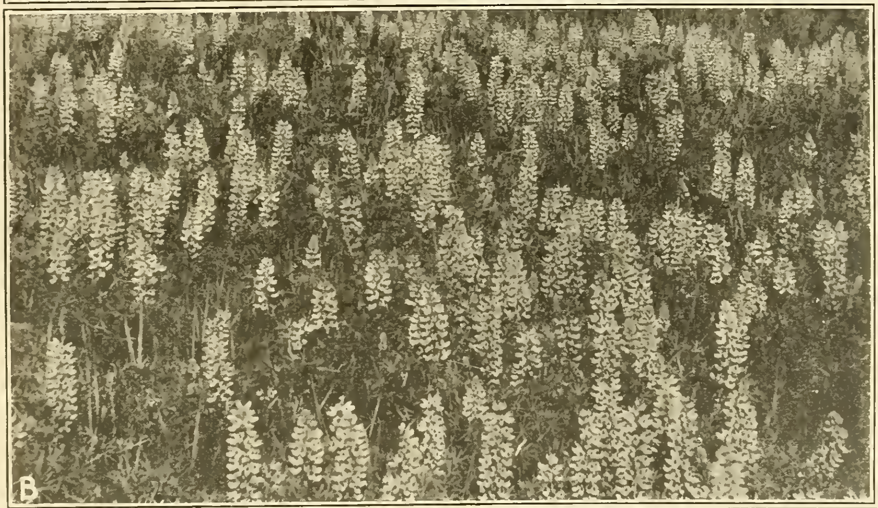
Types of farming.—With reference to indicators, types of farming may be based upon conditions or upon crops. Since the former determines the methods and return (and often the crop as well), it seems to afford the better basis. Accordingly, the usual division into humid and arid farming is employed here, with a further division of the latter into dry-farming and irrigation farming. It is clear that no sharp line exists between the types of agriculture in humid and arid regions. Between the two lies a broad belt of semi-arid country in which there is a gradual adjustment of methods and crops to increasingly arid conditions. The distinction is further obscured by the variation in rainfall from the wet to the dry phase of the climatic cycle. During the wet period humid farming is possible through most or all of the semi-arid belt and the need of drainage becomes felt over a much wider area. During the dry period arid conditions are pushed across much of the semi-arid country and semi-arid conditions develop in the outlying humid areas. However, practices change much less than conditions; the general area of the humid, semi-arid, and arid regions remains essentially the same, with their mutual relations identical.

The humid region is regarded as possessing a lower limit of 25 inches of rainfall, while the semi-arid has a range of 15 to 25 inches, and the arid from 2 to 15 inches. As would be expected from variations in the annual amount and distribution of the rainfall, semi-arid areas with 20 to 25 inches of rain are characterized by the humid type of farming, and those with 15 to 20 inches by dry-farming. The latter type usually reaches its lower limit at 12 inches, or at 10 inches where the rainfall is largely of the winter type. Below 10 inches, farming is profitable only by means of irrigation. Naturally, the latter is also extensively practiced in regions with 10 to 20 inches of rain, and to some degree under even higher rainfall. As Briggs and Belz (1911) have shown, the efficiency of rainfall depends upon the amount of evaporation, and hence decreases more or less regularly from the northeast to the southwest in the western United States.

**Relation of types of farming to indicators.**—Because of the control made possible by irrigation, methods of tillage, and variation in crop or variety, indicator values are less definite in the case of types of farming than in grazing or forestry. Their significance is further reduced by the possibility of irrigation and by such economic considerations as markets and transportation. Moreover, the method of conserving water-content by means of summer fallow enables dry-farming to be practiced in regions where otherwise irrigation would be the only successful method. On the other hand, where annual cropping is the rule, dry-farming methods pass imperceptibly into those of ordinary farming with good tillage in semi-arid and subhumid regions. In spite of this, there is a general correspondence between climax associations and types of farming. The tall-grass prairies are typical of regions in which humid farming prevails. The mixed prairies and short-grass plains denote country in which dry-farming of the annual crop type is more or less successful. The bunch-grass prairies and desert plains characterize regions of scantier rainfall, for the most part of the winter type, and hence are chiefly to be correlated with dry-farming by means of summer fallow. Subclimax sagebrush has practically the same indicator value as the associated grasses. When these are tall-grasses the indications are of dry-farming with annual cropping, and when they are bunch-grasses they indicate summer fallow methods. Climax sagebrush is also an indicator of the latter when the rainfall does not fall below 10 inches. Over the major portion of the central Great Basin, sagebrush indicates a climate in which crop production is impossible without irrigation. This is likewise true of practically the whole desert scrub climax except for small areas at higher altitudes or near its eastern limit, where it approaches or mixes with the grassland. The indications of chaparral are variable. While they are largely non-agricultural, chaparral resembles scrub generally in its indication of dry-farming or irrigation practices, as is true also of woodland where soil and topography are favorable. Montane forest usually receives enough rainfall to make humid farming possible, though both dry-farming and irrigation are practiced in the lower yellow-pine belt. Most of the montane zone lies above the limit of profitable agriculture, and the occasional fields of hardy cereals are restricted to the warmer valleys and lower slopes (plates 61 and 62).

**Edaphic indicators of types of farming.**—These are more local and hence less important than the climatic indicators just discussed. They are primarily related to soil and water-content, and consequently are of the greatest service in regions with marked soil characteristics, such as sandhills, bad lands, saline basins, or in river or lake valleys with relatively high water-content. The same farm may have lowland and upland areas, or may show considerable variations in soil with corresponding indications as to types of farming. This is particularly true of the wet valleys in the sandhills of Nebraska and of the many river valleys with a generally westward direction in Nebraska and Kansas. The wet valleys are marked by meadow communities, and many of them are susceptible of farming by the usual methods. The river valleys are occupied by similar communities of which *Andropogon*, *Agropyrum*, *Calamovilfa*, *Elymus*, or *Spartina* are the dominants, or they may be characterized by the presence of scrub. In either case the indications are for subhumid farming, especially during the wet period of the climatic cycle.

Shantz (1911: 85) has pointed out the agricultural significance of the difference between lighter and heavier soils in passing to the westward. The lighter soils conserve water to a much larger degree, and hence require less intensive methods of cultivation than do the heavier ones. In some regions,



A. Tall valley sagebrush indicating a deep soil for irrigation, Garland, Colorado.
B. A legume, *Lupinus plattensis*, indicating a rich moist soil, Monroe Canyon, Pine Ridge, Nebraska.
C. Relict *Stipa* and *Balsamorhiza* in sagebrush, indicating a bunch-grass climate for dry-farming, Hagerman, Idaho.

and especially during certain years, this may amount to ordinary cropping on one and dry-farming on the other. Kearney and others (1914: 416) have shown that sagebrush (*Artemisia tridentata*) is an indicator of both dry-farming and irrigation farming in Utah when it makes a good stand and vigorous growth. Communities of *Kochia vestita* or *Atriplex confertifolia* generally indicate the necessity of irrigation to rid the soil of the excess of salts. The mixed community of *Sarcobatus* and *Atriplex* has essentially the same significance, though it indicates the desirability of drainage as well. Hilgard (1906: 536) regards *Sporobolus airoides, Spirostachys, Salicornia, Suaeda, Sarcobatus, Frankenia, Cressa,* and *Distichlis* as indicators of the necessity of underdrainage as a prerequisite to successful irrigation farming.

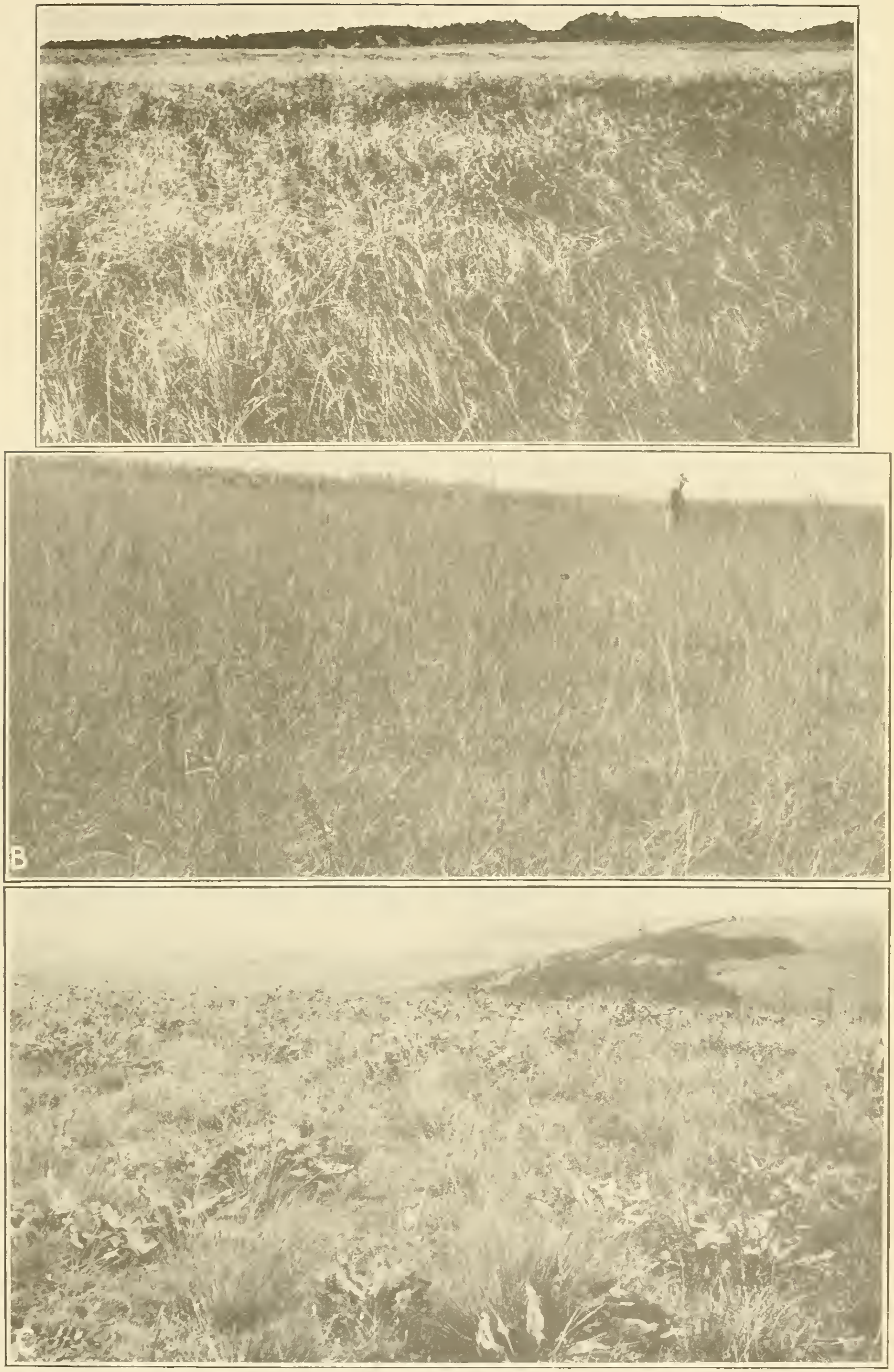
## CROP INDICATORS.

**Nature and kinds.**—While the factor-complex must always be kept in mind in the correlation of indicator communities and crops, water is the paramount factor practically throughout the West. The importance of temperature as a direct factor increases with latitude and especially with altitude, but it is regularly less than that of water. The water relations are primarily a question of rainfall and evaporation, more or less modified locally by topography and soil. As a consequence, it is desirable to distinguish climatic and edaphic indicators of crops. The former denote the general climatic regions for particular kinds or varieties of crops, the latter the soil or topographic differences which break up the climatic uniformity of a particular region and render other kinds or varieties preferable. Climatic indicators are primarily climax communities of varying rank, while edaphic indicators are mostly seral or developmental communities. Crop indicators may serve to denote (1) the type of crop, as grain or forage; (2) the species in a general sense, as wheat, oats, or rye; (3) the kind, as winter and spring, or hard and soft wheat; and (4) the variety, such as Marquis, Fife, or Preston. They also permit correlations with differences in methods of practice, such as dry-farming with and without summer tillage, etc.

Little use has been made of plant communities as indicators of the type or kind of crop. This has been a natural outcome of the enormous amount of crop experimentation carried on by the Department of Agriculture and the various State experiment stations during the past two decades. Nearly 100 stations and substations have been concerned in this work, and it is a logical conclusion that they have made the use of crop indicators unnecessary. It seems, however, that the very extent and thoroughness of the experiments with various crops must increase the accuracy and readiness with which indicators can be used. In spite of the numerous stations, there are many large regions still unrepresented. In addition, the climatic gradations and edaphic variations are so numerous that the native vegetation alone affords an adequate method of taking them all into account. As a consequence, the opportunity for working out a general system of crop indicators seems exceptionally good. This would be based upon the correlations between native communities found about each station and the types and kinds of crops demonstrated to be the most desirable for that region. While such correlations can be obtained from the results of practically all stations, the investigations carried on at those of the Office of Dry-Land Agriculture are of the greatest value. This is due to a number of causes, chief among which are the use of the same crops and methods, the wide extent of the studies, the large number of stations in a single great climax, the grassland, the more or less gradual decrease in rainfall to the westward, and the consequent readiness and accuracy with which comparative results can be obtained. The correlations discussed below have been based chiefly upon the results obtained by this Office, supplemented for the more or less representative central portion by the studies made at the experiment stations of Nebraska and Kansas. In all of them, it should be borne in mind that the correlation and the corresponding indicator community have the greatest accuracy in the region of the particular station or stations, and that this value decreases more or less regularly in the direction of stations with different correlations. However, the practical usefulness of the indicator increases with the remoteness from a particular station, providing always that the plant community remains the same, since the latter indicates that the conditions are essentially unchanged.

Climatic indicators of the types of crops.—The correlations considered here are based upon the fact that crops, like natural dominants, have an area of maximum production about which they shade out in all directions. This diminution is generally less marked in the case of crops, owing to the modifying influence of culture as well as of economic factors. Corn affords the most striking example of a crop grown throughout an extensive region, but with a well-defined area of maximum production. As a crop it extends over the major portion of several climaxes, but its optimum area, the "corn belt," is more or less clearly limited. The limits of this belt fall within the main area of the subclimax and true prairies, which are to be regarded as the indicators of maximum corn production. In this connection, it is at least suggestive that four of the dominants of these communities belong to the genus *Andropogon*, which systematically and ecologically resembles corn more closely than do any of the other grassland dominants. As might be expected, wheat exhibits an even more extensive correlation with the grassland. The region of maximum production is from Saskatchewan to Oklahoma, with secondary maxima in Indiana and Illinois, and in Washington and Oregon. The maximum falls almost wholly within the region occupied by the true and mixed prairies. Here also it is perhaps significant that *Agropyrum*, with its close relationship to *Triticum*, is an important dominant in these communities and is the major dominant in the great wheat region of the Palouse. Oats show a somewhat similar relation to grassland, as does barley, but rye manifests no clear correlation. On the whole, however, there is good evidence for regarding grassland made up of tall-grasses as the primary indicator for the optimum production of cereals (cf. Smith, Baker and Hainsworth, 1916; Waller, 1918).

Hay and forage crops generally are more or less evenly distributed through the deciduous forest and grassland climaxes, but there is a clear regional differentiation in the case of alfalfa and sorghums. The chief center for alfalfa is in central Nebraska, Kansas, and Oklahoma, with local centers in the main irrigated sections of the West, practically all of which occur in grassland or sagebrush. The sorghums, whether grown exclusively for fodder or for grain as well, have their center of maximum production in western Kansas, Oklahoma, Texas, and eastern New Mexico. It corresponds closely with the eastern half of the short-grass association, in which *Bulbilis* and *Bouteloua*



A. Mixed prairie (*Stipa comata*) indicating dry-farming, Scenic, South Dakota.

B. Tall-grass (*Andropogon furcatus*) indicating humid farming, Madison, Nebraska.

C. Bunch-grass prairie (*Agropyrum-Festuca*) indicating dry-farming with winter rainfall, The Dalles, Oregon.

*gracilis* are the dominants. Cotton reaches its maximum in a well-marked region which corresponds with the southern forest, except in central Texas and Oklahoma. Under irrigation it promises to develop a secondary center for long-staple varieties in the desert scrub climax of the Southwest. Of the other types of crops, vegetables are more or less evenly distributed over the eastern half of the country, with marked regional differentiation for certain kinds and many local foci. Fruits and nuts show a similar uniform distribution in the East, but they are almost wholly confined to the forested region and its extension into the southeastern prairies. This correlation is wholly to be expected on the basis of similarity in life-form. The most important fruit districts of the West lie in the sagebrush and chaparral climaxes and depend upon irrigation, as the difference in the life-forms indicates.

Climatic indicators of kinds of crops.—The correlation of the kind of crop with indicator communities has already been touched upon. It is often less definite than with types of crops, but there are a number of correspondences of much interest and value. These are perhaps best shown by the three kinds of wheat, namely, winter, spring, and durum. Winter wheat has its center in the true prairies of Kansas and Nebraska, in which *Andropogon* plays an important part. Spring wheat and durum reach their best development in the mixed prairies or in the northern portion of the true prairies, where *Stipa spartea* and *Agropyrum glaucum* are especially important. They are more or less equal in value in the eastern portion of the true prairies, but durum shows an increasing advantage to the west, and is superior to spring wheat practically throughout the mixed prairies. In the bunch-grass prairies of the Northwest the advantage is reversed, and spring wheat outyields durum. The general use of summer tillage in connection with the winter precipitation favors winter wheat because of its earlier period of growth.

The region of the maximum production of barley comprises the northern half of the true prairies, while that of oats includes the major portion of both the subclimax and true prairies. Flax finds its maximum in the transition from the true to the mixed prairies, but it is extending more and more into the latter in western North Dakota. While there is a marked correlation between the sorghums as a group and the short-grass plains and their transition to the tall-grasses, the various kinds of sorghums show no clear correlations with indicator communities. This is perhaps due in some measure to the relatively short period of trial, but probably results chiefly from the fact that qualities of earliness and dwarfness are more significant than the group differences (Ball, 1911; Ball and Rothgeb, 1918: 88). In contrast with the grain-sorghums, the sorgos show an increasing correlation with the tall-grasses, and in western Nebraska and the Dakotas are to be related to the mixed prairies.

Climatic indicators of varieties.—The significant correlation of indicator plants with varieties is naturally more difficult and less satisfactory than in the case of types and kinds of crops. This is largely because the differences between varieties can be modified or reversed by seasonal variations or cultural methods, as well as by the complex of local conditions. It is also due in part to the fact that the minor differences in indicator communities arising from varying grouping of the dominants and from changes in the subdominants have received little careful study. In spite of these facts, there are certain obvious correlations where varieties differ in some clear-cut quality, such as earliness or dwarfness. Both of these are related to the evasion of drought or frost, and can be correlated in some measure with indicators of changing altitude or latitude, or with decreasing rainfall. It should be borne in mind also that each variety primarily represents a certain degree of adjustment to particular conditions, and that some of them are certain to be replaced by other varieties as a result of longer trial or changing demands.

Wheat exhibits the best indicator correlations with varieties because of its greater differentiation and wider area. Among the durum wheats, Arnautka is indicated as the best variety by the true prairies with greater rainfall and shorter season. Of the spring wheats, Preston is generally indicated by true prairie, Marquis by mixed, and Bart by the bunch-grass prairie. Winter wheats are less clearly indicated owing to their greater drought evasion, but the Turkey and Kharkof are the principal varieties in the true prairies, and various strains of Crimean in the short-grass plains and the sagebrush. The soft winter wheats correspond with the subclimax prairies more or less nearly, while the hard varieties correspond with the true prairies and short-grass plains, which are relatively drier and colder. The varieties of oats show a fair degree of correspondence with the grassland associations. Kherson generally gives the best yields in the true prairie, Burt in the short-grass association, 60-day in the mixed prairie, and 60-day or Kherson in the bunch-grass prairie. In Kansas, Blackhull kafir is the best variety in the subclimax and true prairies, Pink kafir in the broad transition to the short-grass, and Dwarf Blackhull in the short-grass proper, where it enters into competition with Dwarf milo and feterita. Orange sorgo is correlated with the subclimax and true prairies, and Red Amber with the transition and the short-grass plains.

**Life zones and crop zones.**—Merriam's classic paper upon the life zones and crop zones of the United States recognized seven divisions, the Arctic-Alpine, Hudsonian, Canadian, Transition, Upper Austral, Lower Austral, and Tropical (1898 : 18; 1890 : 18). The most important of these were subdivided into faunal areas, of which the Arid Transition, Pacific Coast Transition, Upper Sonoran, and Lower Sonoran are the ones found chiefly in the West. Lists of crops and their varieties were given for each of the areas and the zone ranges of crops were indicated by tables. These represented the most important correlations and were undoubtedly of value as a record of the results of experience and experiment up to 1898, though naturally many of the varieties have since been superseded. Many of these correlations were necessarily the same as for indicator communities in the same regions. Since the basis of Merriam's work was floristic and faunistic rather than ecological, the correlations were for the most part more general and less accurate. As has been indicated earlier, this was a necessary outcome of regarding temperature and fauna as the primary bases for such correlations rather than water and vegetation. One interesting consequence was the much greater use made of perennial crops, particularly the fruits, since these are naturally more subject to unfavorable temperatures than the annual ones. The need for a finer division of the faunal areas is well illustrated by the Upper Sonoran, which includes the grassland, sagebrush, chaparral, and woodland climaxes. The difficulty of correlating crops with such an extensive and varied area is mentioned by Cary in his discussion of this zone in Colorado (1911: 30):

"The distribution of Upper Sonoran crops is at present local; and so dependent are many of the crops upon natural protection, adequate water supply, and suitable soils, entirely aside from temperature, that they can not be grown over the whole of a region so varied as the Upper Sonoran of Colorado."

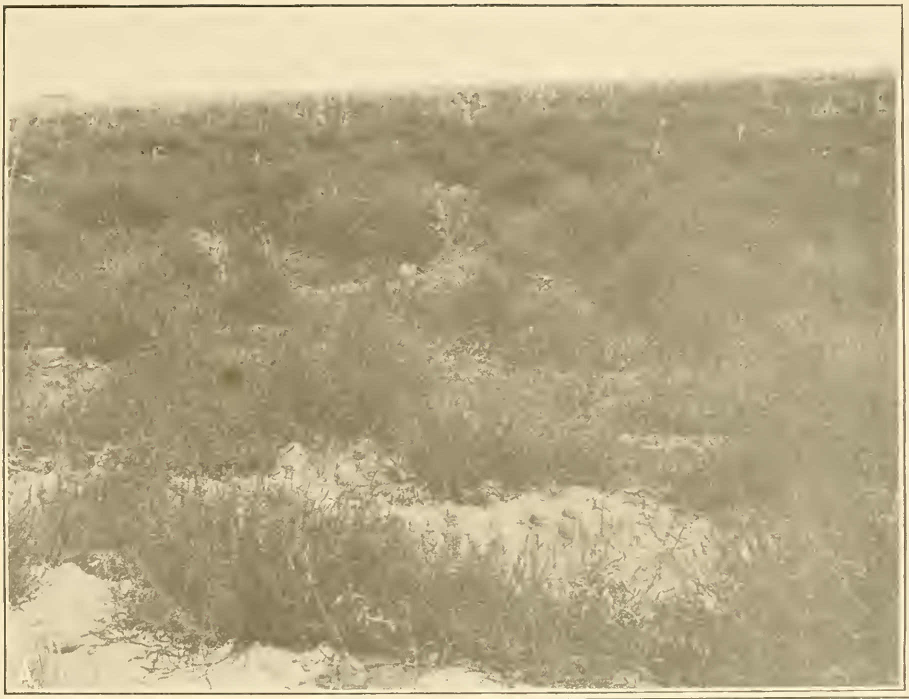
Whatever may be the shortcomings of the life-zone concept, they are more or less inevitable in a pioneer work covering such a vast field. With Hilgard and Chamberlin, Merriam must be given great credit for having recognized the value of natural indicators so early, and for pointing out many of the major correlations. His method has formed the basis for the surveys of Western States made by the Bureau of Biological Survey during the past 15 years. The first of these was that of Texas, made by Bailey (1905), in which little attention was given to crop correlations. In a similar study of New Mexico (1913; cf. Wooton, 1912: 10) he has discussed the crops of the Lower and Upper Sonoran zones in some detail, especially as to the fruits (23, 38). Cockerell (1897) was the first to give a general discussion of the life zones of New Mexico, as well as the first to make use of insects as zone indicators. Cary (1911: 29, 40) has dealt with the agricultural importance of the Upper Sonoran and Transition zones in Colorado. He has also characterized briefly the agriculture of the same zones in Wyoming (1917: 30, 39) and has pointed out the economic importance of the boreal zones (52). Robbins (1917) has described briefly the native plant communities in Colorado with especial reference to altitude and has discussed the general agricultural relations of the grassland, sagebrush, chaparral, woodland, and montane forest.

**Edaphic indicators of crops and methods.**—Variation in crop possibilities within a climate, due to edaphic or soil conditions, may be regional or local. Regional and local variations are both caused chiefly by variations in water-content arising from differences in soil, solutes, or topography, and the only important difference between them is that the one determines the general agricultural practice of a region, and the other that of a neighborhood or of a single farm. The responses of plants to local differences in water-content are readily seen, and the corresponding edaphic indicators are of much value in suggesting desirable or necessary local variations in crops or methods. Since practically all such local differences have to do with water-content or temperature, their indicators have the same general significance as in the case of the more general climatic differences. Such local variations in conditions may often be quite as great as those between adjacent climatic regions and edaphic indicators may consequently denote differences in crops and methods quite as great as climatic ones do. Since the number of such indicators is legion, and every small difference of soil or topography has a corresponding indicator, the adjustment of crop and method to any particular variation in conditions is largely a matter of practicability. Locally as well as generally, the chief differences in soil are represented by saline soil, hard land or gumbo, and sand. All of these have their proper indicators, as is well known, and it is only necessary to recognize that their local occurrence has much the same significance assigned to them by Hilgard, Shantz, Kearney and others for more extensive regions. This is particularly well illustrated in the case of dune-sands, which are found in sandhill areas through the prairies and plains. It is best seen in the great sandhill region of Nebraska, where soil and topography have combined to present an unusual set of conditions. The loose sandy soil, lack of humus, and the maze of steep hills with intervening wet and dry valleys constitute a complex of factors marked by distinctive indicators and demanding a specialized type of agriculture (Cowan, 1916: 5). Such a region not only requires different methods and crops from those of the general climatic area, but the varying areas of wet valleys, dry valleys, and hillsides demand corresponding differences in treatment.

Indicators of native or ruderal forage crops.—The detailed study of secondary seres in fallow fields and similar disturbed areas has revealed a number of species of native herbs and weeds which give more or less promise as forage crops. During the three years of drought from 1916 to 1918, particular attention has been directed to those which made a vigorous growth or a good stand in fields in which forage crops were a failure, or in areas adjacent to such crops. A considerable number of weeds of much promise has been observed over an extensive region, and in addition a number of native species have been suggested as of possible forage value by their behavior during drought. By far the most valuable are *Melilotus alba*, *Helianthus annuus*, and *Salsola kali*. The former is rapidly taking its place as a forage crop in some regions and there seems little doubt that it will ultimately be grown as a dry crop over a wide area. *Helianthus annuus* has but recently been tested under field conditions (Arnett, 1917), but the results agree with the evidence in nature to the effect that it is of much value in dry regions, and especially during drought years. *Salsola* has been grown scarcely at all as a crop, but it has been cut as a weed crop and utilized as hay of a fair quality at least. While its tonnage is less than that of sunflower, it will often grow luxuriantly in places where the latter will not. This is true also of *Helianthus petiolaris*, which may be regarded as a dwarf native form of the common sunflower. The other coarse weeds whose behavior indicates that they will be found to have some forage value are *Chenopodium album*, *Amarantus retroflexus*, *A. hybridus*, *Erigeron canadensis*, *Iva xanthifolia*, *I. axillaris*, and *Brassica nigra*. The native species of weedy habit and of such vigorous growth as to suggest the probability of forage value are *Amarantus palmeri*, *A. powellii*, *A. torreyi*, *A. wrightii*, *A. fimbriatus*, *Acnida tamariscina*, *Psoralea lanceolata*, *Franseria tenuifolia*, *F. discolor*, *Atriplex rosea*, *A. expansa*, *Corispermum hyssopifolium*, and *Cycloloma platyphyllum*. The last four are adapted to saline soils, and the last two to sandhill areas as well (plate 63).

## AGRICULTURAL PRACTICE AND CLIMATIC CYCLES.

Cycles of production.—The close dependence of annual crops upon seasonal and annual rainfall makes it clear that they will reflect the various climatic cycles in some degree. The correlation is less exact than with the natural perennial crops of grasses, shrubs, and trees, owing to the effect of cultural methods and the choice as to times of planting. It is also more or less obscured by rotation and by changes of variety and method such as are constantly taking place in ordinary practice. Moreover, it may be completely destroyed for a particular year by hot winds of a few days' duration if they occur at a critical period, such as that of the tasseling of corn. In addition, the correlation of cycles, rainfall, and crop production is most in evidence in a region such as the prairies and plains, where the rainfall is moderate, ranging



A. Ruderal crop of Russian thistle, *Salsola*, in a field of feterita, Tulia, Texas.
B. Ruderal crop of horseweed, *Erigeron canadensis*, in a fallow field, Goodwell, Oklahoma.

for the most part from 15 to 30 inches. Above 30 inches the compensating effect of accumulated water-content tends to minimize the consequences of drought, while below 15 inches the margin of safety is so small that it is easily destroyed by local or incidental causes.

The evidence of definite cycles in crop production is difficult to obtain for the further reason that accurate records in a particular place for a long period are extremely rare. Few of these extend through a sun-spot cycle of 10 to 12 years, and practically none through the more significant double cycle of 21 to 23 years. However, the drought periods of 1870–72, 1893–95, and 1916–18 were so intense that a corresponding production cycle is shown in the crop averages for the regions concerned. The sun-spot maximum of 1907 marked a minor drought period which in most regions reached its culmination two or three years later. This discrepancy seems to be explained, in part at least, by the interference of a shorter cycle, probably the pleion or quarter cycle of 2.5 years, and by the action of the excess-deficit balance. Arctowski (1912: 745) has shown the relation of the corn crop by States and regions to the interaction of these two cycles. He has found not only that areas of excess and deficit in production bear a definite relation to each other, but also that this relation is preserved as they shift about from year to year. Douglass (1919: 106) has found that the 2.5-year cycle is regularly present in the growth of trees. Hence, it seems probable that the major cycle of crop production is the double sun-spot cycle of 21 to 23 years, and that this is made up of smaller cycles resulting from the interaction of the sun-spot cycle of 11 years and the quarter cycle of 2.5 years. Intensive research only can determine how distinct and universal these may be. At present, it must be admitted that they are often much disturbed by the compensating action which follows an excess or deficit of rainfall. This is termed the excess-deficit balance, and is itself a short-period cycle, based apparently upon the fundamental physical correlation of action and reaction. Since it is usually 2 to 3 years in length, it is not improbable that it may be the 2.5-year cycle heightened by spatial variations in rainfall (fig. 15).

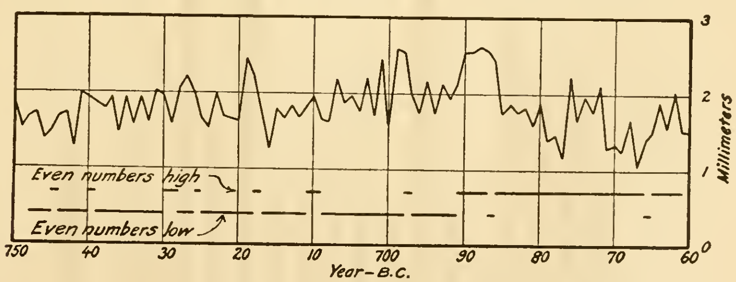



FIG. 15.—2-year cycle in a *Sequoia*. After Douglass.

An analysis of the production of grain-sorghums at Amarillo from 1907 to 1918 has been made to illustrate the possible relation to the various cycles. This has been drawn from the results of Ball and Rothgeb (1918), but is limited to the production in bushels of grain, as representing the more complete response of the plant to growing conditions. The seasonal rainfall has been reckoned for the five months beginning with April and ending with August.

*Rainfall and the production of grain-sorghum.*

| Year. | Annual rainfall. | Seasonal rainfall. | Milo. | Dwarf milo. | White durra. | Durra kafir. | Black-hull. | Dawn kafir. | Red kafir. | Brown kao-liang. |
|---|---|---|---|---|---|---|---|---|---|---|
| 1907 | 18.09 | 11.90 | ...... | ...... | ...... | ...... | ...... | ...... | ...... | ...... |
| 1908 | 19.05 | 15.33 | 35 | 41 | 33 | 33 | 34 | 29 | 33 | 31 |
| 1909 | 19.59 | 10.80 | 6 | 11 | 12 | 4 | 6 | 14 | 5 | 11 |
| 1910 | 11.15 | 10.00 | 18 | 19 | 10 | 12 | 3 | 9 | 5 | 10 |
| 1911 | 22.73 | 15.66 | 32 | 38 | 29 | 30 | 19 | 40 | 19 | 22 |
| 1912 | 14.33 | 8.76 | 19 | 23 | 17 | 7 | 4 | 10 | 4 | 12 |
| 1913 | 18.97 | 7.90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1914 | 19.18 | 10.17 | 11 | 27 | 22 | 15 | 10 | 15 | 15 | 17 |
| 1915 | 27.65 | 17.78 | 61 | 68 | 37 | 28 | 60 | 53 | 51 | 35 |
| 1916 | 16.43 | 9.54 | 7 | 7 | 5 | 4 | 0 | 4 | ? | 4 |
| 1917[1] | 17.06 | 12.88 | 13 | 22 | 11 | 5 | 5 | 5 | 2 | 8 |
| 1918 | 18.11 | 8.73 | 7 | 10 | 0 | 3 | 0 | 1 | 0 | 2 |

[1] Unpublished data from the Office of Cereal Investigations, Bureau of Plant Industry, U. S. Department of Agriculture.

Ball and Rothgeb (1918: 22) have given a very instructive account of the distribution and timeliness of the rainfall of the various years in relation to yield. Their discussion makes clear the number of apparently chance factors which enter into the production of a crop. In spite of this, however, both the 11-year and the 2 to 3 year cycle can be recognized in the production as well as in the rainfall. As seems to be the rule, these show more clearly in the

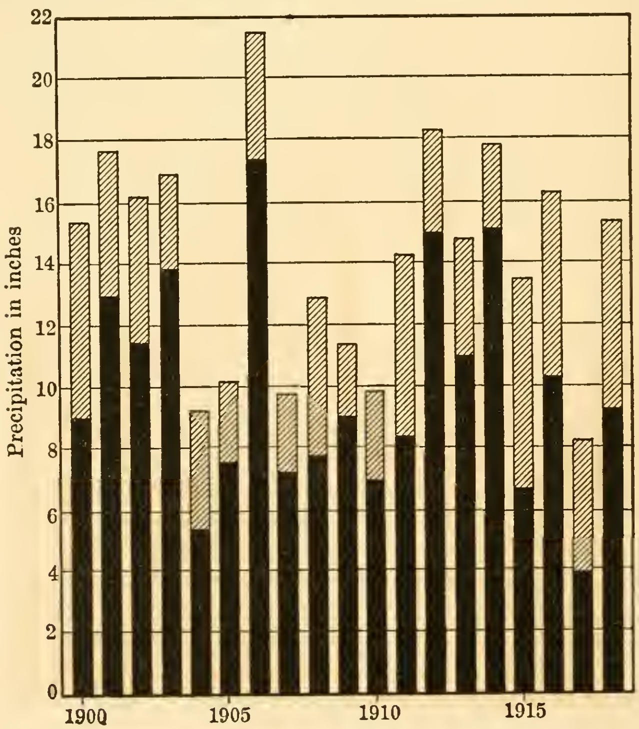



Fig. 16.—Graph of total and seasonal rainfall at Williston, North Dakota.

summer than in the winter rainfall, and hence more clearly than in the annual rainfall. There is a tendency to maximum rainfall about the sun-spot minimum of 1913, and to minimum rainfall about the sun-spot maximum of 1918. However, it is much less decisive at Amarillo than at other places in the Great Plains, indicating the action of a spatial balance in the rainfall of a particular year. The evidence of the excess-deficit cycle of 2 to 3 years is much clearer. From 1908 to 1911 and 1911 to 1914, the cycle was 3 years, while from 1915 to 1916 and 1917 to 1918, it was 2 years. This is reflected in the production, the maximum yields occurring in 1908, 1911, 1915, and 1917. The yield does not correspond with either the annual or seasonal rainfall alone, though it follows the latter more closely. This is due to the fact that while the grains are like the grasses in being chiefly dependent upon the summer rainfall, they also show the effects of a water-content surplus or deficit arising from the year before. There can be little question that the water-content of the soil shows cycles corresponding closely to those of rainfall, and that scientific agriculture must come to take these into account in connection with forecasting the kind of crop and the yield for any particular year. Thus, while the investigation of rainfall and crop cycles presents many complexities, it appears that these are all worked out on the basic pattern of the 22-year, 11-year, and 2 to 3 year cycles. If this proves to be the case as the result of intensive studies throughout the West, it is probable that annual crop pro-

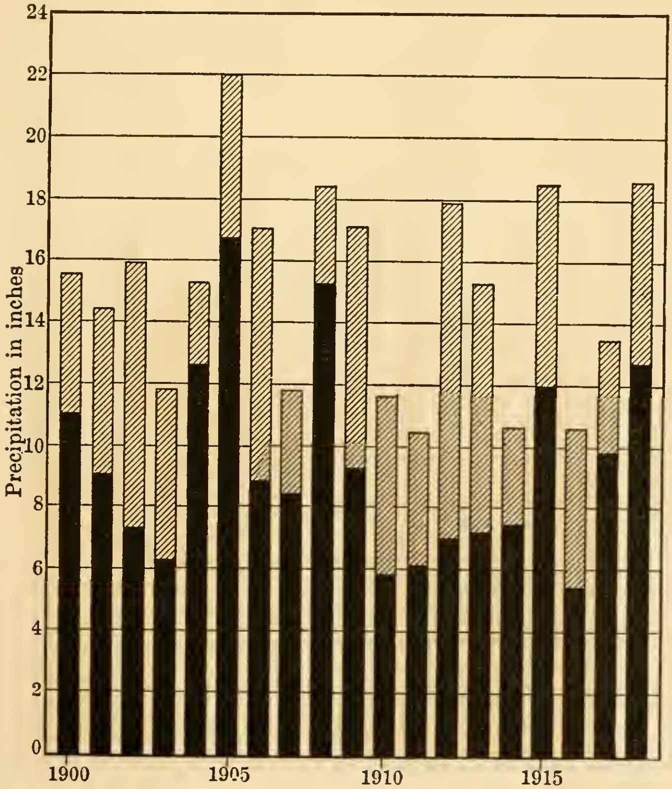



Fig. 17.—Graph of total and seasonal rainfall at Cheyenne, Wyoming.

duction may ultimately be forecasted with something of the accuracy of daily weather forecasts at present.

**The excess-deficit balance.**—The fact has already been emphasized that an excess of rainfall in one year is almost certain to be balanced by a deficit in the next year, while a great excess is often followed by two or rarely three years of deficit. As a rule, an excess is an amount above the normal rainfall and a deficit is an amount below it. Moreover, an excess in one region is often counterbalanced by a deficit in another, or an increase or decrease in one region is not met by a corresponding change in an adjacent one. When the balance operates from one year to another, it produces a cycle of 2 to 3 years. This cycle exhibits marked variations in rainfall, so much so that it may obscure the normal effect of the 11-year cycle at its maximum or minimum, though apparently not that of the 22-year cycle. In order to illustrate the operation of the excess-deficit cycle, use has been made of columnar graphs of the rainfall at widely separated points in the grassland climax. The points selected are Williston (North Dakota), Cheyenne (Wyoming), Akron (Colorado), and Amarillo (Texas). In the case of the first three places, the graphs have been adapted from those prepared respectively by Babcock (1915: 5,) Jones (1916: 4), and McMurdo (1916: 4). The graph of Williston rainfall

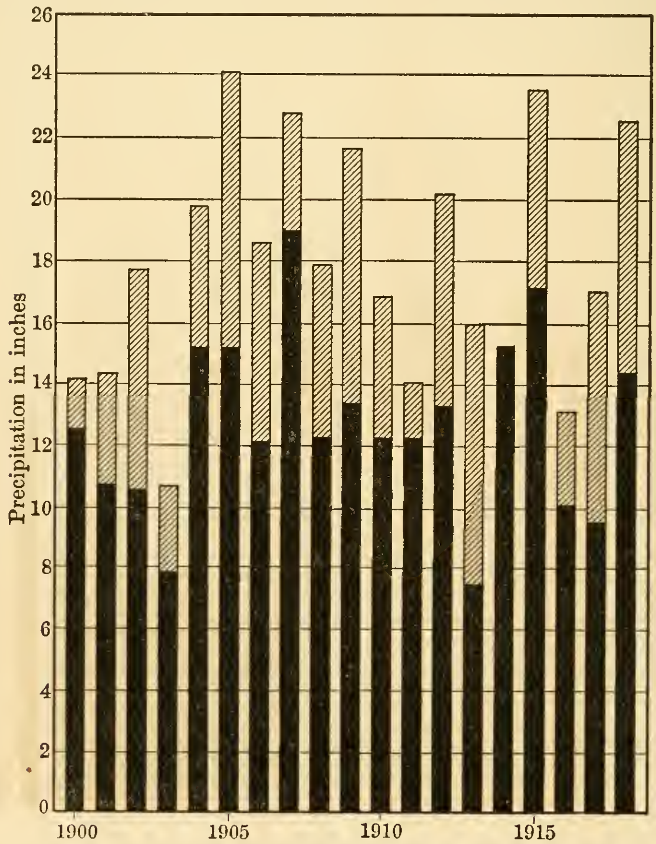



FIG. 18.—Graph of total and seasonal rainfall at Akron, Colorado.

(fig. 16) shows five 2-year and two 3-year cycles since 1900, while the record since 1885 shows an almost complete series of 2-year cycles. The Cheyenne graph shows a preponderance of 3-year cycles, and with the exception of a single year (1908), there is a perfect succession of 2-year and 3-year cycles. At Akron the first two cycles are 2-year and the last three are 3-year. At Amarillo the cycles are much less distinct, but the 3-year cycle is fairly well marked, especially in the seasonal rainfall. A comparison of the respective graphs will disclose the regional rainfall balance during a particular year. The year 1905 was excessively wet at Amarillo, Akron, and Cheyenne, but was very dry at Williston, 1906 being the wet year. Likewise, a slightly less wet year (1915) was excessively wet at Amarillo and Akron, only a little above the normal at Cheyenne, and slightly below normal at Williston, the excess falling the next year again. The year 1911 was the driest of the record at

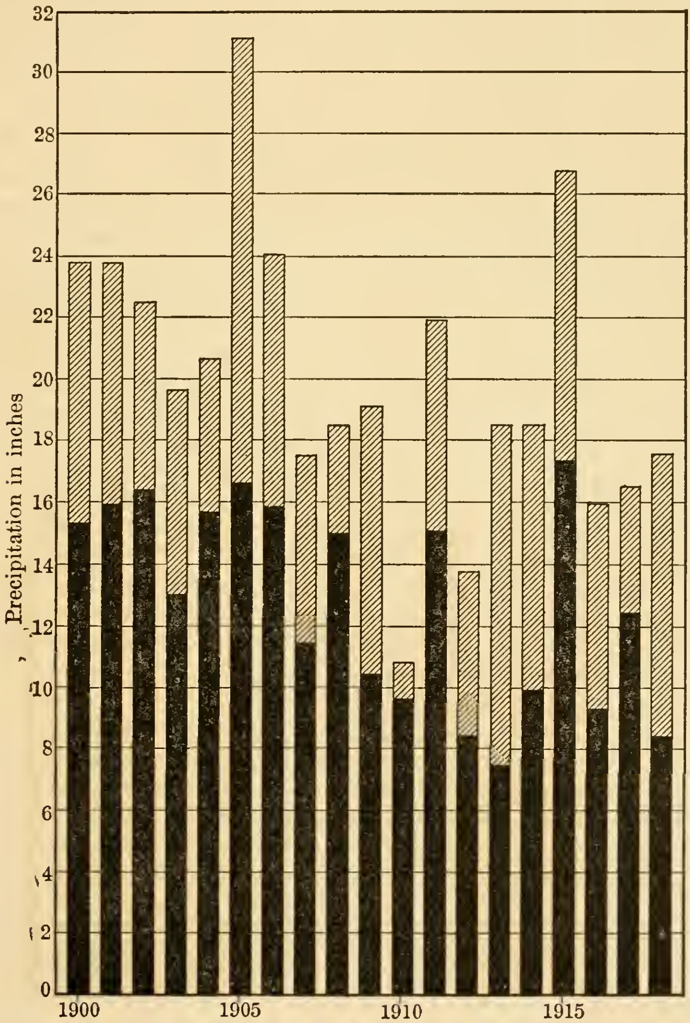



FIG. 19.—Graph of total and seasonal rainfall at Amarillo, Texas.

Akron and Cheyenne, while it was nearly normal at Williston and above normal at Amarillo, 1910 being the driest year at both these places. The year 1914 was dry at Akron and Cheyenne, nearly normal at Amarillo, and above normal at Williston. The regional variations in seasonal rainfall, both absolute and relative, are even more marked. In 1915, the year of greatest seasonal rainfall at Amarillo and Akron, they received 18 inches from April to August inclusive, Cheyenne 10 inches, and Williston 6 inches. The seasonal rainfall was respectively 66, 55, and 50 per cent of the annual for the year. The year of greatest relative seasonal rainfall was that of 1910 at Amarillo, when 90 per cent of the annual rainfall came during the growing season. The corresponding values for Akron, Cheyenne, and Williston were 73, 50, and 70 per cent respectively (figs. 16–19).

Anticipation of cycles.—Crop production makes much greater demands as to the forecasting of rainfall than either grazing or forestry. These deal primarily with perennials, and in the case of trees in particular the dependence upon the summer rainfall is much less marked. As a consequence, a knowledge of the probable occurrence of the wet and dry phases of the 22-year and 11-year cycles or of the approximate total rainfall for any year is of much value. With annual crops the case is very different. While there is a general relation between annual and seasonal rainfall, the latter may vary between 50 and 90 per cent of the annual, as at Amarillo. Moreover, the distribution and timeliness of the seasonal rainfall are even more critical (Ball and Rothgeb, 1918: 24, 6). It must be frankly admitted that at present there are almost no clues to either distribution or timeliness, but this is due largely to the fact that their correlations have received almost no intensive study. It seems not improbable that the same basic processes of action and reaction and of compensating balance apply during the year and season as during cycles, and that they must be considered with reference to spatial variations as well. It is probable that the most important clue to the annual and seasonal rainfall of a particular year lies in the excess-deficit cycle of 2 to 3 years, which Arctowski has noted in crops and Douglass in trees. The assumption that a cycle of similar character may apply to the months receives striking confirmation from the studies of Douglas (1919) on the relation of weather to business. The general correlations of climate with production and prices and the existence of economic cycles have been dealt with by Moore (1914, 1917). All of these represent independent investigations and can hardly fail to strengthen the view that both long-period and short-period cycles occur in crop production (figs. 20 and 21).

In the endeavor to definitize climatic and production cycles and to discover a working basis for their prediction, investigations are under way to determine the climates and subclimates of the West on a plant basis. It is hoped to ascertain the response to the 22-year, 11-year, and 2 to 3 year cycles in terms of tree growth, grass yield, and crop production for different regions, suggested by the type or amount of rainfall. It is expected that the general correlations between rainfall and production will serve to mark the climates proper, but that the latter will show a series of subdivisions leading to restricted localities as the units upon which the practical anticipation of rainfall must be based.

In any event, it seems clear that the attack upon this vital problem from both the intensive and extensive approach will disclose new facts and leads and will bring nearer the actual utilization of cycle predictions in crop productions.

