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The Vegetation
OF
Northern Cape Breton Island, Nova Scotia

BY

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I. GENERAL PHYTOGEOGRAPHIC RELATIONS OF THE REGION

Viewed from the standpoint of ecological plant geography, the vegetation of the forested portions of eastern North America, north of southern Florida, comprises two great climatic formations: the Deciduous Forest Formation and the Northeastern Evergreen Coniferous Forest Formation. Viewed from the standpoint of floristic plant geography, it is possible to subdivide the vegetation of this area still further (in this connection see especially Transeau '05, Harshberger '11, Shreve '17), but from the ecological point of view, as will be emphasized later, the advisability of such subdivision is at least open to question.

The deciduous forest formation attains its highest and most typical development in the lower Ohio basin and the southern Appalachians, where the climax forests are made up almost wholly of deciduous trees. These include a wealth of species, prominent among which are beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*), chestnut (*Castanea dentata*) and tulip (*Liriodendron Tulipifera*), red oak (*Quercus rubra*), white oak (*Quercus alba*), hickory (especially *Carya alba*), and white ash (*Fraxinus americana*). The evergreen coniferous forest formation attains its optimum development in middle-eastern Canada. Here the climax forests are relatively poor in species, consisting mainly of balsam fir (*Abies balsamea*), white spruce (*Picea canadensis*) and black spruce[1] (*Picea mariana*), with which is associated the paper birch (*Betula alba papyrifera*).

[1] In all the current manuals a distinction is made between the black spruce and the red spruce (*Picea rubra*). After several years of experience in the north-woods, the writer is obliged to confess his inability to differentiate with certainty between the two, an inability which he finds to be shared by many other botanists. It is his opinion that the red spruce at best should be regarded merely as a variety of the black spruce, the status which it formerly held. To be sure, the small, impoverished bog form of this tree (the typical *P. mariana* of the manuals) does appear very distinct when compared with the large, thrifty upland form (which typifies *P. rubra*) ; but there are all sorts of intergradations between these two

Midway between these two regions (see map, FIG. 1), is situated the Transition Forest Region, a broad zone in which, due to the overlap in the ranges of the southern and northern climax

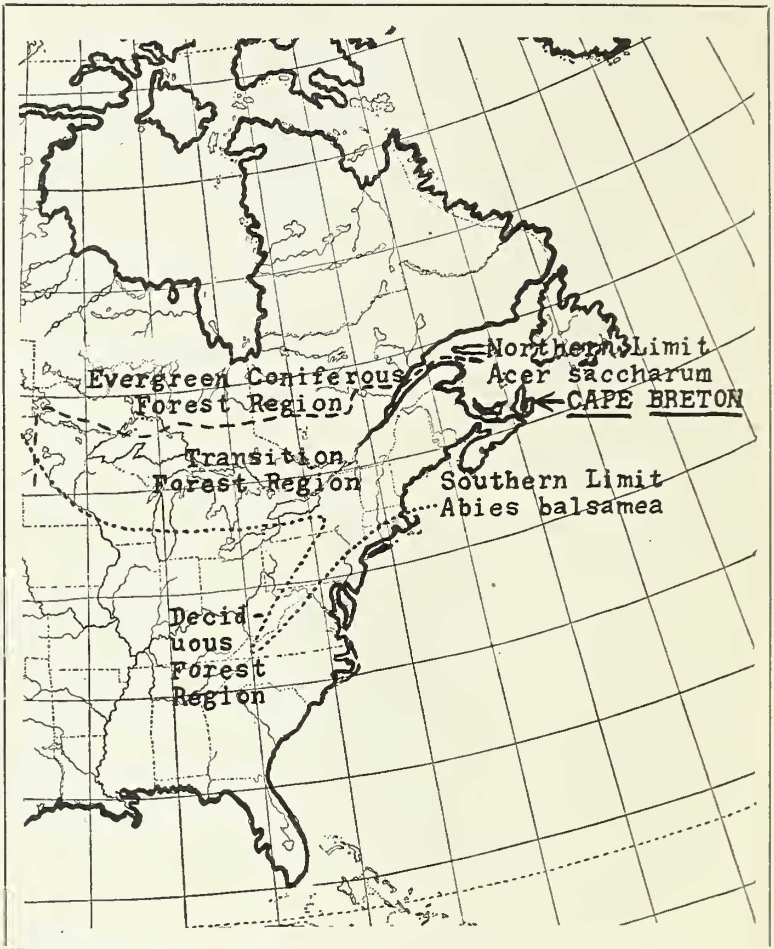

FIGURE 1.—Map of eastern North America, to show position of Cape Breton Island with reference to the Transition Forest Region.

extremes. Moreover, especially in these intermediate forms, the structural dissimilarities upon which the manuals lay stress in attempting to differentiate two distinct species, are far from satisfactory in their application. In the present paper no attempt is made to distinguish *P. rubra* from *P. mariana,* although it is appreciated that much of the upland spruce may perhaps well be referred to the former "species."

trees, the nature of the climax forest, taken in its entirety, is intermediate between that of the evergreen coniferous, and that of the deciduous climatic formation, as most typically developed: where, in other words, the two formations are telescoped. This region represents a great tension zone, in which competition between the northern and southern climax trees is still in active progress, and where, as a result, it is possible to study the ecological relations of the two groups of species concerned. The northern boundary of this transition region is determined by the northern outposts of the deciduous climax trees of the deciduous forest formation: it may be regarded as coinciding approximately with the northern limit of the sugar maple (see, in this connection, Cooper '13, pp. 36–39). In the same way, the southern boundary of the transition region may be said to be determined by the southern outposts of the climax trees of the evergreen coniferous forest formation, in so far as these grow on uplands: it may be regarded as coinciding roughly with the southern limit of the balsam fir. These boundaries are indicated on the map (FIG. 1), but the lines as drawn can represent little more than a rough approximation; for, owing largely to variations in topography, at higher elevations the evergreen coniferous forest formation locally extends far to the south of the northern boundary, while at lower elevations the deciduous forest formation is typically developed considerable distances north of the southern boundary of the transition region, as here represented.

From the standpoint of floristic plant geography it is significant that the geographic center of distribution for the so-called Canadian element in the flora of eastern North America lies within this transition region. Many Canadian species are practically confined to this area, prominent examples of this latter group, among the woody plants, being *Pinus Strobus* and *P. resinosa, Tsuga canadensis, Betula lutea, Acer pennsylvanicum,* and *Viburnum alnifolium*. But while, from the floristic point of view, the vegetation of this region certainly is more or less unique, from an ecological point of view it is doubtfully to be regarded as a distinct climatic formation. And while its intermediate character is generally recognized, nevertheless, largely because of the almost universal supremacy, in situations edaphically favorable to their development, of the climax trees of the deciduous forest formation over those of the northeastern evergreen conifer-

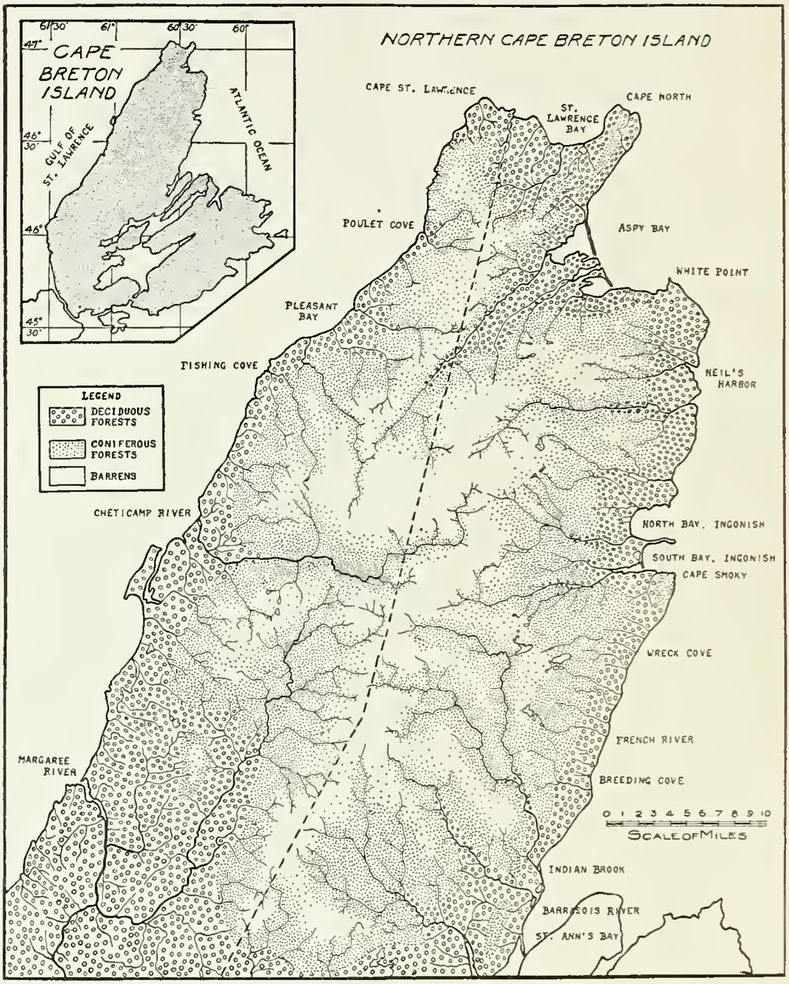

FIGURE 2.—Map of northern Cape Breton, showing approximate distribution of deciduous forest climatic formation and northeastern evergreen coniferous forest climatic formation. The unshaded areas are very largely occupied by barrens. Inserted map: Cape Breton Island, together with a small portion of the peninsula of Nova Scotia.