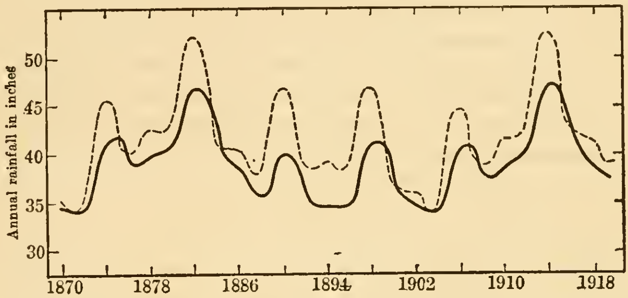



FIG. 20.—Cycles of rainfall in the Ohio valley,........, and in Illinois,_____. After Moore.

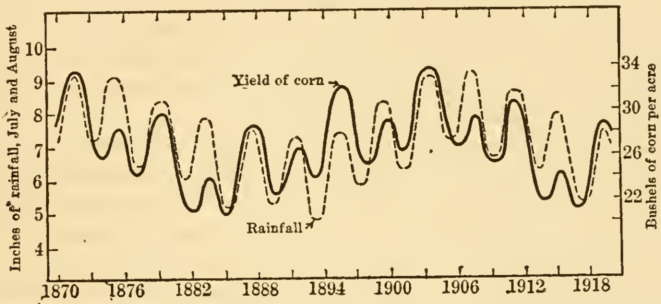



FIG. 21.—Cycles in the yield of corn and in the rainfall of its critical period of growth. After Moore.

# VI. GRAZING INDICATORS.

**Kinds of grazing.**—Grazing practice depends primarily upon the kind of stock, the nature of the vegetation, the season, and the degree of control of the range. It varies more or less with all of these, but often to a much smaller degree than the best management would require. The four kinds of stock usually handled, namely, cattle, horses, sheep, and goats, not only have more or less definite preferences as to the type of grazing, but their effect upon the latter is also markedly different. In addition, they differ much in herding management and its relation to carrying capacity. With respect to grazing type, cattle and horses prefer grasses, sheep prefer herbs and weeds, and goats prefer shrubs or "browse." While this distinction is far from absolute, it marks a fundamental preference upon which the best practice must be built. It is the basis of mixed grazing, in which cattle and sheep, or cattle, sheep, and goats, are grazed upon a range at the same time. Mixed grazing is especially indicated in the ecotone between the chaparral, desert scrub or sagebrush and grassland, but it is desirable in practically all associations except such pure grass types as the short-grass plains. The maintenance of the proper carrying capacity in any type depends upon a knowledge of the difference in habits of stock with respect to the closeness and thoroughness with which each grazes, the amount of trampling, trailing, etc.

The handling of both herd and range depends in the first degree upon the season during which grazing is possible or desirable. The time and duration of the grazing season are determined partly by the behavior of the natural cover and partly by climatic conditions, chiefly the cold and snowfall of winter. In the North, where the winters are long and severe, summer constitutes the sole grazing season and both feeding and protection are either highly desirable or absolutely necessary for approximately half of the year. In the central portion of the West the summer grazing lies largely in the mountains and the winter grazing in the plains and valleys, permitting the regular movement of stock from one to the other. This is determined chiefly by the period during which the high summer ranges are accessible, but in some cases by the furnishing of water through winter snows, as in the Red Desert of Wyoming. In the Southwest the mild climate of winter permits handling stock on the range throughout the year, and the only limitations to this method are set by lack of water or feed. However, while year-long grazing has been the rule for many years throughout this region, the frequent recurrence of drought has shown the necessity of complete utilization of the high summer ranges, and the desirability of more or less winter feeding. This is the one region in which there is a distinct winter forage composed of annual herbs, with the interesting consequence that summer and winter grazing are normally possible on the same area.

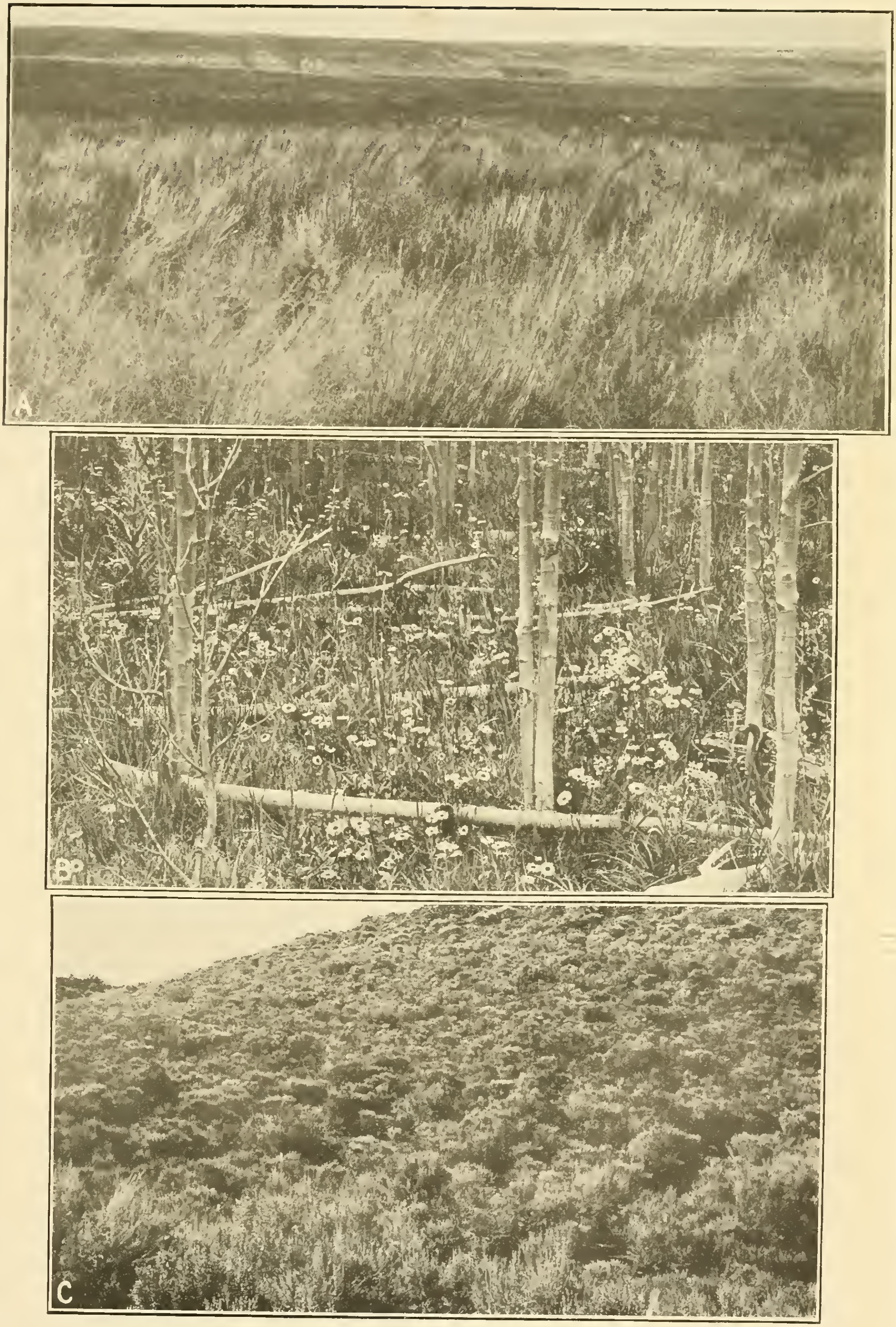
The nature and degree of control of the range have a definite bearing upon grazing. This is largely concerned with the carrying capacity, but in cases of overgrazing it is the latter which determines the sufficiency of summer or winter range and the kind of grazing possible upon it. It is a well-known fact that the open range of the West has greatly deteriorated under existing conditions, in which the only title the stockman can acquire inheres in keeping his particular range so constantly overgrazed that no one else will be tempted to use it. It is evident that a proper carrying capacity can be redeveloped and maintained on such areas only through the assurance of control. This has been secured in Texas by the private ownership of grazing lands, while in the case of the summer ranges of the national forests it has been provided by a system of grazing allotments. For the immense acreage still in the public domain, adequate control can best be obtained by a proper leasing system, as is shown in a later section. After the individual stockman has secured the exclusive use of his range under proper restrictions as to overgrazing, it is of secondary importance whether control is maintained by herding, drift fences, or complete inclosure. As will be seen, however, the latter method alone permits the maximum conservation and utilization of the natural forage crop.

## GRAZING TYPES.

**Kinds of grazing indicators.**—The simplest and most obvious indication of a plant community is that which denotes the possibility of grazing. To-day this is so axiomatic for grassland and scrub associations as to be entirely taken for granted. This has not always been the case, however (Wilcox, 1911: 35), and even at present there are forest and seral communities in which grazing indicators furnish a decisive test of the desirability of utilizing them. In the first instance, grazing types may be grouped as grass, weed, browse, and forest, and used to indicate the kind of grazing. The general principle in effect here is that a uniform community of grass, weed, or browse indicates cattle, sheep, or goats, respectively, while a prairie or a grass-scrub mictium or savannah denotes mixed grazing of two or three kinds of animals. The most striking and useful indicators are those which have to do with carrying capacity and overgrazing. These make it not only possible to measure the amount of carrying capacity and the degree of overgrazing, but they also reveal any failure to secure proper utilization. In addition, they serve to indicate the annual variations in forage production and to permit the correlation of these with the wet and dry phases of the climatic cycle. They likewise disclose the effect of local disturbances, especially those due to rodents, and they furnish a means of tracing the effects of eradication. As a consequence, they afford a complete basis for maintaining a proper balance between the utilization and conservation of the range and are of the greatest service in developing and applying an adequate system of range or ranch management.

The grouping of indicator communities as grass, weed, browse, and forest (Jardine, 1911) is one of both general and practical value. It permits subdivision into as many minor communities as desirable (Shantz and Aldous, 1917), and the chief consideration is to correlate these as naturally and effectively as possible. For this, no system approaches in value that of the developmental relationship as exhibited in the various climaxes and their successional stages. The climaxes discussed in Chapter IV illustrate the three main types, grass, scrub, and forest, while the seral communities and subdominants frequently exemplify the weed type as well. With reference to the grazing value, however, forest and woodland are to be classified on the basis of their undergrowth as grass, weed, or browse. It makes little difference practically whether grazing types are first grouped on the basis of their nature, as grass, browse, etc., or on that of development, as climax and seral. The best system will necessarily employ both, but the vast extent of the climaxes and their obvious dependence upon the vegetation-form suggests them as the preferred basis. This has the further advantage of making the practical and the ecological system the same and of avoiding the confusion which exists in forestry, where the practical types and ecological units are often wholly different. The developmental method is also desirable in that it furnishes a uniform method of dealing with finer and finer divisions upon the basis of climate, soil, and region, as well as upon that of ecology and floristic. As all of these enter into practice sooner or later, it seems clear that the best treatment of grazing indicators is that which relates them to the proper formation and association. In consequence, the following discussion deals first with climax communities as indicators as much the most important, and then with the more localized seral communities. In addition, some account is taken of artificial communities due to planting or other modification, since it is assumed that these will play an increasingly larger part in the grazing industry of the future (plate 64).

Significance of climax types.—The value of the climax community as an indicator rests primarily upon the characteristic life-form. This is clearly seen in the three types, grass, weeds, and browse, but in the case of forest it depends upon the life-forms of the layers and seral stages. Climax formations are far more extensive than the developmental stages which occur here and there in them. Moreover, such stages are constantly moving toward the climax condition, slowly in the case of priseres and rapidly in the case of subseres. The climax communities are extensive and permanent, the seral ones local and temporary as a rule. As a consequence, the grazing practice of large regions must be based upon the indications of the climax formation or its subdivisions, while in a particular locality the importance of certain seral communities may demand some modification in practice. Apart from the vegetation-form as shown in grass, herb, shrub, or tree, the habitat-form and growth-form of the dominants must also be taken into account. Communities of sod-forming grasses indicate different values and treatment than those of bunch-grasses, while there is a striking difference between the associations of tall-grasses and of short-grasses. Climax communities of dominant herbs do not exist, but prairie and alpine meadow often contain so many mixed societies that the grazing value depends largely upon them. The indications of shrubs vary with the deciduous or evergreen nature of the leaf, succulence, form, ability to make root-sprouts, fruit, etc. The dominant trees of climax forest enter the question of grazing very little if at all, and the grazing type of each forest is determined by the greater abundance of grass, weeds, or browse. Finally, the grazing value of a community, and hence its indicator meaning, depend greatly upon whether it is pure or mixed. This is partly a matter of the relative value of the dominants as forage, and partly of the degree to which each is grazed and of its ability to grow and reproduce under the existing conditions. Mixed communities greatly predominate, and their utilization is determined to a large degree by the kind of mixture. They may consist almost wholly of dominants of the same vegetation-form, such as the short-grasses of the *Bulbilis-Bouteloua* plains, or they may contain shrubs and grasses, as in savannah. In addition, grassland which exhibits a marked development of societies is essentially a mixed community with respect to grazing, since it permits selection by cattle or sheep, or mixed grazing by both.



A. Grass type, *Andropogon-Bulbilis-Bouteloua*, Smoky Hill River, Hays, Kansas.
B. Weed type, *Erigeron, Geranium*, etc., in aspen forest, Pike's Peak, Colorado.
C. Browse type, *Artemisia tridentata*, Beulah, Oregon.

**Formations as indicators.**—As has just been seen, the grazing value of a climax formation is determined primarily by the vegetation-form, though other factors enter locally to modify it more or less. The grassland climax is by far the most important of all, and there is little doubt that its development and extension have controlled the evolution of grazing animals in the past. The fact that the word *graze* is formed directly from *grass* proves that grassland has long been the primary grazing type, and that all others are secondary, resulting from the natural extension of grazing into scrub and forest. The alpine meadow ranks next to prairie and plain in primary grazing value, though the short season finds expression in the low growth-form as well as in the short period for grazing. The savannah marks the transition from primary grazing land, *i. e.*, grassland, to scrub. In spite of the unique importance of the latter for mixed grazing, its actual grazing value is secondary, as is indicated by the application of the word *browse* to it. Of the scrub climaxes, the chaparral usually stands first in importance, the sage-brush next, and the desert scrub last, though this varies greatly with the grouping of the various dominants. Of the forest formations, montane forest has the greater value, due largely to the open grassy nature of the yellow pine consociation. The woodland resembles the latter more or less and often ranks next to it in amount of grazing. The subalpine forest varies greatly in importance. The grazing value of its meadows, natural parks, and aspen areas is high, but the climax forest is usually too dense and closed to permit the growth of a uniform ground cover. This is even truer of the luxuriant Coast forest, in spite of the fact that the latter often exhibits a dense tangle of shrubbery.

**Associations as indicators.**—The indicator significance of an association is essentially that of the formation to which it belongs. As a subdivision, it represents a closer response to regional conditions, and the various associations of a climax permit the recognition of more or less different grazing values. This is characteristically true of the grassland and alpine meadow formations. It holds to a somewhat smaller degree for the scrub and is least evident for the forest climaxes, in which the number and extent of seral communities are more significant for grazing than the climax areas themselves.

In determining the relative grazing value of the associations of the grassland climax, this is found to depend upon density, height, and mixture. Upon this basis, the subclimax prairies are perhaps the most valuable, though the true prairies are nearly as valuable, and in some cases even more so. The mixed prairies come next, and are followed by the short-grass plains. The bunch-grass prairies at their best may equal the latter, but generally the stand is too open. While the desert plains are of the same character as the short-grass association, the bunch habit is more pronounced and the total production usually less. Quite apart from the question of yield, however, is that of time of development and ability to cure on the ground. From this standpoint, the mixed prairie of tall *Stipa* or *Agropyrum*, and short *Bulbilis*, *Bouteloua*, or *Carex*, or the transition area of *Andropogon* and short-grasses has a distinct advantage. The tall-grasses either develop earlier or grow with such rapidity as to furnish the bulk of spring and summer feed, while the short-grasses become cured in late summer to furnish feed for fall and winter. Finally, it must be recognized that the tall-grass associations are agricultural indicators as well, and that economic considerations give them greater significance in this rôle. Our knowledge of the Pacific alpine meadow is too small to enable us to draw an accurate comparison with the Petran association. They are so nearly alike in the growth-form and genera of the dominants and in the number and luxuriance of the societies that they exhibit no clear difference in yield per unit area. In spite of this, the Petran association is actually very much more important, for it covers an area many times greater, is more coherent, and for the most part covered by snow to a less degree and for a shorter period.

The grazing value of the chaparral associations depends largely upon the presence of oak, which is usually the most important of the dominants for browse. For this reason, the Petran chaparral is usually more important than the Coastal, though its value decreases greatly with the dropping out of the oak to the northward, just as it increases to the southeast with a larger number of species of *Quercus*. In the sagebrush formation, the Basin association is all-important, the Coastal community being of relatively small extent and containing but one or two dominants of value. The differences between the associations of the desert scrub are not so clear-cut, but the advantage lies in general with the western community, owing largely to the much greater number of succulents. The three associations of the woodland exhibit a thin ground cover of grass and shrubs, resulting from the combined effect of dryness and shade. They produce savannah where they are in contact with grassland or scrub, and in such cases possess more or less of the grazing value of the latter. The presence of oak gives woodland some value as browse, and in this respect the oak-cedar community stands first and the pine-oak next. The montane associations differ strikingly in ground cover, the Petran having the herbaceous layers best developed, and the Sierran, the shrub layer or so-called subclimax chaparral. The former has usually the greater importance for grazing, since many of the shrubs of the chaparral are unpalatable. The comparative value of the associations of the subalpine forest is less certain, but on the whole the Petran has the advantage, especially when the seral grasslands are taken into account.

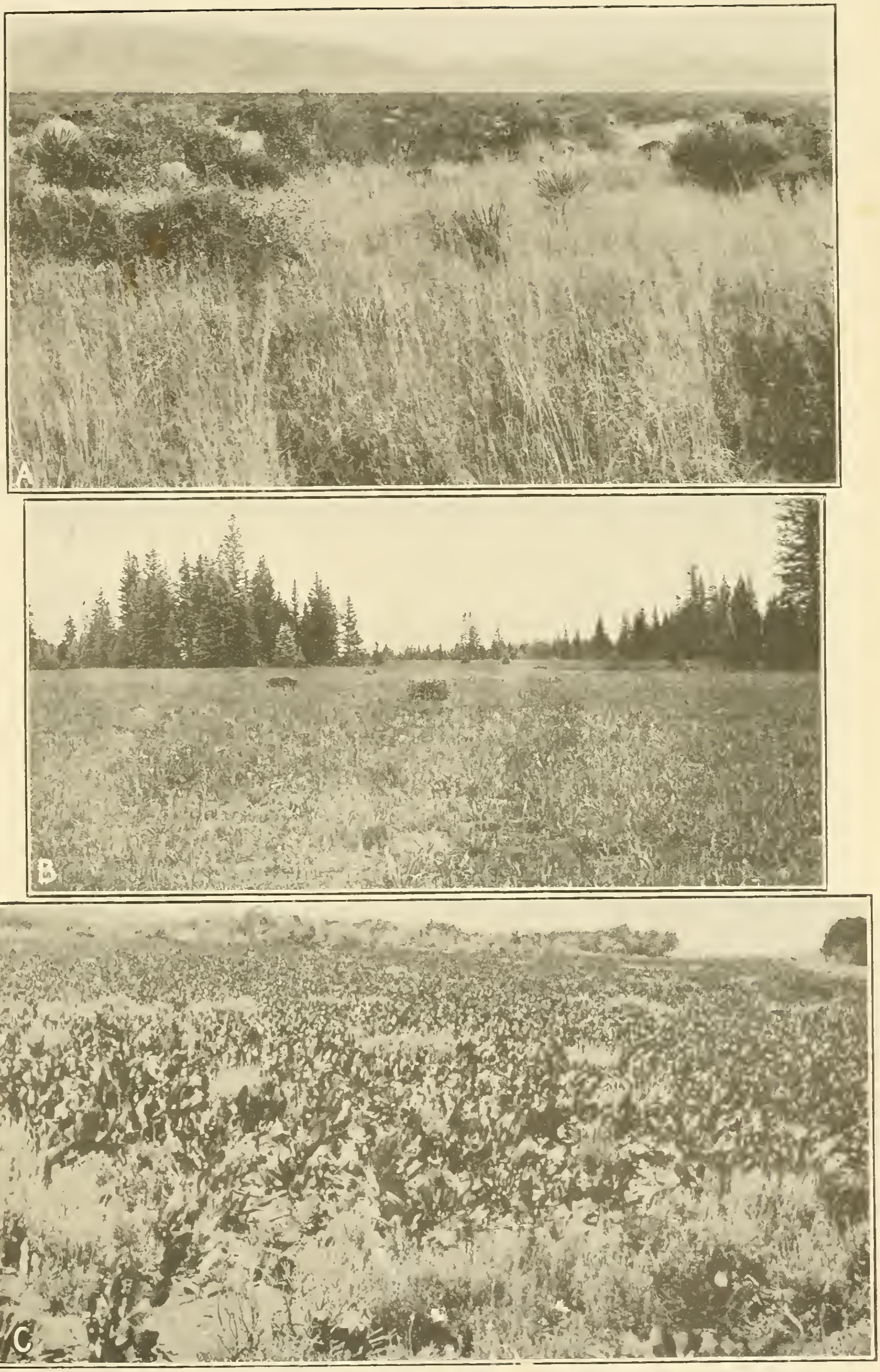
Consociations as indicators.—The value of the consociation as an indicator is determined primarily by the life-form. Grassland derives its unique importance for grazing from the grass dominants, while the value of scrub dominants is much lower and more variable, and that of forest consociations almost wholly dependent upon the undergrowth. In the grassland the chief value lies in the consociation, with the scrub in the consociation and its societies, and in the forest it lies in the shrub and herb societies alone. Moreover, grass consociations are true grazing types, scrub are primarily browse types, and forest and woodland are grazing or browse, depending upon the relative abundance of herbs and shrubs. Consociations may be pure or mixed, and the indicator meaning naturally varies accordingly. While mixed communities are the rule, pure consociations are sufficiently frequent to permit the determination of carrying capacity, response to overgrazing, and other features which make up the total grazing value. In the case of mixed communities the analysis is based upon the normal response of each pure consociation, modified by their varying relations to the grazing animals and their competitive reactions upon each other. In dealing with the actual grazing types of a particular region, pure consociations play an even smaller part on account of their relatively small extent. While they are very helpful in ecological analysis, they are of little importance in practical management.

Local grazing types.—While the main grazing types, such as the formation and association, indicate the comparative value of great regions, as well as the groupings possible in any one, it is the local groupings which determine the carrying capacity of a particular ranch and the proper system of management to be employed upon it. For this reason, they may well be termed practical grazing types. In areas relatively uniform, a single grazing type composed of the two or three major dominants of the association may cover a wide extent. This is the case with *Stipa* and *Bouteloua* in North Dakota and Montana, *Bulbilis*, *Agropyrum*, and *Bouteloua* in the region of the Black Hills, and *Bulbilis* and *Bouteloua* in Oklahoma and Texas. As a rule, however, changes in topography or soil or in the number and grouping of the subdominants bring about important changes every few miles, and very frequently adjoining sections will be found to have a different grouping or an effective difference in relative abundance. Hence, it is clear that the local community must determine the careful classification of the land section by section, especially with reference to carrying capacity, as well as the method of management. For example, while all the climax groupings in the mixed prairie resemble each other in structure and treatment much more than they do groupings of the true prairie or short-grass plains, they show decisive differences among themselves. The carrying capacity and relation to overgrazing of the *Stipa-Bouteloua* community differ from that of *Agropyrum-Bulbilis*, and of both of these from that of *Bulbilis-Agropyrum-Bouteloua*. The marked development of societies reduces the abundance of the dominant grasses, and at the same time affects the carrying capacity. The relation between the two effects depends upon the degree to which the subdominants are grazed, but as a rule they are less palatable than the grasses. Over regions of rolling topography, such as prairies and sandhills, the climax groupings are regularly interrupted by valley and ridge communities which are successional in nature. These are of relatively small extent and may frequently occur with the climax grouping on a ranch of a section or less in extent. In the case of the more level plains, the seral communities are confined to stream valleys and breaks and cover much larger areas. They often serve to mark the distinction between valley and upland ranches. They are not confined to one association, but such a grouping as that of the *Andropogons* may be found repeatedly from the true and mixed prairies through the short-grass and desert plains.

The number of such groupings is legion, and the most important occur again and again in the region where they are characteristic. They have been found in sequence over many thousands of miles in the West, and the most frequent and important have been noted in connection with the frequence and grouping of dominants under each association in Chapter IV. They are of the first importance in determining local variations in grazing value and are regarded as the basic indicators to be used in the range survey discussed later. As already indicated, the major indication of the grouping must always be interpreted in connection with the minor indication of the societies present. In its application to grazing at least, the grouping is so important that the need of a more distinctive term is clearly felt. In so far as grazing is concerned, the term grazing type might well serve the purpose, though formations and associations, as well as seral communities, are also grazing types. The grouping of consociations within the association is typical of all climaxes, however, and seems to warrant a special term for those who need a complete and detailed analysis of vegetation. After an extended consideration of the possibilities, it has seemed desirable to definitize the term *facies* for seral groupings and to make a new word, *faciation*, for climax groupings. These are derived from the same root, *fac*, shine, and possess the same basic meaning, namely, appearance, aspect, or form. The two terms conform to the mutual relation seen in associes and association, consocies and consociation.

Savannah as an indicator.—Throughout the present treatment, the word savannah is used for the community which characterizes the ecotone between two climax formations. In its most typical expression, it consists of grasses and low trees or tall shrubs, and occurs in the hot, dry regions of the Southwest. Other communities are so similar that it is impossible to exclude them, and hence open pine forest and woodland with a grass cover are also called savannah. Closely related to these are the so-called natural parks of the Rocky Mountains in which seral grassland is surrounded and more or less invaded by trees. Such parks occur in both the montane and subalpine zones. When the ecotone lies between forest or woodland and scrub, the general ecological relations are similar to those of savannah, but the grassland is replaced by sagebrush, chaparral, or desert scrub. The trees stand more or less scattered in the scrub, and the indications of the community are primarily those of the latter. The failure to recognize this similarity to savannah has led to confusion with reference to the distinctness of the scrub climaxes in rough regions where they are interspersed with trees. Savannah has been so generally linked with the presence of grasses that it seems unwise perhaps to broaden its meaning to include areas of scrub with taller trees, and consequently the word park has been used for the latter. Thus, a sagebrush savannah is one in which sagebrush is scattered through grassland, while a sagebrush park is a community in which sagebrush is surrounded and more or less invaded by trees or tall shrubs.

In their typical form, both savannah and park are controlled by the grasses or scrub, and the trees are more or less incidental. The transition to forest or woodland is usually gradual, and it is impossible to draw a sharp line between the two. However, it is a simple matter to distinguish the general areas from each other. As long as the trees or shrubs are far enough apart so that their shadows do not touch, the grassland or scrub remains in control. When they are sufficiently close to have their shadows overlapping during most of the day, the grass or scrub dies out for lack of sun, or persists only in small groups of much modified individuals. Tree and scrub savannah often cover extensive areas to which they give the appearance of open woodland, but the true nature of the community is indicated by the continuous carpet of grass, which serves as the indicator. Sagebrush and chaparral parks are usually more local, and they quickly pass into woodland on the one hand and scrub on the other. They recur constantly, owing to the relatively small difference in requirements between shrubs and small trees. Savannah proper is probably due to the effect of climatic cycles and is thought to serve as an



A. Savannah of desert scrub, *Flourensia-Larrea-Prosopis*, and desert plains grasses, *Bouteloua gracilis*, *eriopoda*, and *racemosa*, Van Horn, Texas.

B. Burn park in subalpine forest, Uncompahgre Plateau, Colorado.

C. Burn park of *Wyethia* and *Artemisia* in chaparral, Logan, Utah.

indicator of the wet phase of the cycle. The control of the grasses is so complete that the additional water-content necessary for the germination and establishment of the trees or shrubs is present only during the maximum of the wet phase, often only a single year. Once established, and with their roots at greater depths than those of the grasses, the trees or shrubs persist indefinitely. During succeeding wet phases they tend to increase in number, while in critical drought periods the number may be reduced, as is regularly the case where fires are frequent. Counts of the annual rings of a number of shrubs in different savannah areas confirm the view that ecesis is normally confined to wet phases of the climatic cycle (plate 65).

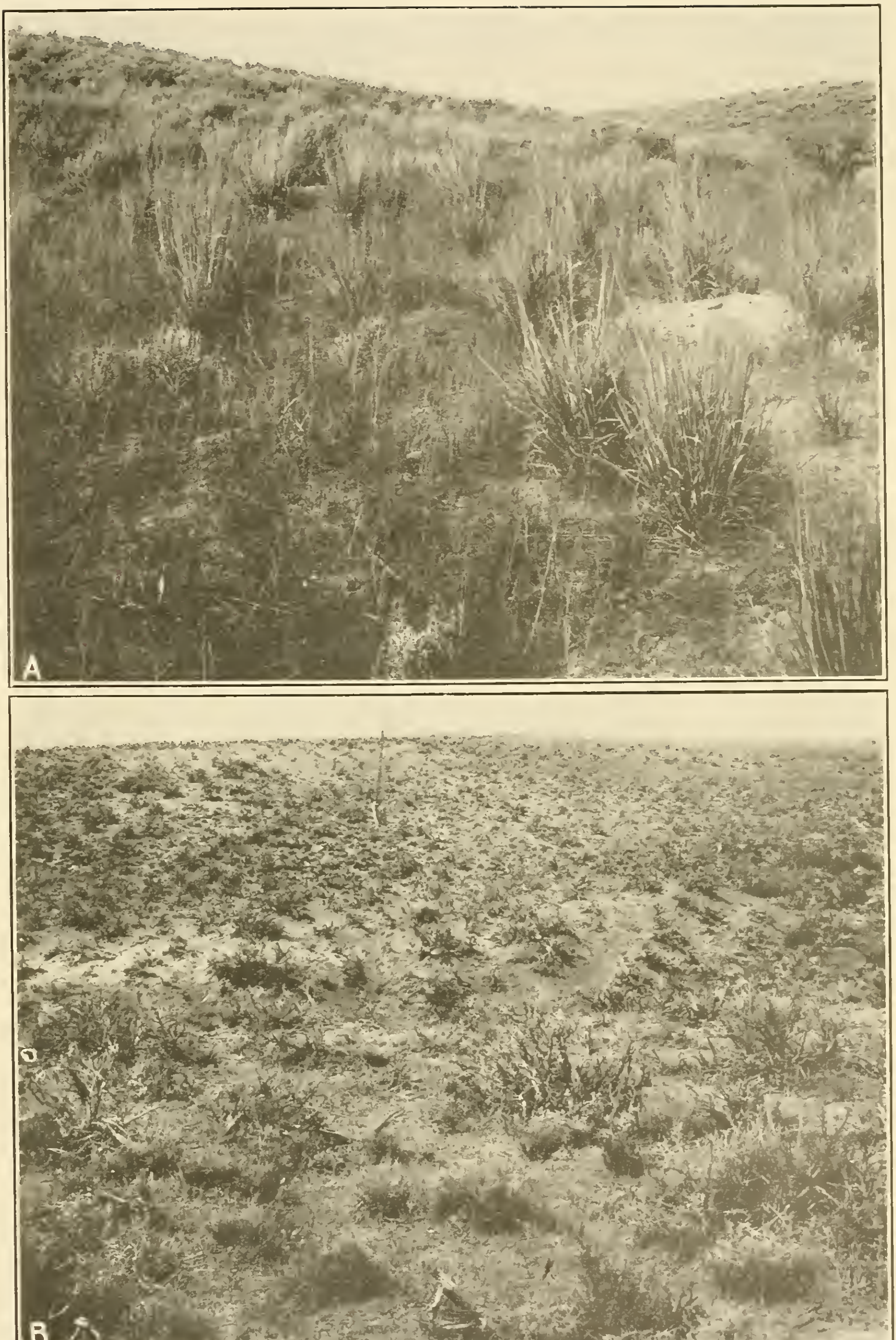
The indicator significance of savannah or park naturally depends upon the kind and the region, as well as upon the dominants. The best examples of tree savannah are to be found along the line of contact of forest or woodland with grassland. Oak savannah is the most common, occurring typically in central Texas, in Arizona, New Mexico, and Mexico, and in California and Lower California. Savannah in which yellow pine is the tree is frequent along the lower edge of the montane forest, where it extends out upon plateaus or plains. It is well-developed in northern Arizona and New Mexico, but is most extensive on the low ranges and high plains east of the central Rockies and around the Black Hills. Both piñon and cedar form savannah, but the latter is much more frequent and extensive. Typical scrub savannah is largely confined to the Southwest, ranging from Texas through southern New Mexico and Arizona, and northern Mexico. Its most characteristic shrub is mesquite, *Prosopis juliflora*, but *Yucca, Acacia, Ephedra,* and other dominants of the desert scrub occur frequently. Owing to its habit of growing in clumps or groups, chaparral tends to form grassy parks rather than typical savannah, especially along the edge of the Petran association. Sagebrush extends into several of the grassland associations to form what is essentially sagebrush savannah, though its low stature tends to obscure the exact relation. This is especially true where it meets the tall-grasses, as in Wyoming and Oregon, but the savannah nature is obvious where tall sagebrush is scattered through short-grass, as in southeastern Utah.

Parks differ from savannah chiefly in that the two communities concerned mix by alternating groups or areas rather than by scattered individuals. Excellent examples of grass parks occur in the subalpine forests of Colorado, where spruce and balsam inclose extensive meadows of *Festuca,* dotted with groups of young conifers or aspens. Somewhat similar parks occur at timberline, where the forest breaks into groups which extend well up into the alpine meadows. Sagebrush parks occur most commonly in the lower subclimax portion of the woodland zone, while sagebrush areas dotted with groups of lodgepole pine or aspen are frequent on the western slope of the Rocky Mountains in Colorado and Wyoming. Chaparral parks are best developed in California, especially in the case of subclimax chaparral in the pine forest and where the climax type meets the pine-oak woodland. In the Rocky Mountain region they occur chiefly as scrub openings in the piñon-cedar or oak-cedar woodland.

Savannah and park are alike as indicators in that they denote a transition from one community to another. They differ for the most part in that savannah is an indicator of climate, and park usually of local or edaphic conditions.

Savannah has to do with the relations of two contiguous climaxes, and park with that of a subclimax to its climax. The former is a permanent condition, varying more or less under the influence of the wet and dry phases of climatic cycles, while the latter is usually a temporary community, occupying its proper place in prisere or subsere, and passing ultimately into the climax. Hence, the indicator values of different types of parks are dealt with in the next section, while those of savannah are considered here. True savannah has value as an indicator of climate as well as of practice. It not only indicates a transition between the climates of the respective climaxes, but also serves to record the course of the climatic cycle. The amount to which it increases its area and density under the same conditions is a measure of the effect of the wet phase, and the dying-out of individuals, of the dry phase. Such measurements are possible only under control, however, owing to the almost universal disturbance of fire or overgrazing.

Kinds of savannah.—With reference to practice, savannah indicates the general possibility of agriculture. For the most part, this is of the dry-farming type, though in central Texas it indicates humid or subhumid farming, and in California farming by means of drought-evasion. With respect to grazing, the indications of savannah depend primarily upon the grass dominants. In fact, the indicator value of savannah is essentially that of the grassland community, unless the trees or shrubs are sufficiently close to reduce materially the amount of grass. When the shrubs themselves have distinct value as browse, the carrying capacity becomes greater than that of the grassland alone, and mixed grazing is also favored. The yellow pine savannah of the Black Hills and eastern Rocky Mountain region occurs in the mixed prairie, while in the Southwest it lies in the short-grass association. In both cases, the grazing value of the grassland is practically unchanged, except for some reduction in cover just beneath the trees. Pine savannah also occurs along the upper edge of the bunch-grass prairie, but it is rarely extensive here. Cedar savannah is found chiefly in the short-grass community, but is frequent also in the desert plains and mixed prairies. Where the cedar is low, it materially reduces the total carrying capacity, though this is often offset by the presence of browse shrubs. Mesquite savannah lies typically in the desert plains, though the mesquite itself extends northward into the short-grass association of the Staked Plains. The shrubs have little effect upon the amount of grass, and they change the indications of the community only to the extent that they are valuable for browse. Toward the lower edge of the savannah the shrubs become denser as they pass into the desert scrub, and the grassland rapidly decreases to the point of disappearance. Oak savannah may be of the tree or shrub type. The latter is most typical on the plateaus and mountain ranges of southwestern Texas, New Mexico, Arizona, and Mexico, where it is formed chiefly by live-oaks. It lies in the desert plains grassland, or in the *Andropogon* zone just above. The grazing value due to the grasses is greatly increased by the abundant browse, and such savannah may well be regarded as one of the best of all grazing types, owing to the assurance it gives against drought in connection with mixed grazing. Tree savannah consisting of oaks usually has little or no browse value, and its indication is essentially that of the grass community in which it is found, with some reduction caused by shading. In California, the



A. Grass park of *Elymus* and *Agropyrum* arising from sagebrush, Boise, Idaho.
B. Sagebrush dying out as a result of competition with *Agropyrum*, Craig, Colorado.

original *Stipa* bunch-grass prairie has been almost wholly replaced by the wild-oats, *Avena fatua,* and the latter determines a relatively lower value for the community. The sagebrush savannah so characteristic of northeastern Wyoming lies in the edge of the mixed prairie, and the sagebrush is chiefly associated with *Stipa,* though *Agropyrum* and *Bouteloua* are also present to a large degree. The relative abundance of grass and sagebrush varies widely, and the indicator value of the mixture in accordance. Since the sagebrush is eaten to a much less degree during the summer, the carrying capacity is somewhat reduced, though this is partly compensated by its availability during the winter.

Savannah in relation to fire and grazing.—The general view in the Southwest is that mesquite and oak savannah are limited or destroyed by fire and that they have spread rapidly in recent years, since the annual burning has ceased (Cook, 1908). In the absence of definite measurements, many of the statements can be accepted only in part, though the general relation to fire seems evident enough. Tree savannah appears to be affected little by burning, except that this must have been a powerful factor in spreading the annual *Avena* in California at the expense of the perennial *Stipa.* The effect of fire upon scrub savannah depends upon a number of factors, chief among which are density and height of both shrubs and grasses, the ability of the shrubs to form root-sprouts, and the frequency of fires. It seems certain that annual fires in scrub savannah that is densely covered with tall-grasses would destroy the shrubs completely in a few years, no matter how great their ability to form root-sprouts. Less frequent burning of open savannah, in short-grass especially, would damage the shrubs much less and might well increase their control by promoting root-sprouting. Moreover, in the more xerophytic grasslands, frequent burning during dry seasons injures the grass and would tend to favor the shrubs in consequence (plate 66).

The general effect of grazing is to increase the shrubs at the expense of the grass. As has been seen, savannah owes its character to a dry climate in which the ecesis of shrubs is regarded as usually possible only during the wet phase of the cycle. This means that shrubs and grasses live constantly under keen competition for water, and that anything which reduces the amount of grass will be to the advantage of the shrubs. Since grasses and herbs are usually eaten to a much larger degree, intensive grazing, and especially over-grazing, will reduce their hold upon the soil and correspondingly improve conditions for the spread of shrubs. The seeds of the mesquite and other shrubs are widely scattered as a consequence of being eaten or through unintentional carriage, and the seedlings are more readily established in areas where the hold of the grasses has been weakened. The local spread of the scrub clumps is chiefly by means of root-sprouts and is promoted by light browsing, but restricted by heavy browsing. Thus, while savannah is primarily an indicator of climate, its secondary indication is one of grazing and absence of fires, upon which its practical utilization must be based. As suggested in a later section, this can be done readily only after quadrat measures have made clear the exact behavior of savannah under different methods of burning and grazing.

Significance of seral types.—While seral communities are temporary in comparison with climax ones, many of them persist for tens or even hundreds of years, and in actual practice may be regarded as permanent. The great majority of them result from disturbance, however, and last for a period of a few years, or at most for a decade or two, unless the disturbance is continuous or recurrent. In addition, they show rapid changes of population from year to year. Such communities are usually local and of small extent and have resulted from fire, overgrazing, or cultivation. They belong to secondary successions or subseres in contrast to the larger and more permanent communities which constitute stages in the primary succession or prisere. These distinctions apparently disappear in the case of great stretches which are kept more or less permanently in the lodgepole or aspen community as a consequence of repeated fires, or in the *Aristida* or *Gutierrezia* stage as a result of continued overgrazing. Even here, however, the differences in the kind and rate of development are of great practical value in determining the proper management. As a consequence, it is desirable to distinguish seral communities as indicators upon the basis of primary and secondary succession, and then to deal with the indicator value of the respective dominants. Each of these is known as a consocies when it is controlling, and corresponds with the consociation among climax types. Two or more consocies regularly occur together to constitute a particular stage or associes, while their subdominants are known as socies, which correspond with the societies of climax communities. A complete treatment of seral indicators is neither possible nor desirable at present, but the following account will serve to illustrate all the important types.

Prisere communities as indicators.—The four great types of primary succession are those which start in initial bare areas of water, rock, dune-sand, or saline lake or basin respectively. The initial communities and some of the medial ones may be used as negative indicators, denoting that conditions have not reached the point where they can support a plant cover of such density or quality as to furnish grazing. The later communities, and especially the subclimax one that immediately precedes the climax, form a more or less complete cover in which grasses or shrubs are usually in control. The density of the cover and the quality of the grazing increase more or less regularly from the medial stages to the climax, and the position of a particular community in the sere indicates its value in a general way.

The most important seral indicators of grazing are the later stages of the priseres in dunes and sandhills, in bad lands and in salt basins. These often cover many thousand square miles and frequently occur in agricultural regions, where the indicator distinction between grazing and farming land is especially important. In addition, there are the sedge and grass meadows which are stages of the hydrosere, and are often characteristic of mountain parks in the montane and subalpine zones. Grassland and scrub also develop in rock fields and on talus slopes where the formation of soil is not too slow. While such parks and gravel-slide areas often afford excellent grazing, they are usually both local and relatively small and serve chiefly to increase the grazing value of the forest areas in which they occur.

Of all the prisere communities, those of sandhills and dunes are probably the most widely distributed and most important. They have been found and studied in each of the 16 Western States, where they may occur as sandhill regions of large extent, as river dunes or ocean dunes. The most extensive

A. Seral stages in sandhills, the subclimax grasses *Andropogon* and *Calamovilfa*, Agate, Nebraska.

B. Seral stages in bad lands, *Atriplex corrugata, nuttallii*, and *confertifolia* the chief dominants, Cisco, Utah.

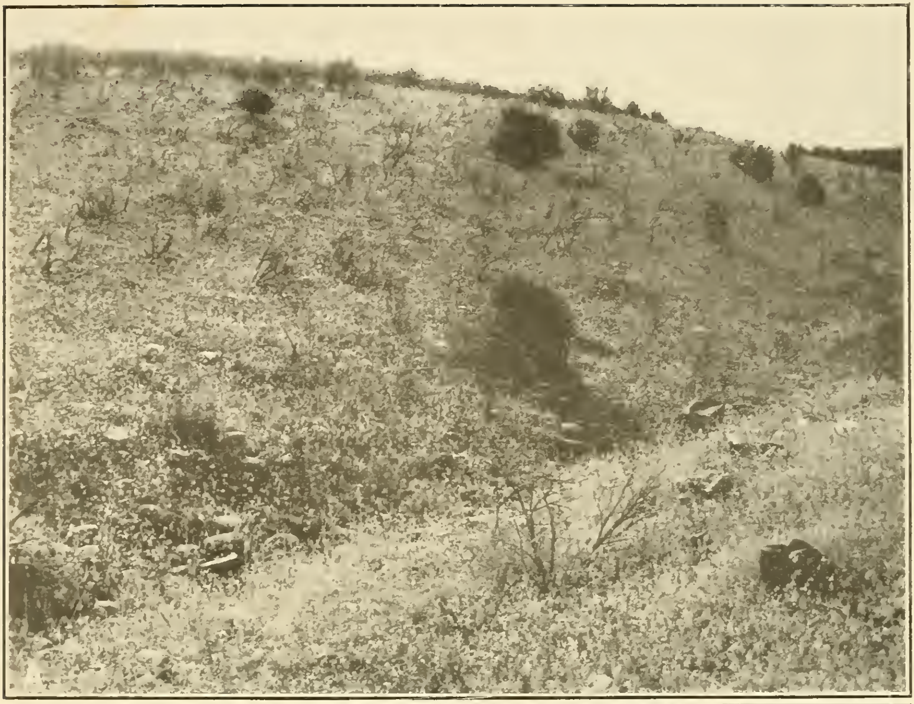
sandhill areas occur in Nebraska, Kansas, and Colorado, though they are scattered throughout the grassland climax from North Dakota to Texas and New Mexico. Such areas differ from dunes chiefly in extent and complexity, and in the fact that they are no longer connected with an active shore-line from which the sand is derived. They are essentially stable dunes with blowouts as characteristic features, and for the most part they exhibit subclimax communities. The succession in sandhills and dunes is practically identical for the same climax, but differs greatly between climaxes, especially in the later stages. The largest and most important sandhill region is that of central Nebraska, which covers an area of about 20,000 square miles. It has received much study during the past 30 years, and the ecological results have been summarized by Pool (1914) in a monograph on their vegetation. The typical community of the sandhills is the bunch-grass subclimax, consisting of *Andropogon hallii* and *A. scoparius.* The blow-sand condition, typical of blowouts especially, is indicated by *Redfieldia, Psoralea,* and *Petalostemon,* which have little or no grazing value. More stable conditions are denoted by *Muhlenbergia* and *Calamovilfa,* and these are correlated with increasing grazing value. The next stage is that of the *Andropogon* subclimax, which possesses a much higher value. By the entrance of *Stipa* and *Koeleria,* the bunch-grass subclimax passes into the true prairie, while in the western portion the invasion of *Bouteloua* and *Bulbilis* indicates the appearance of the short-grass climax, or of mixed prairie when *Stipa* and *Agropyrum* occur also. The hydrosere is a regular feature of the innumerable wet valleys and of the extensive lake region. The first community to indicate grazing is composed of rushes and sedges, and this changes slowly into the typical meadow associes of *Agropyrum, Andropogon, Elymus, Panicum,* and *Spartina,* which is essentially an extra-regional portion of the subclimax prairie. The grazing value of such a group of dominants is obvious, but in practice such meadows are used for hay, since the hills furnish ample summer grazing (plate 67).

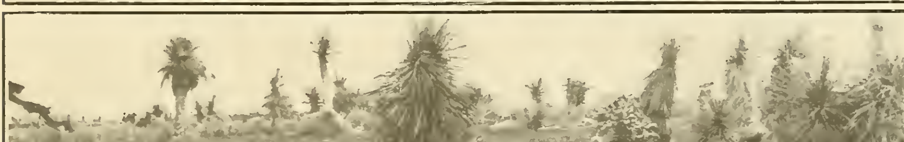
Like the sandhills, bad lands are found throughout the West. Massive bad-land complexes are most typical of the States which touch the Black Hills, but they are frequent also in practically all those along the Rocky Mountain axis, while outlying areas of much interest are found in Texas, Oregon, and California. The actual communities of the sere likewise differ with the climax. The two most important seres are the xerosere of the Tertiary bad lands in the Great Plains region of the grassland climax, and the halosere of the Great Basin sagebrush climax. The former possesses a number of herbaceous stages which have an increasing value for sheep-grazing as they become denser, but grazing proper is indicated only when *Agropyrum* becomes abundant. *Bouteloua* and sometimes *Bulbilis* also enter somewhat later to form mixed prairie, and the latter then becomes definitely constituted by the appearance of *Stipa.* The lower valleys are often controlled for a time by sagebrush, but this ultimately yields to the grasses. The juxtaposition of weed, grass, and sagebrush types indicates the value of bad land areas for mixed grazing, and suggests the importance of hastening the course of succession in them. The bad lands of the sagebrush climax are characterized in the intial stages by colonies of halophytic annuals, which have some grazing value where they make a definite cover. The first stage of much importance is formed by the low perennial species of *Atriplex,* such as *A. nuttallii, A.*

*corrugata*, and *A. pabularis*. These are followed by *Atriplex confertifolia* and *Grayia*, which furnish forage of much better quality and larger amount, and these are finally invaded by *Artemisia tridentata* to form the mixed or pure grazing type so characteristic of the Great Basin and its outlying regions. In the bad lands of the Painted Desert in northern Arizona, the general course of the sere is much the same, but the grasses replace *Atriplex*. The normal sequence in the subclimax stages is the replacement of *Sporobolus airoides* by *Hilaria jamesii*, and this by *Bouteloua*, often with *Muhlenbergia* also. The course of development in the halophytic bad lands is essentially a part of the widespread succession in saline basins, except that the latter often begins in water. Shantz (1916: 233) has indicated the course of the succession in detail, and it must suffice to point out that the first important indicators of grazing are usually scrub dominants, *Sarcobatus* and *Atriplex*. Some of the playas of the Southwest are intensely saline, and show essentially the same communities, but the majority are secondary in nature and belong to the subsere.