ous forest formation, wherever these two groups come into competition with one another, from the standpoint of ecological plant geography it seems best, on the whole, to regard the vegetation of this transition region as constituting merely the northward extension of the deciduous forest formation.

As a glance at the map (Fig. 1) will show, Cape Breton Island, located northeast of the peninsula of Nova Scotia (lat. 45° 30′–47° N.; long. 60° 15′–61° 30′ E.), and separated from the mainland only by the Gut of Canso, a narrow strait scarcely a mile wide, is situated near the northern edge of the transition forest region. In northern Cape Breton, owing chiefly to differences in climate at different elevations, both the deciduous forest formation and the northeastern evergreen coniferous forest formation are well represented: the former predominates from sea level up to an altitude of about 700 feet; the latter prevails at higher elevations. The approximate distribution in this region of these two formations is mapped in Fig. 2. The vegetation of the Barrens, which occupy the highest parts of the plateau, apparently bears much the same relationship to the evergreen coniferous forest formation on the one hand and the arctic tundra on the other that the vegetation of the transition forest region bears to the deciduous forest formation and the evergreen coniferous forest formation respectively: it seems to represent a transition between evergreen coniferous forest, as typically developed, and tundra. For various reasons the barrens have been mapped as distinct, but their vegetation is to be regarded merely as the upward extension of the evergreen coniferous forest formation.

II. PREVIOUS BOTANICAL INVESTIGATIONS, AND FIELD WORK OF THE AUTHOR

Aside from the work of Ganong ('91, '93, etc.) and Transeau ('09), practically no investigations of a purely ecological nature have been conducted in the Maritime Provinces of eastern Canada (New Brunswick and Nova Scotia). The present paper aims to portray in a general way the ecological relations of the vegetation in a portion of this area.

So far as is known to the writer, only three other botanists—John Macoun ('83–'02, '98), C. B. Robinson ('03, '04, etc.), and

J. R. Churchill—have undertaken any explorations in northern Cape Breton. Aside from the work of these three, which was almost wholly taxonomic, scattered observations of general botanical interest are recorded in the report on the geology of this region ('85) by Hugh Fletcher, the pioneer geologist whose detailed maps, constructed more than thirty years ago, have afforded the basis for all subsequent explorations; while B. E. Fernow, on the basis of a survey made for commercial purposes, has briefly described the forests here, with an accompanying map, in his account of the forest conditions of Nova Scotia ('12).

The writer's acquaintance with northern Cape Breton dates back to 1905 when about three weeks were occupied in a tramp along the coast from Baddeck to Ingonish, across the island from North River to Northeast Margaree, and thence back to Baddeck. It was on this trip that the curly grass fern (*Schizaea pusilla*) was first recorded from Cape Breton (see Nichols '05). In 1909, a month was spent in camp near the mouth of the Barrasois River, but beyond the collection and identification of mosses and liverworts no serious botanical work was attempted. The investigations embodied in the present paper were projected in 1913 and have been carried on for parts of four summers. Altogether, during this time, more than six months have been occupied by field work in northern Cape Breton. In 1914, and again in 1915, a base camp was maintained for about a month along the lower course of the Barrasois River (St. Ann's), from which point excursions were made into the surrounding country, while another month was spent at various points along the eastern coast, between St. Ann's Bay and Aspy Bay, and in the interior. During the summer of 1916 the entire length of the coast from St. Ann's Bay to Cape North was traversed on foot, and a week was spent in the interior. On this trip the writer was accompanied by Dr. L. H. Harvey, whose experience in the Mt. Ktaadn region suggested many interesting comparisons. The first draft of the present paper was prepared during the college year 1916-1917, and in the summer of 1917 another month was spent in the field, partly for the purpose of checking up previous observations, partly with the object of visiting the western coast of the area under consideration. On this trip, starting from Baddeck, the author traveled to Middle River, Northeast Margaree and Margaree Harbor, thence along the coast to Cheticamp and Pleasant Bay, across the island to Aspy Bay, and from here to Ingonish, from which point another excursion was made into the interior.

As a desirable adjunct to the ecological investigations, considerable attention has been devoted to the flora of the region: two papers on the bryophytes of Cape Breton have already been published ('16[a], '18), and a similar catalogue of the vascular plants is contemplated. Incidentally, in addition to the studies in northern Cape Breton, the writer has recently visited two other widely separated areas within the transition region: in the spring of 1916 a week was spent at the Yale Forest School Camp near Brandreth, in the western Adirondacks; while during the summer of 1917 nearly a month was occupied, in company with Dr. Harold St. John of the Gray Herbarium, in exploring the upper waters of the St. John River, in northwestern Maine. Also, in connection with the study of raised bogs in northern Cape Breton, a visit was made, in 1917, to one of the New Brunswick bogs described by Ganong ('91, '97).

III. ACKNOWLEDGMENTS

The writer wishes to express his indebtedness to Professor Alexander W. Evans for his continued interest in this work throughout its progress; to Mr. Albert F. Hill, Professor Merritt L. Fernald, Dr. Harold St. John, and Mr. Charles A. Weatherby, who have determined or passed judgment on the vascular plants collected; to Professors A. Le Roy Andrews and Lincoln W. Riddle, who have determined the sphagnums and lichens respectively; and to various others (see Nichols '16[a]), who have assisted in the determination of the bryophytes.

IV. PHYSIOGRAPHY

Cape Breton Island is about 4,000 square miles in area: it is approximately four-fifths as large as the state of Connecticut. Its greatest length (from the Gut of Canso to Cape North) is about 110 miles, its greatest width (from Margaree Harbor to Cape Breton) about 75 miles. The general configuration of the island is brought out by the map (FIG. 2). It comprises two distinct peninsulas, which are united at the south by the narrow Isthmus of St. Peter (now cut by a ship canal), and which almost completely enclose the Bras d'Or Lakes, an irregularly shaped mediterranean sea fifty miles long and in places twenty miles wide. The area treated as northern Cape Breton in the present paper is about sixty miles long with a maximum width of about thirty miles.

A good idea of the general character of the country is conveyed by the accompanying series of photographs. In addition

FIGURE 3.—View of lowland and plateau from Middle Head, Ingonish: in upper right background, Mt. Franey; to left of this, valley of Clyburn Brook; in foreground, low granitic headland, drift-covered, with second growth forests of white spruce and balsam fir.

to those introduced in the present connection, attention is especially called to the following: FIGS. 21, 24, 26, 28, 30, 33, 38, 41, 50, 51.

From a topographic standpoint the outstanding feature of northern Cape Breton is the great interior plateau, which stretches in almost unbroken continuity from Cape North nearly to the Bras d'Or. This massive remnant of the ancient Atlantic Upland (Goldthwait '16), composed of granites, syenites, and other highly resistant, crystalline rocks of Laurentian age, includes the highest land in Nova Scotia. The average elevation of its surface in northern Cape Breton is between 1,000 and 1,200 feet, but in places it is considerably higher.[2] South of the area under discussion the plateau becomes greatly fragmented and its surface gradually approaches sea level. In southeastern Cape Breton the summits of the Laurentian highlands rarely attain an elevation of more than 300 feet.

FIGURE 4.—Characteristic view on the plateau: looking westward from an eminence north of the Barrasois River; primeval forests of balsam fir, etc.