Subsere communities as indicators.—Subseres are developed in secondary areas, such as are regularly produced by fire or cultivation. They occur also in other bare areas in which the disturbance is not sufficient to destroy the soil or to make extreme conditions for ecesis. They are a constant feature of overgrazing and a normal consequence of the presence and activity of man. They are usually local and of small extent, but in the case of fire they may occupy hundreds of square miles. The successional movement is normally rapid, but its progress may be slowed or stopped by the recurrence of the disturbing agency. When this is the case, the area concerned may be held more or less permanently in a subclimax or other seral stage. The most important and extensive subseral communities are those due to fire. The consequences of overgrazing often cover great stretches, but the actual communities change more or less, or they are much interrupted. Those due to cultivation are usually confined to fields, though many of the dominants become extended to roadsides, and some even enter the natural vegetation. While they often have grazing value, it is incidental and temporary and their chief value lies in connection with utilization as supplementary forage crops, as already indicated for *Salsola, Helianthus, Melilotus*, and others (plate 68).

Certain grasses, such as *Poa, Avena*, and *Bromus*, have become widespread dominants as a consequence of the combined action of two or more agencies. In the case of *Avena* and *Bromus*, the species concerned, *A. fatua, B. tectorum, B. rubens*, etc., are annuals which have replaced the native dominants as a general result of the combined effect of overgrazing and fire. As annual grasses, these should have a low grazing value, but this is much less true of *Avena* than *Bromus*, owing largely to the difference in size and habit. Even *Avena* is less valuable than the native perennial grasses which they usually replace, and this suggests the desirability of taking advantage of the principles of succession to restore the original community where it has not been completely destroyed. *Poa pratensis* as a perennial grass of meadows has practically the same ecological habits and grazing value as the prairie dominants which it replaces. Its rapid spread in the valleys and ravines of the true prairies seems to have been the result of a certain amount of disturbance, but






A. *Bromus tectorum* marking a burn in sagebrush, Boise, Idaho.
B. *Erodium cicutarium* indicating trampling in desert plains grassland, Oracle, Arizona.

*Poa* is not a true seral consocies, such as the annual *Avena* and *Bromus*. Among other such consocies of importance are *Plantago patagonica*, *Portulaca oleracea*, *Boerhavia torreyana*, and *Polygonum aviculare*. These are all indicators of disturbance, particularly overgrazing, but in the green condition they also have more or less value as indicators of an available weed type. Other indicators of disturbance are represented by such plants as *Hilaria mutica*, *Scleropogon brevifolius*, *Franseria*, and *Bulbilis*. These occur in playas or "swags" which are subject to flooding and in which a thin annual layer of silt is often deposited as well. The first two are commonly associated, partly owing to the fact that the disturbance of the *Hilaria* consocies by trampling and overgrazing favors the spread of *Scleropogon*. Tobosa swags are typical seral areas in the desert scrub as well as in the zone of savannah which lies between this and the desert plains. In the latter particularly, *Hilaria* is a characteristic subclimax, in which *Scleropogon* is usually an indicator of grazing disturbance, frequently with a similar associate, *Sporobolus auriculatus*. *Hilaria* is an indicator of summer grazing, while the other two are rarely grazed except under drought conditions. The playas of the southern Great Plains are marked by a similar subsere, in which *Franseria* is the important early stage and *Bulbilis* the subclimax. Both of these are grazing indicators, though the value of the *Franseria* is relatively small (plate 69).

Fire indicators and grazing —The typical indicators of fire are trees and shrubs, and they may have a direct or indirect relation to grazing. The indicators may themselves be browsed, or they may be associated with layers of herbs or shrubs which furnish feed. Grasses and other herbs may indicate fire, but are usually associated with woody indicators or their relics. The most important "burn" communities are pine forest, aspen woodland, chaparral, and savannah. In addition, there are grass and sagebrush parks which also represent subseres initiated by fire. Savannah has already been considered, while the grazing value of grass parks is obvious. Sagebrush and chaparral are primarily browse types, though they contain a larger or smaller amount of grass or herbs as well. When young, aspen woodland furnishes a large amount of browse, but it is chiefly valuable for the more or less luxuriant ground cover. This changes with the course of succession from firegrass, fireweed, and other pioneers to the characteristic mixed layer communities of the mature aspen subclimax. The latter exhibits three chief grazing types, herb, grass, and shrub, of which the first is the most common and the second the most valuable. The pine communities which regularly indicate burns are lodgepole and knobcone forests. The subclimax of lodgepole, *Pinus contorta*, is much the most extensive and important, occurring in both the montane and subalpine zones of the Petran and Sierran regions. The community of knobcone pine, *Pinus attenuata*, is a similar fire subclimax, but it is confined to southern Oregon and California. In the Rocky Mountains, the mature lodgepole forest is almost completely without a ground cover, and hence possesses almost no grazing value. In its earlier stages, herb and grass associes are well-developed, and for a time aspen scrub may form a typical stage. In the Coast forest, *Pseudotsuga* and *Larix* are fire indicators and their communities exhibit herb and shrub layers in the early stages especially.

## CARRYING CAPACITY.

Nature and significance..—The practical measure of the value of a range is its carrying capacity. By this is meant the number of animals which can be grazed upon it, expressed in terms of unit area, such as the number of head grazed upon a section (640 acres), or the number of acres required to support a single animal. It is usually expressed in terms of cattle as a basis, though it is better to indicate it in terms of the animal to which the range is best adapted, especially in the case of mixed grazing. As used at present, carrying capacity is only a relative measure of the food value of a range or type. This is due to several facts which introduce elements of uncertainty. Few grazing types are uniform, either in density or composition, and the utilization of any dominant depends to a great extent upon its associates. Even greater variation in carrying capacity results from annual fluctuations in rainfall. On the animal side, each kind of stock has its own preferences, as that of cattle for grass and sheep for herbs, while horses and sheep utilize a forage cover much more completely than cattle. Similar great differences result from the methods of handling stock, especially with reference to the manner of herding by ages or classes, or in the open or band system, with respect to water, salting, etc. Carrying capacity may vary significantly with the breed of stock, and it is obviously affected by winter feeding in regions of year-long range. Finally, perhaps the largest element of uncertainty lies in the great variation in the size and condition of stock when turned off of the range. As a consequence, it is clear that more exact measures must be introduced, which will permit an accurate comparison of different ranges and at the same time furnish a guide to the varying conditions of the same range. The Forest Service (Jardine and Hurtt, 1917) has already done much in this connection, especially with respect to the extensive measurement of carrying capacity, while the office of Dry-Land Agriculture (Sarvis, 1919) has developed a basic method of intensive measurement. By the proper combination of these two methods, it will be possible to secure an exact measure of the carrying capacity of all grazing types, as well as of the fluctuations from year to year and under different kinds of management.

Determining factors.—With respect to the plant cover alone, the carrying capacity of a grazing type is summed up in the total amount of the annual crop of forage. But the total yield must be interpreted in terms of value and utilization. Hence, it is necessary to take into account the composition of the type, the palatability and nutritive value of the dominants and subdominants, the duration and timeliness of the grazing season, and the effects of the climatic cycle. Most of these factors are susceptible of exact measurement, particularly the structure and yield of each type, the chemical composition of the dominants, and the response to annual variations in rainfall. Their practical significance, however, is subject to the test of actual grazing, and hence it is imperative to take into account the relation of each to the type of grazing indicated by the community. All of these relations are summed up in grazing management, in which the kind of stock, the organization of the range, and the method of handling are the determining factors. These are determined by the kind and amount of the annual yield of forage, and in turn react decisively upon it. They are considered briefly in the fol-

A. Tobosa "swag," *Hilaria* and *Scleropogon* subclimax to desert plains grassland, Las Cruces, New Mexico.

B. Playa in the *Bulbilis* subclimax stage, the old shore-line marked by *Euphorbia*, Texhoma, Oklahoma

lowing paragraphs, while their part in overgrazing is discussed in the next section, and their relation to increased carrying capacity under that dealing with range improvement.

**Relation to communities and dominants.**—The general value of climax and seral communities as grazing indicators has already been discussed. This is related directly to the carrying capacity, which is determined by the nature of the dominants and subdominants and their groupings. The value of a dominant is determined primarily by its total yield, palatability, and nutrition content, but it is affected in the most striking fashion by associated dominants. In fact, palatability is regularly the controlling factor, since a grass of high yield and nutrition content may remain untouched in a community of more palatable species, while it may be completely utilized when forming a pure community or in the absence of more succulent forage. Thus, the question of relative palatability becomes of the first importance in the study of overgrazing and of range improvement. It varies with the kind and breed of stock, with the phases of the climatic cycle, and with the year or season.

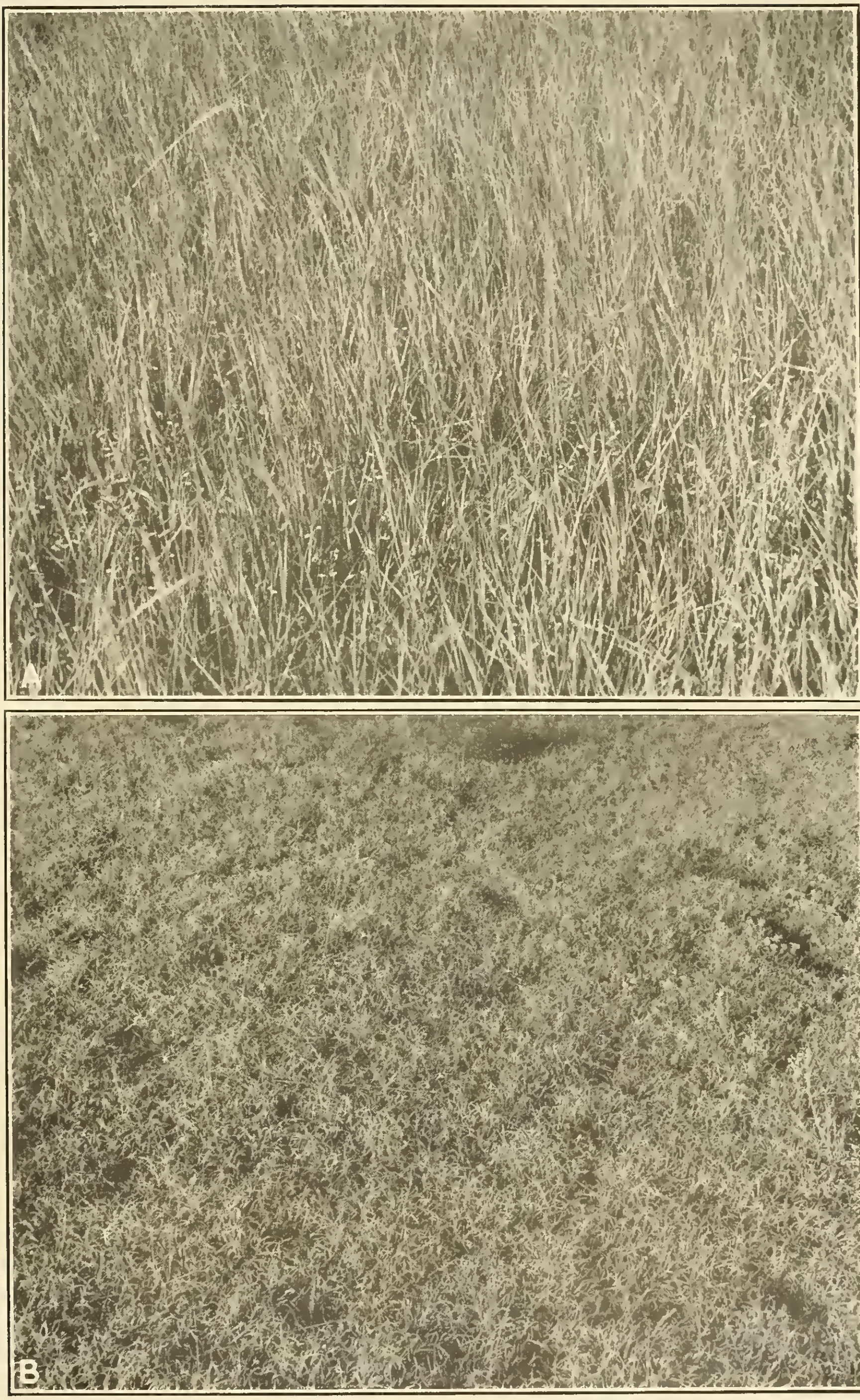
With respect to total yield, the relative importance of dominants may be best illustrated by the grassland climax. The tall-grasses produce more forage than the short-grasses, and the sod-grasses more than the bunch-grasses; but a tall bunch-grass, such as *Agropyrum spicatum* or *Andropogon hallii*, may yield more heavily than a short-grass like *Bouteloua gracilis*, though the latter is more palatable and hence more completely utilized. A short-grass like *Bulbilis*, which forms a compact turf, has a higher carrying capacity than *Bouteloua gracilis* with an open turf, while the latter excels the more open *B. eriopoda* as well as the bunch-like *B. rothrockii*. A mixed community of tall- and short-grasses has much the highest carrying capacity of all, and of these the most productive is one in which the lower layer is *Bulbilis*. Subdominants which approach the grasses in palatability have a similar rôle in increasing carrying capacity, but the great majority are less palatable and decrease the yield in proportion to their luxuriance. Grasses also affect the carrying capacity by virtue of different times of development. A community which contains *Stipa spartea* or *comata* permits earlier grazing than others, while a mixed prairie with *Stipa*, *Agropyrum*, and short-grasses not only affords the longest season, but likewise the most continuous production of forage. The relative yield of tall- and short-grasses is also affected by the rainfall of wet and dry periods. The yield of tall-grasses seems to be reduced proportionately more than that of short-grasses by a drought period and is correspondingly greater during a wet period (plate 70).

The relation of grouping to palatability is perhaps best seen in the mixed prairie and true prairie, though it exists in all communities where two or more dominants differ in this respect. In general, *Stipa comata* is most readily eaten, *Agropyrum glaucum* slightly less so, and *Andropogon scoparius* little or not at all, when they occur in mixture or as alternes. As a consequence, *Stipa* is often eaten out or kept down to such an extent that it fails to fruit. In its absence *Agropyrum* bears the brunt of the grazing and sooner or later decreases to a marked degree, thus making the short-grasses more available. In spite of their high value, the latter are less succulent and seem to be less palatable during the growing season. It is only after *Stipa* and *Agropyrum* have disappeared and the short-grasses have been grazed closely that *Andropogon* is brought into requisition. Under such conditions, which obtain frequently during drought periods, it is grazed fully as closely as the other grasses are normally. In ordinary years a similar result can be secured by burning the dead stems and keeping the bunches grazed while they are green. The relation of *Koeleria* to its associates is less clear, yet the fact that it is often present but rarely dominant, combined with its early growth and succulence, suggests that it resembles *Stipa* in being grazed heavily.

With reference to the dominants, conditions are similar in the true prairies, except for the absence of the short-grasses. Differences in palatability are expressed chiefly in the emphasis of the subdominants, with the result that they often exceed the grasses in total yield. Practically all the herbs are inferior to the grasses in palatability, and they are lightly grazed as a rule, until the grasses have begun to disappear. Various stages of this process are seen in pastures, the more palatable species dropping out first, followed by those less and less palatable until only the most unpalatable ones, such as *Solidago*, *Artemisia*, *Verbena*, etc., remain as indicators of overgrazing. The desert plains have a large number of dominants and a corresponding number of groupings. As a consequence, differences in palatability play a decisive part in them also. The species of *Bouteloua* are most readily eaten, those of *Aristida* less readily, while *Andropogon* and *Heteropogon* are eaten little or not at all until the supply of the others runs low. As a result, the presence of *Aristida* and *Heteropogon* serves to indicate overgrazing of *Bouteloua*, while their increase may be used as a measure of the degree.

Nutrition content.—A scrutiny of the following tables will show that differences in palatability are much more important than those of nutrition content, as shown by the chemical analysis of dominants and subdominants. It is surprising to find some grasses which ordinarily are grazed little or not at all possessing as high a nutrition content as the best species of the range. It is equally surprising to find that many annuals possess apparently a higher nutritive value than related perennial species of much greater grazing value. The native grasses have much the same composition as the cultivated ones, while the sedges run higher in protein and carbohydrates than the grasses. The rushes have about the same protein content as the sedges, but are slightly higher in carbohydrate. The legumes, other herbs, and dicotyl shrubs are the highest in protein, and low in crude fiber, while the shrubs contain as a rule the species of highest fat content. The emergency forage plants, such as *Dasylirium*, *Nolina*, and *Yucca*, are lowest in protein and highest in crude fiber. The cacti are lowest in crude fiber, low in protein, highest in ash, in starch, sugars, etc., and in the water-content of the green plants.

The data in the tables below have been gathered chiefly from the following sources: Cassidy and O'Brine (1890), Shepard and Williams (1894), Shepard and Saunders (1901), Knight, Hepner, and Nelson (1905, 1906, 1908, 1911), Kennedy and Dinsmore (1906, 1909), Griffiths and Hare (1907), Vinson (1911), Griffiths (1915), and Wooton (1918). The table of the average composition of different groups of plants is from Knight, Hepner, and Nelson (1911: 12), and that of average digestion coefficients from Kennedy and Dinsmore (1909: 35).



A. Mixed turf of tall-grass (*Agropyrum*) and short-grass (*Bulbilis*), Winner, South Dakota.
B. Pure turf of short-grass (*Bulbilis*), Ardmore, South Dakota.

GRASSES.

| Species. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Protein. |
|---|---|---|---|---|---|
| | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* |
| Agropyrum caninum | 4.73 | 2.00 | 36.15 | 48.56 | 8.56 |
| glaucum | 8.23 | 2.90 | 34.30 | 44.92 | 9.65 |
| scribneri | 3.86 | 2.99 | 31.26 | 52.12 | 9.77 |
| spicatum | 9.90 | 3.02 | 30.84 | 50.09 | 6.15 |
| Agrostis alba | 11.40 | 1.61 | 32.17 | 47.82 | 7.00 |
| hiemalis | 7.21 | 3.34 | 31.84 | 49.54 | 8.07 |
| Andropogon furcatus | 6.66 | 3.19 | 33.81 | 49.35 | 6.99 |
| hallii | 6.52 | 1.97 | 38.70 | 44.87 | 7.94 |
| nutans | 6.94 | 1.70 | 37.64 | 49.54 | 4.17 |
| saccharoides | 7.16 | 1.64 | 36.78 | 48.00 | 6.42 |
| scoparius | 6.05 | 2.29 | 34.39 | 51.31 | 5.96 |
| sorghum halepense | 6.33 | 3.01 | 32.36 | 44.13 | 14.17 |
| Aristida californica | 8.05 | 0.90 | 34.50 | 50.54 | 6.01 |
| divaricata | 7.20 | 2.55 | 34.89 | 49.71 | 5.65 |
| purpurea longiseta | 8.10 | 1.42 | 36.87 | 46.18 | 7.43 |
| micrantha | 9.11 | 2.01 | 28.24 | 55.36 | 5.28 |
| basiramea | 10.09 | 2.29 | 16.28 | 67.28 | 4.06 |
| Avena fatua | 8.25 | 3.18 | 30.55 | 50.95 | 7.07 |
| Bouteloua bromoides | 7.64 | 1.87 | 30.94 | 54.84 | 4.71 |
| eriopoda | 10.27 | 1.74 | 33.92 | 48.76 | 5.31 |
| gracilis | 4.86 | 1.43 | 34.68 | 50.79 | 8.24 |
| hirsuta | 11.07 | 2.59 | 34.97 | 45.10 | 6.27 |
| racemosa | 9.63 | 1.94 | 32.86 | 49.23 | 6.34 |
| rothrockii | 6.53 | 1.58 | 36.67 | 50.55 | 4.67 |
| aristidoides | 6.84 | 2.12 | 35.11 | 46.96 | 8.97 |
| polystachya | 10.07 | 1.90 | 30.90 | 42.00 | 9.80 |
| Bromus ciliatus | 7.68 | 2.21 | 35.23 | 43.94 | 10.94 |
| inermis | 6.21 | 2.71 | 29.50 | 52.11 | 9.47 |
| marginatus | 7.39 | 1.79 | 35.80 | 44.68 | 10.34 |
| hordeaceus | 11.15 | 4.95 | 29.91 | 38.28 | 15.71 |
| maximus | 9.51 | 2.89 | 28.66 | 49.88 | 9.06 |
| rubens | 4.16 | 2.07 | 33.24 | 55.00 | 5.53 |
| tectorum | 23.96 | 3.56 | 24.11 | 29.86 | 18.51 |
| Bulbilis dactyloides | 10.51 | 2.11 | 25.29 | 54.74 | 7.35 |
| Calamagrostis canadensis | 6.92 | 2.15 | 34.92 | 46.88 | 9.13 |
| purpurascens | 4.34 | 2.35 | 35.52 | 49.29 | 8.50 |
| Calamovilfa longifolia | 6.39 | 1.82 | 39.59 | 46.14 | 6.06 |
| Cenchrus tribuloides | 10.96 | 2.15 | 16.69 | 63.62 | 6.58 |
| Chloris elegans | 12.93 | 1.96 | 32.19 | 42.44 | 10.48 |
| Dactylis glomerata | 10.68 | 3.45 | 27.24 | 44.53 | 14.10 |
| Danthonia intermedia | 4.68 | 2.56 | 18.71 | 64.57 | 9.48 |
| Deschampsia caespitosa | 7.21 | 1.57 | 35.75 | 47.84 | 7.63 |
| Distichlis spicata | 10.66 | 2.15 | 29.06 | 49.50 | 8.63 |
| Echinochloa crus-galli | 9.96 | 2.28 | 31.08 | 47.12 | 9.56 |
| Elymus canadensis | 8.85 | 2.23 | 34.51 | 46.24 | 8.17 |
| condensatus | 7.96 | 2.81 | 37.77 | 41.93 | 9.53 |
| sitanion | 10.10 | 2.27 | 35.61 | 43.21 | 8.81 |
| triticoides | 6.33 | 1.97 | 39.55 | 46.32 | 5.83 |
| Eragrostis pilosa | 10.10 | 2.44 | 28.79 | 43.44 | 15.23 |
| major | 14.53 | 2.60 | 17.70 | 56.24 | 8.93 |
| Eriocoma cuspidata | 8.09 | 2.22 | 32.19 | 48.30 | 9.20 |
| Festuca ovina | 6.30 | 2.09 | 35.81 | 50.66 | 5.14 |
| scabrella | 10.64 | 1.40 | 35.58 | 43.02 | 9.36 |
| megalura | 6.23 | 1.67 | 31.17 | 53.50 | 7.42 |
| octoflora | 7.44 | 2.47 | 29.45 | 50.49 | 7.15 |

GRASSES—*continued.*

| Species. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Protein. |
|---|---|---|---|---|---|
| | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* |
| Heteropogon contortus | 6.01 | 1.44 | 33.28 | 54.79 | 4.48 |
| Hilaria cenchroides | 9.37 | 2.09 | 24.51 | 55.26 | 8.77 |
| jamesii | 8.56 | 2.41 | 31.95 | 48.39 | 8.69 |
| mutica | 8.17 | 1.66 | 32.77 | 50.32 | 7.08 |
| Hordeum jubatum | 10.83 | 3.39 | 31.90 | 42.40 | 11.48 |
| maritimum | 11.77 | 1.96 | 33.02 | 44.65 | 8.60 |
| murinum | 6.86 | 2.00 | 35.99 | 47.72 | 7.43 |
| nodosum | 5.50 | 2.62 | 30.70 | 49.47 | 11.66 |
| Koeleria cristata | 7.45 | 3.03 | 33.94 | 46.98 | 8.60 |
| Lamarckia aurea | 25.79 | 3.17 | 29.90 | 36.21 | 4.93 |
| Muhlenbergia gracilis | 5.12 | 2.59 | 25.72 | 59.72 | 6.85 |
| gracillima | 12.36 | 2.53 | 31.03 | 46.31 | 7.77 |
| porteri | 6.53 | 2.28 | 35.63 | 49.59 | 5.97 |
| Munroa squarrosa | 11.82 | 1.57 | 35.31 | 38.71 | 12.59 |
| Panicum lachnanthum | 11.96 | 2.38 | 29.97 | 45.72 | 9.97 |
| virgatum | 6.26 | 2.25 | 33.52 | 51.52 | 6.45 |
| capillare | 10.45 | 1.73 | 30.26 | 46.97 | 10.59 |
| Phleum alpinum | 4.83 | 2.33 | 32.20 | 51.69 | 8.95 |
| pratense | 7.34 | 1.94 | 37.44 | 46.30 | 6.98 |
| Phragmites communis | 7.80 | 2.92 | 35.97 | 44.40 | 8.91 |
| Poa arctica | 5.36 | 1.80 | 29.89 | 50.65 | 12.30 |
| arida | 7.14 | 2.58 | 36.76 | 47.90 | 5.62 |
| compressa | 5.74 | 2.97 | 33.73 | 50.31 | 7.25 |
| nemoralis | 6.26 | 2.59 | 31.92 | 51.60 | 7.63 |
| nevadensis | 5.05 | 2.06 | 33.68 | 52.17 | 7.04 |
| pratensis | 7.77 | 3.17 | 34.39 | 46.38 | 8.29 |
| rupicola | 4.38 | 2.64 | 26.11 | 58.19 | 8.68 |
| sandbergii | 5.09 | 4.11 | 31.43 | 51.07 | 8.30 |
| tenuifolia | 9.45 | 2.92 | 19.40 | 59.47 | 8.76 |
| Polypogon monspeliensis | 11.57 | 2.58 | 24.41 | 52.17 | 9.27 |
| Schedonnardus texanus | 7.98 | 1.77 | 38.15 | 45.94 | 6.16 |
| Scleropogon brevifolius | 8.59 | 2.02 | 30.41 | 51.20 | 7.78 |
| Setaria glauca | 13.32 | 4.34 | 16.97 | 55.91 | 9.46 |
| italica | 11.17 | 3.24 | 35.22 | 38.21 | 12.16 |
| viridis | 12.15 | 2.87 | 16.40 | 59.91 | 8.67 |
| Spartina cynosuroides | 6.16 | 2.25 | 36.79 | 47.16 | 7.64 |
| gracilis | 7.65 | 2.00 | 35.21 | 47.74 | 7.40 |
| Sporobolus airoides | 8.39 | 1.78 | 32.19 | 48.92 | 8.72 |
| asperifolius | 7.76 | 2.31 | 33.70 | 50.31 | 5.92 |
| auriculatus | 10.46 | 2.26 | 33.42 | 48.11 | 5.75 |
| brevifolius | 7.16 | 2.40 | 33.30 | 50.37 | 6.77 |
| cryptandrus | 7.05 | 1.57 | 33.49 | 50.03 | 7.86 |
| flexuosus | 6.49 | 1.31 | 34.01 | 51.13 | 7.06 |
| wrightii | 8.53 | 1.70 | 32.27 | 47.93 | 9.57 |
| Stipa comata | 6.70 | 2.31 | 34.40 | 49.73 | 6.86 |
| eminens | 6.53 | 2.37 | 38.57 | 45.38 | 7.15 |
| setigera | 8.23 | 1.57 | 36.90 | 47.20 | 6.20 |
| spartea | 4.78 | 2.46 | 23.81 | 60.61 | 8.34 |
| vaseyi | 7.80 | 2.77 | 34.08 | 41.30 | 14.05 |
| viridula | 8.04 | 2.61 | 30.87 | 49.77 | 8.71 |
| Trisetum subspicatum | 5.35 | 2.46 | 32.91 | 47.08 | 12.20 |
| Zea mays | 7.30 | 0.70 | 28.80 | 49.30 | 3.80 |

SEDGES, RUSHES, AND HORSETAILS.

| Species. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|
| | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* | *p. ct.* |
| Carex aristata | 6.49 | 2.45 | 31.55 | 49.51 | 10.00 |
| atrata | 5.99 | 2.17 | 29.08 | 50.03 | 12.72 |
| aquatilis | 6.81 | 1.44 | 31.84 | 43.74 | 16.17 |
| bella | 7.41 | 1.45 | 36.27 | 47.02 | 7.85 |
| douglasii | 6.24 | 3.09 | 29.74 | 51.87 | 9.06 |
| festiva | 5.71 | 1.79 | 29.04 | 51.09 | 12.37 |
| lanuginosa | 8.45 | 1.94 | 34.28 | 45.83 | 9.50 |
| marcida | 7.85 | 3.39 | 28.50 | 53.21 | 7.05 |
| nova | 5.94 | 2.85 | 31.67 | 47.66 | 11.88 |
| pennsylvanica | 9.59 | 2.56 | 27.00 | 44.00 | 16.84 |
| rupestris | 9.12 | 1.96 | 32.33 | 48.51 | 8.08 |
| siccata | 10.30 | 2.40 | 26.79 | 45.66 | 14.85 |
| stricta | 11.13 | 2.52 | 30.13 | 44.97 | 11.24 |
| straminea | 8.72 | 2.32 | 34.16 | 46.56 | 8.24 |
| utriculata | 8.03 | 1.61 | 30.84 | 47.28 | 12.24 |
| vulpinoidea | 9.43 | 2.18 | 30.93 | 47.25 | 10.21 |
| Heleocharis acuminata | 10.55 | 2.39 | 32.65 | 47.51 | 6.90 |
| obtusa | 13.30 | 2.73 | 29.41 | 44.47 | 10.09 |
| palustris | 18.62 | 2.14 | 26.94 | 42.79 | 9.50 |
| Scirpus atrovirens | 7.25 | 1.55 | 34.20 | 53.21 | 3.79 |
| fluviatilis | 10.24 | 1.59 | 29.07 | 48.18 | 10.91 |
| lacustris | 11.30 | 1.14 | 32.56 | 44.95 | 10.05 |
| pungens | 13.42 | 1.69 | 30.81 | 44.56 | 9.52 |
| Juncodes spicatum | 3.73 | 2.78 | 26.34 | 59.44 | 7.71 |
| parviflorum | 5.47 | 2.09 | 29.01 | 54.72 | 8.71 |
| Juncus balticus | 5.51 | 1.53 | 35.64 | 46.47 | 10.85 |
| mertensianus | 6.39 | 1.65 | 24.38 | 54.06 | 13.52 |
| nodosus | 9.32 | 1.11 | 31.25 | 45.95 | 12.37 |
| parryi | 6.38 | 1.66 | 25.90 | 49.31 | 16.75 |
| tenuis | 5.79 | 1.82 | 37.07 | 48.39 | 6.93 |
| Equisetum levigatum | 21.58 | 2.26 | 23.60 | 42.00 | 10.56 |

LEGUMES, NATIVE.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Astragalus bisulcatus | ........ | 8.23 | 1.42 | 28.76 | 43.90 | 17.69 |
| carolinianus | ........ | 9.09 | 1.34 | 28.00 | 40.23 | 21.34 |
| Hedysarum philoscia | ........ | 6.80 | 1.13 | 22.42 | 51.69 | 17.96 |
| Lotus americanus | ........ | 9.05 | 2.96 | 23.28 | 45.67 | 19.04 |
| Lathyrus coriaceus | 6.87 | 7.32 | 4.02 | 27.65 | 44.83 | 9.31 |
| Lupinus argenteus | ........ | 8.12 | 3.18 | 27.01 | 40.05 | 21.63 |
| holosericeus | ........ | 5.28 | 5.62 | 14.43 | 48.80 | 25.87 |
| leucophyllus | ........ | 5.12 | 3.64 | 15.76 | 61.64 | 13.84 |
| lyalli | ........ | 11.59 | 5.08 | 21.37 | 42.58 | 19.38 |
| plattensis | ........ | 9.17 | 1.98 | 17.93 | 57.24 | 13.68 |
| rivularis | ........ | 10.63 | 7.11 | 16.36 | 38.63 | 27.27 |
| Thermopsis divaricarpa | ........ | 5.71 | 2.87 | 26.93 | 49.32 | 15.17 |
| Trifolium dasyphyllum | ........ | 9.76 | 1.91 | 27.37 | 45.72 | 15.24 |
| monanthum | ........ | 9.37 | 6.04 | 18.83 | 41.19 | 24.57 |
| parryi | ........ | 8.42 | 2.59 | 23.78 | 45.17 | 20.04 |
| Vicia linearis | ........ | 7.93 | 1.96 | 27.16 | 40.73 | 22.22 |

LEGUMES, CULTIVATED.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| | p. ct. | p. ct. | p. ct. | p. ct. | p. ct. | p. ct. |
| Medicago sativa | ........ | 9.96 | 1.33 | 33.34 | 37.67 | 17.70 |
| Melilotus alba | ........ | 10.18 | 2.52 | 23.16 | 44.99 | 19.15 |
| officinalis | ........ | 6.57 | 1.72 | 42.47 | 34.56 | 14.68 |
| Trifolium hybridum | ........ | 8.54 | 2.02 | 31.46 | 44.34 | 13.63 |
| incarnatum | ........ | 12.90 | 2.34 | 32.58 | 38.50 | 13.69 |
| pratense | ........ | 10.23 | 2.68 | 19.01 | 49.19 | 18.89 |
| repens | ........ | 12.34 | 3.19 | 15.70 | 44.97 | 23.80 |

OTHER HERBS, PERENNIAL.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Ataenia gairdneri | 6.79 | 9.05 | 4.77 | 25.74 | 46.47 | 7.18 |
| Arenaria hookeri | ........ | 15.99 | 1.65 | 28.01 | 48.24 | 6.11 |
| Aster campestris | ........ | 10.73 | 5.45 | 21.32 | 36.18 | 26.32 |
| Balsamorhiza sagittata | 7.12 | 11.83 | 5.71 | 14.17 | 35.70 | 15.44 |
| Castilleia miniata | ........ | 9.52 | 5.26 | 12.43 | 47.23 | 25.56 |
| nevadensis | ........ | 10.21 | 9.74 | 20.62 | 49.27 | 10.16 |
| Crepis intermedia | 6.74 | 8.81 | 3.37 | 23.47 | 49.19 | 8.44 |
| Franseria discolor | ........ | 20.55 | 4.02 | 11.10 | 43.35 | 20.98 |
| Helianthella uniflora | ........ | 9.89 | 6.46 | 17.52 | 48.78 | 17.35 |
| Iva axillaris | ........ | 20.62 | 6.36 | 11.60 | 47.07 | 14.35 |
| Leptotaenia multifida | 6.15 | 8.88 | 7.04 | 21.71 | 46.35 | 9.87 |
| Pentstemon procerus | ........ | 10.21 | 9.74 | 20.62 | 49.27 | 10.16 |
| Senecio serra | ........ | 1.25 | 5.07 | 22.11 | 53.60 | 17.97 |
| triangularis | ........ | 9.16 | 5.89 | 26.68 | 39.09 | 19.18 |
| Triglochin maritima | ........ | 17.79 | 2.41 | 27.53 | 33.58 | 18.69 |
| Wyethia amplexicaulis | ........ | 10.99 | 12.76 | 10.60 | 50.58 | 15.07 |
| mollis | 6.81 | 16.16 | 3.87 | 15.98 | 46.93 | 16.25 |

OTHER HERBS, ANNUAL.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Atriplex volutans | ........ | 18.47 | .93 | 29.66 | 37.41 | 13.53 |
| Brassica arvensis | ........ | 4.47 | 32.78 | 7.77 | 23.31 | 31.67 |
| Cleome integrifolia | ........ | 10.12 | 9.00 | 17.00 | 47.04 | 16.84 |
| Erodium cicutarium | ........ | 19.04 | 2.11 | 24.13 | 42.35 | 12.37 |
| Lactuca ludoviciana | ........ | 12.56 | 7.12 | 14.00 | 47.65 | 18.67 |
| Polygonum aviculare | ........ | 5.86 | 2.87 | 20.34 | 52.05 | 18.87 |
| convolvulus | ........ | 2.37 | 3.63 | 14.60 | 70.19 | 9.21 |
| erectum | ........ | 5.59 | 1.80 | 32.11 | 48.11 | 11.39 |
| ramosissimum | ........ | 7.40 | 1.91 | 30.19 | 44.98 | 15.52 |

SHRUBS AND HALFSHRUBS, DICOTYLEDONS.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Amelanchier alnifolia | ........ | 8.11 | 10.93 | 14.38 | 50.46 | 16.12 |
| Artemisia rigida | ........ | 6.68 | 3.73 | 21.98 | 46.57 | 21.04 |
| tridentata | ........ | 7.08 | 20.95 | 21.99 | 38.81 | 11.17 |
| Atriplex canescens | 7.54 | 10.66 | 2.01 | 29.89 | 40.15 | 9.75 |
| confertifolia | ........ | 25.39 | 1.52 | 17.89 | 42.41 | 12.79 |
| nuttallii | ........ | 13.76 | 0.82 | 16.45 | 51.52 | 17.45 |
| semibaccata | ........ | 20.27 | 1.22 | 19.21 | 42.85 | 16.45 |
| Eurotia lanata | ........ | 7.61 | 1.61 | 37.56 | 40.41 | 12.81 |
| Prunus demissa | ........ | 11.66 | 13.93 | 20.38 | 45.07 | 8.96 |
| Purshia tridentata | ........ | 4.23 | 3.17 | 14.90 | 57.98 | 12.37 |
| Ribes cereum | ........ | 9.47 | 10.26 | 5.76 | 61.24 | 13.27 |
| Rosa pisocarpa | ........ | 8.37 | 14.04 | 10.18 | 46.91 | 20.50 |
| Salix spp | ........ | 8.34 | 5.60 | 17.74 | 45.53 | 22.79 |

SHRUBS AND HALFSHRUBS, MONOCOTYLEDONS.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| | p. ct. | p. ct. | p. ct. | p. ct. | p. ct. | p. ct. |
| Agave lechuguilla | ........ | 8.9 | 1.7 | 32.5 | 52.5 | 4.4 |
| Dasylirium texanum: | | | | | | |
| Leaves | ........ | 3.5 | 1.6 | 41.7 | 48.1 | 5.1 |
| Stems | ........ | 7.3 | 2.3 | 26.5 | 46.3 | 17.6 |
| Dasylirium wheeleri, leaves | ........ | 4.5 | 2.4 | 39.6 | 48.9 | 4.6 |
| Nolina erumpens | ........ | 5.6 | 2.8 | 41.8 | 41.2 | 8.6 |
| microcarpa, leaves | ........ | 2.9 | 1.5 | 46.6 | 45.3 | 3.7 |
| Yucca baccata | ........ | 7.6 | 1.2 | 34.1 | 53.5 | 3.6 |
| glauca, leaves | ........ | 8.8 | 2.8 | 32.7 | 49.3 | 6.4 |
| glauca, stems and roots | ........ | 7.3 | 0.8 | 25.2 | 61.0 | 5.7 |
| macrocarpa | ........ | 4.6 | 0.6 | 43.1 | 48.8 | 2.9 |
| radiosa: | | | | | | |
| Leaves | ........ | 6.8 | 2.7 | 28.9 | 48.7 | 2.9 |
| Stems | ........ | 9.8 | 2.1 | 25.9 | 55.9 | 6.3 |

CACTI, AIR-DRY.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Opuntia arborescens | 5.26 | 27.71 | 1.40 | 13.72 | 46.43 | 5.48 |
| arbuscula | 5.31 | 14.55 | 1.61 | 19.75 | 46.63 | 12.35 |
| basilaris | 5.08 | 19.98 | 1.90 | 11.75 | 56.52 | 3.77 |
| bigelovii | 5.89 | 15.88 | 1.70 | 17.18 | 54.43 | 4.92 |
| chlorotica | 6.03 | 18.80 | 1.85 | 20.55 | 49.21 | 3.56 |
| fulgida | 5.60 | 13.40 | 1.48 | 5.96 | 70.27 | 3.29 |
| leptocaulis | 6.15 | 16.85 | 6.45 | 12.33 | 53.29 | 4.93 |
| lindheimeri | 5.33 | 21.78 | 2.08 | 10.65 | 53.37 | 6.79 |
| macrocentra | 7.18 | 16.45 | 2.00 | 11.05 | 55.21 | 4.71 |
| mamillata | 6.26 | 16.75 | 1.70 | 15.13 | 54.68 | 5.48 |
| phaeacantha | 6.50 | 15.80 | 1.48 | 12.56 | 60.81 | 2.85 |
| polyacantha | 6.68 | 23.23 | 1.16 | 10.95 | 53.04 | 3.94 |
| robusta | 5.68 | 26.81 | 2.13 | 15.98 | 43.70 | 5.70 |
| versicolor | 5.96 | 17.49 | 1.58 | 17.85 | 50.84 | 6.28 |
| Cereus giganteus | 8.98 | 15.75 | 1.20 | 19.35 | 57.92 | 5.80 |

CACTI, GREEN.

| Species. | Water. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| Opuntia engelmannii | 77.21 | 4.18 | 0.39 | 2.62 | 14.71 | 0.89 |
| fulgida | 77.79 | 4.24 | 0.34 | 1.66 | 14.37 | 1.60 |
| lindheimeri | 80.72 | 4.44 | 0.42 | 2.17 | 10.87 | 1.38 |
| robusta | 89.62 | 2.95 | 0.23 | 1.76 | 4.81 | 0.63 |
| spinosior | 75.54 | 4.63 | 0.49 | 2.56 | 16.01 | 1.77 |
| Cereus giganteus | 87.31 | 2.20 | 0.17 | 1.44 | 8.07 | 0.81 |

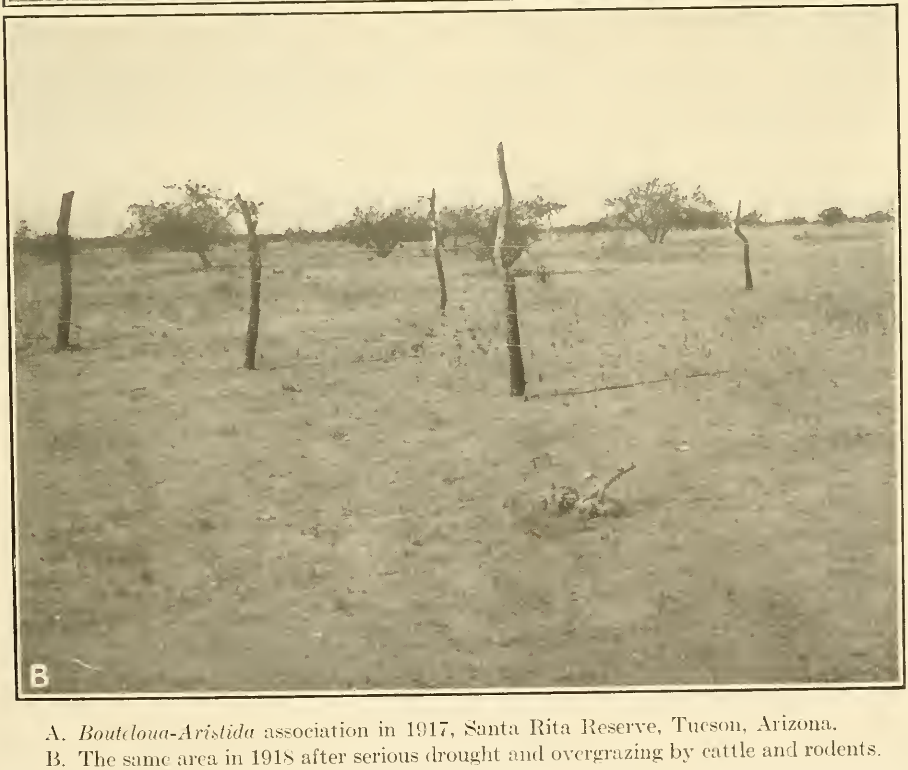
AVERAGE COMPOSITION OF PLANTS.

| | No. of samples. | Ash. | Ether extract. | Crude fiber. | Nitrogen-free extract. | Crude protein. |
|---|---|---|---|---|---|---|
| A. NATIVE. | | | | | | |
| I. Grass-like: | | | | | | |
| 1. True grasses. | | | | | | |
| *a.* Bottom lands | 44 | 8.64 | 1.98 | 34.48 | 45.89 | 9.01 |
| *b.* Bench lands | 69 | 7.48 | 2.05 | 35.92 | 46.53 | 8.02 |
| *c.* Mountains | 54 | 5.12 | 2.23 | 33.00 | 49.15 | 10.50 |
| 2. Sedges. | | | | | | |
| *a.* Bog | 32 | 8.34 | 2.26 | 30.06 | 47.49 | 11.85 |
| *b.* Dry-land | 19 | 6.79 | 2.51 | 29.57 | 49.47 | 11.66 |
| 3. Rushes | 22 | 6.24 | 1.85 | 31.21 | 50.20 | 10.50 |
| II. Not grass-like: | | | | | | |
| 1. The legumes—clovers, vetches, etc | 16 | 8.68 | 2.06 | 25.02 | 44.87 | 19.37 |
| 2. Salt-bushes | 7 | 14.18 | 1.45 | 28.28 | 41.62 | 14.47 |
| 3. Sagebrush, etc | ........ | 6.88 | 11.84 | 21.98 | 42.69 | 16.10 |
| B. INTRODUCED. | | | | | | |
| I. True grasses | 7 | 8.06 | 2.35 | 32.85 | 47.28 | 9.46 |
| II. Other than grasses: | | | | | | |
| 1. Alfalfa, clovers, etc | 18 | 9.91 | 1.92 | 30.63 | 40.28 | 17.26 |
| 2. Salt-bushes, etc | 3 | 26.94 | 1.28 | 17.02 | 37.11 | 17.65 |

AVERAGE DIGESTION COEFFICIENTS.

| | Dry matter. | Protein. | Ether extract (fat). | Crude fiber. | Nitrogen-free extract. | Ash. | Nutritive ratio. |
|---|---|---|---|---|---|---|---|
| Indian potato (Ataenia gairdneri) | 66.59 | 56.74 | 77.19 | 74.38 | 65.21 | 50.10 | 1:15.0 |
| Common sunflower (Wyethia mollis) | 60.65 | 69.46 | 63.19 | 54.41 | 61.19 | 53.01 | 1: 3.8 |
| Balsam-root sunflower (Balsamorhiza sagittata) | 66.38 | 77.28 | 74.21 | 58.69 | 74.90 | 38.29 | 1: 3.9 |
| Wild carrot (Leptotaenia multifida) | 68.76 | 71.10 | 81.49 | 47.39 | 83.04 | 53.07 | 1: 9.2 |
| Mountain indian pink (Castilleia miniata), western variety | 66.94 | 64.76 | 76.82 | 49.05 | 80.28 | 46.82 | 1: 8.9 |
| Bromegrass (Bromus marginatus) | 59.79 | 68.03 | 15.69 | 53.05 | 66.91 | 42.43 | 1: 8.5 |
| Native bluegrass (Poa sandbergii) | 52.71 | 63.90 | 49.87 | 44.68 | 60.16 | 22.69 | 1: 8.7 |
| Dandelion (Crepis intermedia) | 62.30 | 62.88 | 33.13 | 35.90 | 77.45 | 48.66 | 1: 9.5 |
| Bitter brush (Kunzia tridentata) | 76.86 | 81.70 | 71.36 | 69.54 | 86.10 | 57.48 | 1: 6.9 |
| Bitter vetch (Lathryus coriaceus) | 50.38 | 48.03 | 32.42 | 36.39 | 64.55 | 28.35 | 1: 9.4 |
| Little lupine (Lupinus sellulus) | 68.21 | 74.78 | 57.22 | 55.71 | 75.40 | 67.39 | 1: 4.2 |

Relation to climatic cycles.—No other factor produces such rapid and striking changes in carrying capacity as does rainfall. The difference in the total yield of the same range in two successive years of dissimilar rainfall may be greater than 100 per cent, and in the wet and dry phase of the same cycle it may be even greater. Such differences are often greatly augmented by the critical overgrazing which is more or less unavoidable during a drought period under existing methods of management. Since grassland is typically correlated with summer rainfall, the amount of the latter is at once reflected in the growth of the dominants. A single year of deficient rainfall affects the yield at once by decreasing vegetative growth. At the same time,



A. *Bouteloua-Aristida* association in 1917, Santa Rita Reserve, Tucson, Arizona.
B. The same area in 1918 after serious drought and overgrazing by cattle and rodents.

the storage in the propagative organs is reduced and seed production is likewise affected. If the drought continues for a second or third year, these effects become cumulative and the stand diminishes greatly in density as well as in height. During wet phases, the growth of the vegetative organs is favored and this in turn promotes propagation and reproduction, but the former especially. As a consequence, the sun-spot cycle of 11 years is clearly expressed in carrying capacity, and this is often true likewise of the 2 to 3-year cycle, particularly in the more arid Southwest. In short, grass types show a carrying capacity cycle of excess and deficit, which must be taken into account if alternate lack of utilization and overgrazing are to be avoided. Such a cycle has a peculiar significance for overgrazing and range improvement and is further discussed under these heads (plate 71).

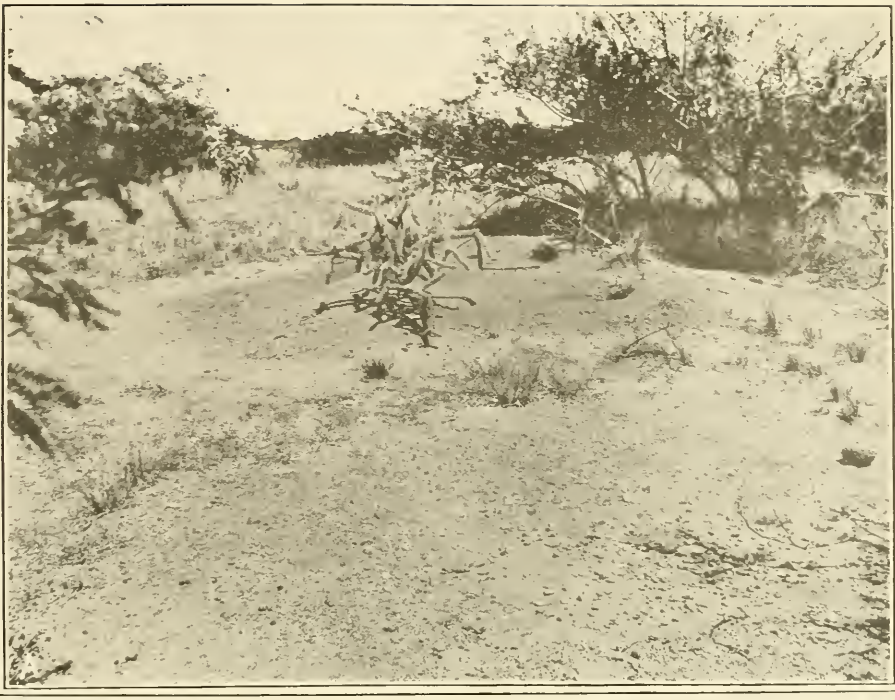
Relation to rodents.—While the damage done by prairie-dogs to native vegetation has long been known and the indicators recognized (Pound and Clements, 1898: 299; 1900: 414), it is but recently that the full importance of rodents has been realized. This has led to the extensive campaigns for the eradication of rodents, organized and carried out during the last five years by the Biological Survey, and to the cooperative studies of the kind and amount of damage to different grazing types. The plans for the first of these were drawn up by the writer, and they have been carried out on the Santa Rita Range Reserve near Tucson through cooperation with the Forest Service, the Biological Survey, and the University of Arizona. The results have already demonstrated the serious and often critical effect which jack-rabbits have upon the range and have added the kangaroo-rat to the list of rodent pests of the first importance (Vorhies, 1919). While prairie-dogs, ground-squirrels, jack-rabbits, and kangaroo-rats are the most important, pack-rats and pocket-gophers also do much damage, and there are doubtless other rodents which must be reckoned with. The reduction of carrying capacity by rodents is a serious matter at all times, but it becomes critical during drought periods. This is due to its added effect upon a range which is already overgrazed by the stock. The frequent occurrence of drought in the Southwest has greatly magnified this effect, and in some areas the grass (and even the desert scrub) has been almost completely destroyed as a consequence. It is probable that there is a rodent cycle, due to the effect of dry and wet phases upon vegetation as the food-supply, but in a local area this must be more or less modified by the effects of migration. Rodents resemble grazing animals in showing a preference for certain life-forms and dominants, as well as in adjusting themselves to less palatable species under the spur of necessity. The general features of the methods by which their habits are studied and their effects measured are given under the discussion of range improvement (plate 72).

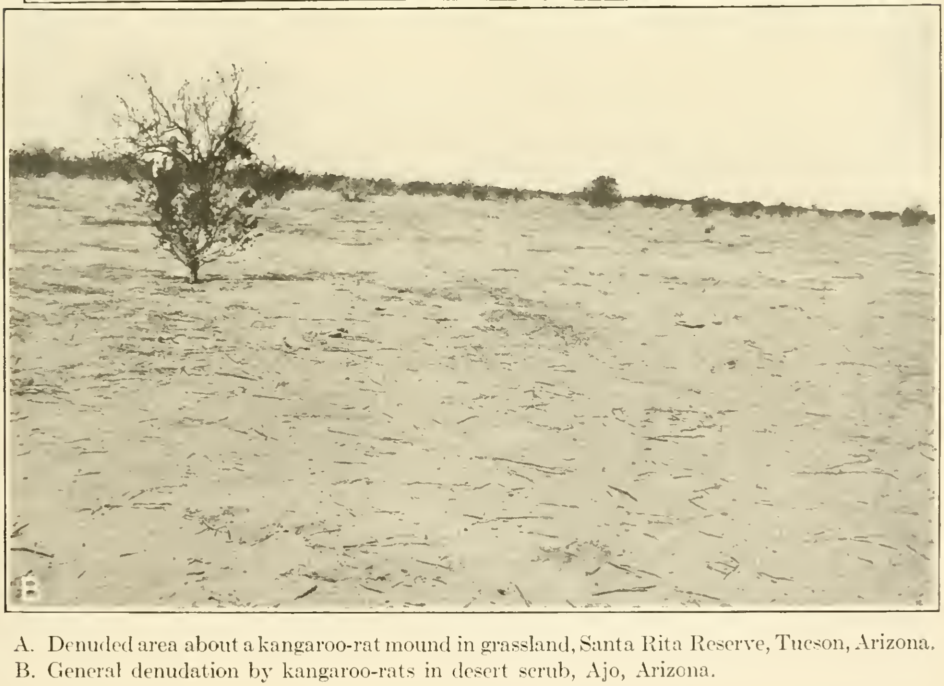
Relation to herd and management.—The recognition of the proper methods of handling stock to secure the maximum carrying capacity was first made by Smith (1899), and the importance of such methods has since been emphasized by Griffiths (1904), Davy (1902), Wooton (1908), and others. Their development into a practical system is due chiefly to the work of the Forest Service in connection with the grazing problems of the national forests (Jardine, 1908; Sampson, 1908; Barnes, 1913). The most complete discussion of the system for handling cattle has been given by Jardine and Hurtt (1917), and for sheep by Jardine and Anderson (1919: 48). The essential features are fencing or proper herding, adequate water development, deferred or rotation grazing, winter and drought feeding, and improvement of the herd. Fencing is first of all important in enabling the stockman to control his own range, but it is also necessary in order to minimize bunching and trampling, as well as to permit rotation. In the case of sheep in the national forests, the carrying capacity of the range is greatly conserved by the open or "blanket" method of herding. Proper water development insures fairly uniform utilization by reducing the distance to water, and hence decreasing the tendency of cattle to overgraze the areas about wells or tanks and to undergraze distant ones. Rotation grazing permits the utilization of types or areas under conditions which maintain the yield, and affords an opportunity for the development of reserve pastures against periods of drought. It likewise encourages the grazing of cattle by classes, such as breeding-cows, steers, etc. Feeding during winter or drought has an obvious effect upon carrying capacity. It not only conserves the actual supply of natural forage, but it also reduces the intensity of grazing in early spring, owing to the fact that the stock come out of the winter in good condition. This is especially important, as the rapid growth of the leaves in spring determines not merely the amount of summer forage, but is even more important in deciding the amount of storage in rootstock and seed, and hence the yield of the following year. In its relation to carrying capacity, the improvement of the herd depends chiefly upon efficiency in transforming grass into flesh, but partly also upon the ability to "rustle." It is evident, moreover, that carrying capacity will vary with the breed as well as the animal, and that certain breeds will be more efficient in one grazing type than in another.

**Measurement of carrying capacity.**—Spillman (Griffiths, 1904: 5) has emphasized the importance of carrying capacity as a basis for the grazing industry:

"A knowledge of the carrying capacity of the ranges is of the most importance, for it must form the basis of any intelligent legislation relating to the range question. This knowledge determines the rental and sale value of range lands, and should also determine the size of the minimum lease or homestead for range purposes in case laws are passed providing for such disposal of the public ranges."

It is evident that definite knowledge of carrying capacity can be obtained only through its measurement, and hence methods of measuring it come to be of the first importance. The best measure of carrying capacity is that furnished by actual grazing test, and all other methods find their warrant in the use of this as a final criterion. However, so many factors enter into practical grazing that experience alone is not a reliable guide to actual carrying capacity, and still less to potential carrying capacity. It must be refined and supplemented by experimental tests under controlled conditions which permit varying one factor, such as grazing type or kind of animal, while the other factors remain esssentially the same. Such grazing experiments may be intensive or extensive in scope, though it is desirable to make use of both kinds in connection with putting experimental results into practical commission. Extensive experimentation has been carried on for several years on the Jornada and Santa Rita Range Reserves by the Forest Service (Jardine and





A. Denuded area about a kangaroo-rat mound in grassland, Santa Rita Reserve, Tucson, Arizona.
B. General denudation by kangaroo-rats in desert scrub, Ajo, Arizona.

Hurtt, 1917), while intensive experiments have been made at Mandan and Ardmore by the Office of Dry-Land Agriculture (Sarvis, 1919). Whether carrying capacity is determined by general experience or measured by actual experiment, the extension and use of the measures obtained depend upon the composition of the grazing type and the abundance and size of the dominants, as determined by the quadrat method. The degree of carrying capacity depends, first, upon the number and kind of the dominants associated in any grouping; second, upon their density; and third, upon the abundance of subdominants. Once it has been found for any particular grouping by experience or experiment, it can be extended to the same or similar types in other regions by using the dominants as indicators and checking this by means of the quadrat as a measure of composition, abundance, and yield. This is especially true where protection inclosures are employed, since they readily show the increase possible in the particular grazing type.

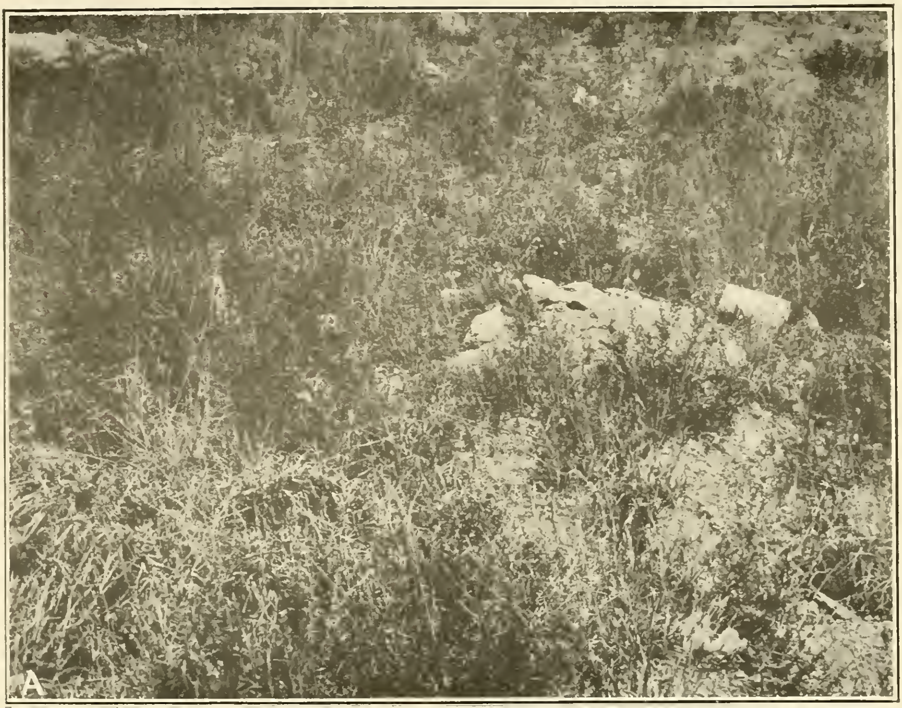
Present and potential carrying capacity—The present capacity of a particular grazing type is determined by its structure and the degree to which it is overgrazed. Its potential capacity depends upon the recovery possible under proper grazing management and the increased utilization brought about by supplementary forage crops. The actual present capacity of a range is determined by the yield during drought periods, while the potential capacity is suggested by that of wet periods, which may be several times greater. While the open range in the grassland climax has been more or less constantly overgrazed since the advent of the buffalo, the evidence indicates that the carrying capacity was higher for a decade or two after the disappearance of the buffalo and that it has steadily decreased up to the present time, except in the regions where settlement and fencing have brought about some degree of protection. During the last decade, the carrying capacity of ranges in the national forests has been increased 20 per cent or more as a result of grazing control, and it appears certain that the open range will permit much greater improvement. The amount of the latter will depend upon the difference between the present and the potential capacity. A mixed type of tall-grasses and short-grasses will have a higher potential capacity than one of either grass-form alone, though overgrazing may reduce its present yield practically to that of a short-grass type. The mixed prairie of North Dakota has been shown by Sarvis (1919) to have a carrying capacity of 1 to 7 during the drought years of 1917–18, while it might well equal 1 to 3 during wet periods. The short-grass type of the Texas Panhandle has an average capacity of 1 to 12 (Smith, 1899: 11), while in New Mexico it seems to be somewhat lower (Wooton, 1908: 27). In the desert plains, the *Bouteloua eriopoda* consociation has a capacity of 1 to 20 (Jardine and Hurtt, 1917: 17), while Wooton (1916: 22) assigns a similar value to the *Bouteloua-Aristida* communities of the Santa Rita Reserve. The short-grass types are grazed for a longer period, however, and their comparative carrying capacity is relatively higher.

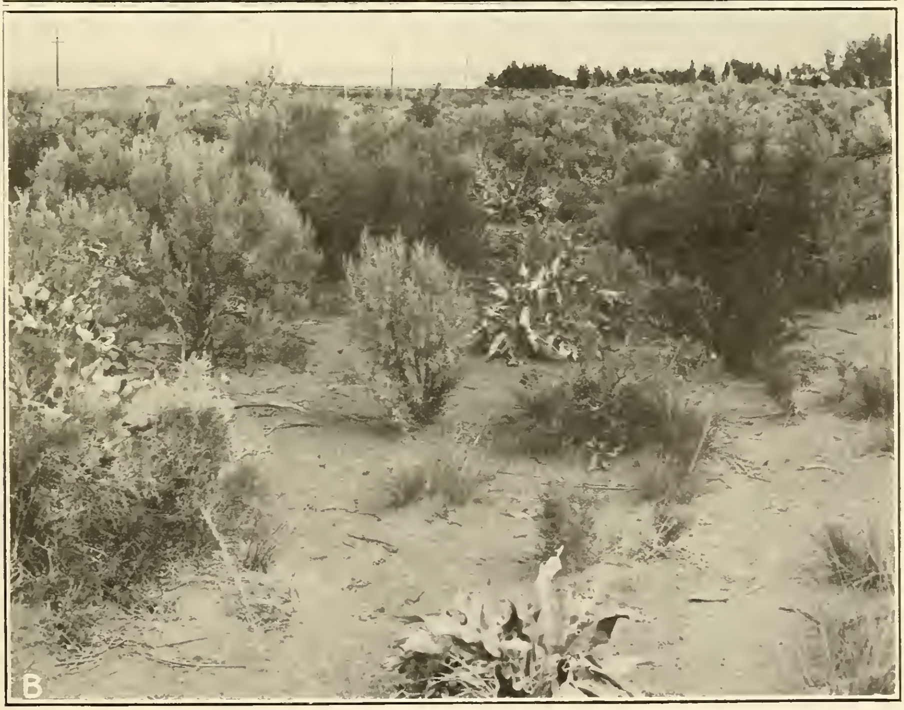
## OVERGRAZING.

Nature.—In practice, a range is regarded as being overgrazed only when its carrying capacity has actually decreased. Such a test is often indefinite because of the conditions under which the stock industry is carried on, and this explains the divergent views as to the condition of particular ranges.

While conclusive evidence as to the degree of overgrazing must be obtained from the failure of a range to maintain the herd upon it, such evidence can rarely be secured except from experimental tests. This is due to many factors, of which variations in carrying capacity with the climatic cycle and differences in management are the most important. As a consequence, it is most satisfactory to draw evidences of overgrazing from the behavior of the plant cover and to determine the degree by means of quadrat measurements. The competition between the individuals and species of the plant community is so keen and the balance so exact that the slightest disturbance can be readily detected. Grazing itself constitutes such a disturbance, and its effects upon growth, propagation, and reproduction can be minutely measured by means of the various kinds of quadrats. Such dominants as the grasses, however, have such an advantage over the subdominant herbs because of their underground parts and methods of growth that only a severe disturbance can throw the balance in favor of the herbs. When this happens, the first evidence is afforded by the increase in the number and vigor of the latter, which consequently serve as indicators. With increasing disturbance due to overgrazing, the annual members of the native flora appear in the most disturbed areas as the pioneers of minute subseres, and are later followed by introduced weeds. In the final condition the grasses will have disappeared, largely or completely, only the more weedy societies will persist, and the ground will be chiefly or wholly occupied by weedy annuals and biennials. Such a community represents one or more stages of the secondary succession and its tenure depends upon the continuance of the disturbance that initiated it. If the latter ceases, the successional process begins and soon terminates in the original climax if the grass dominants have not been killed out. Under such conditions, succession is universal and inevitable in all climaxes, and this fact lies at the basis of all methods of range improvement (plate 73).

On the basis of the maximum annual production of forage, overgrazing occurs whenever the yield drops below this point. It is evident that the maximum production can not have a fixed or average value, but that it must be correlated with the periods of the climatic cycle. A degree of grazing which would be disastrous in a drought period would fall far short of adequate utilization during a wet one. Coville (Sampson, 1908: 5) has applied the term "destructive overgrazing" to the condition in which all or part of the native dominants are killed. It is characteristic of areas overgrazed during the critical drought periods of the double sun-spot cycle. For the sake of clearness, three types of grazing are recognized here. These are overgrazing, close grazing, and reserve grazing. Overgrazing results when the proper maximum yield of a particular year or period is not obtained because of the failure to make enough food for propagation or seed-production, or because the seed-crop has been destroyed. There are varying degrees of overgrazing from a slight reduction in yield to the complete destruction of the range. Close grazing is the type in which the total annual yield is utilized in such a way as to maintain the carrying capacity. Reserve grazing is the process in which part of the annual yield is held in reserve, either by means of a reserve pasture or by understocking. It constitutes an insurance against emergencies and is specially adapted to periods of drought. In actual practice, close grazing is usually preferable for the wet phases of the climatic cycle, and reserve grazing imperative for the dry phases.




A. Relict *Bouteloua* and *Aristida* indicating former grass cover in desert scrub, Tucson, Arizona.

B. Relict *Stipa* and *Balsamorhiza* indicating replacement of grassland by sagebrush, Hagerman, Montana.

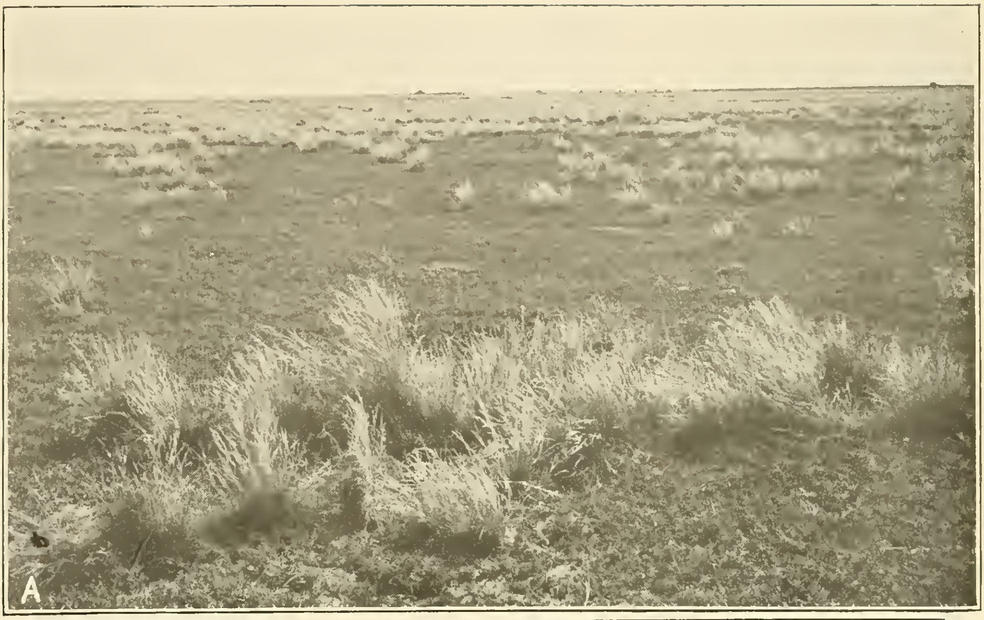
Causes.—The primary cause of overgrazing is stocking the range with more animals than it can carry and still maintain its annual yield. This has been the universal method by which the stockman has maintained a title to his portion of the open range, since an overgrazed range offered little attraction to a new-comer. Overstocking has become such a general practice throughout the West, on private lands as well as upon the open range, that stockmen have almost completely lost sight of the potential carrying capacity of their ranges. A corollary of this is the practice of year-long grazing or of grazing during too long a season, with the result that the grass does not make a proper growth in the spring or fails to ripen and drop its seeds in the fall. Trampling is an inevitable concomitant of overstocking and frequently does more damage than the actual grazing, especially in the vicinity of wells and tanks. In addition, there are several important contributory causes of overgrazing. The most important of these is the drought period of the climatic cycle. The general practice of stockmen takes no account of the great variation in yield between the dry and wet phases. The interval between them usually permits the building up of the herd to the point where the range can not carry it during the dry phase. For a year or more the range is destructively overgrazed, until the herd is moved or a large portion has died. During such drought periods as those of 1893–95 and 1916–18, the range may be so damaged as to require several years to regain a fair carrying capacity and many years to permit the development of its potential capacity. The effect of rodents upon the range is essentially a matter of overstocking. A range which is carrying thousands of prairie-dogs or jack-rabbits is in effect already stocked with a considerable number of cattle. In the usual practice, however, no allowance is made for this fact, and the rodents steadily increase the damage done by the prevailing overstocking with cattle. This double effect becomes most disastrous during the drought period and frequently results in the complete destruction of the range over large areas, especially in the Southwest. The effect of fire upon the range is relatively unimportant by comparison, but it does sometimes do serious damage to the short-grass and desert plains by killing the rootstocks, particularly during dry seasons or dry years.

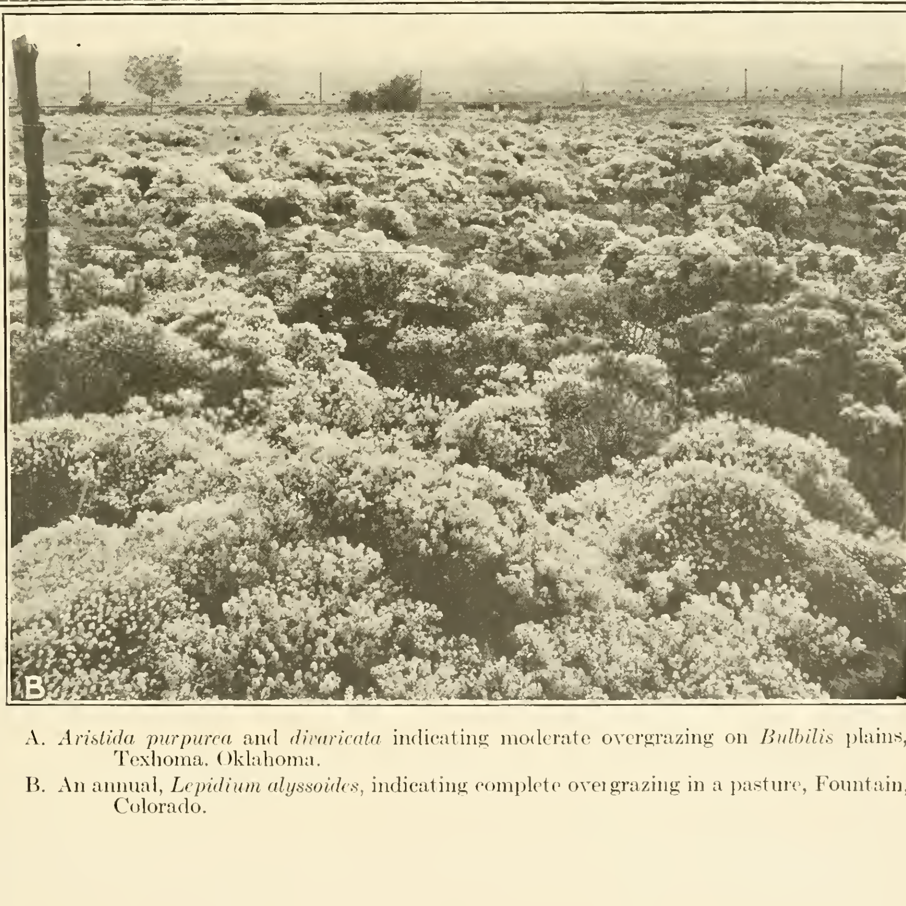
Indicators of overgrazing—In grassland and scrub practically every species may serve as an indicator of overgrazing. This is true also of herbs and shrub associes, especially those of the subsere. In the case of woodland and forest the dominants can act as indicators only in the seedling or sapling stage, but the herbs and shrubs may indicate overgrazing as clearly as in other communities. The primary basis of overgrazing indicators lies in the fact that at any particular stage some species are eaten and others are not. Thus, at any time the degree of overgrazing can be determined from both sets of plants. The best method consists in using one set as positive indicators of excessive grazing, and the other as a check upon these results; but in actual practice the most convenient indicators are naturaly those that are not eaten. In any community such relict indicators owe their importance in the first place to the fact that the more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. They receive an increasingly larger share of water-content and light, and their growth increases accordingly.

This leads to greater storage in the propagative organs as well as to larger seed-production. At the same time, the grazed species are correspondingly handicapped in all these respects, and the gap between herbs and grasses, for example, constantly widens. With the increase of the less palatable species, especially when they are bushy, the grasses are further weakened by trampling. This soon produces small bare spots which are colonized by annual weeds or weed-like plants. The latter set up a new and intense competition with the grass survivors, and these are still further decreased as a result. The weed areas widen, and sooner or later come to occupy most or all of the space between the relict herbs or half-shrubs. Before this condition is reached, however, the latter are brought into requisition for grazing and they then begin to yield to the competition of the annuals. In the case of the severest overgrazing, they too finally disappear, unless they are woody, wholly unpalatable, as in *Gutierrezia*, or thoroughly protected by spines, as in *Opuntia*.

In the grassland climax, where the effects of overgrazing have been most studied, it is possible to recognize three or four stages. The first is marked by the decrease or disappearance of *Stipa* or *Agropyrum*, or of both of them, and the corresponding increase of the short-grasses wherever these are associated; the second stage is characterized by the greater vigor and abundance of the normal societies, as well as by the increased importance of some; the third stage begins with the replacement of the grasses by annuals, while the fourth is marked by the spread of annuals and of introduced weeds generally over the area. Not all of these necessarily occur in the same spot, especially when the process of overgrazing takes place rapidly. Destructive overgrazing may result in a few years, or even in a single year, and in such instances the native vegetation may disappear completely or nearly so. It is replaced by a pioneer associes of native and introduced weeds, whose persistence will depend upon the continuance of the disturbance. These four stages indicate so many primary degrees of overgrazing, while minor degrees are denoted by the dropping out of particular dominants or subdominants. Thus in the mixed prairie, *Stipa* drops out before *Agropyrum*, because it is grazed more heavily in spring, and *Bouteloua* disappears from the desert plains before *Aristida*, owing to its greater palatability. Palatability is the chief factor in determining the successive disappearance of species, and hence the indicators of the corresponding degrees of overgrazing, though the sequence is often disturbed by the vigor of certain dominants. Since there are few species that are wholly unpalatable or inedible, it becomes possible to construct for a particular community a complete sequence of indicators, reflecting each appreciable degree in the process of overgrazing. In severe periods of drought, overgrazing may reach the point where even the annuals are eaten out and the plant covering vanishes completely. This happens regularly in pastures, corrals, and bedding-grounds where animals are kept in masses. It has even been found in desert scrub and savannah where the effects of overgrazing are supplemented by the work of kangaroo-rats (plate 74).

Societies as indicators.—The number of overgrazing indicators for the several climaxes is legion, and it is possible to consider only the most widespread and important. With the perennial grasses as a background, it is convenient to distinguish several groups of such indicators, namely, herbs, subdominant halfshrubs, cacti, seral annuals, introduced weeds, and shrubs. The first





A. *Aristida purpurea* and *divaricata* indicating moderate overgrazing on *Bulbilis* plains, Texhoma. Oklahoma.

B. An annual, *Lepidium alyssoides*, indicating complete overgrazing in a pasture, Fountain, Colorado.

three groups comprise the characteristic relict indicators, and for the most part mark the early stages of overgrazing. The annuals and weeds are typical of the later and final stages, while the shrub indicators are typical of savannahs and other ecotones where grass and scrub mix. The increased importance of societies marks the beginning of overgrazing in those associations where they are regularly present. These consist for the most part of climax herbs, but subclimax half-shrubs and grasses, such as *Gutierrezia* and *Aristida*, are often of especial significance. Moreover, many of the herbs, though regularly present in the climax, have subclimax qualities also, as is readily understood from their competitive relations to the grasses. Practically all the societies listed under the various associations of the grassland, as well as those of the other climaxes, have some value as indicators of overgrazing. In most cases this value is overshadowed by that of the most controlling and extensive societies, and the latter alone need to be taken into account.

In the following list the general order is that of importance, but this naturally varies with the locality and the season. The composites and other late-blooming species are especially serviceable, owing to their persistence (plate 75).

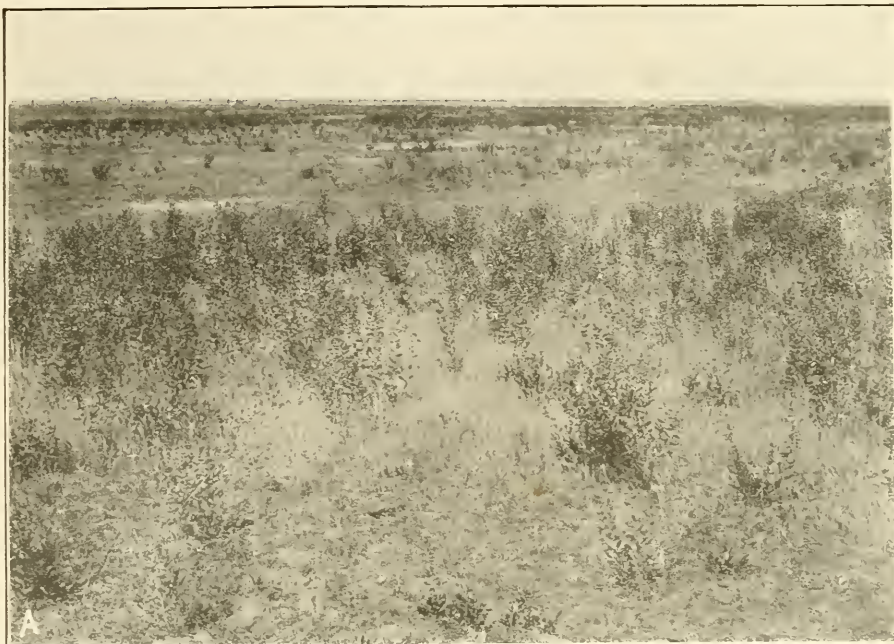
Artemisia gnaphalodes.
Artemisia dracunculoides.
Artemisia canadensis.
Grindelia squarrosa.
Solidago rigida.
Solidago missouriensis.
Solidago speciosa.
Solidago canadensis.
Solidago mollis.
Liatris punctata.
Liatris scariosa.
Liatris spicata.
Liatris pycnostachya.
Lepachys columnaris.
Kuhnia glutinosa.
Malvastrum coccineum.
Vernonia fasciculata.
Vernonia baldwinii.
Achillea millefolium.
Helianthus rigidus.
Carduus undulatus.
Senecio douglasii.
Aster multiflorus.
Aster oblongifolius.
Aster sericeus.
Senecio aureus.
Balsamorhiza sagittata.
Balsamorhiza deltoidea.
Psoralea tenuiflora.
Psoralea argophylla.
Petalostemon candidus.
Petalostemon purpureus.
Amorpha canescens.
Amorpha nana.
Dalea laxiflora.
Tradescantia virginiana.
Verbena stricta.
Verbena hastata.
Glycyrhiza lepidota.
Brauneria pallida.
Chrysopsis villosa.
Lygodesmia juncea.
Aragalus lamberti.
Polygala alba.
Antennaria dioeca.
Astragalus mollissimus.
Astragalus bisulcatus.
Astragalus racemosus.
Astragalus crassicarpus.
Lupinus plattensis.
Erigeron ramosus.
Haplopappus spinulosus.
Hymenopappus tenuifolius.
Rosa arkansana.
Euphorbia corollata.
Salvia azurea.
Asclepias verticillata.
Monarda fistulosa.
Baptisia leucophaea.
Castilleia sessiliflora.
Allium canadense.

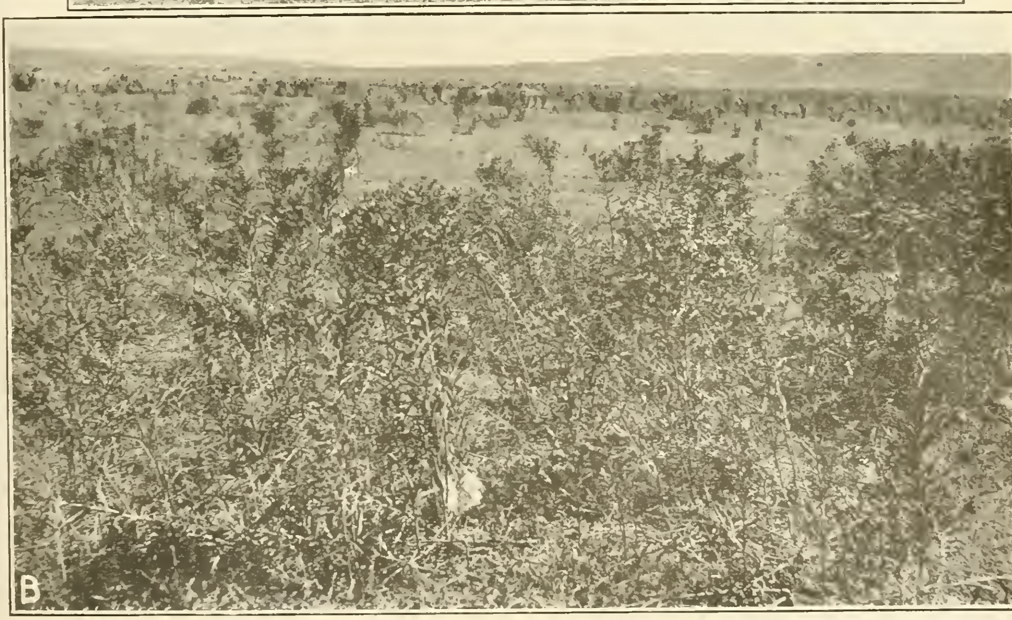
**Halfshrubs as indicators.**—Halfshrubs are best developed in the Southwest, where they are typical indicators of overgrazing in both the desert scrub and the desert plains. A few attain even greater importance in the short-grass plains and the mixed prairies. These are *Gutierrezia sarothrae*, *Artemisia frigida*, and *Yucca glauca*. The relation of the first two to grazing in a short-grass cover has been shown by Shantz (1911: 42). Over the central portion of the Great Plains they are associated as the two most serviceable and universal of overgrazing indicators. *Artemisia* is more abundant to the northward, and *Gutierrezia* to the southward, but they indicate essentially the same conditions whether alone or mixed. Differences in the degree of overgrazing are designated by variations in the density and vigor of the plants. In rough or sandy regions *Yucca glauca* is an indicator of overgrazing, though it is less important than the two just mentioned, largely because the flower-clusters are often eaten by cattle. *Eriogonum microthecum* and its variety *effusum* are common indicators in the central Great Plains, especially in more sandy areas or in sandhills. *Eriogonum jamesii* is even more frequent in a similar rôle, though it is barely shrubby (plate 76).

*Gutierrezia* is also the most important ndicator of overgrazing in the eastern portion of the desert plains and in the *Larrea-Flourensia* scrub. In western Mexico and Arizona it is largely or completely replaced by *Isocoma coronopifolia* and its varieties, which are the characteristic indicators from the lowermost *Prosopis* valleys upward into the *Bouteloua-Aristida* grassland. On the *Parkinsonia-Cereus* bajadas and hills, *Franseria deltoidea* is the indicator on lower slopes and *Encelia farinosa,* or more rarely *Chrysoma laricifolia,* on the upper, while *Franseria dumosa* and, to a less extent, *Hilaria rigida,* play a somewhat similar rôle in the *Larrea* plains of western Arizona and adjacent California. In the higher desert plains, *Calliandra eriophylla* and *Eriogonum wrightii* largely replace *Isocoma* as the most important indicator, while *Baccharis wrightii* is more local. Other halfshrubs that occur through the desert scrub in varying importance are *Zinnia pumila, Psilostrophe cooperi, Krameria glandulosa, Bebbia juncea,* and *Hymenoclea salsola.* While all of the halfshrubs of the desert scrub and grassland are normally indicators of overgrazing, they follow the rule in that practically every one is grazed to some degree when more palatable forage is lacking. This is altogether exceptional in the case of *Gutierrezia, Isocoma,* and *Franseria,* but all of these were found to be grazed more or less during the severe drought of 1918.

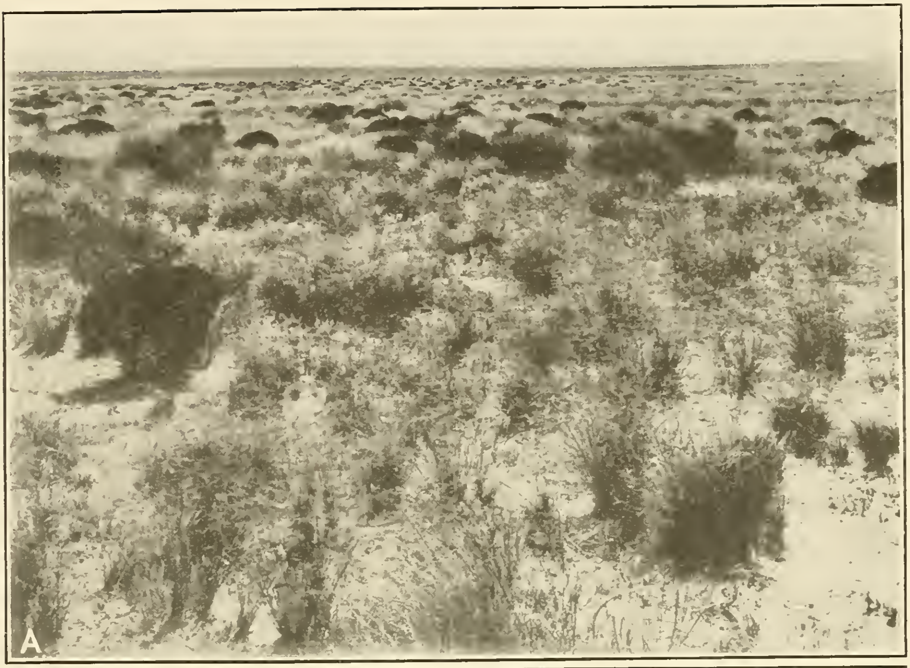
Cacti as indicators.—Cacti owe their value as indicators of overgrazing to the protection afforded by their spines. Under ordinary conditions this is almost complete protection, but during drought periods in the Southwest, cattle in particular make much use of cacti and often keep alive upon them as an exclusive diet. At such times they are utilized by jack-rabbits and pack-rats also, and the work of these rodents frequently renders the prickly pears and barrel cacti available for stock. The cacti which serve to indicate overgrazing belong almost wholly to the genus *Opuntia.* The species with flat joints are commonly known as prickly pears, and those with cylindric ones as chollas. In the short-grass plains and mixed prairies *Opuntia polyacantha* and *O. mesacantha* are the chief indicators, while *Opuntia arborescens* is often the most important species from the Arkansas Valley southward. Both owe their abundance as much to the great ease of propagation as to their spiny protection. In the case of the chollas especially, the joints a e readily broken off and carried about by cattle, and in addition they are blown off by the wind. Moreover, they are well adapted to ecesis in disturbed places, owing to their succulence and the shallow root-system. In the Southwest the most important cactus indicators in the desert scrub and savannah are *Opuntia fulgida, O. f. mamillata,* and *O. spinosior* among the chollas, and *O. engelmannii, O. discata,* and *O. phaeacantha* among the prickly pears. All these extend up into the grassland to some degree at least, but in the foothills the most common species are *Opuntia versicolor, O. arbuscula, O. bigelovii,* and *O. chlorotica. Nolina, Dasylirium,* and *Agave* resemble the cacti more or less in indicator value (plate 77, A).

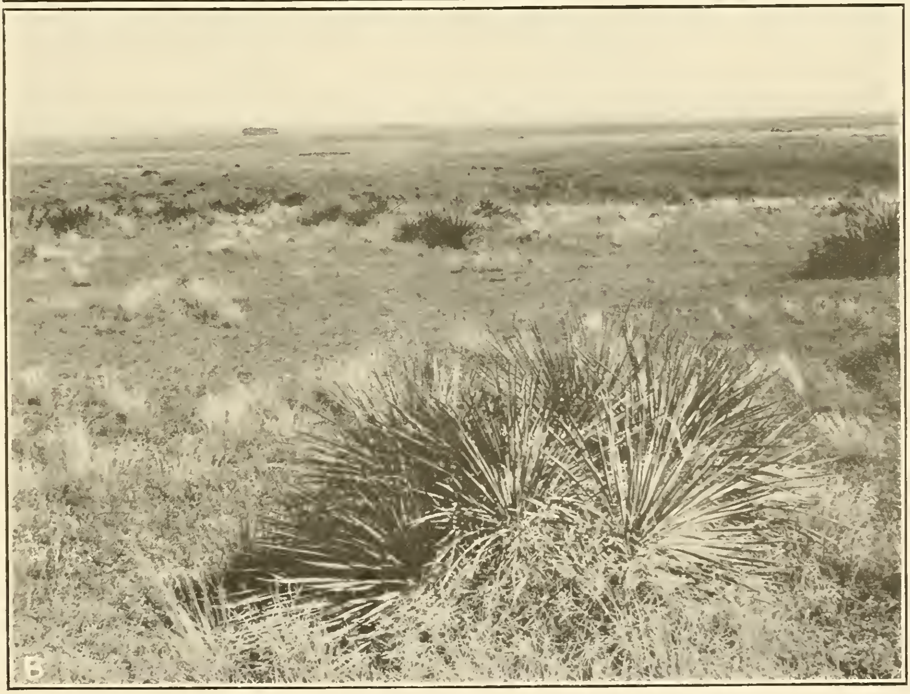
Shrubs as indicators.—The shrubs that indicate the overgrazing of grassland are chiefly such dominants of sagebrush, scrub, or chaparral as mix with the grasses to form savannah. The most important are *Artemisia, Prosopis,*





A. *Grindelia* indicating overgrazing in original *Stipa* bunch-grass prairie, Williams, California.
B. *Vernonia* indicating overgrazing in short-grass plains, Stratford, Texas.





A *Gutierrezia* and *Aristida* in short-grass plains, Albuquerque, New Mexico.
B. *Yucca* and *Aristida* in mixed prairie, Hays, Kansas.

*Acacia, Yucca, Quercus,* and *Adenostoma.* They resemble each other in that grazing gives them the advantage in competition with the grasses, partly by decreasing the hold of the latter through eating and trampling, and partly by disseminating the seeds and rendering their germination more certain. This advantage is largely or completely lost in the case of browsing animals, such as goats, since all of these are readily browsed, with the exception of *Yucca* and *Arctostaphylus.* Species of *Artemisia* are the chief shrub indicators of overgrazing in the mixed prairies, short-grass plains, and *Agropyrum* bunch-grass prairie, though various dominants of the chaparral not infrequently assume this rôle also. The most widespread and important is *Artemisia tridentata,* while *A. cana* is perhaps the most common in the mixed prairies and *A. filifolia* in sandy areas and sandhills. The lower forms, such as *A. trifida, A. arbuscula, A. rigida,* and *A. spinescens,* might well be regarded as halfshrubs. They are more or less widely distributed, but their contact with grassland is more local. In California, fragments of savannah composed of *Artemisia californica* and *Stipa* indicate a similar relation between sagebrush and grassland. This appears to have been true formerly of *Adenostoma* as well, but the observed contacts with *Stipa* grassland are as yet too few for certainty. In the desert plains, *Prosopis,* often with *Acacia* or *Celtis,* is the characteristic shrub indicator of overgrazing. It also extends northward in the short-grass plains to southern Colorado and Kansas. It is perhaps the most typical of all such indicators, owing to its height and the ready dissemination of its seeds by cattle. *Quercus virens, Q. breviloba,* and *Q. undulata,* as well as other members of the chaparral, take similar parts in the grassland of southwestern Texas and adjacent New Mexico. The rôle of *Yucca radiosa* and *macrocarpa* as indicators of overgrazing is somewhat less clear, but their constant occurrence in the sandy grasslands of the Southwest and the connection between their propagation and disturbance by cattle seem to leave little doubt of a similar correlation (plate 77, B).

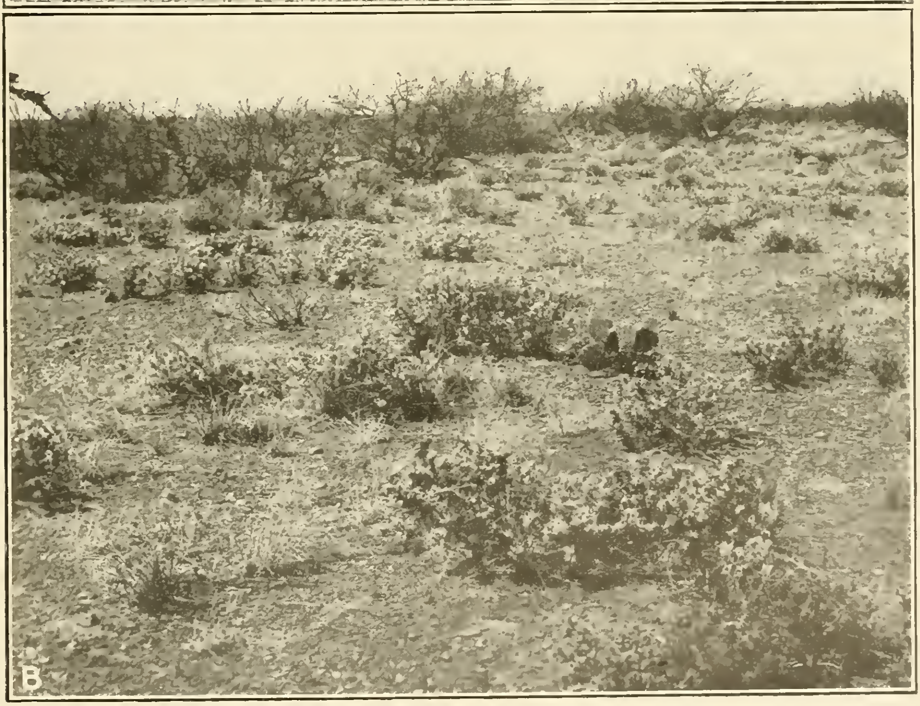
**Annuals as indicators.**—Annuals are typically indicators of serious disturbance, and hence serve to mark the existence of serious overgrazing when abundant. They are the universal pioneers of secondary successions, and they regularly disappear in the course of development. When the disturbance is continuous or recurrent, they may persist for years, but their seral nature is readily disclosed by protecting an area. In a few cases they become suppressed by the perennials and continue as a dwarfed ground layer. In the Southwest the winter rains permit a characteristic development of annuals, which complete their growth and mature their seeds before the perennial communities of the summer become controlling. Annuals usually first appear in spots denuded by trampling and extend from these throughout the community in proportion to the degree of overgrazing. Their mobility is often very great and they may take more or less complete control of a badly overgrazed range in a few years. Indications of varying degrees of overgrazing are given by differences in species as well as in density and vigor. The first annuals to appear are native species, or subruderals, which are given a chance to spread or develop because of the trampling and overcropping of the climax dominants. These often give way to more vigorous subruderals, or they become mixed with introduced weeds or ruderals, and are sometimes completely replaced by them. This is usually only when the disturbance has been long continued and the supply of ruderals maintained by the presence of man. In the case of complete replacement, such as by *Avena* or *Bromus*, fire has often played an effective part. When more palatable species have disappeared, annuals often furnish considerable grazing, though it is usually inferior in all respects to that afforded by the climax dominants displaced. *Avena fatua* is an exception to some extent, while in the Southwest the winter annuals are extremely important in tiding over the cattle until the summer grasses appear.