As one approaches the eastern coast of northern Cape Breton in the little coasting steamer, which affords the easiest means of travel along the shore north of Sydney, the plateau, as viewed in the distance, presents an even, unbroken skyline (see especially FIG. 30). But to one standing on the summit of Mount Franey, or some other eminence along the eastern margin of the table-land, its surface appears as a broad expanse of low, rounded hills, which stretches westward to the horizon (FIGS. 4, 51). Hidden away among these distant hills are innumerable little lakes and ponds, countless deep valleys and wild gorges.

[2] Mount Franey (FIG. 3), the loftiest hill recorded, measures 1,370 feet in height. In the opinion of the writer there are numerous higher summits in the interior of the island.

FIGURE 5.—View looking southward along coast from near summit of Mt. Smoky: Carboniferous lowland in mid-distance; elsewhere the underlying rocks are crystalline.

FIGURE 6.—Ingonish Harbor: Mt. Smoky (granitic) in distance, with lower Carboniferous hills and the shingle spit which partly encloses the harbor in mid-distance; Carboniferous lowland in foreground.

Along certain sections of the coast in northern Cape Breton the crystalline rocks extend bluffly out to the shore. In places, as between Aspy Bay and Neil's Harbor (Fig. 38), these rugged granitic shores are relatively low. Elsewhere, as at Cape North (Fig. 30) and Cape Smoky (Fig. 6), the mountains rise abruptly from the sea: at Cape Smoky and along the northwest shore are magnificent sea cliffs many hundred feet in height. But along much of the coast, a low border of Carboniferous rocks—sand-

Figure 7.—The Big Intervale at Aspy Bay: farms and second growth forests; *Pyrus americana* in right foreground.

stone, shale, dolomite, gypsum, etc.—intervenes between the crystalline area and the sea. On the eastern shore (Figs. 5, 26, 33), and on the western shore north of Cheticamp, this fringe of softer rocks is rarely more than a mile in width; ordinarily it is much less. At certain places even here, however, as at North River, Ingonish, Aspy Bay (Figs. 7, 20), Bay St. Lawrence, and Pleasant Bay, the Carboniferous lowland extends inland for several miles along the rivers, forming broad intervales. In the southwestern part of the area mapped (Fig. 2), in the Margaree district, the lowlands are much more extensively developed than elsewhere (Fig. 21).

It has been inferred by some geologists that Cape Breton Island escaped glaciation, and this has been assumed as a hypothesis by certain botanists (Robinson '06, p. 258; Taylor '12, p. 24), in an attempt to explain certain peculiarities of plant distribution. Such, however, is hardly the case. On the plateau, to be sure, superficial deposits of any depth are scarce, the rock surface often being bare or covered with granite boulders of apparently local origin. Soil, when present, is usually thin:

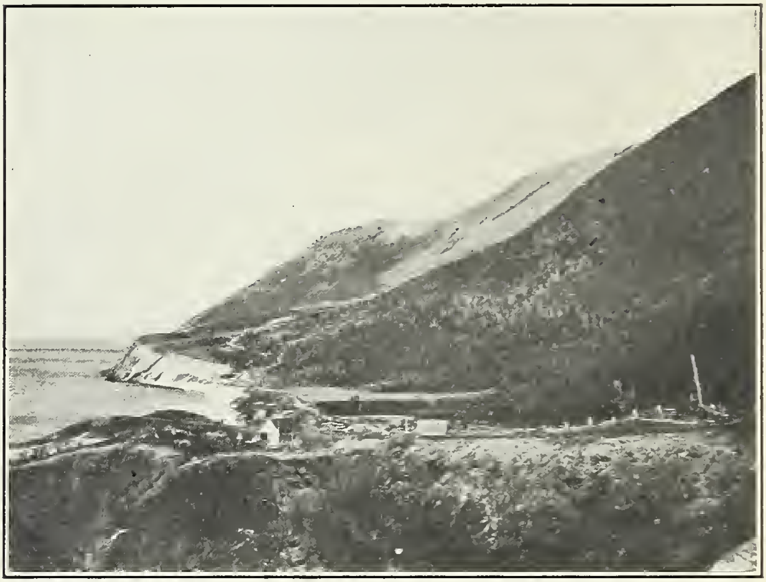

FIGURE 8.—Mountains and granitic, drift-covered lowland north of Cheticamp.

commonly it consists of a coarse quartz sand or gravel derived through the decomposition of the underlying rock. But even on the plateau, as, for example, along the trail between Pleasant Bay and the Big Intervale at Aspy Bay, there may be found considerable deposits of drift. Further, the seemingly complete absence of a truly alpine flora, even on the higher summits, would point strongly toward glaciation. In the lowland, the Carboniferous formations everywhere are hidden by a mantle of glacial débris: in places along the coast, as at French River and

Pleasant Bay, there are sea bluffs, more than fifty feet high, composed entirely of glacial drift, while in some of the brook valleys, e. g., in that of Power Brook, there are accumulations of drift fully as deep. Glacial striae have been observed in several localities (Fletcher '85, p. 77H), but, owing to the rapidity with which most of the rocks crumble when exposed to the weather, such evidences of glaciation are rare.

The distribution of roads and settlements in northern Cape Breton has been determined largely by the character of the topography and of the soil. Along the east coast a road follows the shore from St. Ann's Bay to Cape North, with branches extending inland a short distance wherever intervales occur. From the head of the Big Intervale at Aspy Bay (Fig. 7), a rough trail crosses the plateau to Pleasant Bay, and leads thence southward over the mountains toward the mouth of the Cheticamp River, where, in conformity with the better character of the country, roads are again encountered. The southwestern part of the area mapped affords excellent farming and is well populated, but elsewhere the farms, for the most part, are confined to the intervales and to the low coastal strip. The agricultural possibilities of many of the tracts which have been brought under cultivation would scarcely have been appreciated by any save the Scotch Highlanders, whose descendants constitute the larger proportion of the population of the country. At several points along the coast, as at Cheticamp and Neil's Harbor, the fishing industry supports considerable communities. The mountainous interior of northern Cape Breton is a wilderness, uninhabited and roadless, difficult to travel and little known, seldom visited except by trappers and hunters.

V. CLIMATE

In Table I are given the average temperature and precipitation records for twenty years at Sidney.[3] Although there are known to be certain discrepancies, in a general way these figures doubtless represent the meteorological conditions in northern Cape Breton. For purposes of comparison, climatic data for various

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[3] Part of the climatic data here given has been supplied by Director R. F. Stupart of the Canadian Meteorological Service. The remainder has been secured from various sources.

selected stations in eastern Canada are briefly presented in TABLE II. Of the stations here listed, the first five are in the Maritime Provinces: Sidney, Halifax, and Yarmouth front on the ocean, and St. John on the Bay of Fundy; while Frederickton

TABLE I

AVERAGE TEMPERATURE AND PRECIPITATION RECORDS FOR TWENTY YEARS AT SYDNEY, N. S.

Month	Degrees of Temperature, Fahrenheit					Precipitation	
	Mean Daily	Mean Daily Maximum	Mean Daily Minimum	Monthly Extremes		Total Amount (Inches)	Number Rainy Days (0.01 inch or more)
				Maximum	Minimum		
January...	23	31	15	57	−14	5.19	12
February..	21	30	13	59	−15	4.39	10
March....	28	36	20	58	−18	4.90	13
April.....	37	44	29	77	3	4.04	12
May......	46	55	37	78	22	3.00	11
June......	55	64	45	86	28	2.66	10
July......	64	73	54	92	35	3.16	10
August...	63	72	54	88	36	3.03	11
September.	57	66	48	88	30	3.48	11
October...	48	56	40	77	25	4.11	13
November.	39	45	34	67	12	5.63	14
December.	30	36	24	58	0	5.92	14
Year......	42	51	33	92	−18	49.51	11

TABLE II

TEMPERATURE AND PRECIPITATION DATA FOR VARIOUS STATIONS IN EASTERN CANADA

Station	Temperature (in Degrees Fahrenheit)				Precipitation	
	Normal Mean Daily for Hottest Month	Normal Mean Daily for Coldest Month	Average Extreme Maximum for Years 1907–1914	Average Extreme Minimum for Years 1907–1914	Normal Annual Amount (inches)	Per cent. Falling in Months October–March
Sydney, N. S......	64	21	88	−10	49.51	61
Halifax, N. S......	65	24	91	−10	56.81	57
Yarmouth, N. S....	61	27	78	1	51.94	55
St. John, N. B.....	61	19	80	−13	48.08	55
Frederickton, N. B.	66	13	92	−27	46.44	56
Quebec, Que.......	66	10	90	−24	41.10	49
Montreal, Que.....	69	13	91	−18	40.32	52
Port Arthur, Ont...	62	7	91	−32	23.22	29

lies inland, about fifty miles west of St. John. Of the three remaining stations, Quebec and Montreal are situated in southern Quebec, about 200 miles from the seacoast, and Port Arthur is located in western Ontario, on the north shore of Lake Superior. This latter station is introduced, partly because it exemplifies the relatively continental as compared with the relatively maritime type of climate, and partly because of its proximity to Isle Royale, the scene of Cooper's investigations ('13).

Northern Cape Breton may be said to possess a cool-temperate, maritime climate. In the following paragraphs the general climatic features of this region are briefly summarized, and attention is called to certain differences between the climate of the plateau and that of the lowland.

a. GENERAL CLIMATIC FEATURES OF NORTHERN CAPE BRETON

Temperature.—As compared with regions which are not in close proximity to the ocean, the temperature here is more equable. Some idea of the difference is suggested by the figures in Table II. It will be seen here, for example, that the disparity between the mean temperatures for the warmest and coldest months of the year at Sydney is only 43°, as compared with 53° at Frederickton, and 55° or more at Quebec, Montreal, and Port Arthur. This same dissimilarity between coastal and interior regions is brought out by comparing the extreme maximum and minimum temperatures for the year at the various stations. The winters in northern Cape Breton are long and cold, but extremes of temperature such as prevail toward the interior of the continent are seldom experienced (see Table II). Spring is sometimes very late in arriving, owing partly to the quantity of drift ice in the adjacent waters. The summers are short and cool, but there are only three months in the year when the mean monthly minimum at Sydney is *lower* than 32°. This latter fact is in marked contrast to the conditions at Port Arthur (see Cooper '13, p. 8), where the mean monthly minimum is *higher* than 32° only during June, July, and August.

Precipitation.—In common with other regions along the Atlantic Coast the precipitation in northern Cape Breton is copious and is well distributed over the entire year. More than 60 per cent. of it comes during the period of comparative vegetative inactivity, a condition quite the reverse of what prevails in the interior of the continent (see Table II), and also to that which characterizes the Atlantic Coast farther south (at Charleston, S. C., for example, out of an annual precipitation of 52.07 inches, only 39 per cent. falls during the period from October to March). Snowfall in winter is usually heavy and, on account of the backward spring, the snow commonly remains on the ground for a long time. Fletcher ('85, p. 86) notes that in the middle of June, 1881, patches of snow still lingered in sheltered situations, while in 1914 and 1915 the writer observed snow-ice as late as August at the foot of an open north-facing slope along the Barrasois River.

Humidity.—Fogs are more or less prevalent at all seasons, and even in clear summer weather the humidity of the atmosphere is quite perceptible. Figures regarding the rate of evaporation throughout the growing season are not available, but during the summer of 1915, for a period of nearly three weeks, the writer operated a series of porous cup atmometers in various habitats, and the results obtained from those set up in the open near the coast are given in Table III. The readings in the first four columns of this table were taken near the Barrasois River. The "Shore" station was situated on an exposed, east-facing hillside,

TABLE III

Rate of Evaporation Along the Coast of Northern Cape Breton During the Summer of 1915, as indicated by the Porous Cup Atmometer

Station	July 22–July 27	July 27–August 3	August 3–August 7	Daily Average	August 20–August 23
Shore	28.8 cc.	45 cc.	84.2 cc.	9.8 cc.	79.2 cc.
Intervale	39.4 cc.	53.3 cc.	91.9 cc.	11.5 cc.	(3½ days)

about a quarter of a mile from the seacoast. The "Intervale" station was located in a similar site about five miles from the shore, at the head of a broad open valley. The figures in the fifth column were obtained from an instrument set up on a low hill at Ingonish, within a stone's throw of the open ocean. The average daily rate of evaporation for the entire period at the shore stations was about 12.2 cc. During the period of July 22–August 3 there was considerable rain and fog, while during the periods August 3–7, 20–23, the weather was uniformly clear. For these latter periods the daily rate of evaporation at the shore stations averaged 21.7 cc. The evaporation rate at the intervale station, it will be noted, averaged slightly higher than that at the shore station.

b. CLIMATE OF THE INTERIOR PLATEAU COMPARED WITH THAT OF THE COAST

Temperature.—Aside from a few figures obtained by the writer, few accurate comparative data are available regarding climatic conditions on the plateau, although various interesting observations have been supplied by trappers. In August, 1915, two recording thermometers were set up in the open, one near the shore at Ingonish, the other in the barrens about fifteen miles west of Ingonish (elevation perhaps 1,200 feet). During the writer's stay in the barrens daily readings were made from these instruments, and subsequently readings were taken at intervals of a few days by a competent guide, who made trips into the barrens for this purpose. The readings were continued at each station until a temperature of 32° or lower had been recorded. The figures given in TABLE IV and covering part of this period

TABLE IV

MAXIMUM AND MINIMUM TEMPERATURES (°F.) IN THE INTERIOR AND ALONG THE COAST OF NORTHERN CAPE BRETON; AUGUST 18–23, 1915

	Mean Daily Maximum	Mean Daily Minimum	Mean Daily Range	Extreme Maximum	Extreme Minimum
Barrens........	74°	48°	26°	80°	43°
Ingonish........	71°	56°	15°	75°	52°

are suggestive, if nothing more. It is of interest to note that the daily maximum temperature in summer is frequently higher, and the daily minimum invariably lower, while the average daily range of temperature is perceptibly greater on the plateau than along the coast. Observations recorded for nine days show the average daily minimum to range from six to ten degrees lower on the plateau than along the coast, and the average daily maximum about one degree lower. For the barrens station the first freezing temperature was recorded on

September 8 (30°), eighteen days earlier than at the Ingonish station (September 26: 31°). There is little doubt that on the plateau, during some seasons, the temperature falls below freezing during every month of the year. And not only are the daily minimum temperatures here during the growing season lower than in the lowland, but the growing season is considerably (probably from six weeks to two months) shorter here than there.

Precipitation, Evaporation and Wind.—No exact observations have been made regarding precipitation on the plateau, but from the writer's experience and from numerous inquiries it can be stated with certainty that during summer the rainfall is somewhat heavier here than along the coast. The evaporating power of the air in *clear* weather, at least during the summer, is apparently greater than along the coast. This observation is deduced from atmometer readings, taken for the brief period of three and a half clear days in August, when an instrument on the barrens indicated a daily evaporation rate of 28.4 cc., as compared with 22.6 cc. near the shore at Ingonish. But, on the whole, the humidity of the atmosphere is greater on the plateau than on the lowland. This is due to the prevalence here of fogs. During dull weather the clouds hang low, covering the slopes and summits of the mountains above an elevation of seven or eight hundred feet, sometimes for days at a time. Even though it may not actually rain, everything is saturated with moisture. The higher rate of evaporation during clear weather is correlated with the heavy winds which sweep across the plateau at all seasons. So effective are these that a wet, spongy bed of cladonias may become dry and brittle within a few hours. The effect of wind on the vegetation, as seen in the barrens, is even more pronounced in winter than during the growing season. This will be discussed later in connection with the vegetation of the barrens.

VI. ECOLOGICAL CLASSIFICATION OF MATERIAL; NOMENCLATURE

The ecological classification adopted in the present paper has already been described in considerable detail elsewhere (Nichols '17), and need be only briefly outlined here. The fundamental unit of vegetation from the standpoint of physiographic ecology is the *plant association:* any group or community of plants, taken in its entirety, which occupies a common habitat. Associations which are correlated with a common type of habitat and which are ecologically equivalent to one another may be referred to a common *association-type.* The culminating member of any specific successional series is termed an *edaphic climax association.* In favorable situations this edaphic climax coincides with the *regional climax association-type:* the most mesophytic type of vegetation of which the climate of the region permits the development on ordinary uplands. But, in unfavorable situations, the edaphic climax may be represented by an association which is less mesophytic than the regional climax type.

Parenthetically, it may be remarked that while emphasis is usually placed, as above, on the relatively high degree of *mesophytism* which characterizes the regional climax association-type, it is quite likely that this conception, while in general doubtless holding true, should be altered somewhat. In the lowland of northern Cape Breton, for example, a coniferous forest association on ordinary uplands represents either a temporary stage, destined to give way to deciduous forest, or else an edaphic climax (see definition below); yet not infrequently, in so far as their relative mesophytism is concerned, such forests seem quite on a par with forests of the regional climax type. The differentiating factors concerned in this particular case are suggested in the writer's discussion of the ecological relations of the balsam fir (p. 285).