There are several hundred annuals which serve in some degree as overgrazing indicators. The most important ones are found chiefly in the grassland climax and its contacts with the scrub formations. Some of these extend upward into the grasslands of the montane zone, while the indicators of overgrazing in the higher zones usually belong to the same or similar genera. A few of the annual indicators extend more or less throughout the grassland formation, but most of them occur in their particular region. Hence, it seems most convenient to group them under the three heads, namely, prairies and plains, desert plains, and bunch-grass prairies.

**Prairie and plains indicators.**—While different species of annuals indicate small differences in the degree of overgrazing, the abundance and height of the plants is usually of greater importance. In addition, annual indicators have received little quantitative study, and hence it is possible only to list them in the general order of their importance. Some of those listed are either annual or biennial, and a few are typically biennial (plate 78, A).

| | | |
|---|---|---|
| Plantago patagonica. | Eragrostis pilosa. | Aster tanacetifolius. |
| Festuca octoflora. | Eragrostis major. | Aster canescens. |
| Hedeoma hispida. | Ambrosia artemisifolia. | Phacelia heterophylla. |
| Lepidium intermedium. | Salsola kali. | Allionia linearis. |
| Lepidium alyssoides. | Solanum rostratum. | Cassia chamaecrista. |
| Lepidium ramosum. | Argemone platyceras. | Coreopsis tinctoria. |
| Lappula texana. | Dyssodia papposa. | Salvia lanceolata. |
| Verbena bracteosa. | Hordeum jubatum. | Lupinus pusillus. |
| Helianthus petiolaris. | Schedonnardus texanus. | Lotus americanus. |
| Helianthus annuus. | Munroa squarrosa. | Draba caroliniana. |
| Erigeron canadensis. | Euphorbia marginata. | Myosurus minimus. |
| Erigeron divergens. | Croton texensis. | Androsace occidentalis. |
| Erigeron ramosus. | Collomia linearis. | Pectis angustifolia. |
| Chenopodium leptophyllum. | Verbesina encelioides. | Sophia pinnata. |
| Chenopodium album. | Orthocarpus luteus. | Physalis lobata. |
| Eriogonum annuum. | Polygonum aviculare. | Solanum triflorum. |
| Eriogonum cernuum. | Polygonum ramosissimum. | |

**Desert plains indicators.**—These fall into two groups, depending upon their time of appearance. The summer annuals correspond to those listed above. They occur with the grasses, and hence are a more exact measure of overgrazing than the winter annuals. Most of them are distributed throughout the region, but are more typical in New Mexico. The winter annuals develop most abundantly in overgrazed areas also, but they finish their growth before the grasses appear and hence indicate conditions of the previous year. They are characteristic of southern Arizona and adjacent Mexico. The most important ones, such as *Plantago fastigiata*, *Eschscholtzia mexicana*, *Lesquerella gordoni*, *Lepidium lasiocarpum*, *Pectocarya linearis*, etc., often form a dense cover and are invaluable for spring grazing (plate 78, B).



A. *Opuntia polyacantha* indicating overgrazing in mixed prairie, Guernsey, Colorado.
B. *Prosopis* and *Calliandra* indicating overgrazing in desert plains, Santa Rita Reserve, Tucson, Arizona.

Summer Annuals.

| | | |
|---|---|---|
| Aristida bromoides. | Kallstroemia brachystylis. | Haplopappus gracilis. |
| Bouteloua aristidoides. | Kallstroemia hirsutissima. | Eriogonum abertianum. |
| Bouteloua polystachya. | Cladothrix lanuginosa. | Eriogonum polycladum. |
| Boerhavia torreyana. | Croton corymbulosus. | Pectis angustifolia. |
| Boerhavia intermedia. | Solanum elaeagnifolium. | Pectis prostrata. |
| Kallstroemia grandiflora. | Tribulus terrestris. | Chloris elegans. |
| Kallstroemia parviflora. | Portulaca oleracea. | Eragrostis pilosa. |

Winter Annuals.

| | | |
|---|---|---|
| Plantago fastigiata. | Daucus pusillus. | Malacothrix sonchoides. |
| Eschscholtzia mexicana. | Erodium cicutarium. | Malacothrix fendleri. |
| Lesquerella gordoni. | Erodium texanum. | Oenothera primaveris. |
| Lepidium lasiocarpum. | Phacelia distans. | Calandrinia menziesii. |
| Pterocarya linearis. | Phacelia crenulata. | Baeria gracilis. |
| Bowlesia lobata. | Lupinus sparsiflorus. | Lappula texana. |
| Plagiobothrys arizonicus. | Thelypodium lasiophyllum. | Festuca octoflora. |
| Amsinckia tessellata. | Thysanocarpus curvipes. | Gilia gracilis. |
| Sophia pinnata. | Lotus humistratus. | Salvia columbariae. |

**Bunch-grass prairie indicators.**—The most remarkable development of annual indicators of overgrazing has taken place in California. This is undoubtedly a consequence of its early settlement, together with its mild climate and winter rainfall. In addition to a large number of summer and winter annuals derived from the native vegetation, the most widespread and typical indicators are European weeds, which are nearly all grasses. Many of these were probably introduced from Europe during the period of Spanish occupation, and spread rapidly as a result of overgrazing and fire. These agencies would have first brought about the replacement of the native *Stipas*, but sooner or later fire and clearing would have caused weeds to spread through much of the chaparral as well. This problem of successive invasions and replacements is now under investigation by means of permanent protected quadrats. Meanwhile, the conclusions reached by Davy (1902: 38) afford the best summary of the probable course of development (plate 79):

"1. The primitive forage plants were the 'bunch-grasses' (*Danthonias, Stipas, Melicas, Poas* and perennial *Festucas*), with annual and perennial clovers, wild-pea vines and wild sunflowers; these were much more abundant in former times than now, and on account of their palatableness they largely disappeared with overstocking.

"2. With the advent of white settlers and their domestic animals, wild oats (*Avena fatua*) and alfilerilla (*Erodium cicutarium*) took possession of the country; these increased in relative abundance as the native forage plants became scarce; as the latter diminished in quantity, the cattle took to eating the former until they in like manner succumbed, while other plants took their place.

"3. Small barley grass (*Hordeum maritimum gussoneanum*), squirrel tail (*Festuca myurus*), and soft chess (*Bromus hordeaceus*) were among the next weedy introductions; the two former, when in a maturing condition being disliked by cattle, have had a chance to spread and cover the ranges; but cattle having acquired a taste for soft chess, it is being kept in check, if not diminishing, on closely grazed ranges.

"4. A third immigration is now taking place, in which musky alfilerilla (*Erodium moschatum*), broncho grass (*Bromus maximus gussoni*), barley grass (*Hordeum murinum*, locally called fox-tail), tacalote (*Centaurea melitensis*), hawkbit (*Hypochaeris glabra*), bur-clover (*Medicago denticulata*), and other weeds are establishing themselves along the roadsides and around ranch houses. Of these, the bur-clover and musky alfilerilla have some forage value. Barley grass is eaten green in the spring before heading out, but afterwards becomes one of the most objectionable weeds for a stock range. The other aliens are destined to cause irreparable injury to the ranges unless kept in check and prevented from becoming firmly established."

With few exceptions the species listed below are summer annuals. The winter annuals of southern California are largely those noted for the desert plains, but they are here relatively unimportant. It should be borne in mind that, while the indicators given originally denoted overgrazing, some of them, such as *Avena* and *Erodium*, have become valuable forage plants as a consequence of the displacement of the native bunch-grasses, and in turn their overgrazed condition is indicated by still more weedy invaders.

GRASS INDICATORS.

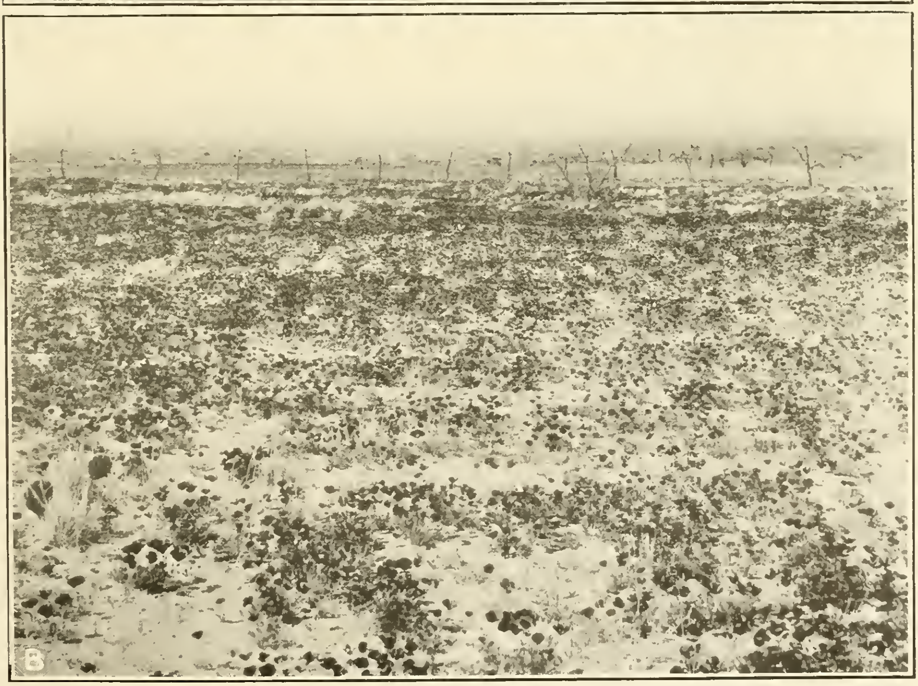
| | | |
|---|---|---|
| Avena fatua. | Bromus tectorum. | Hordeum murinum. |
| Bromus maximus. | Festuca myurus. | Polypogon monspeliensis. |
| Bromus rubens. | Hordeum maritimum gussoneanum. | Lamarkia aurea. |
| Bromus hordeaceus. | | |

HERB INDICATORS.

| | | |
|---|---|---|
| Erodium cicutarium. | Trifolium amplectens. | Trichostema lanceolatum. |
| Erodium moschatum. | Trifolium gracilentum. | Plantago patagonica. |
| Centaurea melitensis. | Trifolium tridentatum. | Epilobium paniculatum. |
| Medicago denticulata. | Medicago lupulina. | Phacelia heterophylla. |
| Hypochaeris glabra. | Melilotus indica. | Lagophylla ramosissima. |
| Hypochaeris radicata. | Raphanus raphanistrum. | Ptilonella scabra. |
| Eriogonum vimineum. | Eryngium vaseyi. | Orthocarpus purpurascens. |
| Eriogonum nudum. | Hemizonia fitchii. | Centaurea cyanus. |
| Lupinus micranthus. | Hemizonia clevelandii. | Eremocarpus setigerus. |
| Lupinus affinis. | Madia exigua. | Lithospermum ruderale. |
| Lupinus truncatus. | Madia dissitiflora. | Navarretia leucophaea. |
| Trifolium microcephalum. | Lotus strigosus. | |

Great Basin indicators.—These are limited in the present discussion to the annuals that spread over the grassy intervals of the sagebrush, especially along the northern border where it is mixed with *Agropyrum spicatum*. While a number of the annuals of the preceding list assume this rôle along the western edge, three species of introduced weeds are more important than all others combined; these are *Bromus tectorum*, *Sisymbrium altissimum*, and *Lepidium perfoliatum*. These occur singly or variously mixed. The most extensive community is that of *Bromus tectorum*, while the mixed community of *Bromus* and *Sisymbrium* is almost equally important. *Lepidium* is most abundant in the Northwest, but is rapidly spreading to other regions. While they owe their establishment originally to overgrazing, fire is a large factor in their rapid spread. They have now replaced the native grasses and herbage almost completely over thousands of square miles, and have reduced the grazing value practically to that of the sagebrush alone. *Bromus* is the only one with any real value, and this is frequently slight. It furnishes some grazing for sheep in the spring, but quickly becomes dry and nearly worthless.

Overgrazing in the past.—The condition of the great ranges of the prairies and plains before the settlement of the West and the effect of settlement upon the grasses have long been mooted questions. It has frequently been assumed that certain grasses have disappeared with the coming of the early settlers



A. A summer annual, *Euphorbia marginata*, indicating complete overgrazing in a pasture, Fountain, Colorado.

B. A winter annual, *Eschscholtzia mexicana*, indicating both overgrazing of grasses and grazing capacity, Santa Rita Reserve, Tucson, Arizona.

and that others had entered to take their place. For example, it has been the almost universal opinion of farmers and stockmen that buffalo grass vanished from the prairies with the going of the buffalo and that the bluestems had come in from the East to replace it. This opinion has been shared to a large degree by scientific men. Bessey (1887: 216) early noted the general relations of the grasses to cultivation and fire:

"Several entirely distinct species are popularly known as buffalo grass. All are, however, short grasses, unfit for making into hay, and although apparently quite nutritious, they supply so small an amount of food per acre that as the land becomes more valuable the farmer can not afford to retain them. But even should he wish to retain them, he can not; for they are unfitted to battle successfully with bluegrass and white clover, with the bluestems and rank weeds which always spring into prominence upon the prairies when the settler stops the annual prairie fires. Moreover, they can not endure the close cropping and tramping to which they are subjected when the land is inclosed and used for regular farming purposes. Already the genuine buffalo grass (*Buchloe dactyloides*) has practically disappeared from the eastern third of the State. Of course I know very well that there are patches of it here and there in these older counties; it may be found in such patches within a mile or two of the capitol building; but these little patches are as nothing when compared with its former extensive distribution. A second grass commonly known by the name of buffalo grass (*Bouteloua oligostachya*) is fast following the first.

"Buffalo grass, *Bulbilis dactyloides*, is widely spread throughout the Sandhill region. This valuable forage plant is rapidly disappearing. Its hard-awned fruits were especially suited for distribution by the buffalo, and since these have disappeared and the prairie fires are no longer allowed to sweep the plains, the buffalo grass is being rapidly choked out by the ranker species. It is the most valuable native pasture grass, but is rapidly passing toward extinction" (1893: 288).

Webber (1890: 37) states that "the buffalo grass, once the prevailing plant, is, in eastern Nebraska, found only in small patches, and is fast becoming rare," while Crandall (1890: 136) says that "this, the true buffalo grass, which once formed so large a portion of the prairie turf, is now found in this region only in isolated patches."

Pound and Clements (1898 : 246, 1900 : 350) found evidence to indicate that the buffalo grass had disappeared only where the land had been broken for cultivation.

"The buffalo grass was, until recently, supposed to have once covered the greater portion of Nebraska; its disappearance has, as a matter of sentiment, been connected with that of the buffalo. That such a supposition is entirely erroneous is beyond a doubt. The patches of buffalo grass, which are found scattered here and there over the State, are to be regarded as intrusions rather than stragglers left by a retreating species."

In 1897, Williams wrote:

"This famous range grass is still quite abundant in the regions west of the James Valley in both Dakotas. It is by no means as rare as most people suppose, being frequently overlooked on account of its similarity to certain of the grama grasses and because it seldom fruits in any great quantity." (14)

In speaking of the changes accompanying overgrazing in the Texas prairies, Smith (1899: 28) makes the following statement:

"Before the ranges were overgrazed, the grasses of the red prairies were largely bluestems or sage grasses (*Andropogon*), often as high as a horse's back. After pasturing and subsequent to the trampling and hardening of the soil, the dog grasses or needle grasses (*Aristida*) took the whole country. After further overstocking and trampling, the needle grasses were driven out, and the mesquite grasses (*Hilaria* and *Bulbilis*) became the most prominent species. The occurrence of any one of these as the dominant or most conspicuous grass is to some extent an index of the state of the land and of what stage in overstocking and deterioration has been reached. There is often a succession of dominant grasses in nature through natural causes, but never to as marked an extent as on the cattle ranges during the process of deterioration from overgrazing. On overstocked lands there is uniformly an alternation of needle grass and mesquite at short intervals, unless the overstocking is carried too far, when these perennials give way to annuals and worthless weeds."

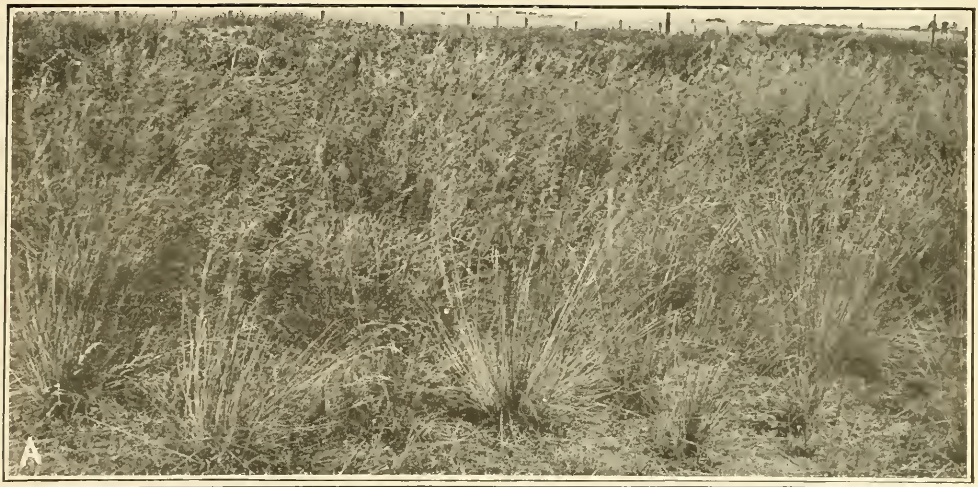
Smith (1893: 281) has suggested part of the explanation as to the varying opinions upon the condition of the range since the disappearance of the buffalo, in discussing the Sandhills of northern Nebraska:

"The theory is quite commonly advanced by stockmen and others interested in the country that the sandhills were quite bare of vegetation at a comparatively recent date and have only commenced to be grassed over since the days of the Indian and buffalo. I doubt very much the correctness of this idea. We have accounts of the sandhills written in the early part of this century which gave the salient features of the landscape about as they exist today. The region is one where physical conditions may vary greatly in a term of years. We were told by stockmen who have been located in the hills for a long time, that the soil is very susceptible to drying, that the lakes sometimes entirely disappear during periods of drought, and that one year a crop of hay may be cut where the year before there was a fine body of water. In wet years the vegetation of the valleys, which is always more luxuriant than that of the drier hills, may extend far up their slopes, while in dry years opposite conditions may prevail. If one sees the sandhill region for the first time when bare of vegetation in winter or early spring, or after the drying out of July and August, one may easily get the idea that the sandhills have never been grassed over. When the freshening up comes after the rains, he may conclude that they are becoming turfed over for the first time."

Wilcox (1911: 26) has compiled the opinions and statements of a very large number of explorers and travelers with reference to grazing conditions over the prairies and plains during the past century. These show great divergence, and many of them are directly contradictory. On the whole, however, they support his general conclusion that the range has not changed essentially, whatever its fluctuations may have been.

"The present condition of the Great Plains is essentially the same as that described by early travelers. The prevailing grasses are still the buffalo and grama, of low habit. The immense number of buffalo in the early days and later of cattle have not been sufficient to produce any marked change in the character and amount of range forage upon this area." (47)

"To one who is familiar with the present range conditions of the arid west as a whole, or any particular section of it, these statements must indicate a



A. *Stipa setigera* indicating the original bunch-grass prairie, Fresno, California.
B. *Avena fatua* on bunch-grass hills, Rose Canyon, San Diego, California.
C. *Festuca myurus* and *Bromus hordeaceus* on bunch-grass land, Corning, California

striking similarity in the appearance of the range in former times and at present. So far as the numerous statements which have been consulted indicate, the general appearance and conditions of the range country have changed but little since the time when they were first explored by white men." (45)

Succession and cycles.—The range studies of the past six years have furnished a complete explanation of the sharp difference in views as to the past conditions of overgrazing. There is no question that Smith, Wilcox, and others are correct in stating that there has been no essential permanent change in the composition and structure of the great grassland associations. On the other hand, it is equally certain that there have been great local or temporary changes, which critically reduced the carrying capacity, or actually destroyed the climax community. A broad view of the grassland climax would warrant the opinion that it had never undergone serious change, while the observation of a particular range would justify the statement that the original grasses were completely destroyed. This apparent contradiction is readily explained by the student of succession, as is likewise the fact that one observer may find good grass in the same locality where another had seen a barren waste. It is obvious that an area destructively overgrazed would be abandoned by grazing animals for an untouched portion of the same climax, and that the bare area would then pass through the various stages of succession to again reach the climax in 20 to 30 years. This is recognized by Wilcox (31) in connection with the overgrazing caused by buffalo:

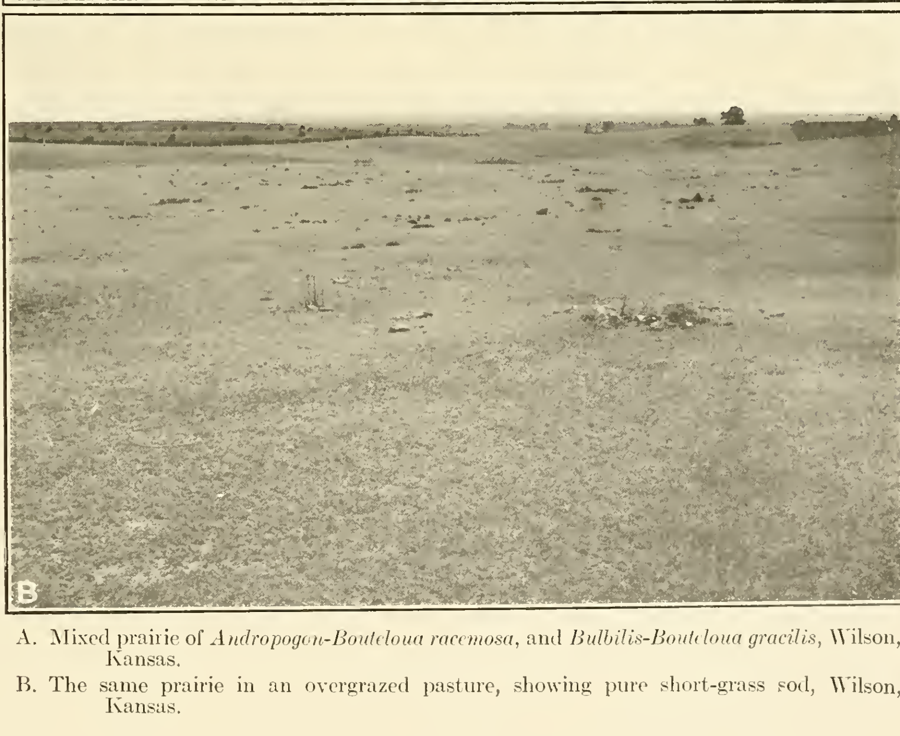
"These accounts indicate what would naturally be expected, viz, that where buffaloes congregated in immense herds the grass was totally destroyed for the time and the ground was much cut up or packed down, according as dry or wet weather prevailed. The result of such accumulations of large herds was the apparent total destruction of the grass. It should be remembered, however, despite the fact of apparent total destruction wrought by the buffalo along the line of their migration and during their close association at breeding seasons, the range recovered so that the evidence of their destructive grazing was entirely lost within a few years. This fact indicates also the possibility of range improvement at present."

While great variations in the condition of the range can be explained by local overgrazing and subsequent recovery as a consequence of succession, further explanation can be found in the action of climatic cycles. The chief effect of the dry phase of the cycle was found in the impetus given to overgrazing, while the wet phase favored successional processes and hastened recovery. Climatic changes also serve to explain many of the contradictory statements as to the same locality. Even under ordinary conditions of grazing, the same area would be strikingly different during a drought period and the preceding or following wet phase. If it were visited at a time when drought and overgrazing coincided, and then at one in which more or less complete recovery were followed by a wet period, no greater contrast could be imagined. Moreover, while the effects of overgrazing were usually local, those of drought periods were general for the most part, and hence climatic cycles are especially important in furnishing the explanation of the discordant statements of explorers. The effect of drought in changing the dominants of the range is illustrated by the grassland south of the Niobrara River. In 1893, this was dominated by *Aristida purpurea* and *A. basiramea* as a result of drought and overgrazing, while by 1915 the awn-grasses had been completely replaced by the mixed prairie of tall-grasses and short-grasses, which was undoubtedly the original climax.

Relations of tall-grasses and short-grasses.—The explanation of the apparent replacement of buffalo grass by the bluestems, as well as the general replacement of tall-grasses by short-grasses, has been found in the effect of grazing upon such a mixed community. This effect is naturally increased by drought periods, and it is especially in connection with such periods that the impression of a permanent change arises. Mixed prairies of tall *Andropogon* or *Stipa spartea* with short *Bulbilis* and *Bouteloua* are found in central Nebraska and Kansas, and also in the eastern Dakotas, while in western Nebraska, the Dakotas, Montana, and Wyoming they consist of *Agropyrum* or *Stipa comata* with *Bulbilis, Bouteloua,* or both of them. It is in these regions that the view has been more or less general that the tall-grasses have replaced the short-grasses as a consequence of the disappearance of the buffalo and the coming of man. This view has been held by so many keen observers, both practical and scientific, as to indicate that it has an actual foundation of fact. This has proved to be the case, but it was impossible to recognize the basic facts until the principles of successions were brought into use. A particular study of the effects of overgrazing upon mixed prairie with respect to wet and dry periods has been made since 1914. This quickly revealed the fact that the short-grasses were often completely hidden by the tall ones in times of unusual wetness, such as 1915, and that overgrazing regularly brought the tall-grasses to the point of apparently complete disappearance during drought periods. These facts have been repeatedly confirmed in adjacent grazed and ungrazed areas throughout the mixed prairie from North Dakota to Kansas, and they are regarded as furnishing a complete explanation of the apparent disappearance of the short-grasses and the invasion of the tall ones.

There is general agreement as to the damage done to the range by buffalo, as well as to the enormous number found on the prairies and plains from 1865 to 1875, when settlement was taking place most rapidly. In fact, the application of the term buffalo grass to the short-grasses is in harmony with the action of overgrazing in suppressing or destroying the tall-grasses. The westward movement of the buffalo and their decrease in numbers coincided with the incoming of settlers and the decrease of prairie fires. The immediate result was renewed growth of the tall-grasses, especially *Andropogon*, in areas where it had not been completely killed, and its invasion into others where it had disappeared. This tallies with the statement that the bluestems followed in the wake of the settlers, and drove out the buffalo grasses. The error involved in this is best illustrated by the statements of Bell (1869: 1:26, 43):

"Before we reached Salina, trees had become very scarce; but as we moved farther, the short tender buffalo grass gradually appeared—at first only here and there, but at last it abounded everywhere; and ever and anon we crossed the well-beaten path of the monarch of the plains. Doubtless no grass could bear so well the heavy tramp of thousands of buffalo continually passing over it; but it is a good thing for the land that, as settlers advance and domestic herds take the place of big game, the coarser, more vigorous, and deeper-rooted grasses destroy it and take its place. These new-comers grow with great luxuriance, yielding very fine hay; and at the same time loosening the sod, opening up the soil, and retaining the moisture in the ground."



A. Mixed prairie of *Andropogon-Bouteloua racemosa*, and *Bulbilis-Bouteloua gracilis*, Wilson, Kansas.

B. The same prairie in an overgrazed pasture, showing pure short-grass sod, Wilson, Kansas.

The route followed by Bell from Manhattan to Salina, Fort Harker, and Hays was retraced in 1918 for the express purpose of determining the relations of the bluestems and buffalo grasses. Both buffalo grass and grama were found on the ridges and upper slopes about Manhattan, though they were secondary to the tall-grasses in importance. This relation continued westward to the Dakota hills about Kanopolis, where the short-grasses became more abundant, equaling the tall-grasses, and mixed or alternating with them. This general condition continued to Hays, but with the short-grasses increasing in abundance Beyond Hays, they soon became controlling, though the rough bluffs along the streams maintained their mixed cover. Throughout the region from Kanopolis to Hays, overgrazed pastures exhibited a pure short-grass cover, while protected or less grazed areas showed a mixture of tall-grasses and short-grasses. It is clear that the short-grasses could not have been replaced by the tall ones as a consequence of settlement, and then have reentered the same areas under conditions of increasing cultivation. The obvious explanation is that while they have been associated in the mixed prairies for thousands of years, the tall-grasses were kept down by the buffalo in the zone of concentration resulting from advancing settlement. They reappeared with the going of the buffalo, and the disappearance of the buffalo grasses was nothing more than their being overtopped by the bluestems (plate 80).

Drought periods doubtless played a part in the behavior of the bluestems and buffalo gra ses, as they certainly did in the mixed prairies of Nebraska and the Dakotas. In 1893 the gumbo plains north of the Niobrara River were dominated chiefly by *Bulbilis* and *Bouteloua gracilis*, as a consequence of excessive drought and overgrazing. In some places a pure cover of *Bulbilis* stretched for many miles, almost unbroken by societies. This region has been revisited several times from 1915 to 1918. The stretches of buffalo grass and grama have disappeared, and in their stead is a mixed prairie of *Andropogons*, *Agropyrum*, and *Stipa*, below which is a more or less well-developed layer of short-grasses. The drought of 1893–95 had a similar effect upon the mixed prairies of western Nebraska, in which *Stipa* was the most conspicuous dominant. This disappeared so completely, leaving a pure short-grass cover, that it was regarded as a new grass invading for the first time when it reappeared in great quantity during the rainy years of 1897–98. Williams (1898: 54) has shown that dry periods have the same effect upon the appearance of *Agropyrum* in the mixed prairies of the Dakotas. It was thought that the tall-grasses might again disappear apparently during the drought period of 1916–18, but this took place only in overgrazed pastures, showing that overgrazing is an essential feature.

Overgrazing cycles.—The existence of cycles of overgrazing is beyond question, and it is possible to recognize several kinds. The simplest and shortest is brought about by such destructive overgrazing that the area will no longer support the animals upon it. In the case of wild animals, such as the buffalo, horse, etc., the herds sought a new range, while on restricted areas the cattle died from starvation or were shipped out. In either event the grasses were given an opportunity to regenerate, or in the worst cases the processes of succession brought about a gradual return to the original conditions. Such overgrazing cycles correspond to the cycle of a subsere, and are relatively short, lasting 10 to 15 years on an average. Such cycles also occur when overgrazed or worn-out pastures are permitted to "rest." A much more important cycle is that of the double sun-spot period, namely, 22 to 23 years. This is due to the fact that overgrazing has much more serious consequences during maximum periods of drought, such as 1871–73, 1893–95, and 1916–18. The effects upon the range and the herd are much more marked than when overgrazing alone is concerned, but an enforced period of rest ensues, during which successional processes bring about the restoration of the original grass cover, unless again disturbed by overgrazing. It is this cycle which, in its beginning, has been especially disastrous to the grazing industry of the West, just as the subsequent and inevitable regeneration through succession offers the solution of all overgrazing problems. In addition, there are major cycles of overgrazing, such as are involved in the permanent migration of great herds from one region to another, or in the appearance of new species or groups of grazing animals. Some such cycle must have marked the reintroduction and spread of the horse over the plains of the Southwest. The consideration of such cycles is beyond the scope of the present treatment, and is reserved for another place.

The recognition of past and present cycles of overgrazing is of great practical importance. Its greatest value lies in the certainty that a range will return to its normal condition once it is given a chance to regenerate. It also emphasizes the fact that it usually takes several to many years to really "wear out" a range, and that the rate of recovery is roughly proportional to the length of the period of overgrazing. All the statements agree as to the excessive damage done to the range by buffalo, but it seems certain that the more or less complete rest which followed brought about a fair degree of recovery in a few years. This is not an excuse for overgrazing, since the latter always involves a distinct economic loss, the amount depending upon the period and the intensity, but it does make it clear that all overgrazed ranges can be certainly and greatly improved by proper rest or rotation. This is the basis of all range improvement, as is shown in some detail in the next section.

## RANGE IMPROVEMENT.

History.—The first proposal to improve the ranges of the West by rotation grazing was made by Smith (1895: 323), although suggestions for their improvement by planting cultivated species had been made by Bessey (1887, 1893, 1897), Georgeson (1895), and others. It is probable that the first suggestion as to the good effects of resting the range came from the ranchmen (Williams, 1898: 72), and it is not impossible that the practice of the buffalo in leaving overgrazed regions had also led to this conclusion. In his two papers of 1895 and 1899, Smith outlined the major features of range improvement, while at the same time Williams (1897, 1898) proposed those which had to do with the artificial treatment of the range. The system advanced by Smith comprised (1) proper stocking, (2) rotation, (3) adequate water development, (4) destruction of rodents, (5) destruction of weeds and cacti (6) disking the soil, (7) sowing and planting, (8) provision of forage, and (9) winter protection. He was also the first to organize definite grazing experiments to determine carrying capacity and the effects of rotation. The method suggested by Williams involved (1) proper stocking, (2) harrowing the soil,

(3) top-dressing with stable manure, (4) sowing wild or cultivated forage plants, (5) keeping weeds mowed, (6) water development, (7) rest. Since the work of these two pioneers in range improvement, the subject has been discussed more or less completely or from various sides by Bentley (1898, 1902), Nelson (1898), Shear (1901), Griffiths (1901, 1902, 1903, 1904, 1907, 1910), Davy (1902), Cotton (1905, 1908), Wooton (1908, 1915, 1916), Sampson (1908, 1909, 1913, 1914, 1918, 1919), Jardine (1908, 1911, 1912), Thornber (1910, 1914), Wilcox (1911), Barnes (1913), Darlington (1915), Barnes and Jardine (1916), Potter (1917), Jardine and Hurtt (1917), Clements (1917, 1918, 1919), Sarvis (1919), and Jardine and Anderson (1919).

The first experimental study of grazing was carried on at Abilene and Channing, Texas, from 1899 to 1901 by Smith and Bentley (p. 20). Experiments under practical grazing conditions have been made on the Jornada and Santa Rita Range Reserves of the Forest Service for the past seven years. Intensive studies in smaller pastures and hence under closer control have been carried on by the Office of Dry-Land Agriculture at Mandan, North Dakota, since 1915, and at Ardmore, South Dakota, since 1918. Both the field and experimental studies have conclusively demonstrated the essentials of range improvement and have made it possible to outline a complete system based upon investigation as well as practice.

Prerequisites.—In addition to the actual processes concerned in improving the range, certain factors are prerequisite to any improvement or necessary for the best results. By far the most important of these is adequate control, without which improvement is all but impossible. It is immaterial whether control is secured through ownership or leasing, provided it permits fencing. However, leasing has the indirect advantage that it enables the State to exact certain conditions as to utilization. The value of control in preventing overstocking and permitting rotation is obvious. Next in importance is a practical appreciation of the inevitable recurrence of dry and wet periods and their critical effect upon the range. It is imperative that the ranchman be prepared to reduce the pressure upon his range as the dry phase of the climatic cycle approaches and that he be ready to take full advantage of the excess carrying capacity of the wet phase. In fact, the whole system of improvement must be focussed upon the destructive effect of overgrazing in dry years and the possibility of greater utilization and of successful sowing and planting during wet years. Furthermore, there must be some recognition of the universal processes of succession and their importance in regeneration. It is necessary to take into full account the fact that destructive overgrazing, trampling, and other disturbances will destroy the grass communities and make place for one of weeds. Even more important is the recognition of the fact that weed communities will be maintained indefinitely by continued overgrazing or disturbance, or that they will slowly give way to the returning grasses if the area is protected for a time. In short, an elementary understanding of successional processes furnishes a tool for manipulating the grazing cover more or less as desired. Finally, a trustworthy idea of the condition and tendency of the range is impossible without adequate methods of measurement. In practice, such methods can best be supplied by indicator plants, and by a careful check upon the condition of animals when they enter and leave the range. In both investigation and demonstration, however, more accurate measurements are necessary, especially in connection with the varying carrying capacity of wet and dry periods. Changes in composition and variations in production year by year can be determined only by the use of permanent quadrats. Some of these are charted, while others are clipped and the herbage weighed. The most significant measurement, however, is that furnished by weighing the individual animals from month to month, or at the beginning and end of the season.

Essential factors.—Range improvement may be effected in some degree by any one of a large number of processes. Thoroughgoing improvement, however, must take them all into account, in so far as they are concerned in a particular range. It is obvious that some of these, such as proper stocking and rotation grazing, are of universal importance, while others, such as the eradication of prairie-dogs or poisonous plants, apply only to certain ranges. The essential features of the complete system of range improvement proposed here are: (1) proper stocking; (2) rotation or deferred grazing; (3) eradication of rodents, poisonous plants, weeds, etc.; (4) manipulation of the range by clearing, burning, etc.; (5) improving the cover by sowing and planting; (6) forage development; (7) water development; (8) herd management. Contributing factors are found in classification and range surveys, the economic aspects of ranch management, and an adequate land system. Practically all of these have been regarded as more or less essential to range improvement since the first proposals of Smith, 25 years ago, and the present treatment assumes only to correlate them more closely and to work some of them out in greater detail. The distinctive features of the system are the use of climatic cycles and succession as universal bases, the employment of indicator plants, the use of inclosures and exclosures together with permanent quadrats as measures, and the development of new methods of manipulating and modifying the range, especially in the production of mixed grazing types.

Proper stocking.—The primary object of range improvement is to secure and maintain the maximum carrying capacity. The chief factors in this are proper stocking and rotation grazing. The optimum degree of stocking, however, can be determined only by actual trial accompanied by measurement of the results. Such trials can be made by the ranchman himself wherever he has control of his range, but until their necessity becomes generally recognized they must be made for the different grazing types by the experiment stations and similar agencies. The investigation of carrying capacity by actual grazing test can be made by either the extensive or intensive method. The first is more practical on ranges as they exist; the latter is more accurate and demands a greater equipment. The results of an extensive study of carrying capacity on the Jornada Reserve have been brought together by Jardine and Hurtt (1917: 12). Eight different grazing types occur on the reserve and the carrying capacity varies greatly for the different communities. Permanent quadrats were employed to determine variations in yield from year to year, as well as the rate of increase under rotation or protection. Since both rotation and reserve grazing were necessarily practiced, no definite studies were made of the basic carrying capacity under full grazing for the entire season. Such studies are possible only under the intensive method and in an essentially uniform type. Their great value lies in making it possible to check the assumed optimum carrying capacity by rates of grazing which reveal both over- and under-utilization, and in demonstrating the additional gain resulting from rotation methods. Installations for the intensive study of carrying capacity and rotation grazing have been made by the Office of Dry-Land Agriculture at Mandan and at Ardmore. Both are located in the mixed prairie, the one in *Stipa-Bouteloua,* and the other in *Bulbilis-Agropyrum-Bouteloua.* Since the methods are essentially alike, it will suffice to describe briefly the experiments at Mandan, which have been under way since 1915.

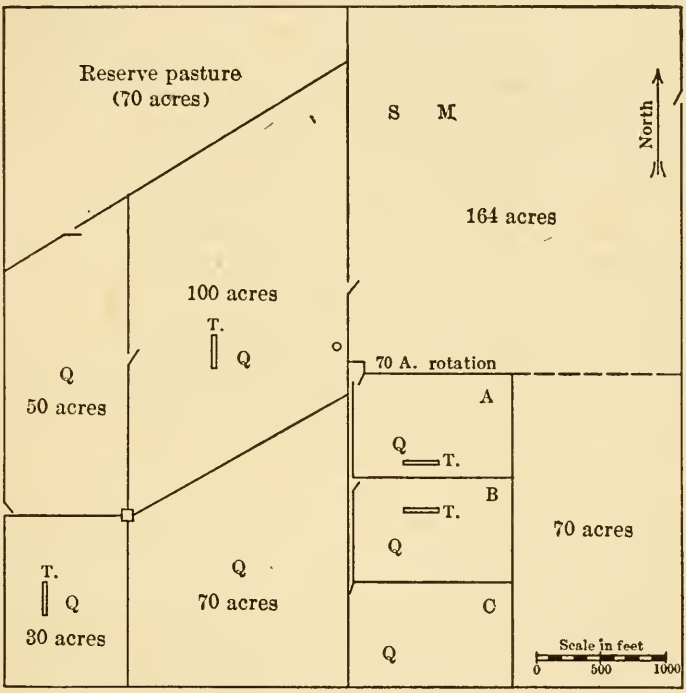



Fig. 22.—Pastures for the intensive study of carrying capacity and rotation grazing, Mandan, North Dakota. After Sarvis.

There are four pastures for the investigation of carrying capacity under continuous grazing, two for rotation grazing, a reserve pasture, and one for the study of hay development (fig. 22). At Ardmore two pastures are devoted to continuous grazing and the same number to rotation. The four pastures contain respectively 30, 50, 70, and 100 acres. Since each pasture is grazed by 10 two-year-old steers, the corresponding rates of grazing are 1:3, 1:5, 1:7, and 1:10. Each pasture contains an exclosure termed an isolation transect (fig. 23), which is 300 feet long and 60 feet wide. This consists of three strips, of which the central one, *P*, serves as permanent transect for annual comparison with the grazing and regeneration transects on either side, as well as for the installation of permanent quadrats of various types. One unit of the grazing transect, *G*, is unfenced for each year of the climatic cycle, while one of the regeneration transect, *R*, is fenced for each successive year of the cycle. The central position of the permanent transect permits ready comparison between the protected area and those fenced and unfenced for each successive year, as well as actual measurement in all three areas by means of chart and clip quadrats. Similar quadrats are located in the open pasture, thus completing the measurement of all areas year by year. It is evident that the grazed transect will also show in series the effects of unfencing for 14, 13, etc., years down to 1, and that the regeneration transect will show those of fencing for a similar series of years. Finally, special quadrats are located in the transect to reveal the effects of burning or clipping at various times and intervals.

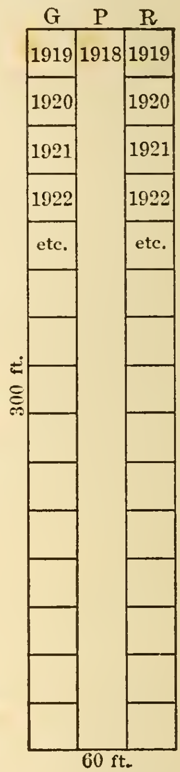
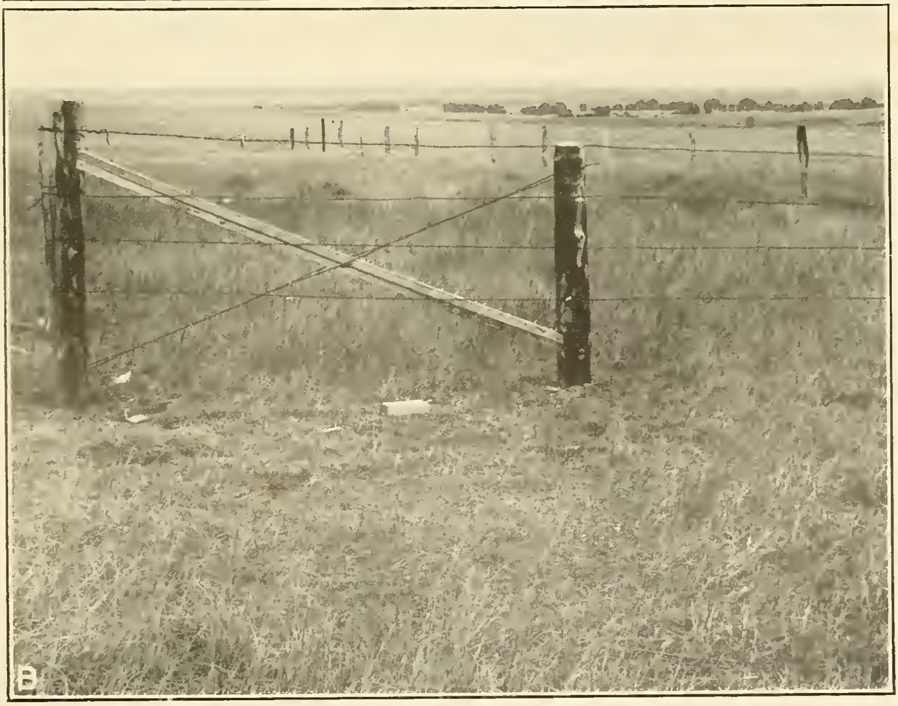


Fig. 23.—Isolation transect for measuring cyclic changes in yield under protection and under grazing.

With reference to the cattle to be used, it is necessary that they be of the same breed, age, and class, and in as nearly the same condition as possible. It will probably prove desirable to determine the carrying capacity of the same grazing type for different species, as well as for different breeds, etc., but this will require pastures of the same size and involves an expansion of the work which is unnecessary at present. The cattle are weighed at the beginning and end of the grazing season and at monthly intervals during it. This is accomplished by means of four corrals, one for each pasture, leading to the scales for weighing (fig. 24). A special method of management has been developed for handling the cattle in the pastures and at the times of weighing, the main details of which have been given by Sarvis (1919). The detailed results of the experiment have not yet been published, but the evidence furnished by the various pastures, in terms of cover and indicator plants, has been most striking (plate 81), and these have been verified by the behavior and weights of the different herds.

**Rotation grazing.**—First suggested by Smith in 1895 and begun experimentally by him and Bentley in 1899, rotation grazing has been developed chiefly by the Forest Service since 1910. The scientific basis for deferred and rotation grazing was largely developed by Sampson (1908, 1909, 1913), and it has been applied to actual grazing on the national forests. It has had its most thorough demonstration on the Jornada and Santa Rita Range Reserves, but especially on the former. Pastures for the study of rotation were installed at the Mandan and Ardmore stations in 1918, but conclusive results can not be expected for several years. Rotation grazing is an inclusive term which is regarded as applying to all methods of alternate grazing and rest, partial or complete. Deferred grazing is the type in which the pasture is completely protected or only lightly grazed during critical periods in the life-history of the chief dominants. This is usually the period of seed-production, but on certain types it may fall at the opening of the growing season. Reserve grazing is that in which a pasture is kept in reserve for emergencies, especially those due to drought, or where the grazing during the season, though uniform, is sufficiently light to permit a fair amount of seed to be produced.



A. Isolation transect in *Stipa-Bouteloua* pasture, Mandan, North Dakota.
B. Isolation transect in *Agropyrum-Bulbilis* pasture, Ardmore, South Dakota.

The classic experiment in rotation grazing is that carried on by the Forest Service in cooperation with Mr. C. P. Turney on the Jornada Reserve near Las Cruces, New Mexico. This has been described in detail by Jardine and Hurtt (1917: 28), and their conclusions as to range improvement by natural revegetation are given here:

"Primarily as a result of (1) reducing the number of stock during the main growing season of about four months—July to October—to about half of the average number the area will carry for the year, (2) not overstocking during the other eight months, and (3) better distribution of stock watering places, grama-grass range on the Jornada Range Reserve has improved in three years at least 50 per cent as compared with similar adjoining unfenced range grazed yearlong.