In any unit area where more than one association is represented, the associations, taken collectively, constitute an *association-complex.* Within any specific geographic region the associations are grouped naturally into a series of more or less definite complexes with reference to the physiographic features of the region, i. e., with reference to topography and soil. Any association-complex which is thus related to a specific physiographic unit area constitutes an *edaphic formation.* Edaphic formations which are correlated with a common type of physiographic unit area may be referred to a common *edaphic formation-type.* The edaphic formations of any unit area, where more than one is present, taken collectively, constitute an *edaphic formation-complex.* The edaphic formation-complex of any climatic region constitutes a *climatic formation.* To sum up: the association is a unit determined by habitat; the edaphic formation is a unit determined by physiography—a unit of a higher order than the association; while the climatic formation similarly is a unit determined by climate—a unit of a still higher rank than either of the preceding.

In the account of the ecological relations of the vegetation of northern Cape Breton which follows, the two climatic formations here represented are discussed separately. The scheme followed in classifying the innumerable associations which, taken collectively, comprise the vegetation of the respective regions concerned is partially outlined in the table of contents, which may be looked upon as in the nature of an analytical key. For the benefit of readers to whom the writer's paper on classification may not be available, a few further remarks regarding the system on which this synopsis is built up may be added.

First of all, taking into account their successful relations to one another and their distribution with reference to specific physiographic unit areas, the various individual units of vegetation, the associations, have been assembled into definite association-complexes. An individual association-complex, as thus defined, constitutes an edaphic formation. For obvious reasons, however, the various individual associations have been treated collectively, as association-types, and, similarly, emphasis has been laid on the edaphic formation-types rather than on the individual formations (see definitions above). Proceeding further, the edaphic formations (and formation-types) of the region have been divided primarily with reference to the water relations of the areas which they occupy into two successional series: formations of the xerarch series, and formations of the hydrarch series.[4] Under each of these two heads, in the case of the region of deciduous forests, it has seemed desirable to distinguish between primary and secondary formations, the latter embracing formations in which the vegetation has been modified

[4] The term xerarch, to quote Cooper ('13, p. 11), "is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; . . . [the term hydrarch] to those which, originating in hydrophytic habitats, such as lakes and ponds, also progress toward mesophytism."

by cultivation, lumbering, or fire. The formations of the xerarch and hydrarch series respectively are further subdivided with reference to the general topographic features of the region, these being considered from the standpoint of their relationship to one another through physiographic development. Thus, among the formations of the xerarch series, three groups of formation-types are distinguished: the formation-types, respectively, of ordinary uplands, of uplands along streams, and of uplands along the seacoast. In the same way, the formation-types of the hydrarch series fall more or less naturally into three groups: the formation-types of lakes, ponds and swamps inland, the formation-types in and along rivers and streams, and the formation-types along the seacoast. The classification of formation-types primarily on the basis of water supply is open to certain objections, but so also is their classification primarily on the basis of physiography, a method which might perhaps equally well have been followed.

In discussing the vegetation of each region, the regional climax association-type is taken up first, since an understanding of this, representing as it does the highest degree of mesophytism permitted by the climate—the climatic indicator, so to speak, is prerequisite to an adequate interpretation of subordinate association-types and of successional relations. The edaphic formation-complex of the region, which of course includes all the edaphic formations and formation-types, with the associations and association-types which comprise them, including the regional climax association-type, is then considered, after the manner outlined in the preceding paragraph.

In matters of nomenclature the author, in general, has followed the seventh edition of Gray's Manual ('08), with the emendations of Robinson and Fernald ('09), for the vascular plants, his own papers on the bryophytes of Cape Breton ('16[a], '18) for the mosses and liverworts, and Fink's Lichens of Minnesota ('10) for the lichens. In the case of the vascular plants, changes in nomenclature since the publication of the Manual for the most part have been neglected. Only in exceptional cases are authorities cited for the names used. In cases where a plant is referred to by its common name, the scientific name is usually given only in connection with its first mention in the text.

THE DECIDUOUS FOREST CLIMATIC FORMATION IN NORTHERN CAPE BRETON

I. THE REGIONAL CLIMAX ASSOCIATION-TYPE: THE CLIMAX FOREST

Present and past distribution of the climax forest.—To one visiting northern Cape Breton at the present day the prevailing aspect of the lowland forests (Figs. 9, 39, 42, etc.) appears to

Figure 9.—Second growth woodlands of balsam fir and white spruce; Barrasois.

be coniferous: white spruce and balsam fir predominate on every side. But practically all of these forests are secondary in their origin. Although settlements in this region for the most part date back scarcely one hundred years, during this short period the greater part of the country has been either cut or burned over, and much of it, at one time or another, has been cultivated or used for pasturage. In view of the widespread destruction or modification of the original vegetation, the nature of the primeval forests must be judged very largely from the scattered vestiges which for one reason or another have remained intact. From the study of many such fragments, together with certain little modified tracts of second growth forest, it has become unmistakably evident that in former times a very large

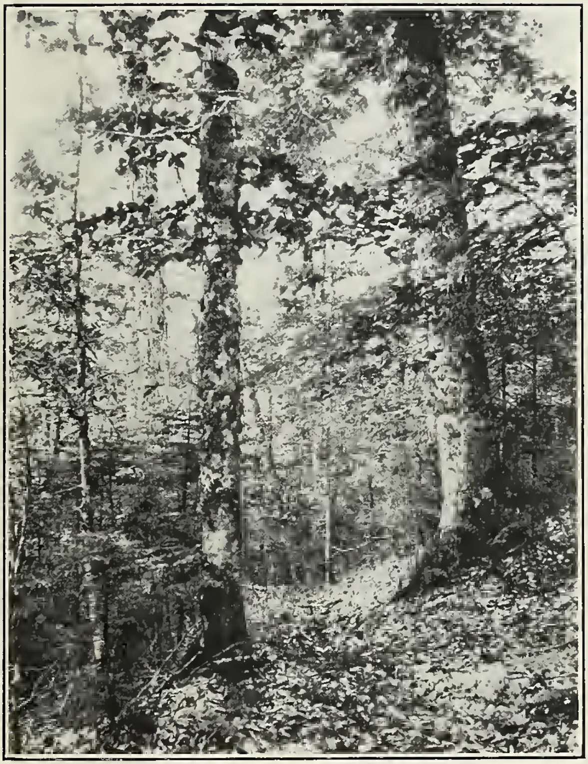

FIGURE 10.—Primeval forest of the regional climax type, on lower slopes of mountains along Northeast Margaree River; mostly beech and maple; balsam fir well represented in undergrowth and to some extent in mature stand.

portion of this area was clothed with forests in which the predominant trees were deciduous. It is certain (and this conclusion is confirmed by statements of many of the older settlers) that forests of this sort were developed in practically all edaphically favorable situations; they were by no means local in their occurrence, but rather of very general distribution. The structure of these regional climax forests is considered in brief detail in the following paragraphs. Their general aspect is illustrated by FIGS. 10–12.

The trees of the climax forest.—The nature of the individual associations which comprise the climax association-complex of the lowland varies considerably. In some places the forest is made up wholly of deciduous trees, but more commonly it consists of a mixture of deciduous and evergreen species. The various trees which may enter into the composition of the forest are named below, together with remarks as to their frequency and ecological importance. (1) Deciduous Species:—Beech (*Fagus grandifolia*) is almost invariably the predominant species, in some cases including fully 65 per cent. of the mature trees. Sugar Maple (*Acer saccharum*) is always present and usually ranks second in abundance to the beech. Yellow Birch (*Betula lutea*) is likewise omnipresent and sometimes outnumbers the sugar maple. Red Maple (*Acer rubrum*) is rarely absent, and frequently occupies a prominent position in the forest. Paper Birch (*Betula alba papyrifera*) ordinarily grows scattered through the forest. In some stands these five species are the only large-sized trees represented in the mature growth. The northern Red Oak (*Quercus rubra ambigua*) is widely distributed, and in some localities, as at Pleasant Bay and in the vicinity of Cape North, is an important constituent; but in most places it is only sparingly represented, and often it is absent. White Ash (*Fraxinus americana*) is not uncommon in many low intervale forests, but elsewhere it is comparatively rare. Balsam Poplar (*Populus balsamifera*) is occasionally encountered in virgin forests. (2) Evergreen Species (conifers):—Balsam fir (*Abies balsamea*), in the majority of cases, is a conspicuous, though not necessarily abundant, member of the forest, growing intermixed with the various deciduous species. Hemlock (*Tsuga canadensis*) is locally abundant and sometimes is the predominant tree; but often it is absent or represented only by scattered trees. White Pine (*Pinus Strobus*) is also an important constituent, locally, at any rate. It is particularly characteristic of the steep, well-drained, rocky slopes and ridges which flank many of the larger streams; but repeated cutting has thinned out this tree to a greater extent than any other single species. White Spruce (*Picea canadensis*) grows sprinkled here and there through the forest, though seldom present in quantity. Black Spruce (*Picea mariana*) also is frequently represented by scattered specimens.

In the account which follows, for the sake of convenience, forests of the usual climax type, predominantly deciduous but with a more or less pronounced admixture of evergreen trees, are frequently referred to simply as "deciduous forests."

FIGURE 11.—Primeval forest of the regional climax type, along Indian Brook; mostly beech, maple, and hemlock, with some yellow birch and balsam fir; dense undergrowth of yew.

Size of trees in climax forest.—The relatively large size attained by some of the trees in the primeval forests of northern Cape Breton is suggested by the following diameter measurements[5] which were noted for various species: beech, 25 inches; sugar maple, 36 inches; yellow birch, 42 inches; red maple, 18 inches; paper birch, about 3 feet; red oak, 35 inches; white ash, 24 inches; balsam poplar, about 2 feet; balsam fir, 16 inches; hemlock, 30 inches; white pine, about 30 inches; white spruce, 26 inches; black spruce, about 12 inches.

[5] Diameter measurements of trees were taken at breast height.

Woody undergrowth in the climax forest.—Two small trees, the mountain maple (*Acer spicatum*) and the moosewood (*Acer pennsylvanicum*), are usually conspicuous in the undergrowth. The latter species sometimes attains a diameter of nearly a foot, but, in the forest, both are usually little more than shrubs. The mountain ash (*Pyrus americana*) is not infrequent, but is more characteristic of the evergreen coniferous climax forest of the

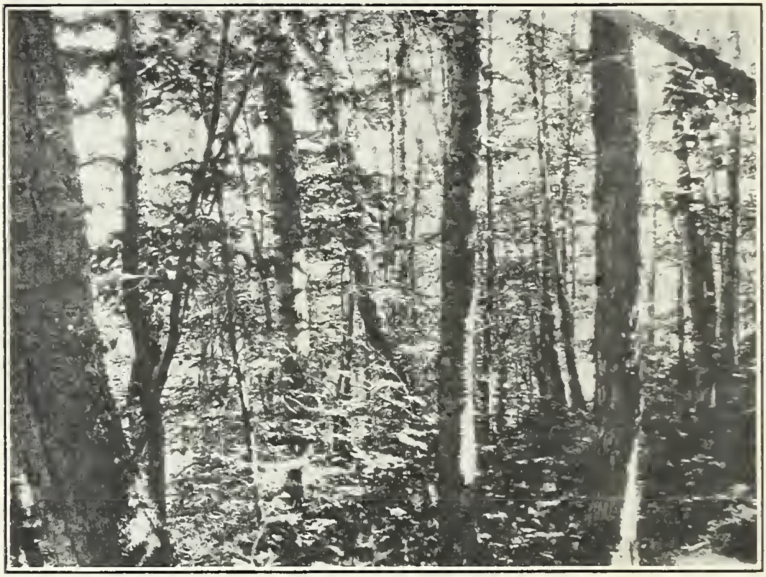

FIGURE 12.—Primeval forest of the regional climax type, at Tarbet, along the Barrasois; mostly beech, maple, and yellow birch; balsam fir abundant in undergrowth but absent from mature stand.

highland. Of the shrubs, the yew (*Taxus canadensis*) is the most characteristic species: usually this is common, and frequently it forms a dense tangle which excludes other plants in much the same way that the mountain laurel (*Kalmia latifolia*) does in the woods of southern New England. Sometimes, however, the yew is entirely absent over considerable areas. The northern hazel-nut (*Corylus rostrata*) occupies a position in the forest here somewhat parallel to that held by the witch hazel in woods farther south. A few other shrubs are ordinarily represented by scattered specimens, namely: fly honeysuckle

(*Lonicera canadensis*), withe-rod (*Viburnum cassinoides*), gooseberry (*Ribes lacustre*), dogberry (*Cornus alternifolia*), and red-berried elder (*Sambucus racemosa*). The hobble bush (*Viburnum alnifolium*), one of the most representative shrubs of the climax forest throughout much of the transition region, is very local in northern Cape Breton.

The herbaceous vascular plants of the climax forest.—The following list includes the more characteristic ferns and herbaceous seed plants of the regional climax forest.[6]

Phegopteris polypodioides	*cc*	*Epipactis tesselata*	*co*
Polystichum acrostichoides	*fc*	*Coralorrhiza maculata*	*co*
Polystichum Braunii	*lf*	*Actaea rubra*	*cf*
Aspidium noveboracense	*fc*	*Actaea alba*	*lr*
Aspidium Filix-mas	*lc*	*Oxalis Acetosella*	*cf*
Aspidium marginale	*lc*	*Viola canadensis*	*of*
Aspidium spinulosum var.	*cc*	*Viola incognita*	*cf*
Botrychium virginianum	*of*	*Aralia nudicaulis*	*cc*
Lycopodium lucidulum	*cc*	*Sanicula marilandica*	*of*
Carex arctata	*fo*	*Pyrola elliptica*	*cf*
Clintonia borealis	*cc*	*Monotropa uniflora*	*cf*
Smilacina racemosa	*ff*	*Monotropa Hypopitys*	*fo*
Maianthemum canadense	*cc*	*Trientalis americana*	*cc*
Streptopus roseus	*cc*	*Epifagus virginiana*	*lf*
Medeola virginiana	*ff*	*Mitchella repens*	*cf*
Trillium cernuum	*of*	*Linnaea borealis americana*	*of*
Habenaria orbiculata	*co*	*Aster acuminatus*	*cc*
Epipactis decipiens	*co*		

Several species have been omitted from this list which are characteristic of low-lying intervale forests, but not of climax forests in general. These will be noted later.

[6] In this and in several subsequent lists of the plants characteristic of the climax association-type, an attempt has been made to indicate both their general prevalence and their relative abundance when present. The following symbols are used: *c* = *common*; *f* = *frequent*; *o* = *occasional*; *r* = *rare*; *l* = *local*. In each case two symbols are given, the first indicating merely the frequentness with which the species is represented (i. e., is either present or absent) in associations of the climax type, the second indicating its relative abundance, when present, in the individual association. For various reasons it has not seemed feasible to carry out this scheme in connection with other association-types.

The bryophytes and lichens of the climax forest.—Corticolous mosses and liverworts form a striking feature of these forests. Loose mats of *Neckera* and *Leucodon, Porella* and *Frullania* often literally plaster the trunks of maple and other trees; *Ulota* grows in scattered, compact tufts, particularly on trunks of beech; while two lichens, *Sticta pulmonaria* and *Parmelia saxatilis,* are of very common occurrence. Tree bases, logs and rocks also are usually hidden by masses of *Bazzania, Anomodon* and various Hypnaceae. A list of some of the more conspicuous species follows:

Bazzania trilobata	*cc*	*Thuidium delicatulum*	*cf*
Ptilidium ciliare	*cf*	*Brachythecium reflexum*	*cf*
Porella platyphylloidea	*cc*	*Rhytidiadelphus loreus*	*fc*
Frullania Tamarisci	*cc*	*Rhytidiadelphus triquetrus*	*fo*
Dicranum longifolium	*ff*	*Hylocomium splendens*	*cf*
Dicranum scoparium	*cc*	*Hylocomium umbratum*	*cf*
Ulota ulophylla	*cc*	*Ptilium crista-castrensis*	*co*
Mnium cuspidatum	*cc*	*Stereodon cupressiformis*	*cf*
Leucodon sciuroides	*cf*	*Heterophyllon Haldanianum*	*cf*
Neckera pennata	*cc*	*Hypnum Schreberi*	*cf*
Heterocladium squarrosulum	*cf*	*Webera sessilis*	*fo*
Anomodon attenuatus	*ff*	*Polytrichum ohioense*	*cf*
Leskeella nervosa	*co*		

But while mosses and liverworts are present in profusion in these deciduous climax forests, it is important to note that they develop luxuriantly for the most part only on substrata which are elevated above the general level of the forest floor. On the forest floor itself the bryophytes usually are sparsely represented and they may be totally absent over considerable areas. This is in striking contrast to the conditions which prevail in the evergreen coniferous climax forests of the highland, where the ground is almost always carpeted by a rich growth of bryophytes. Various explanations for this dissimilarity have been considered by the author. At first it seemed that it might be due to differences in soil acidity, but all the forest soils tested were found to be more or less acid to litmus. Similarly, differences in light fail to afford an adequate explanation. The conclusion has finally been reached that the scarcity of mosses and liverworts on the forest floor in deciduous forests is correlated in large measure with the deciduous habit. Every year the ground is covered with a more or less continuous blanket of fallen leaves; mosses and liverworts may be buried alive, so to speak, and repeated instances have been observed where without question they have been partially or wholly exterminated in this way. In a general way it may be stated that in the climax forests of northern Cape Breton the abundance of bryophytes is inversely proportional to the abundance of deciduous trees.