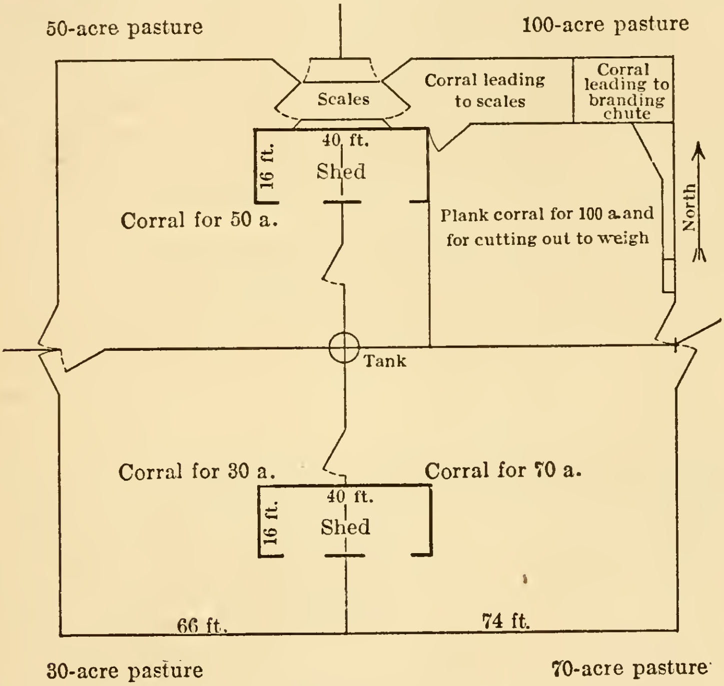



Fig. 24.—Arrangement of corrals, sheds, and scales, Mandan, North Dakota. After Sarvis.

"On fenced grama-grass ranges of the Southwest where the stock are carried mainly on range feed throughout the year, light stocking during the growing season is profitable. It will probably not reduce the total animal-days feed furnished on a given area during the year, and will reserve feed for the critical period from February to July, and later in case of prolonged drought.

"Where the whole of a range unit is made up of grama or similar grass, about one-third of the area should probably be reserved for light grazing during the growing season two years in succession. Each third in turn should be given as nearly as practicable this amount of protection. By light grazing is meant grazing by not more than half the average number of stock that the area will carry for the year as a whole."

**Rodent eradication.**—Smith (1899: 15) was apparently the first to emphasize the damage done by rodents to the range and to urge the systematic extermination of prairie-dogs and jack-rabbits. While much has been said and written on the control and extermination of prairie-dogs in particular since 1900, effective campaigns against these and other rodents are recent developments. During the last five years especially, the Biological Survey has carried on systematic and effective work in the eradication of both prairie-dogs and ground-squirrels, in cooperation with various States, as well as with the Forest Service and with private individuals (Bell, 1917; Lantz, 1918). In addition, California has organized an extensive campaign through its Rodent Control Section. It has also come to be recognized that jack-rabbits are often exceedingly destructive to the range, and the work of Vorhies (1919) has shown that the kangaroo-rats of the Southwest must also be included among the major pests. While various methods have been used to exterminate or control rodents, that of poisoning has become the standard, because of its economy and efficiency. However, it has become clear that complete eradication is possible only through poisoning for two or three successive seasons, and that re-immigration can be controlled only by dealing with large and more or less natural areas and by the extermination of invading colonies from time to time.

The absence of accurate knowledge as to the amount and kind of damage done to the range by rodents, and especially of the rate and degree of recovery in various types after eradication, led the writer to suggest the desirability of cooperative studies to the Biological Survey, the Forest Service, and the University of Arizona. As a consequence, fenced areas for such investigations were established in 1918 in the *Bouteloua-Aristida* grassland of the Santa Rita range reserve and in the *Bouteloua gracilis* climax of northern Arizona near Seligmann and Williams. The latter were designed to study the recovery after the eradication of prairie-dogs, while the former were to permit a more intensive study with reference to jack-rabbits, and especially kangaroo-rats, which had just been shown by Vorhies to cause even more serious damage. A series of three exclosures was installed in the *Bouteloua rothrockii-Aristida californica* type of the reserve (plate 82). The first was fenced against both rodents and cattle, and the second and third against cattle alone, but differing in that the rodents were killed out of one. A second exclosure was established in the *Bouteloua eriopoda-Aristida divaricata* type, which was also fenced against rodents and cattle. For the sake of a direct determination of the amount of forage consumed by jack-rabbits and kangaroo-rats, two inclosures were located in one of the best areas of *Bouteloua rothrockii*. In one of these were placed two rabbits, in the other two kangaroo-rats. Permanent quadrats were located for measuring the effects in the various inclosures as well as in the pastures by means of charting and clipping. The critically dry summer of 1918 almost completely prevented the growth of grass and summer annuals, and practically all quadrats contained less growth in the fall than in the spring. The winter rains were nearly normal and so well distributed that the growth of winter annuals was exceptional. As a consequence, the various fenced areas showed striking improvement in total production over the pastures. This was not only true of the cattle-proof exclosures, but of the rodent ones likewise, proving that the rodents also take heavy toll from the winter annuals as well (plate 82, B).

A. Rodent exclosure showing combined effect of cattle and rodents on the crop of winter annuals, chiefly poppy (*Eschscholtzia mexicana*), Santa Rita Reserve.

B. Difference in yield of poppies in rodent exclosure, cattle exclosure and pasture, Santa Rita Reserve.

Special studies were made of the life history and food habits of the kangaroo-rat in particular, and the latter were found to have a decisive bearing upon the dominance of the grasses (Vorhies, 1919). Burrows excavated in the winter of 1917–18 showed that the kangaroo-rat stored large amounts of food and that this consisted chiefly of the spikes of *Bouteloua*. Those excavated in 1918–19 exhibited no grass spikes, owing to their failure to form during the drought of the preceding summer, but the bulk of the stored food consisted of the crowns of *Bouteloua rothrockii*. When the size of the denuded area about each burrow is taken into account, it is readily seen that the damage done by kangaroo-rats is exceedingly serious, especially in periods of drought. While they occur throughout the desert scrub, it seems probable that the majority have migrated upward into the desert plains as the grasses were eaten off at the lower levels. The persistence of the grasses in sheltered spots and their reappearance in fenced areas in the desert scrub suggests that they can be successfully reintroduced into the deserts about Tucson after the kangaroo-rats have been exterminated. The rats which persist in the desert now live in part upon the shrubs, it seems, and in consequence the latter are now being killed out over great stretches from Ajo to Yuma and beyond.

In addition to the major pests, the pocket-gopher, wood-rat or pack-rat, and several of the field mice do more or less damage to the range. The gopher damages the range by eating grass roots and disturbing the soil with his burrows, but the injury is usually restricted to small areas. The pack-rat lives on leaves of *Yucca* by preference, especially *Y. radiosa* and *Y. arborescens*, and may do considerable damage in regions where these are important supplementary forage. In the desert scrub and plains, it seems to feed largely upon various species of *Opuntia*, which are heaped up about its nest (plate 72).

Eradication of poisonous plants.—The loss of range stock from eating poisonous plants is so evident and often so serious that the importance of its prevention requires no argument. The chief difficulty in the way lies in the general ignorance of poisonous species and of the best methods of dealing with them. Quite apart from their poisonous properties, such species are usually undesirable weeds which compete successfully with the grasses and thus reduce the carrying capacity of the range. As a consequence, eradication is theoretically the most satisfactory way of dealing with them, but this is perhaps economically possible only in small pastures and other local areas. Where they grow over hundreds of square miles, as in the case of the loco-weed, *Aragalus lamberti*, on the plains and foothills along the eastern front of the Rocky Mountains, eradication is practically impossible under existing conditions, and controlled grazing is the only practicable method of prevention. Marsh (1918: 21) has stated:

"Most of the losses from poisonous plants occur at times when the animals are short of feed and the larger part of the stock poisoning is indirectly due to scarcity of proper forage. This fact of the intimate relation of scarcity of feed to stock poisoning can not be too strongly impressed upon the people who handle range animals in the West. There is apparently a popular idea that range animals will voluntarily seek out poisonous plants and eat them by preference. It may be stated as a general fact that this is not true. Animals seldom eat poisonous plants except as they are driven to do so by the lack of other food. Almost all poisonous plants are actually distasteful to live-stock and under ordinary circumstances will be avoided. The only exception to this, perhaps, is the group of loco plants. Animals do frequently acquire a taste for loco and under some circumstances will eat nothing else, even in the presence of other forage; and yet the initial feeding in the case of loco plants is almost invariably brought about by the scarcity of food.

"It has long been known that loco eating is ordinarily commenced in the winter season or in the early spring, when the loco plants are green and luscious and before the grass has started. The loco plants at that time are the most prominent plants on the plains and animals commence to eat them because of lack of other food. In the matter of other plants, the relation between starvation and the eating of the poisonous plant is still more marked. For instance, the larkspurs spring up immediately after the snow leaves the mountains and grow much more rapidly than the surrounding grasses, and if cattle are allowed to go up to the upper ranges before the grasses have had a fair start they find already occupying the ground the succulent larkspur plants in large numbers. Sometimes the cattle come from dry winter feed and are anxious to gorge themselves with any green material they find. Under such circumstances, if they come upon a field of larkspur they frequently eat enough to produce fatal consequences. Later in the season there is very much less danger from larkspur because of the abundance of other food. If, however, cattle are driven from one range to another and the trail passes through a mass of tall larkspur, it is not at all unusual for the hungry animals to grab hastily at the plants and this may result in disastrous consequences. Under such circumstances it is important that the cattle shall not be driven rapidly, for they will snatch all the more, and they should also have been thoroughly fed before going on such a drive.

"It is also evident from what has been said earlier in this paper, that if cattle can be kept off fields of larkspur until after the plant has blossomed, little trouble may be expected. This method has been employed for many years in Colorado, where it is a common practice to "ride for poison," as it is called; that is, the herders ride and keep the cattle down from the higher ranges until the larkspur has blossomed and matured, after which there is no further danger. The same thing has been accomplished in certain regions by putting up drift fences which are designed to keep the cattle on the lower ranges until the danger is past. There are valleys known as death traps for cattle. Frequently it will be found that in these valleys the tall larkspur is thriving in large clumps and cattle drifting in will feed freely upon it. It is often possible, under such conditions, to clear out this larkspur or enough of it so there will be no danger. In order to kill the plants the roots of most species should be cut off at least 6 or 8 inches below the surface.

"The losses of sheep from death camas (*Zygadenus*) occur under very similar conditions to those of cattle from larkspur. *Zygadenus* grows very early in the spring. It precedes the grasses in its growth and is present in a succulent condition at a time when other forage is extremely scarce. Inasmuch as it occurs frequently in large masses, if sheep are trailed over these places they are liable to get enough to cause heavy losses. It is particularly important in the handling of sheep in such localities that, if possible, they be grazed in loose order. When the animals are massed together, they will eat everything in their course, and because of jealousy will take particular pains to get every available plant.

"This applies equally well to lupine poisoning. When sheep are allowed to feed freely upon a lupine patch and are moved without haste, no harmful results will occur. If, however, they are massed together and driven in close formation over such a patch, they are almost certain to be poisoned if the plants are in pod at the time. The remedy in such cases clearly is to see that the sheep, when it is necessary to trail them through a patch of lupine, are drifted rather than driven, and that they are well fed when they come upon this locality. It seems probable that intelligent handling of bands of sheep may reduce to almost nothing the losses occasioned by *Zygadenus* and lupine. If, however, hungry sheep come in contact with fields of *Zygadenus* in the spring or with fields of lupine in the late summer and fall, at a time when the plants are bearing pods, fatal results must be expected."

Poisonous plants can be eradicated or kept down to a point where they are not dangerous in various ways. The most thorough and likewise the most expensive is that of grubbing out the roots. At the Utah Experiment Station of the Forest Service, Sampson has found that cutting or mowing two or three times during the first growing season and once or twice the second prevents storage in the rootstocks and leads to the dying-out of the plants. Where the ground is not too uneven or covered with brush, it is much cheaper than grubbing, and nearly as efficacious. Sheep have also been used to graze off larkspur on cattle ranges, and it appears probable that overplanting with vigorous innocuous species during favorable seasons would largely eliminate poisonous plants as a result of competition.

Aldous (1917: 22) has summarized the results of the methods of grubbing out and grazing off larkspur on the national forests:

"Grubbing out the plants is the most feasible method of preventing loss of cattle from tall larkspur poisoning. The first grubbing costs from $3.65 to $10.10 per acre, the cost depending upon (1) the number of plants per acre, (2) the texture of the soil, and (3) whether or not the plants are growing in the open or in willows or other brush. The cost of the second grubbing should not exceed $1 per acre. Extensive eradication on four forests has been done at a cost of less than one-half the value of the cattle saved annually. An average of 93 per cent of the plants in the experimental work and of from 80 to 95 per cent in extensive work were killed by the first grubbing. By a regrubbing of the area one year after the first grubbing practically all of the larkspur plants were killed.

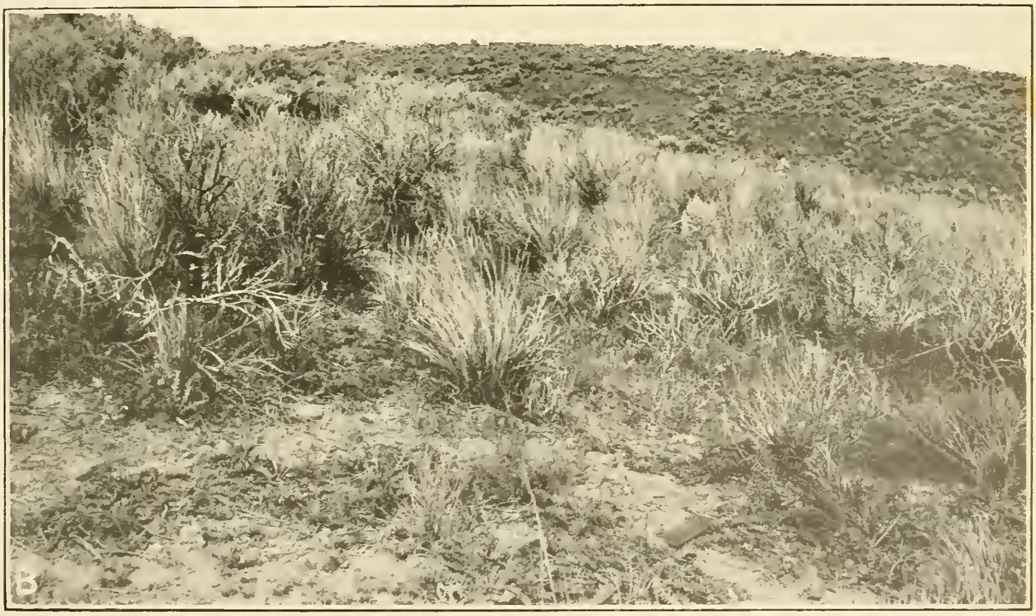
"The use of sheep to graze off larkspur-infested cattle range has a limited application. Its success depends (1) on the palatability of the larkspur, (2) the availability of sheep to graze the infested area at the proper time, and (3) whether the infested areas furnish sufficient forage to justify trailing sheep to them."

On the lower ranges, especially those of the grassland climax, overgrazing is either a direct or a contributing cause of stock poisoning. This is naturally the consequence of the disappearance of the more palatable species and the correspondingly greater abundance and attractiveness of the poisonous weeds. Since the evil effects of overgrazing are most in evidence during the dry phase of the climatic cycle, methods of control and eradication should be focussed especially upon drought periods. For example, the grubbing out of plains larkspur or loco would be a simpler matter at the end of a drought period, and the grasses would be enabled to develop a much more effective competition during the ensuing wet period.

**Eradication of weeds and cacti.**—It has been repeatedly shown that annual herbs are replaced in the course of succession by perennial ones, and these to a large degree by grasses. The weedy nature of the annuals is evident, but perennials are often also to be regarded as weeds in a grass range, especially one used by cattle or horses. Under climax conditions, the grasses are able to maintain their dominance in competition with the herbs, but in the case of overgrazing or other disturbance, the latter gradually get the upper hand. When the area is protected or the grazing reduced, the advantages of the grass life-form again come into play in the competition, and the herbs disappear or become subdominant. As a consequence, the best method of eradicating weeds is by protection or regulated grazing. Complete protection is more rapid in its effects, but it is usually out of the question. Regulated grazing is the most practicable method as a general rule, but it is sometimes too slow in operation, or the area is too thoroughly dominated by weeds to permit it. This is particularly the case with areas densely covered with prostrate species of prickly pears, such as *Opuntia mesacantha* and *O. polyacantha*, or with half-shrubs, such as *Gutierrezia*.

When it is desired to get rid of annual weeds more rapidly than by means of regulated grazing, they may be grazed off by sheep, especially where mixed grazing is practiced. They may be greatly reduced by burning at the time when their seeds are ripening, and they may even be mowed where the area permits. During favorable seasons, their disappearance may be hastened by overplanting with more vigorous species, especially perennials, which increase the natural rate of succession. Perennial weeds are more difficult to get rid of, since they are less affected by burning or mowing, and it is too expensive to grub them out on the range as a rule. Fortunately, the most serious pests are cacti and half-shrubs, which lend themselves to various methods of clearing. Since cacti furnish succulent forage when more or less spineless, the most satisfactory method of eradication is by burning, when the tract contains enough grass to permit this, or by singeing with a torch when the area is almost pure. Once the spines are removed from the prickly pears, they will be grazed down to the ground by cattle, and in a few years will practically disappear from the range if overgrazing is prevented. Halfshrubs, like other weeds, can best be eliminated by protecting the areas or grazing them lightly, but many ranges are so densely covered with *Gutierrezia* or *Isocoma*, for example, that other methods must be employed. Since these rarely root-sprout, burning is the quickest and most economical method, though in small areas they may be cut out with profit.

Eradication of brush.—The range value of brush is determined primarily by its palatability, but it depends in a large measure also upon whether it is pure or mixed with grass. As has already been emphasized, a range made up of grass and browse in more or less equal degree permits mixed grazing and furnishes the best insurance against drought and other disasters. The burning of unpalatable brush to clear the ground for herbaceous growth seems to have been long practiced in California, and it has also been employed to maintain the stand of grass against the encroachments of shrubs in mixed types. In the case of the Coastal chaparral, the dominants form root-sprouts in great abundance and repeated burning is necessary to maintain the herb cover. This is less true as a rule in the Petran type, where burning is chiefly important in enlarging the grass areas, as is the case likewise in the subclimax chaparral of Texas. In the typical savannah of the Southwest, the mesquite and its associates are kept down by burning and the grassland climax favored. In the case of sagebrush, grazing by cattle favors the shrubs at the expense of



A. Wheat-grass (*Agropyrum glaucum*) following sagebrush after clearing, Brookings, Oregon.
B. Bunch-grass (*Agropyrum spicatum*) following fire in sagebrush, Boise, Idaho.

the grasses, and the latter can be maintained only by some practice which handicaps the brush. Since *Artemisia* and its associates usually form few root-sprouts, fire furnishes the simplest way of restoring the balance from time to time. Clearing is even more effective, but out of the question because of the expense. Sagebrush may also be driven out by the grasses where irrigation or flooding occurs, but this is rarely feasible in range practice (plate 83).

Manipulation of the range.—Fire is but one of several processes which may be used to bring about modifications of the forage cover. In addition to the similar process of clearing are (1) cultivating, (2) irrigating, (3) fertilizing, (4) cutting and pruning, and (5) sowing and planting. Besides its use in handicapping scrub in mixed types, fire is of especial value in destroying the old stems of bluestems and bunch-grasses, and making the new growth available for grazing. Throughout the grassland climax from Canada to Mexico occur frequent and extensive areas of *Andropogon* which are utilized little or not at all, except when hunger drives the cattle to graze them during drought years. However, when the dead stems are burned in the winter or early spring, the new growth is readily eaten, and with proper management the bluestems and similar coarse grasses can be kept in constant commission in the grazing practice. There is still a wide difference of opinion as to the ordinary effect of fire upon grassland, and this is one of the many grazing problems which need exact investigation in various types. Theoretically the burning of prairie every few years should constitute a desirable practice, if the year and season are chosen in such a way as to avoid injury to the underground parts. In the short-grass and desert plains, fire would probably always do more harm than good, owing to the dry soil and the certainty of injuring the roots and rootstocks. Annual fires in grassland are probably always harmful, especially in regions where less desirable annual species are present. Fire has undoubtedly played a large part in the spread of *Bromus tectorum* and related species, as well as of *Avena fatua*, and it now is largely responsible for maintaining them against the perennials. However, in the regions where *Avena* is a desirable range or hay grass, fire is of value, since this annual would slowly yield to other dominants if fire and other disturbing agents were removed. Apart from farming operations, clearing is practicable only in the case of particular species and over limited areas, as has already been noted for poisonous plants. In such cases, grubbing, cutting, and mowing are all modifications of clearing, which are of restricted application. In the case of browse plants, however, cutting and pruning offer means of increasing the amount of fresh browse, as well as its accessibility. These again are methods for small areas, but they promise to have real value in the case of such shrubs as the salt bushes, oaks, mesquites, catclaws, etc.

The improvement of the range by the use of some of the methods of cultivation has been tried from time to time. The first experiments in the application of surface tillage to the range were those of Smith (1899: 20) and Bentley (1901: 18), which led to the conclusion that it would be profitable to cultivate pastures with disk and iron-tooth harrows, especially in the semi-arid regions. While the practice of stirring the surface soil and loosening up the root-bound sod has been frequently recommended (Georgeson, 1895: 43; Williams, 1897; cf. Thornber, 1910: 324), it has never been adopted for many reasons, chief among them the labor and expense involved and the great difficulty of applying intensive methods to large areas. This is equally true of the application of fertilizers to increase the growth of grasses, and of the use of irrigation. The application of manure to worn-out pastures was a logical extension of good farm practice, and there is little question that the composition as well as the yield of native and artificial pastures can be varied more or less at will by the scientific manipulation of different fertilizers (Skinner and Noll, 1919). However, such methods are limited to pastures in which intensive yields are possible, and are not applicable as yet to even the smaller pastures of climax grassland. Irrigation has a somewhat broader application to western ranges, because the lack of water is the chief limiting factor to production. The cost of irrigation, however, is regularly too great to permit its use, except in restricted areas, where an exceptional production can be obtained. Even in the majority of such cases, the forage is worth more as hay, and is handled in that form.

**Plant introduction on the range.**—The sowing or planting of desirable native or cultivated species on the range has universally been suggested and often attempted. One of the earliest trials was that of Georgeson (1895: 43), who sowed a mixture of perennial grasses, clover, and bluegrass in the prairie near Manhattan, Kansas. The tame grass made a splendid growth early in the season, but by autumn it had everywhere yielded to the native dominants. Bentley (1901: 16, 30) made extensive tests of native grasses when sown or transplanted in the native cover. Transplanting gave much the best results, practically all the native dominants establishing themselves successfully when due care was taken as to the time and method of transplanting. The most extensive series of experiments in seeding native grassland have been carried on in the Southwest by Griffiths, Thornber, and Wooton between 1900 and 1915. As this is the most trying region for the introduction of new plants, it affords the best idea of the difficulties involved. Griffiths has summarized the results of seeding operations on the range reserves near Tucson, as follows:

"Experimental work carried on thus far in attempting to introduce perennial forage plants upon the mesas has given very little encouragement. *Panicum texanum*, an annual, has given the best results of anything thus far introduced, and it is believed that more success will be secured with annuals than with perennials. They are not as good feed, but short-lived plants with good seed-habits now furnish the main feed upon the mesas (1904: 61).

"Many attempts have been made to introduce forage plants in this section, both in the large enclosure and upon the holdings of private individuals. There is but one species, alfilerilla (*Erodium cicutarium*), that has given any beneficial results. In all, 200 species of forage plants have been tried in this enclosure. Many native species were tried, but the vast majority used were of foreign introduction. At one time the Office of Forage-Plant Investigation of the Bureau of Plant Industry furnished more than 100 varieties for testing. In some cases the seed was covered and in others scattered without any further attention. The plan has been, whenever the quantity of seed permitted, to sow one-half in the fall and one-half in the early summer. In some cases the ground was worked up sufficiently to kill about half of the original vegetation. The net economic result of all this foreign introduction has been practically nil. Most of the species in our experience have never come up, and the few things that did make any growth usually died before seed was produced.

"A number of native grasses have been caused to spread successfully by gathering the seed in advantageous localities and simply scattering it where the ground was badly denuded. Better results have been obtained when seeding was done the last of June or the first of July. When sown in autumn the ants pick up too many of the seeds. Beneficial results have been secured in this way by the use of the seed of *Andropogon saccharoides*, *Bouteloua vestita*, and *B. rothrockii*. Less positive results have been secured by the use of native seed of *Bouteloua curtipendula* and *Leptochloa dubia*. Indifferent results have been secured with *Bouteloua oligostachya*. The above illustrations of the successful use of native species are important and interesting, but they have no applicability to open-range conditions. However, where the land is under fence, and seed can be secured in the vicinity without too much expense, improvements can be made in very badly trampled areas. When the roots of the native growth are not completely destroyed, it is questionable whether in such situations as this, recuperation would not occur fully as rapidly by proper protection from overgrazing without the use of seeds as with it." (1910: 12.)

Thornber (1910: 312) has furnished a detailed and comprehensive account of seeding and planting operations in connection with the small range reserve near Tucson:

"The almost complete failure of the above experiments in a reasonably favorable year led the writer to undertake a series of experiments on similar land receiving more water than the annual rainfall. To this end the storm water embankments or dams already noted were built and the small areas over which their flood waters occasionally extended were cultivated and sown from time to time with the more promising of the native grasses, saltbushes, and other forage plants, in addition to a number of introduced ones. For purposes of comparison, most of these varieties were sown on adjacent areas not so flooded, and also in the forage garden on the University grounds where moderate irrigation was given.

"Good stands of blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), and side-oats grama (*B. racemosa*) were secured with heavy summer rainfall in addition to flooding, on the small range enclosure. These, however, gradually died out with average summer rains and little or no flooding from storm water. Crowfoot or mesa grama (*B. rothrockii*), though more or less common on the lower mesas, killed out badly with prolonged droughts. With moderate irrigation practically all the grama grasses did well in the forage garden, while without such irrigation their growth was short and they showed signs of dying out. It is quite evident therefore that the rainfall at the lower altitudes is too limited for the successful growth of these species. Silver-top or feather bluestem (*Andropogon saccharoides*) has become established whereever sown on areas subject to annual flooding, after which with average rainfall it has yielded at the rate of three-fourths to one ton of hay to the acre. It has resisted in a remarkable degree prolonged drought, never having suffered any injury therefrom when once established, and is gradually spreading over cultivated areas, and swales and mesa depressions. When sown on the higher creosote land not subject to flooding, or during seasons with less rainfall than the average, it has failed. Tangle head (*Heteropogon contortus*) has also made a good showing on the small range enclosure, while in the forage garden it has yielded even more heavily than silver top. The sacaton grasses made little or no growth from the start with rainfall heavier than the average on land not flooded, and this was true of a number of other grasses, including *Hilaria*, *Stipa*, and *Aristida*.

"No introduced forage plants, including species from cool, moist climates and higher altitudes, made any growth on the small range enclosure, and but few of them persisted in the forage garden for any considerable length of time. Both the native and Australian saltbushes failed repeatedly to secure a hold or make any growth of extended duration, though they were planted on land occasionally flooded with storm water. The growth of summer annuals with average rainfall and no flood water was short, and they matured little or no seed. Of the winter-growing species alfilaria and Indian wheat (*Plantago*) made good growth when the rains were favorable, and invariably matured seeds. Root-planting experiments were generally unsuccessful."

Wooton (1916: 38) gives an account of reseeding studies on the Santa Rita Range Reserve which is in entire accord with that of Griffiths and Thornber:

"Practically all attempts to introduce new species of forage plants or to increase the relative abundance of particular endemic species beyond their natural importance in the plant associations of the region have resulted negatively. In a few cases introduced plants, like alfilaria or some aggressive annuals, have seemed to promise returns, but in the course of a few years the native perennials have crowded them out. The scattering of seeds of the local native species upon bare ground has proved to be well worth the trouble, since the practice has resulted in the more rapid recovery of such areas. This procedure has also put a crop of grass upon some soils where it was predicted that nothing would grow."

Introduction and reseeding have been generally successful in mountain meadows and other regions where the rainfall is relatively high, as well as in local areas of the sandhills and in river valleys where the water-content is above normal as a result of runoff or underground drainage. Griffith (1907: 22) concludes:

"Profitable partial cultivation of native pastures must be confined to productive areas in regions of sufficient rainfall to permit at least the occasional cultivation of some of the hardier crops. The areas where reseeding methods on an economic basis are applicable extend to the western plains, and are scattered throughout the mountains in meadows, high valleys, and other situations where the requisite moisture occurs."

Cotton (1908: 23) states that experiments carried on in the mountain meadows of the Pacific coast "show that the carrying capacity can be greatly increased by reseeding with tame grasses. The grasses best suited to this purpose are timothy and redtop."

Vinall (1911: 9), in discussing forage crops for the sandhill region of Nebraska, strongly urges that "a good percentage of clover be mixed with the native hay, as all the clovers grow naturally on the moist lands of the hay flats. In fact, no part of the United States seems able to produce clover with less care or attention than this wet-valley region, and its use here is strongly urged. Red clover seeded in 1895 in meadow sod, without plowing or other cultivation, has reseeded itself from year to year in haying land, and is today in better condition and shows a better stand than ever before."

**Prerequisites for seeding and planting.**—The above accounts make it clear that water is the chief limiting factor in the establishment of seedlings or mature plants and that competition for water determines their persistence. Where the water-content is more or less in excess of the needs of the native population, as in mountain meadows with high rainfall, or in wet valleys with little drainage, tame grasses or forage plants can be introduced into the community successfully and without disturbing it unduly. Such areas constitute a relatively small amount of the total range, and they are rarely in such need of revegetation as the grasslands of low water-content. In dealing with the latter, the first great need is to take advantage of times of greater rainfall. This has generally been done with reference to the season, but no method has heretofore been available for anticipating periods of several years with rainfall above the normal. Such a method now exists in the use of the sun-spot cycle to determine the probable duration of the wet and dry phases of the 10 to 12-year climatic cycle. While the annual rainfall varies more or less during the wet phase, it is regularly higher than during the dry one. Moreover, drought periods of 2 to 3 years' duration have been found to fall only at the dry phase for the past 60 years. Hence, it is obvious that the difficulties attendant upon reseeding or introduction will be least during the wet phase and greatest during the dry one, and that all operations of this kind should be confined to the former. Moreover, it is especially desirable that sowing or transplanting be repeated for the first two years of the wet period in order that an adequate stand be secured in the event of the seasonal distribution of the rain being unsatisfactory. This would also accord with the probability of two or three fairly wet years for the proper establishment of the plants, before the beginning of the dry period.

A second prerequisite of great importance is the eradication of rodents. Where seeding is the method used, it is probable that the failure to secure a good stand is often due as much to the destruction of the seeds as to the lack of water. This is probably true even in the arid Southwest, since it is here that rodent damage is greatest. As a consequence, it is imperative to kill out the rodent population before seeding operations are begun on an area. It is almost as important to make sure that the rodents are kept out of such areas, since they may turn the scale against the establishment of plants which have germinated successfully. The food habits of the kangaroo-rat help to explain why the grama grasses fail to make seed and gradually disappear in the experiments mentioned above. In certain regions, at least, they would likewise render the establishment of transplants much more difficult. It is also obvious that areas in which reseeding is being carried on must be protected against grazing for several years. As a consequence, reseeding and transplanting should be fitted into the rotation system, and carried on with reference to the period of complete or partial rest given the different areas. It is assumed that all such operations must still be regarded as actual investigations and that they will be begun only where fencing assures control, and a preliminary study of conditions presupposes some degree of success. Under such conditions, it is possible to take the factor of competition into account also. The success attained in artificially reseeding bare and especially trampled areas in pastures has been largely due to the absence of competition for water. When reseeding is employed to increase the density of an existing community or to introduce new dominants, competition becomes a critical factor. It can be adequately modified only in small pastures where disking or harrowing is economically desirable, or irrigation possible. On the ranges of the Southwest, with two growing seasons, it can be avoided by the use of winter annuals, which do not come into direct competition with the summer grasses at all.

**New investigations.**—In connection with grazing studies throughout the grassland and scrub climaxes of the West, it is proposed to extend experiments in reseeding and transplanting to all the associations. These are being established with especial reference to the prerequisites discussed and they have been planned for the next four or five years in the expectation that these will constitute the wet phase of the cycle. Protection and eradication have been emphasized, and particular attention has been devoted to methods of evaluating the rôle of competition, since actual practice will require the reseeding of both bare areas and overgrazed communities. This is done in protected inclosures, where tillage methods may be employed in so far as desirable, and where permanent quadrats can be maintained for charting changes in composition and measuring the annual variations in yield (Clements, 1917, 1918, 1919). By the use of transplanting in addition to reseeding, it is expected to determine the ecological requirements of practically all the dominants and many of the subdominants, within the same association or local grouping, as well as between associations.

In addition to improving the carrying capacity of overgrazed areas, it is hoped that it will prove possible to extend and develop mixed grazing types, such as the mixed prairie, and the mesquite and sagebrush savannahs. The mixed prairie has the highest carrying capacity of all grass types, and also possesses essentially the same high resistance as the short-grass plains to trampling, overgrazing, and drought. It owes this property especially to the presence of buffalo grass, *Bulbilis dactyloides*. The runners of this grass make it one of the very best for transplanting experiments and it should prove possible to establish sods as centers of ecesis throughout the grassland where the rainfall ranges between 15 and 30 inches. *Hilaria cenchroides* has similar values, but its range is more restricted and trials with it should perhaps be confined to the Southwest. The production of mixed prairies, and of all mixed types indeed, contains promise only in those climates or edaphic regions where there is some water-content in excess of the needs of the existing dominants. For this reason, it is practically certain that success can be attained only by transplanting short-grasses into tall-grass areas, or into existing mixed areas, rather than the reverse (plate 84).

The value of mixed grass and palatable scrub in permitting the grazing of cattle and sheep, often with goats, and in providing a double insurance against drought or other disaster is so great that the possible extension or production of such types is of the greatest importance. In many cases it is expected that the carrying capacity of the type will be increased by replacing one shrub with another more palatable. Where savannah already exists or desirable scrub is already in contact with grassland, the extension of the scrub can be secured by a system in which grazing and fire are used to maintain the balance at the point desired. Fire in conjunction with planting furnishes a ready means of developing grassland in the midst of scrub. The actual planting of shrubs in grassland is more difficult because the demand for water then tends to exceed the climatic supply. As a matter of fact, the demands of shrubs and tall-grasses are so nearly alike that shrubs can be readily introduced into true, subclimax, and mixed prairies during wet periods, as nature has often proved. Once established, their deeper root-systems and taller stems enable them to persist. Certain subclimax shrubs, such as the saltbushes, will

A. Mixed grazing type of oak chaparral and grass, Sonora Grazing Station, Edwards Plateau, Texas.

B. Mixed type of tall-grass (*Agropyrum*) and short-grass (*Bulbilis-Bouteloua*) with relicts of *Sarcobatus*, Ardmore Station, South Dakota.

probably permit similar treatment in moister situations in the short-grass and desert plains. Finally, the latter may be regarded as constituting a curiously mixed type in which the two elements, winter annuals and perennial grasses, occupy the same ground but become dominant at two different seasons. Since grasses depend almost wholly upon the summer rainfall for their growth, such a mixture is especially valuable in utilizing the annual rainfall to give the maximum amount of forage. While Thornber (1910) and others have emphasized the unique value of the winter annuals in the Southwest, their importance and the possibility of extending or developing this mixed type have not been generally understood. The chief annuals possess the vigor and the seed-production of weeds. Hence, the seeds germinate readily and the new plants quickly become established. Like all plants, however, they can not grow without rain, and their yield follows the variation in winter rainfall even more closely than grasses do that of the summer.

Forage development.—It is obvious that the utilization of hay and other forage to supplement the range during winter or periods of drought reduces the demand upon the range and hence helps to improve it. Fundamental as this is, it is far from a general practice among stockmen. While there has been utilization of native hay areas, few attempts have been made to develop them. Moreover, the use of native forage plants of an emergency character has been exceptional until recently, while the production of cultivated forage and silage crops by the stockman has barely been begun. Smith (1899: 22) was the first to emphasize the importance of the production of hay and stack silage as aids to the improvement of the range. Thornber (1910: 305) has discussed the use of methods for developing artificial meadows and fields by means of storm-water dams, but concludes that these are in general not very satisfactory. However, the majority of ranches perhaps contain areas on which a fair amount of native hay can be developed, or on which cultivated forage can be grown by means of irrigation, use of storm-water, or by the methods of dry-farming. This is especially true during the heavier rainfall of the wet phase of the climatic cycle. When the value of hay and silage as insurance against drought is fully realized, it will usually be possible to produce enough during the wet years to tide stock over drought periods. This is especially true of silage, because of the long period for which it can be kept. In view of the enormous difference in the production of forage crops in wet and dry years, it is imperative for the ranchman to realize that his most certain insurance against the disasters of drought is an adequate forage reserve. While increased hay production plays a part in this, maximum production of silage during the wet phase especially is much more important. Silage can be kept almost indefinitely in properly constructed silos, but it would probably never need to be kept more than four years, since even the most serious drought periods have been only three years long. With the use of the method of climatic cycles to determine the approximate date and length of wet and dry phases, it will be possible to develop this drought insurance into a practical certainty. In the case of single years, it is a much more difficult matter to anticipate the probable rainfall, and during the dry phase additional insurance can be obtained by planting such forage crops as sunflower and Russian thistle. In fact, in the Southwest at least, it will be the part of wisdom to plant a certain amount of these every year, against the chance that the distribution of the rainfall may be abnormal.

Thornber (1911) and Griffiths (1905, 1908, 1909) have discussed in detail the utilization of native cacti as emergency forage plants and have shown how they can be cultivated in dry regions. The value of cacti as a supply of reserve food for drought periods is generally understood, but too little trouble is taken to see that it is available when needed. Other plants that are grazed little during wet periods but are eaten more or less by the cattle directly during drought are bear-grass or sacahuiste (*Nolina*), sotol (*Dasylirium*) and soapweed (*Yucca*). The first direct utilization of any of these species as emergency forage was made by Mr. C. P. Turney on the Jornada Reserve in 1915 (Jardine and Hurtt, 1917: 26). The critical nature of the drought period of 1916–18 gave an impetus to the development of machinery for chopping the plants into feed and resulted in a great extension of their use (Thornber, 1918; Wooton, 1918; Forsling, 1919). While they should be regarded strictly as emergency forage and not be permitted to take the place of proper forage development, there can be no question of their value as roughage in times of severe drought. If used as such, the supply in many regions of the Southwest is practically inexhaustible, but the tendency will almost certainly be to continue using soapweed in particular until it completely disappears from the accessible areas (plate 85).

Water development.—The importance of water development for range improvement has been generally recognized and has been discussed in considerable detail by Smith (1899), Bentley (1898), Griffiths (1904), and Jardine and Hurtt (1917). These are all in complete agreement, and the conclusions of Smith and of Jardine and Hurtt are quoted in some detail, as representing the earliest and latest experiments in range improvement:

"Another precaution that must be taken, if the stock ranges are to be restored to anything like their former value, is that water must be provided in sufficient amount so that cattle will not have to travel long distances for it in times of severe drought. Nearly the entire western portion of Texas is underlaid by artesian waters ranging from 150 to 1,500 feet below the surface. Wherever the drainage slopes are not too precipitous, artificial tanks may be formed across the draws by building dams, and if the bottom of the tank is carried down to hardpan, or is puddled before being filled, a supply sufficient to last through the dry season may be secured at small expense. Such tanks, or wells, either artesian or where the water is lifted by windmill pumps, should be provided at least every 4 miles over the range, so that cattle will never have to travel more than a couple of miles to water. Where the wells, water-holes, or tanks are 8, 10, or more miles apart, as they very frequently are on some of the western ranges, cattle greatly overstock the range in the vicinity of the water, especially during midsummer, while the back country is thickly covered with good feed. Thus a portion of the range will be overstocked while another portion will be undergrazed. In the one case the grasses are eaten down and trampled for a few miles back from the water so that it may require several good seasons to undo the injury done in one bad year. In addition, the forage on the large area back from the water is entirely lost through not being grazed. The cost of constructing dams or providing windmills will often be but a small percentage of the loss incurred when no water is provided. It has been often observed that the period of flow of the rivers in countries which have been overgrazed is very much less than it was formerly. This is because the trampling of the herds has compacted the soil, and also because the waters are not retarded from running off the surface as they

A. Park of *Nolina* and grass in oak chaparral, Sonora Grazing Station, Edwards Plateau, Texas.

B. *Yucca radiosa* in desert plains, Empire Valley, Elgin, Arizona.

would be when the land is covered with a thick coating of grasses. Hence the drainage of the surplus water takes place in a very much shorter time. There are many streams and springs which in former years afforded a continuous supply throughout the dry season, which now only run during or immediately succeeding periods of abundant rainfall. Thus less dependence is to be placed upon the streams as a source of stock water. New artificial sources of supply must be provided." (Smith, 1899: 26.)

"Fairly efficient use of plains and mesa range in the Southwest can be secured where stock do not have to travel more than $2\frac{1}{2}$ miles to water. This means one watering-place for each 13,200 acres. Such an acreage of grama-grass range will carry about 500 cattle throughout the year if properly managed. As the distance in excess of $2\frac{1}{2}$ miles which stock have to travel to water increases, the barren area around water increases, as does also the partly used forage beyond $2\frac{1}{2}$ miles from water. Consequently the number of stock the range will support is reduced. When feed is short, a long distance between feed and water tends to increase the loss of stock, to decrease the calf crop, and to retard development of the young animals. Observations to date appear to justify one permanent watering place for each 500 head of cattle. Where conditions are favorable, the construction of tanks to catch flood waters for the purpose of supplementing the permanent watering places will be a paying investment. They will aid (1) in getting more green feed for the stock during the year, (2) in more even utilization of the range as a whole, (3) in the protection of feed and range near permanent water, and (4) in reducing the cost of maintenance and operation of wells." (Jardine and Hurtt, 1917: 29.)

Herd management.—Better methods of handling stock may improve the range or prevent its deterioration directly, as in the open herding of sheep, or may be of indirect benefit, as in the production of a more efficient animal. Since the ultimate objective of range improvement is the maximum permanent production of stock, all methods which lead to this end are more or less concerned in it. While many of the factors in proper herd management have been worked out by the experiment stations in feeding and breeding experiments, the chief contributions to the management of range stock have been made by the Forest Service. These deal mainly with the handling of cattle in large range pastures, and of sheep in coyote-proof pastures and under new systems of herding. The immediate objectives have been (1) maintenance and improvement of the carrying capacity, (2) improvement in grade of stock, (3) increased calf or lamb crop, and (4) prevention of loss. The results secured on the Jornada Range Reserve have been summarized by Jardine and Hurtt (1917: 30), as follows:

"The big opportunity for increasing the calf crop is to keep poor cows in thrifty condition. This can be done by not overstocking the range used by breeding stock and by feeding a small quantity of cottonseed cake or other supplemental feed to the cows that need it. All bulls should be fed during the winter and early spring.

"The small loss at the Jornada reserve is attributed to careful, systematic vaccination against blackleg, to the reservation of grama-grass range for poor stock during the critical spring months, to feeding the animals a small quantity of cottonseed cake, and to prevention of straying.

"In order to provide for extra range for the breeding stock in poor years, one-third of the stock on a range unit should be steers. It is then possible to reduce the number of stock when necessary by selling steers, without great sacrifice and without interfering with the breeding stock. In good years the number of steers can be increased and in bad years decreased.

"To provide against loss in extremely bad years, some kind of roughage to supplement the range forage, for feeding with cottonseed cake or other concentrated feed, would be a decided advantage on southwestern ranges. Feeding cottonseed cake to calves weaned during the late fall, winter, and early spring is an important factor in cutting down loss and increasing the size of the stock, as well as in increasing the calf crop. Where this is done, young calves can be taken from poor cows, thus reducing loss from starvation among both cows and calves and stimulating earlier breeding."

The value of coyote-proof fences for sheep pastures and range lambing-grounds has been studied by Jardine (1908, 1911). His conclusions are that the carrying capacity under this system is about 100 per cent higher than under the ordinary one, and that the percentage of lambs is higher, the sheep are much better, the loss almost nothing, and the expense of handling materially decreased. The advantages of the "bedding-out," "blanket" or "burro" system of herding sheep have been studied by Jardine, Fleming, and Douglas, and have been summarized by Jardine and Anderson (1919: 50). The latter have given the most complete account available of the management of cattle and of sheep on the ranges of the national forests, with respect to the range as well as the herd (pp. 30, 49).

## ESSENTIALS OF A GRAZING POLICY.

A proper land system.—It has long been recognized by students of grazing that overgrazing and its attendant evils were the result of an unfortunate land policy. This fact has never been understood by the public, even in the West, and it is but recently that the stockmen themselves have realized it. A large portion of the country still holds the vague opinion that the West contains the possibility of unlimited homesteads, a delusion which western politicians and real-estate dealers have found it profitable to encourage. It is a national misfortune that the entire open range was not brought under adequate control at the time when the conservation movement was at its height, as the West contained few resources of greater importance. At present, every competent and disinterested student of the situation realizes that an adequate and just leasing system furnishes the only economic solution of the problem. The administration of the grazing lands upon the national forests has convinced the vast majority of stockmen of the advantages of leasing or allotment, and has dissipated the fears that the "little man" would suffer under such a system. In spite of this, public opinion has hardly advanced beyond that of the days of the "cattle kings," who were more or less justly regarded as the foes of the homesteader. This is not to be regarded as strange in view of the failure of the West to comprehend the grazing industry as perhaps its major problem. When the West realizes, and causes both public and lawmakers to realize that half a billion acres of its land can never be used profitably for anything but grazing, it will become possible to enact the necessary legislation for an intelligent economic and social treatment of the public domain, such as was provided in the Kent grazing bill of 1913.

Essentials.—Coville (1898) and Smith (1899: 43) have pointed out the essentials of a proper land system with respect to the needs of grazing, and Smith has summarized these as follows:

"The only way in which the non-mineral lands can be filed upon is either under the right of preemption, under timber claim laws, desert-land laws, or those relating to irrigated lands. There is no system for disposing of areas unsuited for agriculture other than under some one of these laws, and the result is that the grazing lands are held as commons open to any stockman who can run his cattle upon them. The first and foremost necessity, if the extravagant waste of the public domain is to be prevented, is to devise some system by which grazing lands can be placed in a class separate from agricultural lands, and under which property rights in lands now free to everyone may be assumed by individual stockmen. It has been the experience in all pastoral countries that proper care and conservation of the forage resources can only be secured and will only be practiced where the tenure of the land is sure. The necessary fixity of tenure might be legally provided for by long-term leases directly from the General Government at a nominal rental per acre.

"Aside from the effect of overgrazing on the lands themselves and on the natural grasses with which they are covered, it is well to note that millions of cattle and sheep are grazed on free lands in every Western State and Territory. These lands contribute no taxes for the support of the State governments. The cattle when marketed may be sold at a much lower figure than those raised on taxed lands owned by the stock grower and still make a profit. It is not fair to the people who are compelled to bear the expenses of local government for large untaxed areas, nor on the other hand to the cattle men and woolgrowers of the East whose products come into competition with those grown almost without expense on free Government lands. The policy which governed the settlement of the prairie States might well be modified to meet the demands of the stock raisers, especially as a very large percentage of the Government land now remaining is not agricultural and can not be made so by irrigation. The best policy is that which will the best promote permanent settlement. It is necessary that timely action shall be taken to open up the public lands for settlement in tracts extensive enough to encourage men to build ranches and make permanent improvements upon them. The continued existence of great bodies of free lands covered with free grass is demoralizing to all those who take advantage of the opportunities presented thereby. As suggested above, probably the most feasible plan would be to provide for long-term leases of the public lands for grazing purposes."

The Kent grazing bill.—As an epitome of the best experience and results in grazing practice and administration, the grazing bill introduced into Congress in 1913 by Mr. Kent, of California, is unrivaled. It is such a complete and concise exposition of the proper land policy for the West, and of the needs of the grazing industry, that it is given here in its entirety, because of the conviction that such a measure, and such a measure alone, can solve the land problem of the West.