Reproduction of the climax trees.—In the normal course of events, the future character of any forest is determined in large measure by the present character of the immature trees. The nature of the rising generation may be said to furnish a criterion of permanency. A permanent forest is one which is able to perpetuate itself. It is therefore a significant fact that in the primeval forests of this region the composition of the younger generation of trees, at least so far as the dominant species are concerned, is essentially the same as that of the mature stand. Beech, sugar maple, birch, and red maple almost everywhere exhibit good reproduction underneath the forest canopy. The same is true, more locally, of the oak and hemlock, and to a less extent of the ash and white pine. Reproduction in the balsam fir is discussed in subsequent paragraphs. Young trees of paper birch and white spruce are seldom found, and it seems probable that, in general, they either represent relicts of a more primitive type of forest, or that they are able to establish themselves only under the more favorable light relations which are occasionally created by gaps in the forest canopy overhead.

The ecological relations of the balsam fir in the climax forest.—The balsam fir may be regarded as the character tree of the northeastern evergreen coniferous climatic forest formation (in this connection, see especially Cooper '13, pp. 36–39). In parts of Cape Breton where this climax formation holds sway, the balsam far outnumbers all other trees. In the competition for supremacy between the deciduous and the evergreen coniferous climax forest-types, the balsam fir, in this region at any rate, is the last element of the more northern type of forest to disappear. For this reason, the ecological relations of this tree in the climax forests of the lowland have been given considerable attention, although it must be admitted that the observations have not been wholly conclusive.

Seldom, if ever, is a tract of climax forest encountered from which the balsam fir is wholly absent. Frequently, however, it is represented only in the younger growth. This latter condition is well brought out by TABLE V, which shows the relative

TABLE V

RELATIVE ABUNDANCE OF VARIOUS TREES IN TWO QUADRATS IN A HARDWOOD FOREST ALONG THE BARRASOIS RIVER[7]

Name of Species	Diameter Less than 2 Inches	Diameter 2–5 Inches	Diameter 5–10 Inches	Diameter More than 10 Inches
Fagus grandifolia......	55	5	7	3
Acer saccharum........	33	0	2	2
Betula lutea...........	2	1	1	2
Acer rubrum..........	3	0	0	1
Abies balsamea.........	23	0	0	0

[7] Quadrat 32.8 feet (ten meters) square. Figures for the two quadrats are added. No trees less than one foot high counted.

abundance of various trees on two quadrats in a hardwood forest along the Barrasois River (FIG. 12). The most interesting facts to be deduced from this table are: (1) that, of the trees less than five inches in diameter and more than one foot high, balsam fir includes 18.5 per cent. (as compared with beech, 50 per cent.; sugar maple, 26.6 per cent.; yellow birch, 2.4 per cent.; red maple, 2.4 per cent.); while (2), of the trees more than five inches in diameter, none at all are balsam (as compared with beech, 55.5 per cent.; sugar maple, 22.2 per cent.; yellow birch, 16.6 per cent.; red maple, 5.5 per cent.). In the mature stand, taken as a whole, it was estimated that beech includes fully 65 per cent. of the trees, sugar maple and yellow birch each about 15 per cent., red maple and paper birch together about 5 per cent. So far as observations extended, no mature balsam fir whatever is present, the largest living specimen noted being about fifteen feet high; but several dead, standing or fallen, trunks having a diameter of about eight inches were found. The larger living specimens average six or eight feet in height, and are greatly suppressed, many of them showing twenty-five or more annual rings.

The conditions noted in this tract of forest are essentially similar to those which prevail in many other areas: balsam fir is abundantly represented in the younger generation, but is virtually absent from among the mature trees. The absence of mature balsam, however, is far from being the rule. In the majority of cases it grows along with the more southern climax trees, forming an important constituent of the stand, and contributing to the formation of the mixed deciduous-evergreen forest which is the prevailing climax type throughout the lowlands. In competition with the deciduous climax trees, however, the balsam seldom retains a position of dominance, and occasional tracts of primeval forest are encountered in which not only all the mature trees, but practically all the younger ones as well, are hardwoods or hemlock. Forests of this sort are essentially similar to the type which formerly prevailed in many parts of southern New England (see Nichols '13).

In view of the facts set forth above, the query naturally arises: Assuming the climatic conditions to be equally favorable to all the species concerned, why is it that, in competition with maple, beech, hemlock, and the other species which characterize the deciduous climax forest, the balsam fir is unable to hold its own? For obvious reasons this is an important question, and one to which various answers may be suggested.

(1) The relative tolerance of shade exhibited by the various species concerned, at first thought, seems to afford the most likely explanation. Beech, sugar maple, and hemlock are notably tolerant species: they are capable of successful reproduction in their own shade. Regarding the tolerance of the balsam fir there seems to be a discrepancy of opinion. According to Cooper ('13, pp. 17–22, 42, 43), the balsam demands abundant light for successful reproduction: "Later in life the young trees can endure severe shading, but for a successful start abundant light seems to be a necessity." Zon ('14, p. 39), on the other hand, states that, "For the first five or six years of its life, balsam will grow in dense shade, but as it develops it demands more and more light." In northern Cape Breton, the sparsity of balsam seedlings and young trees in many hardwood tracts might well harmonize with Cooper's conclusions, were it not for the fact that in other equally shady forests the young balsam growth is quite abundant. In this connection the observation of Moore ('17, p. 157), made on Mount Desert Island, that, "Under many spruce stands which have reached about middle

age, the fir reproduction is nearly all composed of large seedlings approximately 1–3 feet in height; young seedlings are scarce," is of interest. As indicated above, parallel conditions have frequently been observed in the lowland climax forests of northern Cape Breton. Moore suggests that, "In these cases it appears that the fir came in profusely under a set of environmental conditions different from the present ones . . . . One of them may have been stronger light than at present. Indications of this were found in the fact that some of these cases of fir reproduction occur in stands which were formerly more open than they are now." In one striking case of this sort, observed by the writer, the abundance of young balsam in a primeval hardwood forest is certainly correlated with the occurrence, about fifteen years ago, of a fire which, while it was not sufficiently severe to seriously injure the larger trees, must have resulted temporarily in a considerably increased illumination of the forest floor. Certain it is that the balsam reproduces best and grows most vigorously in well-lighted situations, and there seems to be little question that it is less tolerant of shade than sugar maple, beech, and hemlock. Nevertheless, repeated observations have led to the conclusion that at any rate tolerance alone, even in the broadest interpretation of the term (see Burns '16, pp. 3, 4, 22), cannot be regarded as the cause for the elimination of the balsam.

(2) It has been suggested by Murphy ('17) that the burial of the seeds of the spruce by a mulch of hardwood leaves may be a very important factor in the suppression of this tree in competition with deciduous trees. That the yearly accumulation of leaf litter on the floor of a deciduous forest is, in a somewhat similar manner, responsible for the poor development of the bryophytic ground cover, was a conclusion already arrived at by the writer (see page 284); and it seems not impossible that this may also be a factor of some significance as affecting the reproduction of the balsam fir.