H. R. 10539.

In the House of Representatives, December 15, 1913.

Mr. Kent introduced the following bill; which was referred to the Committee on the Public Lands and ordered to be printed.

A bill for the improvement of grazing on the public lands of the United States and to regulate the same, and for other purposes.

*Be it enacted by the Senate and House of Representatives of the United States of America in Congress assembled,* That the unreserved, unappropriated public lands of the United States shall be subject to the provisions of this Act, and the President of the United States is hereby authorized to establish from time to time, by proclamation, grazing districts upon the unreserved, unappropriated public lands of the United States, conforming to State and county lines so far as practicable, whereupon the Secretary of Agriculture, under rules and regulations prescribed by him, shall execute or cause to be executed the provisions of this Act, appoint all officers necessary for the administration and protection of such grazing districts, regulate their use for grazing purposes, protect them from depredation, from injury to the natural forage crop, and from erosion; restore and improve their grazing value through regulation, by the eradication of poisonous plants, and by the extermination of predatory animals and otherwise; eradicate and prevent infectious and contagious diseases injurious to domestic animals; issue permits to graze live stock thereon for periods of not more than ten years, which shall include the right to fence the same, giving preference when practicable to homesteaders and to present occupants of the range who own improved ranches or who have provided water for live stock grazed on the public lands; and charge and collect reasonable fees for such grazing permits, based upon the grazing value of the land in each locality: *Provided*, That for ten years after the passage of this Act such charge for grazing shall not exceed four cents per acre nor be less than one-half cent per acre, or the equivalent thereof on a per-capita basis, and the Secretary of Agriculture shall revise and reestablish maximum and minimum rates of charge for grazing for each succeeding period of ten years.

Section 2. That homestead or other settlement, location, entry, patent and all other disposal of public lands under the public-land laws shall be in no wise restricted, limited, or abridged hereby; nor shall anything herein be construed to prevent bona fide settlers or residents from grazing their stock used for domestic purposes, as defined under the regulations of the Secretary of Agriculture, on the public lands affected hereby: *Provided*, That after the establishment of any such grazing district no form of location, settlement, or entry thereon shall give a right to grazing privileges on public lands except when made under laws requiring cultivation or agricultural use of the land: *Provided further*, That permits to graze live stock upon land which is subsequently appropriated under any public-land law shall not be affected by such subsequent appropriation, except as to the land actually appropriated, until the end of the current annual grazing period: *Provided further*, That no permit shall be issued which will entitle the permittee to the use of any buildings, corrals, reservoirs, or other improvements owned or controlled by a prior occupant until he has paid such prior occupant a reasonable pro rata value for the use of such improvements. If the parties interested can not agree, then the amount of such payment shall be determined under rules of the Secretary of Agriculture: *And provided further*, That when buildings, corrals, reservoirs, wells, or other improvements, except fences, shall have been established on any forty-acre tract to the value of more than $100, as determined by rules of the Secretary of Agriculture, such forty-acre tract shall not be subject to settlement or appropriation under the public-land laws during the permit period without the consent of the owner of such buildings, corrals, reservoirs, wells, or other improvements.

Sec. 3. That all water on public lands or subject to the jurisdiction of the United States within such grazing districts may be used for milling, mining, domestic, or irrigation purposes under the laws of the State or Territory wherein such grazing districts are situated, or under the laws of the United States and the rules and regulations thereunder.

Sec. 4. That no grazing permits issued under this Act shall prohibit settlers, prospectors, and others from entering upon such grazing districts for all proper and lawful purposes, including the use and enjoyment of their rights and property, and prospecting, locating, and developing the mineral resources of such districts; and wagon roads or improvements may be constructed thereon, in accordance with law, and all persons shall have the right to move live stock from one locality to another within such grazing districts under such restrictions only as are necessary to protect the users of the land which will be driven across.

Sec. 5. That the users of the public lands under the provisions of this Act may select a committee of not more than four members from the users of any such grazing district, which committee shall represent the owners of different kinds of stock, and, with the officers appointed by the Secretary of Agriculture in charge of such grazing district, shall constitute an executive board, which shall determine whether the permits for such grazing districts shall be issued upon an acreage or upon a per capita basis, shall make such division of the range between the different kinds of stock as is necessary, and shall decide whether the distribution of the range shall be by individual or community allotments. The executive board shall also determine the total number of animals to be grazed in each grazing district and shall decide upon the adoption of any special rules to meet local conditions and shall establish lanes or driveways and shall prescribe special rules to govern the movement of live stock across the public lands in such districts as to protect the users of the land in their rights and the right of persons having the necessity to drive across the same. The executive board, after thirty days' notice by publication, shall also determine the preference in the allotment of grazing privileges provided for in section one of this Act, and shall, under rules of the Secretary of Agriculture, determine the value of the improvements and the use of the same whenever that may become necessary under the provisions of this Act in the administration of the same. Fences, wells, and other improvements may be constructed with the permission of the Government officer in charge, who shall record the ownership and location of such improvements. Any differences between a majority of the executive board and the officer in charge shall be referred to the Secretary of Agriculture and shall be adjusted in the manner prescribed by him. Any interested party shall have the right to appeal from any decision of the board to the Secretary of Agriculture. If the users of the land fail to select the committee as herein provided, the President of the United States shall name such committee from such grazing districts, representing the owners of the different kinds of stock, as above provided.

Sec. 6. That the Secretary of Agriculture shall fix a date which shall not be less than one year from the establishment of any grazing district, and after such date the pasturing of any class of live stock on public land in said grazing districts without a permit, or in violation of the regulations of the Secretary of Agriculture, as herein provided, shall constitute a misdemeanor and shall be punishable by a fine of not less than $10 nor more than $1,000, or by imprisonment for not less than ten days nor more than one year, or by both such fine and imprisonment in the discretion of the court.

Sec. 7. That twenty-five per centum of all moneys received from each grazing district during any fiscal year shall be paid at the end thereof by the Secretary of the Treasury to the State or Territory in which said district is situated, to be expended as the State or Territorial legislature may prescribe for the benefit of the public schools and public roads of the county or counties in which the grazing district is situated: *Provided*, That when any grazing district is in more than one State or Territory, or county, the distributive share to each from the proceeds of said district shall be proportional to its area therein. The sum of $500,000 is hereby appropriated, to be available until expended, for the payment of expenses necessary to execute the provisions of this Act.

Sec. 8. That the President is hereby authorized to modify any proclamation establishing any grazing district, but not oftener than once in five years, to take effect in not less than one year thereafter, and by such modification may reduce the area or change the boundary lines of each grazing district.

Classification and range surveys.—The necessity of a classification survey to determine the primary division of the public domain into agricultural, grazing, and forest lands has been discussed in the preceding chapter. Here it will suffice to emphasize the importance of classifying as grazing land all areas in which there is not convincing evidence of permanently successful agricultural production. In view of the fact that dry-farming in many regions is largely confined to forage production, by far the best plan would be to treat the remainder of the public domain as grazing land and to organize it into districts and units in such a way that the forage areas could be intensively utilized.

The primary task of a range survey is to determine the grazing types and subtypes of a region and to approximate the carrying capacity of each. It must ascertain the character, composition, extent, and value of each type, as well as its present condition and its future development. It is essentially ecological in nature, and hence must be based upon the climax formations and their subdivisions, and upon their successional development. The most important unit is the grouping or faciation, which represents the local type with which an individual range must deal, though the larger ranches might have a number of different types. A range survey will necessarily devote much time to the need and the possibility of range improvement in the different types. It will pay especial attention to the indicators of overgrazing, and to the successional evidences of the best method of regeneration. It will locate the areas infested with rodents or with poisonous plants, and will suggest the most promising methods of eradication. It should likewise take note of all areas in which there is actual or potential development of hay and forage, and of the location and extent of communities of emergency forage plants. It must also deal with the possibilities of water development, by means of mills as well as by tanks. Finally, it will take account of sandhill, bad land, and other areas in which some form of grazing reclamation is possible. In its complete expression the range survey should lead to the production of ecologic sheets and folios which would do for the range what topographic sheets and geologic folios do for the topography and geology of a quadrangle.

Production cycles.—The recurrence of wet and dry periods in general harmony with the sun-spot cycle has already been shown to have a profound effect upon the carrying capacity and water supply of the range. As a consequence, the climatic cycle is clearly reflected by a corresponding grazing cycle. The carrying capacity and water supply are high during wet periods, and they are at a minimum during drought periods. For successful ranch practice in the drier regions especially, the grazing cycle must be made the basis of a production cycle. In fact, it is already the basis of such a cycle, owing to the fact that production is necessarily reduced to the minimum during a drought period. It is imperative that the actual existence of such a cycle be recognized, and that its operation be anticipated and modified in such a way as to stabilize production. In existing practice, a series of wet years is a period of voluntary expansion, and a drought period one of involuntary contraction. With the increasing probability of forecasting wet and dry phases, the ranchman should make his plans accordingly. Expansion must still be the rule for wet phases, and contraction for dry ones, but the change from one to the other must be definitely anticipated and prepared for. This is particularly true of the critical change from expansion to contraction, but it is also true in a large measure for the reverse process.

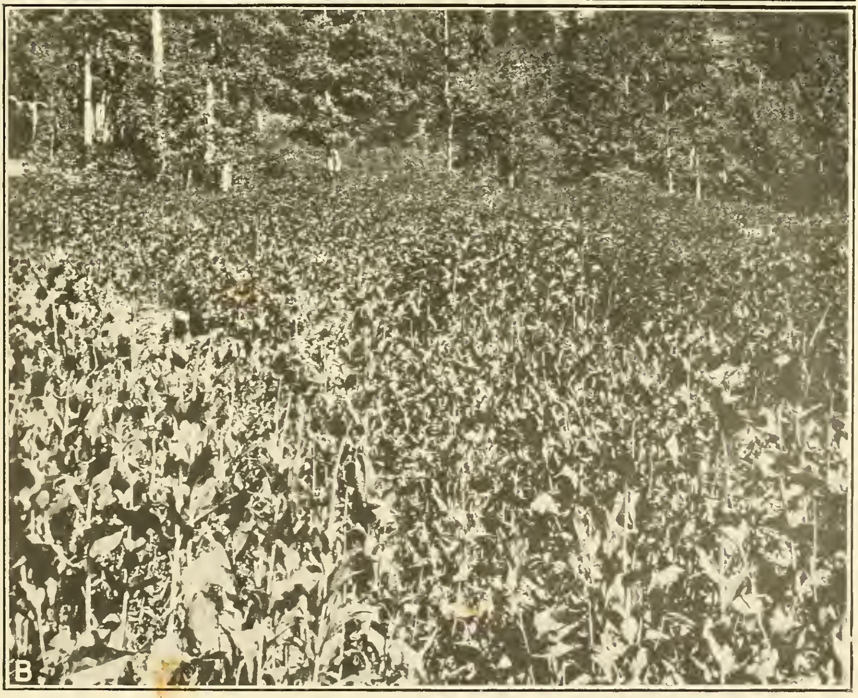
Most of the essentials of a contraction-expansion system have already been discussed under range improvement. It is imperative to have the largest possible amount of insurance against drought in the form of rotation grazing and reserve pastures, and of water development. Even greater possibilities of adjustment are afforded by the management of the herd to secure necessary contraction and desirable expansion. On the Jornada Reserve this has been obtained by maintaining the number of steers at about one-third the total of the herd, but increasing the number in good years and decreasing it in bad years as the range warrants or demands (Jardine and Hurtt, 1917: 31). Still greater elasticity is provided where it is possible to employ mixed grazing, running cattle and sheep together, or cattle, sheep, and goats. Mixed grazing not only permits readier adjustment to climatic conditions, but also serves in some measure as insurance against unfavorable market conditions.

Ranch management surveys.—The task of placing the grazing industry upon a sound economic and social basis is not solved until costs of production can be determined. Until this is done and net income ascertained, it is impossible to know the efficiency of any particular ranch in either economic or social terms. It is felt that the only proper objective of any productive system is to secure an equitable balance between the needs of the producer and the consumer. Such a balance is possible only when the actual cost of production is known, so that its relation to the proper cost can be determined. In its present condition the stock industry of the West is little better than a game of chance, in which both the stockman and the public are regularly losers. It can be converted into a productive business that does its full duty to the individual and the nation only by means of proper land legislation, adequate methods of range improvement, and by ranch management surveys, which will disclose the exact status of each ranch as a productive unit. Such surveys may well serve to usher in a period of cooperation in ranching, which will make possible great improvements in range and herd management as well as in marketing and distribution. They would probably lead also to the stabilization of land values and the reduction of interest rates, and to the production of social values such as rarely obtain at present.

# VII. FOREST INDICATORS.

**Nature.**—Forest indicators are of three chief types, namely, (1) those that have to do with existing forests; (2) those that indicate former forests; (3) those that indicate the possibility of establishing new forests. A community of trees is axiomatically an indicator of forest, but it carries with it indications of habitat, structure, and development which are not so obvious. Moreover, it involves important indications as to use, such as lumbering, water regulation, grazing, etc. Indicators of former forests are either actual relicts of the forest itself or seral communities which mark particular stages of the successional reforestation. They may consist of the dominant trees as individuals or communities, of the subdominant shrubs or herbs of the climax forest, or of the dominants or subdominants of any successional stage. Their great value lies in the fact that they not only indicate the possibility of reforestation, but also the stage which has been reached and the further methods to be employed. They are by far the most important and practical of all forest indicators when the vast extent and significance of deforested areas are taken into account. They pass more or less gradually into indicators of the possibility of forest production in regions which have been repeatedly deforested and which show neither relicts nor seral stages of the original climax. Such are the transition regions between forest and scrub or prairie, in which the latter appear to be climax, but are really subclimax and will consequently yield to forest when artificial regeneration is employed. In addition, chaparral and grassland may also indicate afforestation in regions which have not borne forest for hundreds or thousands of years. These are primarily edaphic areas in which the indicator community owes its presence to a higher water-content resulting from soil or topography. Such are the sandhills of Nebraska and the river valleys throughout the prairie associations.

**Kinds of indicators.**—Both the individual and the community may be used as indicators. The latter is naturally more complete and definite, but in many cases the change following clearing or fire is so complete that a single relict individual gives information of great value as to the original climax. This is true also of subclimax forests which have more or less completely disappeared in the reestablishment of the climax forest. The forest formation which is climax for a certain region is itself the indicator of the permanent type of the region, and hence of the forest which will naturally develop or redevelop in all bare or cleared areas. As a consequence, it is an indicator of site and likewise of the type of management to be employed. Each association is an indicator of climate, while the various groupings and alternations of the consociations indicate different edaphic conditions as well. The societies indicate variations in water-content or light primarily, but the layer societies are especially related to light. Differences in the density and growth of dominants and subdominants serve as indications of minor changes in the factor complex. Indicator values may be derived from growth in height, diameter, or volume. The former is the most convenient for use, but the latter is probably the most accurate. Seedlings are among the best of dominant indicators, especially when their growth, habit, and abundance are taken into account. The minute structure of leaves is an excellent indicator of



A. Climax subalpine forest of *Abies* and *Pinus* as a climatic indicator, Yosemite National Forest, California.

B. Consocies of *Rudbeckia occidentalis* as an edaphic indicator of clearing and fire, Utah Experiment Station, Ephraim.

light and water relations, and that of stems is an indicator of annual fluctuations in rainfall, and hence climatic cycles. Flowering and seed-production also have their indicator values, but these are of secondary importance.

Seral communities differ chiefly from climax ones in indicating edaphic conditions or habitats rather than climate. Their peculiar value lies in the fact that they may at the same time indicate the nature of the initial area or disturbance, the particular stage of development in the succession and the habitat, and the final association or climax. Such stages are denoted by the associes, and minor stages or variations by the consocies, while the socies denotes subordinate differences within these. These three types of community, and the series of associes which constitute the sere, form a complete scale of variations and changes, upon which the problems of forest maintenance, of reforestation and afforestation, must be based. In short, while the climax indicates the permanent forest of a region, the seres indicate the methods and materials which must be used in hastening, maintaining, or postponing the climax community, which is inevitable under natural conditions. It is obvious that seral communities furnish indications from composition, density, and growth essentially similar to those of the climax (plate 86).

## FOREST TYPES.

Bases.—The nature of forest types and the bases for their distinction have been fruitful subjects of discussion among foresters. Graves (1899) seems to have been the first to characterize forest types definitely:

"If nature is left undisturbed, the same type of forest will tend to be produced on the same classes of situation and soil in a specified region. There will be variations within the type, but the characteristic features of the forest will remain constant, that is, the predominant species, density, habit of trees, reproduction, character of undergrowth, etc. If a portion of the forest is destroyed by fire, wind or otherwise, the type may for the time being be changed, but if left undisturbed, it will revert to the original form, provided the condition of the soil is not permanently changed."

Zon (1906) states:

"The first step in any silvical study or attempt at forest management is to reduce the great variety of stands to a small number of types, each having characteristic features of its own and requiring a distinct treatment. The nearer we come to establishing natural types of forest growth, the deeper we penetrate into the true relationship existing between these types and the factors that produce them, and this is the most important contribution to silvics."

The changes brought about in a forest by man or by accidents are not regarded as a basis for the establishment of fundamental forest types, but it is recognized that such changes do produce temporary or transient types. The essential agreement of the basis proposed by Graves and Zon with the principles of succession and the distinction between climax and developmental communities was pointed out by Clements (1909: 62):

"Reproduction is the forester's term for development or redevelopment; it is the complex response of a formation to its habitat, which leads to succession. The result of reproduction is a forest type of succession, an ultimate or stable formation, i. e., a forest type and a stable formation of a succession are identical. This identity is made clearer by the author's insistence upon stability as the ideal for which the forester must strive in regenerating and caring for his forest. The change in stabilization is perhaps the most essential feature of a succession, and the succession terminates only because the habitat is finally occupied by a formation which, accidents excepted, is best suited to it and hence is permanent."

The varying concepts and applications dealing with the forest type are well illustrated by a symposium on the subject, the papers of which are briefly abstracted here. Dana (1913: 55) defines the different kinds of types which seem to serve a useful purpose and should be recognized:

"A *forest type*, known often as simply a *type*, is a stand of trees with distinctive characteristics of composition. A *cover type* is a forest type now occupying the ground. The term conveys no implication as to whether the type is temporary or permanent, or one which we shall strive to maintain under forest management. A *temporary type* is a forest type which has come in as a result of some interference with natural conditions, such as fire or lumbering, and which will eventually, if nature is left undisturbed, be replaced by a different type. A *permanent type*, or *natural type*, is a forest type which will eventually take possession of and perpetuate itself on any given area if natural conditions are undisturbed. A *management type* is a forest type that we shall strive to maintain under forest management, irrespective of whether or not it is the type that would occupy the area under natural conditions."

Munger (1913: 62) emphasizes the following point:

"The term forest type must above all be used for a classification of timberland that will be useful to the practicing forester in forest management in a broad sense. Forest typing must not merely be a theoretic grouping of similar areas convenient for wall-map purposes or a classification of merely botanical or ecological interest. Their distinctions must be based on fundamental points of difference which have significance to the forester. In every form of intensive reconnaissance which a forester is doing preparatory to making working plans, he should include the collection of data showing both the present composition by species and the physical conditions of the site. Though both of these classes of data may be shown on his maps, I feel that the term 'forest type' should be reserved for a classification based upon permanent basic physical factors. I should define, therefore, a forest type as an aggregation of areas of forest land upon which the physical conditions of climate, soil, and moisture are so similar that an identical form of silvicultural management may be applied on all."

Woodward (1913: 69) states:

"In the examination of lands offered for purchase under the Weeks law, it has been found desirable to classify the kinds of forest stands and sites from two points of view. In the first place, it is necessary to know the composition of the present stands in order to arrive at the value of the timber. The second way in which sites need to be classified in valuing the lands offered is to determine the value of the site for producing timber. In a virgin stand, the present composition is a very good index of what can be grown on the area in question. However, it is conceivable that under forest management it may not be advisable to wait for the struggle for existence to proceed so far that temporary species are eliminated. As a means of classifying stands and sites, a system of types and subtypes is now in use. A forest type is understood to be an area in which the climatic and soil factors are uniform and which may therefore produce stands of like composition. A subtype is a subdivision of a type in which the struggle for existence is not yet completed and whose composition is therefore changing. Generally this temporary condition is caused by fire, lumbering, windfall, etc. The most common species in subtypes are light-needing ones which occupy the ground quickly, but which will ultimately give place to more tolerant species."

Moore (1913: 75) summarizes his views of forest types as follows:

"A forest type is a tree society having such differences of composition from other tree societies as to make necessary a separate study of yield. Physical factors are the cause of forest types, but not forest types themselves. They cause confusion when used in classifying forest types. Yield studies are at the foundation of forest management, and must be based on forest types distinguished by composition. Reconnaissance must furnish material to which yield studies can be applied. For this purpose it must distinguish forest types by composition, whatever other method may be used in addition. Fortunately, this is, for most regions, the easiest way of distinguishing forest types."

Greeley (1913: 76) points out:

"There have been three general stages in the work of the Forest Service, each involving a somewhat different point of view in the classification of forest types. During the first stage the 'cover type' in its simplest terms was adequate. In the second stage, the 'cover type' in itself is inadequate. We need rather the 'management type.' In the third phase of the work to which I have alluded, we need possibly an additional type—the 'physical type' or 'land type.' The type needed for the classification and description of National Forest lands is the 'management type.' The classification of forested areas should be attacked from the standpoint of what those areas will grow best under scientific administration. Let us have, then, a classification of forest types based upon present cover interpreted where necessary by the uses which we will make of it in management. Let us leave the intensive study of physical factors to the working-plan expert or the silvicist. The 'management type,' in my judgment, is the key to the classification of complex stands arising from changes in composition at different periods in the life-history of the forest. I would apply this principle to any complex situation where a temporary type is followed by a permanent type, selecting for the purposes of our classification the stage in the natural rotation of species which, as far as we can now see, will be the basis of the forest management. In a word, the existing cover interpreted by our knowledge of the life-history of the type and of what the land should produce under management will, I believe, furnish the best basis for classification."

Pearson (1913: 84) emphasizes the value of communities as indicators and summarizes the bases for the classification of forest land into types, as follows:

"The only scientific basis for such a classification is that of potential productiveness, considering both agricultural and forest crops. The productive value may be ascertained in two ways: The first measures directly, as far as possible, all physical factors on the site and gauges the productive capacity by the measure in which the sum of these factors meets the requirements of various crops. The second method uses characteristic forms of vegetation on the ground as an indicator of the physical conditions present, and upon this basis ascertains the adaptability of the site for different crops. The obvious objection to the first method is the need of climatological data and soil analyses on each site to be classified; and, owing to the diversity of sites in our forest regions, together with the almost entire absence of climatological records in many sections, the collection of data would involve an expense which, at this stage of our advancement in forestry, would be almost prohibitive. The second method requires a thorough preliminary investigation in each region to be covered, in order to secure a working knowledge for the actual land classification, and obviously reliable results can only be obtained by the employment of trained men. This method is the simpler and probably the more reliable of the two, and it is considered entirely applicable to the needs of the forester."

Rockwell (1913: 85) defines four types, as follows:

"The *temporary type* is a transitional condition, in which a forest of a temporary character is established as a result of some disaster which overwhelmed the original stand, but which will, if the disaster is not repeated, in time revert to the original climax form. The *climax type* is named for the species which will eventually predominate as a result of the physical factors concerned, provided the stand is left indefinitely undisturbed. The *cover type* may be either temporary or permanent; in mature and over-mature stands the name is based on the present composition; in immature stands it is based upon the probable composition at maturity. A fundamental type which, similarly to the climax type, is based on physical factors of site, but named for the commonly occurring species most important from a management standpoint, instead of for the climax species, will here be called, for want of a better name, the '*physical type*.' In addition to furnishing a better basis for the estimate of future yield and the regulation of the annual cut, the knowledge of site conditions which a 'physical' type map supplies is of great assistance in handling all the problems of forest management. After the types have been thoroughly studied, we will know definitely the range of climatic conditions in each type—knowledge of great value in forestation, fire protection, and land classification work. We will know what species can grow in each type, their rate of growth, and what they will yield. We will know about the behavior of different species within the type, and can then plan intelligently the management of cutting operations, methods of brush disposal, and other problems of forest management. Not until the physical types are properly classified and mapped can these problems be definitely worked out."

Mason (1913: 91) recognizes—

"Two classes of forest types. One of these types is based upon physical factors and will be called the 'physical type'; the other, based on the forest cover found on the area in question, will be called the 'cover type.' A physical-type map is principally valuable in forest management to indicate the species which can be grown most profitably on a given area. It is useful in case planting is to be done, or if a method of cutting merchantable timber is to be selected which will reproduce the proper species. A physical-type map, then, shows the potentialities of the area mapped. It need show nothing with relation to the present forest cover, or even the presence or absence of forest growth. The cover-type map, on the other hand, shows whether or not the area is timbered at all. It shows what kind of timber is now present on the area and its age. It indicates the nature of the crop which will be harvested during the present rotation. The physical-type map, then, shows what the land is capable of producing, while the cover-type map shows what the land is producing. If the cover type is important in connection with the present rotation, the physical type is important with relation to the next rotation. The physical-type map indicates the species which may be best grown upon a particular area. This, however, is a matter of comparatively secondary importance in forest administration. Furthermore, questions as to proper species for planting and suitable methods of cutting are solved by special studies rather than in the course of the work of the general reconnaissance crew. Physical-type maps are doubtless of great silvical and ecological interest, but cover-type maps are more valuable at present to the men who are managing forests in a practical way."

Tillotson (1913: 95) has emphasized the importance of permanent forest types:

"Ordinarily it is undoubtedly true that better success will attend silvicultural operations if due regard be given to the establishment and maintenance of permanent forest types. It therefore becomes important to learn to distinguish and to classify them. It seems that this will necessitate the division of the country into rather large areas, over which the same general conditions of temperature prevail at similar altitudes, these units to be subdivided into smaller areas, where similar conditions of precipitation both as to amount and distribution exist, and these still further into smaller units, where differences in exposure, topography, or soil exist. On similar areas of this last division the ultimate forest growth may be expected to be the same, both in composition and in character, and it makes little difference in speaking of the permanent types whether they are called, for instance, the north-slope and the south-slope type, or the north-slope Douglas-fir type and the south-slope Douglas-fir type, providing the character of the growth in the region under discussion is known. The physical factors of the habitat will determine the type, and if these are known the character of the ultimate growth will be known by one familiar with the region. To one not familiar with the region any designation of types will in any case necessitate a description of them."

Zon (1913: 103) points out:

"One of the most urgent and fundamental silvical tasks of the present moment is the working out of a natural classification of our forests. Since there are no characteristics within the stands themselves which could be used as unmistakable guides for dividing the forest into homogeneous silvicultural units and for acquiring exact knowledge of their silvical requirements, one must necessarily seek such characteristics outside of the stands. Such guides are found in the external environment, with its climatic and soil peculiarities. These alone determine the composition and combination of the species as well as the silvical requirements of the stand. It does not make any difference whether the name of the forest type is derived from the distinctive commercial species or topography, provided that in differentiating the forest into types the physical conditions of growth, which are the fundamental and primary causes of the real differences in the stands, are taken as the basis. If forest types are based upon physical conditions of growth, they will necessarily also determine the character of growth and make superfluous the further subdivision into quality classes.

"In a proper forest classification, two things must be distinguished: (*a*) types of forest as the product of physical conditions of growth, and (*b*) the condition of the stands as the product of the interference of man or natural accidents. In the latter group will belong temporary types—sprout forests, abnormally open forests, the absence of undergrowth on account of grazing, etc. The classification into types is fundamental and is of importance not only for the present but also for the remote future. Classification on the basis of secondary characteristics, which are merely stages in the evolution of the type, is important only for the immediate future.

"A comprehensive classification of forests into types should begin by establishing, first, silvicultural units of various orders. The country as a whole should be divided into botanical-geographical regions—as, for instance, northern conifers, central hardwoods, etc.; each region must be subdivided further into subregions—thus the northern conifers into spruce subregion, pine subregion, etc. Within each subregion the forest should be divided on the basis of marked differences in topography and geology into types of forest massives. Each forest massive should then be divided into forest types, and within the boundaries of each type the stands may be further grouped by age, by origin, or by any other distinction which may be due to the interference of man or accident.

"Without denying the importance of the secondary characteristics in describing and differentiating forest stands, these characteristics must be placed, it seems to me, in a different perspective—at the end and not at the beginning of the work. All attempts at forest classification so far made have been based either upon artificial characteristics or upon characters in which the interference of man was not separated from the natural factors. Such a classification inevitably included in one group stands extremely heterogeneous silviculturally. In order to secure a natural classification and at the same time a complete knowledge of the silvical requirements of the stand, it should embody in the classification both the natural characteristics and the characteristics produced by the interference of man, but subordinate the latter to the former—that is, the characteristics produced by man should be used for classification only within uniform conditions of growth—the physical conditions for growth for the same type must be so similar as to guarantee a biological uniformity of stands."

Comparison of views.—A careful scrutiny of the opinions just summarized makes it evident that they differ more in emphasis than in fact. While the majority prefer to make use of the community, either actual or potential, they do this as an index to conditions and management. Those who regard the physical factors as the most important recognize the necessity of knowing the composition. The fact that the physical type is defined as one in which the climatic and soil factors are uniform shows that even this view takes proper account of the community, since there is at present no other measure of the uniformity of the factors concerned. In fact, practically every author regards both habitat and community as essential to the adequate understanding of forest types, and this agreement extends also to the desirability of recognizing and using various kinds of types. This is especially true with respect to permanent and temporary types, and largely also for management types, all of which may be cover types, when the community is emphasized. They are likewise physical types when the chief emphasis is placed upon the habitat or site, but technically, temporary types would usually be excluded. It thus becomes clear that forest types must take full account of both habitat and community, and that the community is the visible sign of any type. It is the indicator of the physical factors of the site as well as of the kind of management which such a community demands to produce the maximum return. In short, it is the indicator value of the community, which the forester, consciously or subconsciously, has constantly in mind when he is defining or classifying forest types. As a consequence, the major objectives of forester and ecologist are the same in the study of vegetation, and the system of classification and of indicators which the latter establishes as the result of successional and quantitative studies should be equally serviceable for the former.

Forest sites.—To the ecologist it seems that much confusion has resulted among foresters from the fact that they have constantly used the indicator method, but usually without a clear recognition of this or of its connotations. As a consequence, there is frequent doubt as to the meaning of the terms type and site. The causes for this confusion have been discussed by a number of foresters. Dana (1913: 58) points out:

"The use of the term 'physical type' in this sense is practically the same as the generally accepted meaning of 'locality' or 'site.' This is defined in Forest Service Bulletin 61 as 'An area, considered with reference to forest-producing power. The factors of the locality are the altitude, soil, slope, aspect, and other local conditions influencing forest growth. Locality class, or quality of locality, includes all localities with similar forest-producing power.' Such a classification is undoubtedly a useful one for many purposes, but it would be better to drop the misleading term 'type' and to substitute for it either of the approved terms 'locality' or 'site.' In any event, it should be clearly understood that the term refers to the area and not directly to the stand."

Moore (1913: 75) says:

"The main point at issue becomes, therefore, one of terminology: Shall we call the environment or physical factors a 'forest type,' or shall we apply the term 'forest type' only to the tree growth? It is evident that we require a separate term for each. Common usage in this country has generally made the term 'forest type' apply to the forest cover. It would therefore simplify matters, I believe, if some other term such as 'site' were recognized as applying to physical factors, while the term 'forest type' is reserved for the forest cover."

The argument for a clear-cut distinction between forest type and site receives strong support from a comparison of the statements of Moore and Zon. The former (*l. c.*, 75) states:

"Mr. Zon, in his article 'Quality Classes and Forest Types,' uses the term 'forest type' to indicate environment or the sum of all physical factors; used in this sense, the 'forest type' becomes synonymous with site quality."

Zon (1913: 102), however, merely says:

"An attempt to use such site classes for forest types as an expression of the physical conditions of growth must necessarily lead to confusion."

Zon's further conclusions as to forest types and site classes have a direct bearing on this question:

"The division of a forest into stands having different average heights or site classes is perfectly justifiable as long as the end sought is purely an economic one. Site classes based upon the average height of the stand can not always represent physical conditions of growth, as the same site classes may be found in stands which have entirely different physical conditions of growth; in other words, belong to two distinct forest types. Site class, therefore, while it indicates the actual character of the timber found on the ground, is not a silvicultural unit which can be used in management. The average height of the stand or site class may be the result of the interference of man, fire, animals, etc., and for this reason can not always be taken as the true measure of the productive capacity of the soil, even within the same type. The classification of stands on the basis of their average height is still further deceptive, because it does not take into effect the taper or the soundness of the timber, two qualities closely connected with the physical conditions of growth of the stand. The use of quality classes alone as indicators of the physical conditions of growth is as misleading as to use the composition of the stand for determining forest types. Both at best show only the actual condition of the stand, but are entirely mute as to the physical factors that are the cause of it."

The question of sites and their recognition has received much attention at the hands of foresters. It is essentially a matter of indicator values, in which growth, or its consequences, furnishes the indications desired. For this reason it is discussed briefly in a later section on growth as an indicator.

Succession as a basis.—A complete and satisfactory solution of the forester's difficulties in the recognition and use of types and sites is possible only on the basis of successional studies. Succession at once removes the confusion between sites and types, since it emphasizes the basic relation of the two as cause and effect. The site or habitat is the controlling cause and hence the explanation of the type or community, but is itself reacted on by the latter in such a way that it passes through a number of developmental stages to the final climax condition, each stage marked by its characteristic community. An adequate study of the community can no more neglect the habitat as cause than it can the community as effect, and also as the cause of modifications in the habitat. Moreover, it leads to confusion in the minds of others to use such terms as physical type and cover type, which appear to ignore one or the other. This is abundantly shown by the opinions cited above, in which essential uniformity is often completely hidden by superficial disagreement.

But succession does not merely put type and site in this proper relation to each other. It is even more important in furnishing the only basis for the natural classification of types, and hence of sites also. Other bases may be natural in some degree, depending upon the criteria used, but development is the only one which takes into account all the factors and processes concerned and in their proper relation (Plant Succession, 111). Its essential feature is the recognition of the forest as a complex organism with a characteristic structure and development. The mature or adult stage is the climax forest while its development is represented by a series of typical stages or communities arising in bare or denuded areas. The climax communities correspond with permanent types, and the developmental or seral ones with temporary types, while both are cover types where they actually occur on the ground. The management type, whatever its name may be, is peculiarly successional in nature, since it depends not only upon the climax and its succession, but also upon the degree to which the latter can be controlled in the interests of optimum production.

The greatest importance of the successional basis for the classification of forest types lies in its indicator values. The climax communities of different degree are the indicators of the climates and subclimates, while the seral communities indicate soil and other local or edaphic conditions. At the basis of succession lie competition and reaction, and within the control of the climate, these are the forces which largely determine the density and growth of stands. But even greater indicator values inhere in the sequence typical of succession. Each stage indicates not only its particular habitat, while its variations in composition or structure indicate similar variations in the controlling factors. In addition, it serves to indicate communities and habitats which have preceded it, and those which will follow it. Seen in its successional relation, each community or cover type is an indicator not only of physical conditions, but also of the past history and future possibilities of the area concerned, and hence of the system of management or of planting.

Significance.—The primary value of forest indicators lies in denoting the physical factors in control. The climax communities of different degree indicate the corresponding climates and their subdivisions. The seral communities indicate local or edaphic conditions, usually of water-content, and at the same time mark the presence of progressive changes due to reaction. The dominants of both climax and seral communities serve to measure the light relations, and this is especially true of tree seedlings and of the subdominants that form the societies of the forest floor. Processes, such as fire, lumbering, grazing, etc., that produce disturbance, are either marked by relicts of the original vegetation, or by subseres more or less typical of the particular process. Growth is one of the most sensitive and hence one of the most important of indicators in the detailed study of communities and stands. Furthermore, the climax and the seral stages of a region taken together determine the general type of management possible or desirable. The composition and successional position of the community in any particular spot furnish a clear indication of the type of management necessary to the utilization of a certain species or stage as the preferred crop. Since succession is essentially progressive in nature, the maintenance of a particular crop or rotation depends upon a knowledge of the competition and reaction of the dominants, and the relation of these to the successional movement. In any climax, there will be seres in all possible stages of development. Some of these will need to be held in the present stage, while in other cases the progressive movement must be favored or hastened, and in still others it will need to be retarded. Whatever the desired method, when the dominants in possession are used as indicators of the forces which initiate and maintain the succession, it becomes possible to adjust the system of management to all the differences in composition and development.

## CLIMATIC AND EDAPHIC INDICATORS.

Climatic indicators.—It is axiomatic that all forest climaxes are indicators of forest climates. The four climax formations, woodland, montane forest, Coast forest, and subalpine forest, indicate as many corresponding forest climates, while the scrub formations and especially the chaparral indicate climates in which water conservation is important. It is well understood that the three mountain climaxes indicate climates with a progressive increase of rainfall from woodland to subalpine forest, while the Coast forest has the highest rainfall of all. In similar fashion, woodland, montane, and subalpine forest indicate a progressive decrease in the length of season and the temperature values, though the Coast forest marks the longest growing season and the most equable temperatures. The rainfall and temperature relations of the several formations have already been suggested in Chapter IV and need not be repeated here. The associations indicate subdivisions or subclimates of the formational climates. In general, the Petran associations are drier and colder than the Sierran associations of the montane and subalpine climaxes. For the three woodland associations, the total rainfall varies less than its seasonal distribution, and the temperature relations seem more decisive than the rainfall. The piñon-cedar indicates the coldest climate with much of the precipitation as snow, the oak-cedar the warmest, and the pine-oak the most equable. The first two have from 40 to 70 per cent of their rainfall in the summer, and the latter about 20 per cent. The two associations of the Coast forest show two subclimates strikingly different in both rainfall and temperature.

The consociations serve to indicate still finer climatic divisions, both as to altitude and latitude, though in general their indications are merged in those of the association or formation to which they belong. This is well illustrated by the montane forest, in which *Pinus ponderosa* indicates drier and warmer climatic conditions than *Pseudotsuga taxifolia*, while *Abies concolor* is more or less intermediate. Consociations also indicate potential climates, with especial reference to the wet phase of the climatic cycle, where they form savannah, as in the case of *Pinus ponderosa* in the grassland climax, or *Juniperus* in the sagebrush. The varied groupings of consociations throughout an association also have some climatic indications, but these are often obscured by edaphic indications of more importance.

Two outstanding investigations have been made of the physical factors of climatic types. The first is that of Bates, Notestein, and Keplinger (1914: 78), the second, that of Sampson (1918). The former deals with yellow pine, Douglas fir, and Engelmann spruce groupings of the central Rocky Mountains. The factors of the air and soil were measured during 1910–1911, and the following conclusions were reached as to the differences of the several types:

"There are wide differences in the heat requirements of the species and in the temperatures of the types. The types vary somewhat in air temperatures, but much more distinctly in soil temperatures. The length of the growing season as determined from soil temperatures is a fairly accurate basis for determining what tree should be grown on the site. It is possible that after a series of careful observations a rule may be laid down by which the growing season may be determined from a very few soil-temperature measurements, or a direct relationship between the degree of solar radiation at any time and the length of growing season may be established. This last, of course, will simply be a scientific method for 'sizing up' the combined effects of slopes, aspect, and altitude—a thing which is done roughly by the forester every day.

"The soil moisture of the types varies greatly, the spruce requiring the most and the pine the least soil moisture; but the soil-moisture percentage is not a good basis for comparing types except in the same immediate vicinity, where it is known that the physical properties of the soils are uniform. In any locality the spruce type probably always receives a greater amount of precipitation than the pine, and if all sites had the same aspect and gradient the amount of precipitation might determine the type. There are, however, too many influences affecting the final value of precipitation to make this element a safe criterion.

"From the above it is readily seen that the measurement of soil temperature affords the simplest means for determining the qualities of the site. In this measurement are involved the effects of the slope and aspect; the direct or indirect solar insolation; the effect of retained snow or precipitation which cool the soil; the effect of wind movement and humidity as they may cause evaporation from the soil, and the effect of wind movement as it may bring heat or cold from areas of different temperature."

Sampson (1918: 69) has determined the physical factors of the chaparral, montane, and subalpine associations of the Wasatch Mountains in central Utah, employing standard plants as well as instruments for habitat analysis, and showing the differences with respect to the various factors and responses in graphic fashion. His general conclusions are as follows:

"The mean annual temperature increases gradually from the highest to the lowest type, and this results in the longest growing season in the lowest type and a gradual decrease in the period of growth with increase in elevation. Thus from the time of the beginning of growth to the occurrence of killing frosts there are about 120 days in the oak-brush type, 105 in the aspen-fir type, and 70 in the spruce-fir type.

"The normal annual precipitation is greatest in the aspen-fir association, but is only slightly heavier in this association than in the spruce-fir. Less than half as much precipitation is recorded in the sagebrush-rabbit-brush as in the aspen-fir association; and in the oak-brush type it is only slightly greater than in the sagebrush-rabbit-brush type. The precipitation is rather uniformly distributed throughout the year.

"Of the three associations critically studied, the evaporation during the main growing season is greatest in the oak-brush type; but owing to high wind velocity in the spruce-fir type the evaporation is nearly as great as in the oak-brush type. In the aspen-fir type the evaporation factor is notably less than in the types immediately above and below. This is accounted for largely by the lack of high wind velocity, which is due to the luxuriant vegetation and to topographic features.

"In the case of all species employed, the total, and, indeed, the average leaf length and total dry weight produced are notably greatest in the aspen-fir association, these activities being rather similar in the spruce-fir and oak-brush types. The decreased production in leaf length and the production of dry matter in the respective types are in direct proportion to the evaporation.

"The elongation of the stem is greatest in the oak-brush type, intermediate in the central type, and least in the aspen-fir type. Thus stem elongation appears to be determined largely by temperature and seems to be little influenced by the intensity of the evaporation.

"The efficiency of the leaves per unit area as manufacturing agents, that is, in the production of dry matter, appears to vary inversely with the evaporation, though, indeed, temperature appears to be one of the important factors. The largest amount of dry matter per unit of leaf area is produced in the aspen-fir type and the least in the oak-brush type, while in the spruce-fir type, where the evaporation is only slightly less intensive than in the oak-brush type, the dry matter produced is only slightly greater than in the oak-brush type."

Edaphic indicators.—These are either climax or seral dominants and subdominants. Seral dominants are typical edaphic indicators, since they mark the changing conditions of the habitat in its progressive development to the final climax condition. Climax dominants differ in their requirements and necessarily show indicator responses to local edaphic as well as general climatic conditions. Subdominants, whether seral or climax, mark minor differences in the habitat, and serve also to indicate the dominants in many cases where these have been destroyed or removed. The most striking edaphic indicators are the seres which arise in bare or denuded areas. Each prisere not only marks a particular type of initially bare area, such as water, rock, or dune-sand, but it also indicates the changes of the habitat complex, as well as the final climax. As already mentioned, each seral stage or community indicates a certain set of factors, and at the same time the stages which are to come in the development of the climax. This is likewise true of subseres, which differ from priseres chiefly in arising in areas denuded by fire or other accident, or by the agency of man. They are much more numerous than priseres, the successional movement is much more rapid, and the stages fewer. Each subsere is an indicator of the disturbance process that originated it, and its stages mark the different degrees of development of community and habitat on the way to the climax. Such stages, or associes, occur in both subsere and prisere. Each marks a particular stage of the habitat which controls it, and in turn reacts upon the habitat to produce the next stage. It consists of two or more consocies, or seral dominants, which indicate minor changes in the stage and hence perhaps different areas of habitat. In addition, each seral community contains a varying number of subdominants which constitute socies, corresponding to the societies of climax communities. The socies mark the more minute differences of the habitat, and perhaps also the minor movements within the associes.

The most important edaphic indicators are those which denote differences in water-content, light, or soil, or mark the effect of disturbing agencies, such as fire, grazing, etc. In addition to the presence or composition of a community, its growth or the growth of one of its dominants serves as an indicator of variations in the habitat complex or of site quality.

Water-content indicators.—In the several forest climaxes, the physical properties of the soil in relation to water-content are so much more important than the chemical that the latter require little attention. As a consequence, the indicators of water-content serve as indicators of soil texture, aeration, and temperature as well. The water relations of the climax and subclimax dominants have been considered briefly under each forest association. The climatic relations of the dominants of a community are reflected in the edaphic ones, and this may even be true of the dominants of different formations. The dominants of drier climates or subclimates take the drier slopes and ridges of the local area, and those of moister climates grow on northerly slopes and in canyons or valleys. *Picea engelmanni* frequently reaches the lower limit of the montane forest along the moist canyons of north slopes, while *Pinus ponderosa* extends to the middle of the subalpine forest zone or even higher on dry and warm south slopes. In short, dominants indicate the total water relation, and hence their climatic indications may be completely subordinated to local conditions.

It is assumed that all dominants have different water requirements, and that each in consequence indicates a different water-content. It is believed that the results of further quantitative studies will show that the dominants of a sere can be arranged in a linear sequence from the pioneer stage to the climax. At the same time, it seems completely established that this sequence falls naturally into stages or associes, characterized by dominants of the same life-form and similar requirements. As a consequence, it becomes possible to use the dominants or consocies of a sere to indicate the successive small steps in the changing water-content from the initial bare or denuded area to the climax, while the associes indicate the stages of longer duration which are characterized by a certain set of water conditions. In the prisere, such conditions and their indicators have some relative permanence, but in the subsere the successional movement is much more rapid and the stages sometimes obscured. In both cases, however, the basic principle holds that a complete series of indicators marks the changes of water-content from an originally hydrophytic or xerophytic bare area to the relatively mesophytic forest climax. The exact value of each community or dominant as an indicator must await more general quantitative study, but the approximate values that can be assigned them at present are of genuine service in forest problems.

Light indicators.—The general principles which underlie light indicators in the forest have been discussed at some length in Chapter III, and the light relations of the dominants of the various forest associations have been touched upon in Chapter IV. The tolerance of western dominants has been indicated by Zon and Graves (1911: 21), Sudworth (1908), Larsen (1916: 437), and others. In a study of the tolerance of New England forest trees, Burns (1914, 1916) concludes that tolerance "really expresses not a light relationship, but the total relationship of a tree to all the factors of its habitat." While the results of Fricke (1904) and Burns have shown that competition for water must be taken into account in studies of tolerance, light is still to be regarded as playing the paramount rôle. Burns's further conclusion that light readings in the forest are of little value is not in accord with extensive experience in making and utilizing such readings in ecological studies. On the contrary, one of the chief difficulties in the correlation of edaphic communities with their habitats is the absence of measurements of light intensity. Where these have been made with care and in large number through several years, as in the Pike's Peak region of the Rocky Mountains, they have proved invaluable in the study of reproduction, development, and plant indicators, as well as in that of leaf adaptation and photosynthetic efficiency. Measurements of light intensity in the forests of the West have been made by Clements (1905, 1910), E. S. Clements (1905), Pearson (Zon and Graves, 1911: 46), and Bates (1917: 233). Studies of the quality of forest light have been carried on for several years by means of a portable spectrophotometer (Clements, 1918: 291), but the detailed results have not yet been published.

Site indicators.—The term site, like forest type, has a wide range of meaning among foresters. While it is regularly employed to denote the habitat, it is applied to all possible divisions of the latter. This is understandable, since this is the present ecological practice in the case of habitat. But just as it has proved necessary to distinguish habitats of different character and various degree, so is it desirable to recognize several categories of site. Climax and seral habitats or sites are fundamentally different, though they are often found side by side. The habitat of one consociation differs from that of another of the same association, and mixed areas of the two show subordinate differences. Finally, the same consociation exhibits marked variations in growth and density, each corresponding to smaller differences of the factor-complex.

In practice, the forester has emphasized two of the several categories of sites. The first is the consociation habitat or the site occupied by a dominant, and the second the minor sites marked by significant differences in the growth or density of a particular dominant. The more specialized use of the word has been in the latter connection (Roth, 1916: 3; 1918: 749; Watson, 1917: 552; Bates, 1918: 383). As a matter of fact, the two types are developmentally connected, the growth sites, commonly designated as I, II, III, and IV, representing a sequence of minor habitats within that of the dominant consociation, such as *Pinus ponderosa*, *Pseudotsuga*, etc. The recognition of growth sites is chiefly important in connection with yield tables and working plans. In planting operations, consociation sites must first be determined, and then growth sites may be employed to ascertain the most promising areas.

Growth as an indicator.—As stated in a previous chapter, the presence of a dominant furnishes one set of indications, and its growth, another. The latter naturally affords a more sensitive scale of measurement, and hence indicates the effective differences of the habitat in terms of timber production. It is obvious that total growth is the most complete indicator, as Bates has insisted (1918: 383), though it is equally clear that height-growth or even width-growth may be used with much success. Since readiness and convenience are essential in the practical use of indicators, height-growth has received the most attention at the hands of those interested in the classification of sites. The whole question of site indicators as well as the advantages of height-growth in this connection has been well stated by Frothingham (1918: 755):

"Any method of determining forest sites must employ an indicator, whether this be the probable ultimate forest ('climax type'), the height-growth of one or more species present, the current annual volume increment of a fully stocked pure stand, some herb or shrub typical of a locality, or merely the composition of the existing stand. Similar sites are then to be recognized either by the identification of similar indicators or by determining the similarity of the physical-site factors. These may be measured in precise terms or simply estimated. Precise measurements appeal to the investigator. Accepting the permanent type as an indicator, for example, it would only remain to learn quantitatively the physical factors determining it. These physical factors wherever found interacting in precisely the same amounts will always produce, in time, barring accident or design, precisely the same form of forest. The plan of classification based on physical factors appeals to the investigator because it is truly fundamental. The apparent difficulties in deciding what is the permanent type in the isolation and measurement of the several physical factors, etc., may not be so formidable, after all, and the work may be simplified by the discovery that only one or two of the factors are of particular significance. In many large regions, the permanent forest type is strikingly apparent. In other places it remains exceedingly obscure. Even where plainly evident, subdivisions with reference to yield are a necessity from considerations of future as well as present management. This subdivision of permanent forest types or of any other kind of types can be effected by the use of an indicator. Indicator plants, volume growth, and height-growth are means to this end. Under certain circumstances the use of indicator plants may prove very useful, as experiments by Korstian and others indicate.

"The use of the current annual increment as a means of determining site involves the double difficulty of securing a basis and of applying the measure of the site, when found, to the identification of similar site conditions elsewhere. As an exact indicator it may prove the last word in refining previous site determinations in localities where it can be employed, but as a general method, suitable for immediate use, it fails to meet the requirements of simplicity and widespread utility previously set forth. The utility of height—one of the functions of volume, but far less unwieldy as an index—ought to be plainly evident to everyone as the logical immediate basis for subdivision. Height-growth, as a matter of fact, appeals in two ways: First, as an immediate means of classifying forest sites in general, and second, as a guide and a short cut in arriving at a possible future classification of sites on a physical or permanent type basis.

"In conclusion, the principle of height-growth as a guide to site has the following features:

"1. It is simple, natural, easily understood, and easily applied in the field.

"2. It is independent of the determination of physical sites producing definite permanent forms of forest; but the two are not antagonistic; both are 'indicators' and both demand equally a determination, more or less refined, of the physical factors of site.

"3. The sites determined by height-growth are species sites, not permanent-type sites; hence they are useful with reference to short-lived intolerant and long-lived tolerant species growing in the same stand.

"4. By adopting one or more index species (intolerant species of wide occurrence on a variety of sites) the height-growth of other species can be gauged, their relative value in each site can be determined, and this value can be expressed by naming the site in terms of the growth of each species present, and, by analogy, of other species which do not happen to be present.

"5. It affords a means of comparing the growth of all American species on the basis of the soil and climate to which each is best suited, as well as in less favorable sites.

"6. It permits a ready comparison (*a*) between even-aged second-growth stands in widely different regions, thereby avoiding such inconsistencies as those to be found in the published yield tables for the same species in different States; and (*b*) between second-growth and old-growth stands in the same or different regions.

"7. Since height-growth is sensitive to interferences in the natural life of the stand (fire, culling, changes in density, etc.) care and judgment are necessary in the choice of trees to serve as the index; but except for very precise site determinations, the method, if used with ordinary caution, will undoubtedly prove serviceable for the majority of wild-woods conditions as well as for even-aged stands.

"8. As the knowledge of the laws of growth of our species increases, the refinement of site determination by height-growth can be increased."

The correlation of height-growth with rainfall and other factors has been made by Pearson (1918: 688) for *Pinus ponderosa* in Arizona:

"Western yellow pine in northern Arizona makes its height-growth during the period of lowest precipitation in the year. During this period of high activity, the trees are dependent almost entirely upon moisture stored in the soil during the preceding winter and spring. Normally the great bulk, and in some years all of this moisture, is stored during the winter months, December to March. When winter precipitation constitutes the sole supply, height-growth in young saplings is apt to be small. If winter precipitation is supplemented by 2 inches or more in April and May, a pronounced stimulus to height-growth results. It may be stated as a general rule for the sites covered by this study, that 2 inches or more of precipitation between April 1 and May 31 is several times as effective as the same amount in excess of the normal precipitation between December 1 and March 31. Factors reflecting atmospheric moisture conditions, including evaporation, wind movement, relative humidity, cloudiness, and length of rainless period, from April 1 to June 30, show a close, though not entirely consistent, relation to height-growth. Temperature on the sites studied appears to be important only in so far as it affects moisture conditions. Since the increase in temperature results in increased water consumption, height-growth, if, as is usually the case, there is a shortage of moisture, varies inversely with temperature. Observations indicate that where moisture is abundant, height-growth increases directly with temperature. Complete records of soil moisture, if available, would probably show even a closer relation to height-growth than does precipitation."

It is highly probable that water-content is the factor that exerts the primary control upon height-growth, and width-growth also. However, it seems practically certain that the competition for water and food between the growing points and the cambium ring determines that height-growth shall largely precede width-growth during each year as well as during the life history of the individual (Mitchell, 1918). The studies of Brewster (1918:869) indicate that "the height-growth of larch seedlings does vary in accordance with variations in weather conditions from year to year, and that the most favorable conditions for rapid height-growth are produced in the North Idaho region by a combination of temperatures somewhat above the average, coupled with a high percentage of clear days, with an average amount of precipitation evenly distributed in the form of good rains at intervals of four to ten days preceded and followed by lighter showers." The greater rainfall, lower temperature, and greater cloudiness of northern Idaho in comparison with northern Arizona readily explain the relatively greater importance of temperature and light in height-growth, as well as the difference in the seasonal occurrence. This must be expected for the various climax associations, for which the task of correlation is primarily one of discovering the limiting factor by the measurement of the habitat complex.

In the determination and classification of sites, as well as in their discussion, it will conduce to clearness to recognize that this is almost wholly a matter of applying the indicator method. While the word site appears to refer to the physical conditions, it does so only in so far as these are indicated by the presence or growth of the species concerned. And while it is felt that the species affords a better measure than instruments do, such a measure is one of actual growth and not one of the controlling or limiting factors. Hence, it must be recognized that height-growth indicates habitat only in a general way, and that its specific indications apply only to the productiveness of the area in terms of a particular tree crop.

**Burn indicators.**—It is a general rule that subclimax dominants serve as the typical indicators of forest burns. This is in conformity with the principle that almost any consocies and many socies of the subsere may indicate fire as well as other similar disturbances, the particular initial stage depending upon the degree of disturbance or the frequency of its repetition. The universal occurrence of tree and shrub consocies as burn indicators is explained by the fact that fire not only produces areas temporarily free from the competition of the climax species, but also characterized by conditions favorable to less exacting species. Their characteristic dominance is chiefly due to the rapidity and completeness with which they occupy the ground, as a consequence of excessive seed production, the opening of cones by fire, or the ability to produce root-sprouts. The conifers rely almost wholly upon the first two methods and chiefly the second, while the deciduous trees depend mainly upon root-sprouts. Among trees, the three types are represented respectively by *Pseudotsuga* and *Larix,* such pines as *Pinus contorta* and *attenuata,* and by aspen, birch, and alder. The scrub indicators owe their character almost wholly to root-sprouting, reinforced more or less by seed production and mobility.

The burn subsere consists of the usual stages of annual and perennial herbs, grasses, shrubs, and trees. However, the number and distinctness of the stages and the duration of the subsere depend chiefly upon the severity of the burn. In the most severe burns the initial community often consists largely or wholly of mosses and liverworts, *Bryum, Funaria,* and *Marchantia,* and is followed by one of annuals, and this by one of perennials. The species, and to a less extent the genera, of these vary with the climax association, but such species as *Agrostis hiemalis, Epilobium spicatum, Achillea millefolium,* and *Pteris aquilina* are more or less universal. The development of a grass stage is less regular, since its place is often taken by scrub when the root-sprouting shrubs are abundant. The scrub is normally replaced by aspen, birch or alder, and these may yield to a subclimax forest, such as that of lodgepole pine, or be replaced directly by the climax. It is obvious that fire may sweep through the scrub, aspen, or lodgepole communities, and initiate new subseres, producing an intricate pattern of seres and communities. In the great majority of cases, the succession is more or less telescoped, and often completely so. The root-sprouting ability of the shrubs and aspen and the release of the seeds inclosed in cones or buried in the duff enable the shrubs and trees to begin development the first year, at the same time that the herbs appear. In such cases practically all the dominants appear at once, but the development still exhibits many of the features of succession. The stages, though brief, give character to the area in the normal sequence and each disappears in turn as the competition of the next one becomes too great for it.

For the reasons just given, the herbs are relatively unimportant indicators in complete burns, though they are characteristic in the case of light ground fires. The burn subsere is characterized almost wholly by scrub, deciduous woodland, or subclimax forest, not only because of the duration of the latter, but also because repeated fires tend to make them relatively permanent. On account of differences of distribution as well as the general similarity in requirements, the three types rarely occur in the same subsere. Two, however, are frequent, aspen and lodgepole being the most common. The rule is that the dominant with the greatest requirements is the subclimax. This is in accord with the occurrence of lodgepole as the characteristic burn community in the northern Rocky Mountains, aspen in the southern, and scrub in the Southwest and in California. As burn indicators, they have several features in common, in spite of their differences in life-form. They not only indicate the possibility of reestablishing the climax by preventing fire in some cases or by planting in others where the original climax dominants have disappeared. But they also make it clear that artificial means and fire especially must be resorted to in areas where it is desirable to maintain the subclimax as a relatively permanent type (plate 87).

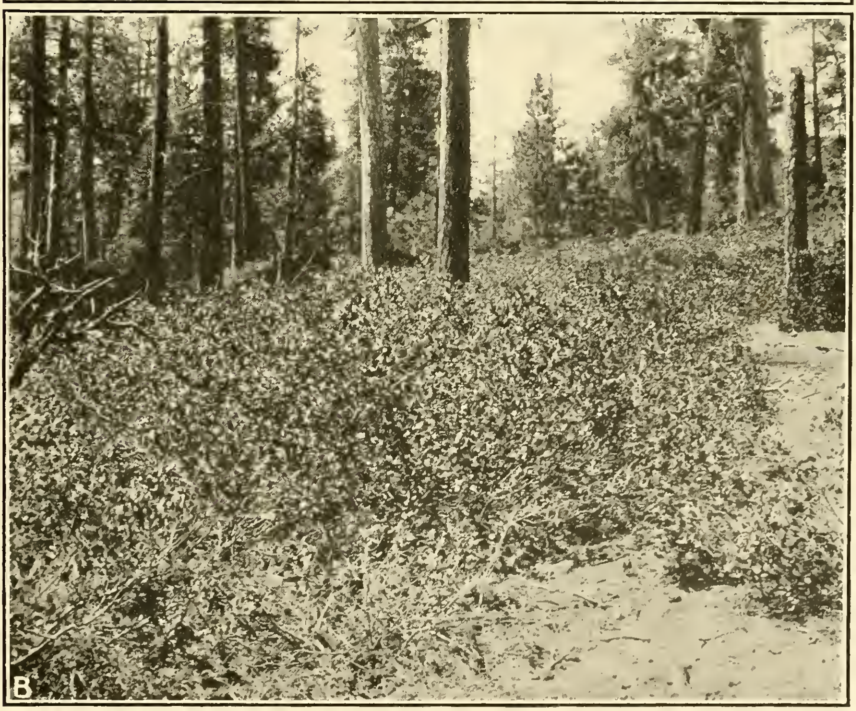
The importance of burn subclimaxes has been emphasized by Clements (1910: 56) in the case of the lodgepole pine:

"The lodgepole forest is the key to the silvicultural treatment of the forests of the eastern Rocky Mountains, especially in Colorado and Wyoming. Its position in a zone between Douglas fir and yellow pine below, and Engelmann spruce and alpine fir above gives the forester a peculiar advantage. Its enormous seed-production, the power of the seeds to remain viable in the cones for years, its preference for soils of moderate water-content, the dependence of reproduction upon sunlight, and its rapid growth are all points of the greatest value in enabling the forester to accomplish his results. And it is by means of fire properly developed into a silvicultural method that the forester will be able to extend or restrict lodgepole reproduction and lodgepole forests at will."

The relation of aspen to lodgepole in burn subseres and its rôle as a temporary type have been dealt with in the same study (20, 47). The significance of aspen as a burn subclimax and its importance as a temporary type have been discussed by Pearson (1914: 249), Sampson (1916: 86), and Baker (1918: 294, 389). In the Northwest where *Pseudotsuga* forms a remarkably permanent subclimax in burns of enormous extent, Hofmann (1917: 23) has reached the following conclusions:

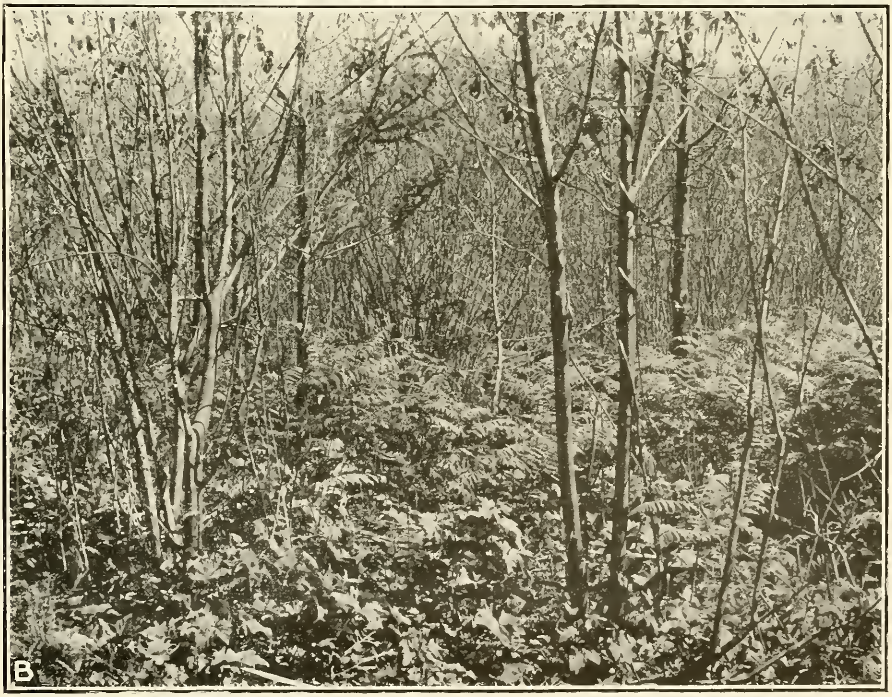
"The study of burns and cut-over areas in the Douglas-fir region of the Pacific Northwest has brought out the following facts: The distance to which seed trees are capable of restocking the ground is limited to from 150 to 300 feet. They can not, therefore, account for the restocking of the large burned areas. The irregular dense stands of young growth are due to seed stored in the forest floor or in cones. This seed retains its viability through the fire and is responsible for the dense reproduction that springs up after the first fire. The even-aged stands of reproduction immediately following a fire, regardless of location of remaining seed-trees, the irregular alternation of dense stands of reproduction with grass areas, and the failure of reproduction on areas burned over by a second fire before the stand reaches seeding age, or by consuming all of the duff and precluding any possibility of seed remaining after the fire, all point to the seed stored in the duff as the principal source of seed responsible for the restocking.

"Since the seed must be produced by the stand before it is destroyed, the age at which the different species begin to produce seed is of the utmost importance. It varies greatly, and this variation alone is often the controlling factor in determining the composition of the second growth. For example, when western white pine, Douglas fir, and knobcone pine (*Pinus attenuata*) appear in a mixed stand which is destroyed by fire, all of these species may again appear in the next stand; but if this second growth is destroyed by fire

A. *Chamasbatia foliolosa* indicating fire in pine forest, Yosemite National Park, California.

B. *Ceanothus velutinus* indicating fire in pine forest, Burns, Oregon.


A. *Anaphalis* and *Epilobium* indicating a recent burn, Wind River Experiment Station, Washington.

B. *Pteris* and *Rubus* indicating fire following one marked by *Arbutus*, *Prunus*, etc., *Pseudotsuga* forest, Eugene, Oregon.

when it is from 10 to 12 years old, the next stand will consist principally, if not wholly, of knobcone pine. The knobcone pine begins producing seed when it is 6 years old and is producing good crops of seed at 10 years, while the white pine and Douglas fir bear only occasional cones at ages under 12 years. Therefore the knobcone pine is the only species which has any seed present to produce a forest stand following the second fire. Instances of such types are the knobcone pine types on the Siskiyou National Forest."

Scrub communities are regularly indicators of fire where they are in contact with forest. In fact, sagebrush appears to be a fire subclimax in the piñon-cedar woodland, as well as in the southern portion of the Coastal chaparral. Chaparral, however, is the typical scrub indicator of fire in woodland and forest. This is as true of the subclimax chaparral along the eastern edge of the grassland climax as it is of the Petran and Coastal associations. The most characteristic development of chaparral as a burn indicator is found in the montane forest in California, where the scrub persists as a more or less complete forest layer (p. 213; cf. Mitchell, 1919: 39; Foster, 1912: 212). Chaparral owes its importance as a fire indicator to its remarkable ability to form root-sprouts, and hence the form of the dominant shrubs is itself a response to fire. Fire in chaparral leads to a short subsere, in which the herbaceous stages persist for only a few years before the new shoots overtop them. Repeated fires may produce a subclimax characterized by *Eriodictyum*, or by *Artemisia*, *Salvia*, and *Eriogonum*. In the region of its contact with woodland and forest, chaparral is an indicator of forest burns, and consequently is subclimax. This is true in both associations, but is more marked in the Sierran, perhaps because of its greater massiveness. Munns (1919: 9) has assumed that all of the latter is a temporary type due to fire, but this certainly seems not to be true of the regions with 12 inches or less of rainfall. This assumption is largely due to a misconception of what constitutes the test of a climax. Both of the tests used, the successful planting of trees and the existence of scattered trees and tree stands, would prove the grassland climax to be a temporary one. The critical processes in the establishment of a forest are seed-production, dissemination, and ecesis, and artificial planting is powerless to throw light upon the outcome of these. Further studies of the chaparral formation during the past three years have confirmed the view expressed in 1916 (Plant Succession, 180) that it constitutes a real climax, though portions of it are undoubtedly subclimax. This view is supported by the conclusions of Cooper (1919), who has made an intensive study of the California chaparral upon the instrumental and successional basis (plate 88).

Grazing indicators.—With reference to the forest itself, only those grazing indicators are of importance that indicate overgrazing, and hence actual or potential damage to the reproduction. The presence of the usual overgrazing indicators would serve this purpose, but these are usually accompanied by evidences of damage to the seedlings as well. However, while abundant evidence of this nature denotes overgrazing, it is still a question as to just when this becomes critical in the reproduction of the forest. In fact, it is clear that the critical degree of overgrazing depends much upon the nature of the community, time of year, age of the seedlings, and other factors. Much light has been thrown upon the problem by three careful studies in the national forests.

Hill (1917: 23) has reached the following conclusions with reference to the damage done to seedlings in the yellow-pine forests of northern Arizona:

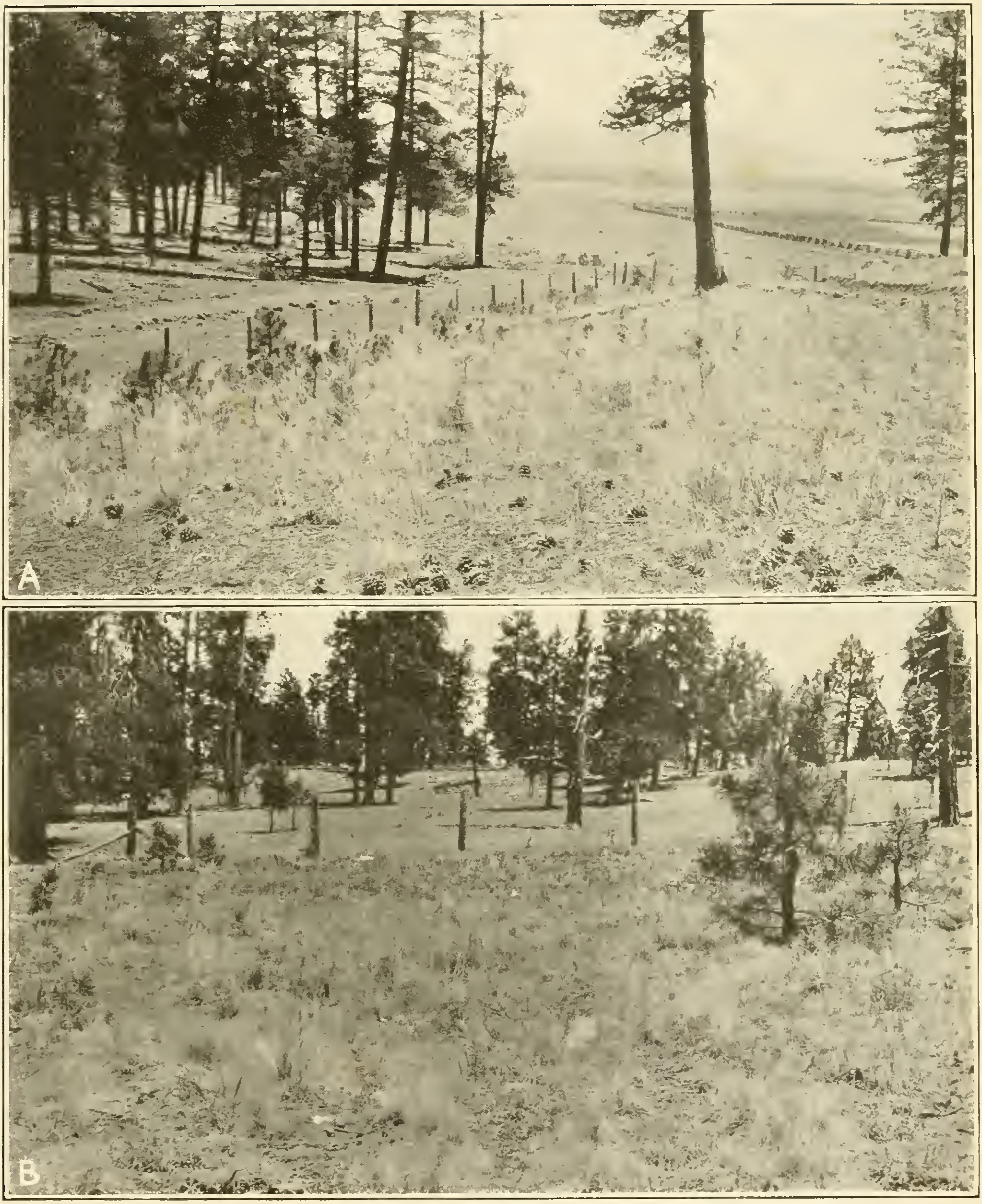
"Of 8,945 trees of a size subject to grazing, observed over a period of three years, 1,493 or 16.7 per cent were severely damaged each year and 1,222 or 16.1 per cent were moderately damaged. The most injured are the seedlings, 21 per cent of which are seriously damaged. The damage gradually decreases with an increase in the size of the trees. Trees above 4.5 feet in height are free from damage by browsing. The greatest amount of damage occurs during the latter half of June and the first part of July, or when the effects of the spring dry period are most pronounced. Under normal conditions of grazing, cattle and horses do an inconsiderable amount of damage to reproduction. Sheep under the same conditions may be responsible for severe injury to 11 per cent of the total stand. On overgrazed areas all classes of stock are apt to damage small trees severely. Cattle and horses may damage about 10 per cent of all reproduction. Where sheep are grazed along with them, however, at least 35 per cent of the total stand may be severely damaged. The amount of palatable feed available during the grazing season, and especially during June and July, has an important bearing on the amount of damage that grazing will cause to reproduction" (plate 89).

Sparhawk (1918) has shown that the damage to seedlings more than a year old is negligible in the yellow-pine forests of central Idaho, while the mortality of seedlings less than a year old averages 20 per cent. He states that, on the whole—

"More than three times as many seedlings were killed by other causes as were killed by sheep grazing, and five times as many were injured. As a general rule, the range should be grazed just enough to remove the greater part of the palatable forage. Extensive browsing of the least palatable species or of conifer reproduction is the best evidence that the area is being grazed too closely not only for the good of the range, but also for the best interest of the stock. Steep slopes with loose soil, particularly where the seedlings are less than a foot and a half high, and reproducing burns, clear-cut areas, or plantations with seedlings up to 5 or 10 years old, depending on the site, should be grazed rather lightly, especially in the first part of the season or during a wet period. In many instances it will be desirable to eliminate grazing entirely from plantations or other areas of seedlings less than three years old. During a dry season spots where danger of fire is greatest may be grazed as closely as possible."

Sampson (1919: 25) has summarized the results of his study of the effect of grazing upon aspen reproduction as follows:

"The leafage, young twigs, and branches of the reproduction are browsed with varying degrees of relish by both cattle and sheep. Over 90 per cent of the damage inflicted by stock is chargeable to browsing, the injury due to trampling, rubbing, and similar causes being negligible. Sheep are responsible for severe damage to the reproduction, both as it occurs in standing timber and on clear cuttings, regardless of the variety and supply of choice forage. Cattle cause some damage, but the extent of injury is usually slight, except where the lands are overgrazed or where the animals are inclined to congregate for more or less lengthy periods. The injury and mortality chargeable to the presence of live stock is roughly proportional to the closeness with which the lands are grazed. Observations covering a 50-year period in standing timber on sheep range showed that 27.2 per cent of the reproduction was either in-




A. Pine reproduction in a fenced area, Fort Valley Experiment Station, Arizona.
B. Fenced quadrat showing effect of grazing upon reproduction, Cliffs, Arizona.

jured or killed on lightly grazed plots, 31.8 per cent on moderately grazed areas, and 65 per cent on heavily grazed plots. During 1915 and 1916 the average percentage of injured and killed sprouts by cattle browsing was 1.6, 2.4, and 26.8 on lightly, moderately, and heavily grazed plots, respectively. On clear-cut lands, where the reproduction is conspicuous and the stand even, the annual mortality due to sheep grazing is exceedingly heavy. As a rule, three years of successive sheep grazing on such lands results in the destruction of the entire stand."

Cycle indicators.—Trees, and shrubs also, may serve as indicators of climatic cycles by virtue of their growth, seed-production, or reproduction. In addition, there appears to be a certain correlation between the frequence and intensity of forest fires and the dry and wet phases of the cycle. The growth of trees as recorded in the annual rings is the classic material for the studies of Douglass, Huntington, and Kapteyn upon climatic cycles. The width of the ring indicates the varying rainfall of different years so clearly that Douglass (1919) has found it possible to cross-identify rings from trees grown many hundreds of miles apart. He has also found that the yellow pines of central Arizona often indicate two growing periods in one year by the formation of a double ring, and Shreve (1917: 706) states that this appears to be regularly the case with trees at 6,000 feet in the Santa Catalina Mountains. It seems almost certain that height-growth and volume will likewise show cycle correlations, and this is suggested by Pearson's results in the study of the relation of height-growth to spring precipitation in northern Arizona (p. 351). The suggestion that seed-production is related to climatic cycles is based upon its well-known periodicity (Zon and Tillotson, 1911: 133), as well as upon the fundamental fact that as a growth response it is controlled primarily by water and temperature. It seems probable that the seed-production cycle of pines especially is a response to the interaction of the 11-year cycle and the excess-deficit cycle of 2 to 3 years.

Reproduction reflects more or less faithfully the variations in rainfall during the 2 to 3 year, the 11-year, and the 22-year cycles. This correlation is clearly seen in the case of woodland and montane forest, especially at the lower limit, but it is naturally less evident in climaxes with a higher rainfall. It is most striking where woodland or forest is in contact with a community of lower water requirements, such as grassland, sagebrush, or chaparral, and shows less in the reproduction on the forest floor. All the cases of tree savannah and "natural parks" so far investigated warrant the working hypothesis that reproduction in such areas is cyclic and corresponds as a rule to the 11-year cycle, though minor variations conform to the 2 to 3 year cycle. There is also considerable evidence that the success or failure of planting operations has often been determined by their accidental coincidence with the wet or dry phases of the 11-year cycle, while it is obvious that in the future planting should be carried out with reference to the phases of the 2 to 3 year and 11-year cycles (plate 90).

## PLANTING INDICATORS.

Kinds.—Indicators of sites for planting are of two kinds: (1) those that indicate the former presence of forest; (2) those that suggest the possibility of developing forest in grassland or scrub areas. The first are indicators of reforestation, the second of afforestation. The obvious indicators of reforestation are relict survivors, or trunks and stumps. Less obvious but equally conclusive are charred fragments or pieces of charcoal in the soil. In those cases where there is no direct evidence of the original forest, the desired clues are readily afforded by indicator communities which bear a definite relation to the forest. Such are seral and especially subclimax communities which exhibit a successional relation to the forest climax, and societies of shrubs or herbs which formed layers in it. While the latter are frequent in burns and clearings, they are usually accompanied by tree relicts which furnish more direct evidence. In some cases, however, they are the sole indicators of the former existence of forest in a particular spot. Subclimaxes are by all odds the best indicator communities of forest climaxes, since they show that the habitat has reached the condition in which the climax dominants can thrive. The earlier communities of a subsere have nearly the same value, since the habitat undergoes relatively slight change. In the case of a prisere, only the grass and scrub stages indicate that the slow reaction upon the originally bare area has reached a point in which remaining changes may be compensated by planting operations. Afforestation indicators are savannah, chaparral, or grassland of tall-grasses, in which the water requirements are sufficiently near those of trees that the gap may be bridged by planting methods, and especially by making use of the increased rainfall of the wet phase of the climatic cycle.

Furthermore, the indicators of sites for planting or sowing serve also to indicate the preferred species. In the case of reforestation, the general rule is that these are the climax trees that were in possession, but reasons of management may make it desirable to employ a subclimax dominant, such as lodgepole pine. Similarly, the growth-form best adapted for planting in a region is the one developed by that region, as the Forest Service has repeatedly demonstrated at its experiment stations. In the case of afforestation, the indications as to species must be derived from tree communities somewhere in contact with the grassland or scrub, as from pine in the case of the sandhills of Nebraska, from the indications of an intermediate community, such as scrub, or from the comparative study of habitats.

Prerequisites for planting and sowing.—The critical part played by rodents and by competition in natural reproduction was recognized more than a decade ago (Clements, 1910). Extensive tests of sowing in many national forests by the Forest Service has shown that destruction or control of the rodents is imperative (Tillotson, 1917: 50). In fact, it seems evident that for practically all regions rodents are the most serious enemies of both natural and artificial reproduction, and that they should be systematically and permanently cleared out of all areas in which reproduction is important. Competition is a process which is less readily controlled on a large scale. Competition for water is much more decisive as a rule than for light, the latter usually becoming critical only in dense scrub or similar communities. The disturbance of the soil involved in planting seedlings or in sowing by the seed-spot method usually suffices to reduce water competition sufficiently, except in a grass sod. The latter is usually encountered in clearings and in grassland associations in which afforestation is the method to be employed. In climax grassland, where the annual rainfall is less than 25 inches, the grasses use all of the water-content during the drier portions of the season. As a consequence



A. Reproduction cycle of *Picea engelmanni*, Uncompahgre Plateau, Colorado.
B. Extension of *Juniperus* into sagebrush during wet phase of cycle, Milford, Utah.

seedlings or transplants have little chance of survival unless the sod is destroyed about them, or unless planting is done during a period of unusual rainfall. As a desirable precaution under all conditions, the competition of the grass cover should be decreased by such treatment as the density of the sod and the nature of the soil will permit (Bates and Pierce, 1913: 43). By far the most important practice in this connection, however, is the utilization of climatic and seasonal cycles to evade serious drought during the first few years (Hofmann, 1919).

Use of climatic cycles.—The critical importance of wet and dry periods for planting plans is strikingly shown by the variations in rainfall for the two areas in which afforestation has been tried on a large scale. The lowest rainfall at Valentine, on the northern edge of the sandhill region of Nebraska, was 10 inches in 1894; the highest was 28 inches in 1905. The lowest rainfall at Garden City, in the sandhill region of Kansas, was 9 inches in 1893; the highest was 29 inches in 1898. In both cases the rainfall of the wettest year was practically 3 times that of the driest, and the wettest and driest years departed practically 10 inches from the normal. A somewhat similar condition is shown at higher altitudes, where most of the reforestation planting and sowing is done. The base of Long's Peak, altitude 8,700 feet, shows a variation from 14 to 30 inches, while Pike's Peak, altitude 14,100 feet, exhibits a range of 9 to 44 inches. In all of these, the minimum rainfall occurred at the maximum of the 11-year sun-spot cycle, while the maximum rainfall either occurred at the sun-spot minimum or was related to it through the excess-deficit cycle of 2 to 3 years. In planting operations, the minimum is to be avoided at all costs, and this can be done almost certainly by utilizing the date of the maximum of the sun-spot cycle of 11 years. It is almost as important to anticipate a period of several wet years. The correspondence of the wet phase with the sun-spot minimum is not so good as that of the dry phase with the maximum, but it is sufficiently close in time and amount to make a great improvement over present methods. When the excess-deficit cycle is taken into account, the correspondence becomes so close as to warrant the assumption that planting can be planned in such a way as to avoid dry periods and to coincide with wet ones. As already shown in Chapter V, it is necessary to determine the operation of the climatic cycle in the particular region concerned.

**Reforestation indicators.**—The first definite proposal to use native plants as indicators of specific planting sites appears to have been made by Zon (1915):

"The selection of sites suitable for planting in a region which has been stripped of its natural timber is among the most perplexing problems. As long as there is a remnant of the virgin forest left, the latter may serve as a guide in selecting the species to plant on the given site.

"When, however, as is the case of the Ephraim Canyon and several other canyons on the Manti Forest, the original virgin timber has nearly disappeared altogether, both as the result of severe burns and grazing, and has been replaced by shrubs, herbaceous vegetation, and wide stretches of aspen cover extending over an area originally occupied by several forest types, the question of deciding what species to plant on a given site becomes very difficult indeed. In such cases the shrubs and the herbaceous vegetation which occur throughout the canyon can be used to advantage as an indicator of the moisture content of the different sites and therefore for prognosticating the kind of timber the site can best support. The native shrubs and herbaceous vegetation, since they are not merely forerunners of the forest type that will eventually develop on a given site, but are also associates and are characteristic of different types as their typical undergrowth, are useful in deciding upon the species to plant. This is true not only where the original forest has entirely disappeared, but also on sites where there are still some traces of the original stand but which, because of the change in the physical condition of the site brought about by clear-cutting or burning, may better support a species which naturally grows at a somewhat lower elevation.

"For the purpose of artificial reforestation, Ephraim Canyon may be divided into five vegetation belts. The upper and lower limits of these vegetation belts vary, of course, on the southern and northern exposures; on the southern slopes the upper limits of each vegetation belt will extend to a higher elevation than on the northerly slopes, but wherever a certain vegetation is found it may be indicative of one or another natural timber belt, irrespective of the altitude or exposure. These five belts are as follows: (1) the lower timberless belt; (2) the yellow-pine belt; (3) the Douglas-fir belt; (4) the Engelmann-spruce belt; and (5) the upper timberless belt."

The indicators of the various zones are shown in figure 25.

Tillotson (1917: 53) has pointed out the importance of indicators in the selection of planting sites (plate 91):

"The suitability of an area is very strongly indicated by the natural growth present. This is a pretty fair criterion of the quality of the site, and it points out the species which are most likely to succeed—either those which naturally occupy the area or others whose demands upon soil and climate are quite similar. A heavy growth of trees on similar adjacent sites will indicate that the area is quite probably suitable for sowing or planting; while a sparse growth of a drought-resistant species of tree on such sites will indicate that the area is only suited to reforesting with very drought-resistant species and that even then success will be uncertain."

He has also given a detailed summary of the planting indicators for the various regions and the most important species of the West. The nature and importance of his account may be gained from the following extract, which gives the indicators for Utah and southern Idaho:

"Western yellow pine in Utah: (1) Burned-over areas in the natural yellow-pine types; (2) areas covered with brush, mainly of oak, maple, and service berry; (3) areas covered with open stands of scrubby aspen; (4) sagebrush areas.

"Western yellow pine in southern Idaho: (1) Those sites producing yellow pine naturally; (2) brush areas within the limits of yellow pine and adjoining stands of that species; (3) open grassy areas in the neighborhood of timber stands.

"Douglas fir: (1) Burns within the fir type; (2) sites covered with aspen of moderate density; (3) burns in the Engelmann spruce type; (4) areas covered with brush of oak, maple, service berry, cherry, and other deciduous species; (5) open grassland and mountain meadows. The planting of this species naturally centers mainly around the aspen type, particularly in Utah. The last two sites are not considered favorably for planting at present.

"Engelmann spruce: (1) Burned-over, non-restocking Engelmann spruce and balsam-fir cuttings; (2) the denser and better stands of aspen occurring at high altitudes; (3) lodgepole-pine burns.

A. *Arbutus* indicator of reforestation sites, *Pseudotsuga* forest, Eugene, Oregon.

B. Reproduction of *Pseudotsuga* from seed stored in soil, Wind River Experiment Station, Washington.

"Lodgepole pine: (1) Lodgepole-pine burns which are non-restocking; (2) non-restocking Engelmann-spruce burns; (3) aspen-covered areas at higher altitudes. This species is not thought suitable for planting on brush areas nor on open grassy land where sheltering objects are missing."


FIG. 25.—Indicators of planting sites in the various zones, Utah Experiment Station, Ephraim. After Zon.

Korstian (1917: 281) has made use of the herbaceous and shrubby species in distinguishing between Sites I and II for yellow pine in the Datil National Forest in New Mexico.

"A perusal of the list shows marked differences in the individuality of the vegetation of the two sites. Site I is shown to produce such typical mesophytes as *Mnium* sp., *Agrostis hiemalis, Bromus polyanthus, Muhlenbergia wrightii, Populus tremuloides, Arenaria confusa, Cerastium longipedunculatum, Silene laciniata, Aquilegia chrysantha, Thalictrum wrightii, Draba helleriana, Potentilla atrorubens, P. crinita, Rosa fendleri, Geranium richardsonii, Viola neomexicana, Amarella scopulorum, Gentiana bigelowii, Prunella vulgaris, Mimulus langsdorfii, Penstemon virgatus, Campanula petiolata,* and *Solidago neomexicana.* Site II bears such transitory species and xerophytes as *Poa rupicola, Commelina dianthifolia, Yucca* sp., *Quercus grisea, Portulaca oleracea, Heterothrix longifolia, Cercocarpus breviflorus* and *Hymenopappus radiatus.*

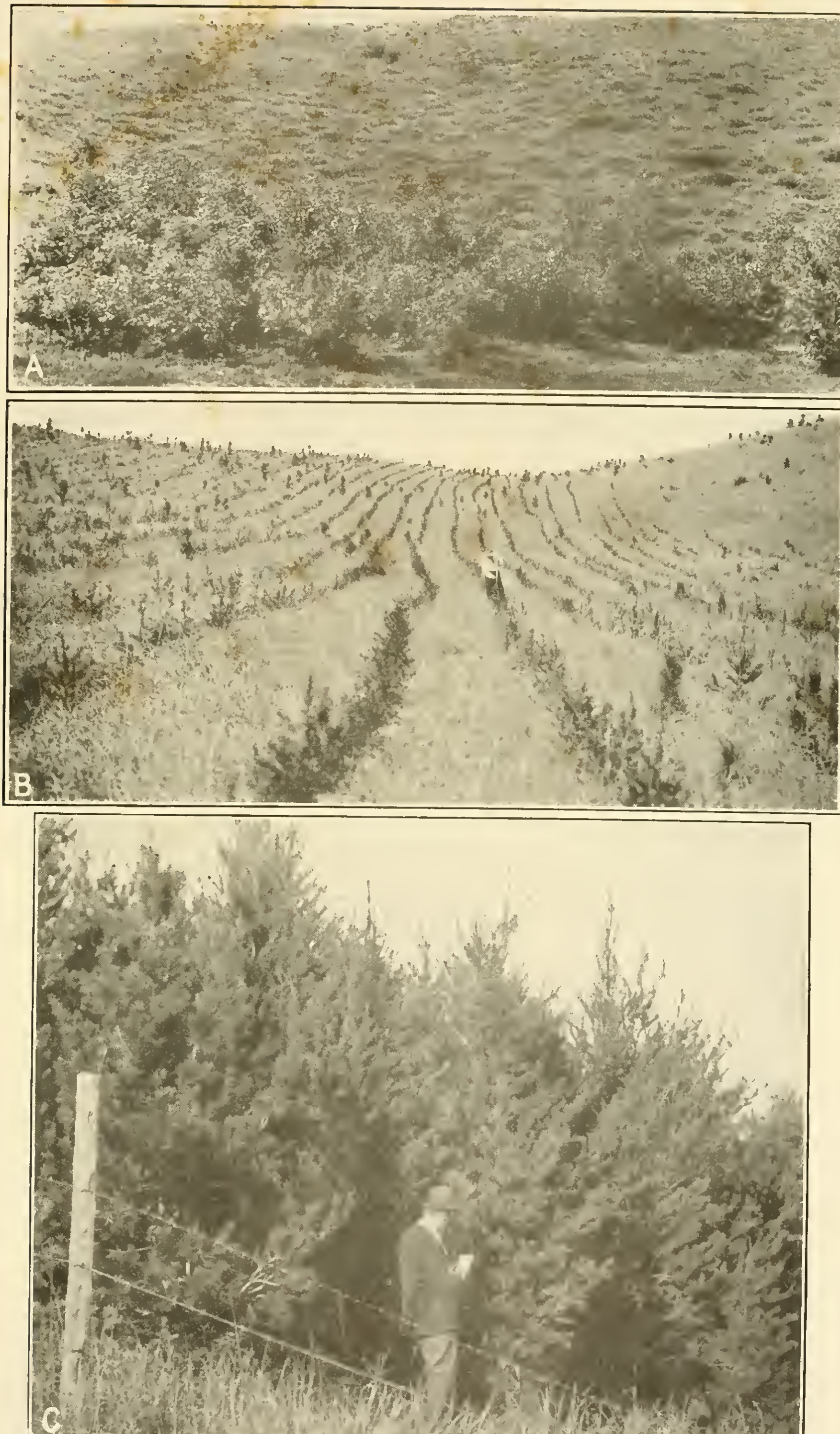
The moss (*Mnium* sp.) was found only in cool, moist, and shaded situations, thereby indicating unusually favorable site conditions. The monkey flower (*Mimulus langsdorfii*) was the only plant which was confined to the proximity of water, indicating excessive soil moisture conditions.

"Practically all of the species listed as occurring entirely on Site II, which do not overlap on other sites, were found in hot, dry, and unshaded situations and might be regarded tentatively as indicators of poor western yellow-pine sites in the San Mateo Mountains. The mesophytes listed as possible Site I indicators were not found on poorer sites in this locality. However, it may be true that further detailed studies in the San Mateo Mountains might require a different listing of the vegetation than that here given. A number of the species listed as occurring on only one site are, to the writer's personal knowledge, known to occur on different sites in other parts of the Southwest. The vegetation on Site II was comparatively sparse and more open than on Site I where it was also more luxuriant and vigorous. Those species which were found to overlap on both sites normally made their optimum development on Site I. Approximately twice as many species were found on Site I as on Site II."

Afforestation indicators.—As already stated, the indicators of the possibility of forest production in grassland and scrub climaxes are either such extra-regional communities of trees as are found in savannah or in the fringing woods of river valleys, or such grasses and shrubs as indicate an approach to the water requirements of trees. As a matter of fact, practical afforestation has been confined chiefly to the sandhill regions of Nebraska and Kansas, in the first of which all four of these indicators have been present in some degree. Indeed, the success of planting in Nebraska and its failure in Kansas are related to the fact that these indicators were present in the one State and largely lacking in the other. While it is clear that no sharp line can be drawn between reforestation and afforestation, the latter is regarded as having to do only with those climaxes, grassland and scrub, in which trees occur at the margins or in valleys. While pine savannah and valley woodland were doubtless more extensive in the sandhills of Nebraska during the wet phases of some of the major climatic cycles of the present geological period, it is practically certain that this region has belonged to the grassland formation since the Miocene at least (plate 92).

Bessey (1887, 1895) was the first to point out the evidence which indicated that the sandhills of Nebraska could be forested, or reforested as he regarded it. This evidence consisted wholly of valley and canyon relicts of woodland, chiefly yellow pine. It was summarized as follows:

"There are many isolated canyons which contain trees; there are western as well as eastern trees and shrubs in these canyons; the yellow pine of the Rocky Mountains now grows with other trees upon the hills of Pine Ridge from the Wyoming line in Sioux County to the Dakota line in Sheridan County; the yellow pine is now to be found in the canyons of the Niobrara River and its tributaries as far east as the border of Holt County; it extended eastward along the North Platte River and Lodge Pole Creek to Deuel County until the pioneers destroyed it, forty or fifty years ago; it grew in considerable quantities in at least one station on the Republican River until destroyed by the early settlers; in the Loup Valley there are yellow pines on the South, Middle, and North Loup Rivers; logs and fragments of pine trees occur here and there in the sandhills."



A. *Salix* and *Ceanothus* indicating planting site in sandhills, Halsey, Nebraska.

B. Three-year old plantation of jack pine (*Pinus divaricata*) in sandhills, Halsey, Nebraska.

C. Jack pines 10 years after transplanting, Halsey, Nebraska.

Pool (1914: 267) has considered in some detail the sandhill communities of shrubs which show the close approach to the water requirements of trees, among the most important of which are *Celtis*, *Prunus*, and *Salix*.

Bates and Pierce (1913: 15) have discussed the sandhill shrubs in their general relation as indicators of forestation and of planting sites:

"Of the numerous woody undershrubs the yucca, or soap-weed (*Yucca glauca*), is probably the most striking plant of the sandhill region and is least abundant where the soil is the most stable and firm. Other shrubs, most of which are more or less gregarious and form clumps or mats on the ground, are the sandhill willow (*Salix humilis*), very common on north slopes and indicative of good moisture conditions, the redroot or New Jersey tea (*Ceanothus ovatus*), typical of sandy hilltops; the sand cherry (*Prunus besseyi*), found in almost any site, but especially in the loose sand around blow-outs; and the shoe-string bush (*Amorpha canescens*). Wolfberry (*Symphoricarpos occidentalis*), choke-cherry, and wild plum frequently form thickets on the slopes of pockets facing the southeast, where they are favored by the moisture from snowdrifts. The first-named seldom becomes more than 2½ feet high, the other two frequently 15 feet.

"From the standpoint of forestry one of the most important of the woody plants is the low bearberry or kinnikinnik (*Arctostaphylos uva-ursi*). While this grows in only a few limited localities, on moist north slopes, it is thought to be indicative of conditions favorable for western yellow pine, since it is an almost invariable associate of that tree in the Rocky Mountains.

"Typical of the stream valleys in both Kansas and Nebraska are the false indigo (*Amorpha fruticosa*), the buffalo berry, peach-leafed willow, sand-bar willow, wolfberry, plum, and chokeberry. The diamond willow, one of the Nebraska sandhills' most valuable small trees, is not found in Kansas. On the whole, shrubby growth is much more typical of the Nebraska than the Kansas sandhills, which usually have a heavy grass sod that does not permit the growth of shrubs."

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# INDEX

# PLANT INDICATORS

## THE RELATION OF PLANT COMMUNITIES TO PROCESS AND PRACTICE

BY

FREDERIC E. CLEMENTS

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