(3) In the opinion of the writer, however, *longevity*, in the last analysis, is the critical factor which enables the maple, beech, hemlock and the associated climax trees of the deciduous forest climatic formation of eastern North America to win out in competition with the balsam fir. In this connection, the behavior of the hemlock, as studied in the primeval forests of north-

western Connecticut (see Nichols, '13), is enlightening. The hemlock is capable of growing in a suppressed condition under the shade of other trees for more than a century. A tree which has been thus suppressed may have attained at the end of a hundred years a diameter of perhaps six or eight inches and may have grown well up into the forest canopy overhead. With the improvement of light conditions, which may be accomplished either through its own upward growth or through the downfall of contiguous trees, such a tree grows vigorously, and may attain an age of more than 300 years, with a diameter of more than four and a height of more than a hundred feet, before its death is brought about through disease, wind, or other agency. What is said of the hemlock applies also to the sugar maple and beech, although these trees are perhaps more susceptible to disease than the hemlock. The behavior of the balsam fir is in marked contrast. Although, like the hemlock, the balsam is able to grow for many years in fairly dense shade, it is handicapped by its susceptibility to fungus diseases, largely in consequence of which its lease on life is limited. At the age of a hundred years, a hemlock, even if it has been growing suppressed all this time, will usually have a sound, healthy trunk. In northern Cape Breton, at any rate, the balsam fir, even under favorable conditions, seldom reaches the age of seventy years without having become infected by heart rot,[8] and by the time it has rounded the century mark its trunk usually has become badly rotted within. In addition to the "ground rot," which, in conjunction with the brittleness of the wood, renders the tree liable to windfall (Fig. 13), the balsam fir, when growing in a suppressed condition under hardwoods, is likely to be affected by "top rot," which may cause it to die back from the top. Like the hemlock, however, a balsam may ultimately find an opening in the forest canopy overhead. But by

[8] According to Zon ('14), two species of fungi are concerned: *Trametes Pini* (Brot.) Fr. and *Polyporus Schweinitzii* Fr., which may cause either "ground rot" or "top rot." According to the observations of Dr. G. P. Clinton in the western Adirondacks, and of the writer in northwestern Maine and northern Cape Breton, in these regions heart-rot in the balsam fir seems to be attributable to still another fungus, *Fomes pinicola* Fr., a species which Duggar ('09, p. 467) has also mentioned as one which causes disease in the balsam.

this time it is an old tree. For, while the hemlock at a hundred years is still comparatively young, the balsam is already a veteran, since (at least in northern Cape Breton) it seldom lives to be more than 125 years old.

To sum up, if it is assumed that the climatic conditions are equally favorable to all the species concerned, the apparent inability of the balsam fir to compete successfully with the species which characterize the deciduous climax forest formation

FIGURE 13.—Wind-felled balsam fir; Adirondack Mountains, New York. The specimen in the background shows the manner in which the trunk commonly splinters.

can be attributed in large part to its shorter tenure of life, coupled with which are its greater susceptibility to fungus diseases and its less pronounced tolerance of shade. That the climate in this region is favorable to the deciduous climax trees is attested by their vigorous growth and the large size which they commonly attain. That it is favorable to the balsam fir is manifest from the manner in which this tree thrives wherever there is freedom from competition. It should be added that, considering the transition region in its entirety, account must also be taken of climate. Climatic factors without doubt have been of great importance during the northward migration of the deciduous climax trees which has ensued in post-glacial time (see especially Adams '02), and there is little question that in parts of the transition region farther south, where balsam is absent or restricted in its distribution, such factors are still of large significance.

General features of transition climax forests in northern Cape Breton and elsewhere.—The trees which characterize forests of the climax type in the lowland of northern Cape Breton may be divided into four groups, as follows: (*A*) Deciduous species, such as the beech and sugar maple, whose center of distribution lies south of the transition region; (*B*) Deciduous species, notably the yellow birch, whose center of distribution lies within the transition region; (*C*) Evergreen species, notably the hemlock, whose center of distribution lies within the transition region; and (*D*) Evergreen species, such as the balsam fir and white spruce, whose center of distribution lies north of the transition region. To these might perhaps be added a fifth group: (*E*) Deciduous species, such as the paper birch and the balsam poplar, whose center of distribution lies north of the transition region.

It has been intimated in earlier paragraphs that the relative abundance of the different climax trees is subject to considerable local variation. By way of summary, it may be stated that in forests of the regional climax type the trees of group *A* commonly predominate, though sometimes they are outnumbered by those of group *C*. The yellow birch, representing group *B*, is practically always present, varying greatly in abundance, usually common though seldom predominant (but see in this connection p. 387). The trees of group *D* are seldom completely absent: usually they occupy a prominent, but rarely a predominant, position in the forest. The trees of group *E* are commonly represented, but always as a minor element in the forest: frequently they are missing altogether.

While the above observations are made primarily with reference to conditions in northern Cape Breton, they are capable of much wider application. Throughout much of the vast expanse in eastern North America which is embraced by the transition region, the five groups of trees specified in the preceding paragraph are represented. Broadly speaking, throughout this area the nature of the regional climax forests is essentially similar, in so far as their ecological aspect is concerned; but, just as in Cape Breton, there is considerable local variation in their composition—in the presence or absence of certain species and in their relative abundance when present. Leaving out of consideration the species of the fifth group, which occupy a relatively insignificant position here, it is possible to distinguish, with reference to the presence or absence in the forest of members of the first four groups outlined above, eleven different group-combinations of trees which may comprise an equal number of floristically different types of climax forest. Indicating the respective groups by letter, these various group-combinations are as follows: (1) *A-B;* (2) *A-B-C;* (3) *A-B-C-D;* (4) *A-B-D;* (5) *A-C;* (6) *A-C-D;* (7) *A-D;* (8) *B-C;* (9) *B-C-D;* (10) *B-D;* (11) *C-D.*

In sections of the country where all four groups of climax trees (*A, B, C, D*) are well represented, forests comprising any and each of these group-combinations may be encountered. As might be expected, however, while the trees of groups *B* and *C* are about equally well represented in forests throughout the transition region, those of group *A* are most generally represented southward, those of group *D* northward. It is along the southern borders of the transition region, in that part of the area where climatic conditions presumably are most favorable to the trees of group *A* (and least so for those of group *D*), and which these have occupied for the longest time that the first group-combination (*A-B:* the "northern hardwood" type of forest) is most extensively developed. Here the trees of group *D* tend to be localized in situations which are edaphically favorable: they develop best in areas which are somewhat swampy. Conversely, along the northern borders of the transition region, in that part of the area where climatic conditions presumably are less favorable for the deciduous species of group *A* (but more so for those of group *D*), or which, it may be, these species in their post-glacial migration have reached only in comparatively recent time, the trees of group *D* are commonly a conspicuous and even the predominant element in forests of the regional climax type. Here the trees of group *A* tend to be restricted to the better drained soils. It is important to note in this connection, however, that even along the northern border of the transition region, as in Cape Breton, purely deciduous forests are by no means lacking, and that the trees of group *A* growing here compare quite favorably in size, vigor and ability to reproduce themselves with those growing in forests farther south. It is of further interest that along the southern border of the transition region the trees of group *D* may occupy a prominent position in climax forests: in one locality in northwestern Connecticut, for example, at an elevation of less than 2,000 feet, the black spruce is thriving on uplands, reproducing well, attaining a large size, and growing in association, not only with beech and maple, birch and hemlock, but with such species as chestnut (*Castanea dentata*) and mountain laurel.

Considerable interest attaches itself to the relative importance, in transition forests where the trees of group *D* are represented, of the balsam fir and black spruce. In northern Michigan (Whitford '01), Ontario (Howe & White '13), and elsewhere the balsam fir, as in Cape Breton, seems to be the predominant northern conifer. But in other localities the black spruce occupies the position of relative predominance. This seems to be true, to cite localities with which the author is personally familiar, in the western Adirondacks and in northwestern Maine. In the primeval forests about Big Moose (elevation about 2,000 feet), in the Adirondacks, for example, where it grows abundantly, in company with beech, sugar maple, yellow birch, and hemlock, the black spruce attains a diameter of more than three, and a height of more than 125 feet. Here, as in Maine, the balsam fir is present in the forest, but it is more characteristic of the "flats" and moister sites. As noted earlier, the black spruce is represented in the climax forests of the lowland in northern Cape Breton, but here it is infrequent and never reaches the size exhibited by the spruce in the Adirondacks.

In proceeding northward from the region of deciduous forests to that of coniferous forests (Fig. 1) there is a gradual transition from one type of forest to the other. Broadly speaking, however, due largely to the predominating influence of the deciduous element, forests of the regional climax type are essentially similar in their ecological aspect throughout the transition region. Various attempts have been made to define subdivisions of this region on the basis of vegetational dissimilarities, but while such subdivisions may be of floristic importance, their significance from the standpoint of ecological plant geography is at least open to question. Thus, it is doubtful whether the "Northern Mesophytic Evergreen Forest" region (characterized in the east by the presence, as the most common species, of white pine, hemlock, jack pine [*Pinus Banksiana*] and balsam fir), which Shreve ('17) maps as distinct from the "Northeastern Evergreen-Deciduous Transition Forest" region, should be so separated, since throughout this area, as elsewhere in the transition region, climax forests of the deciduous type are commonly encountered in situations which are edaphically suited to their development. Similarly, the "White Pine Region" of New England, as mapped by Hawley and Hawes ('12), while distinct from the standpoint of the forester, does not seem to be so from the standpoint of ecological plant geography. White pine is a frequent constituent of the climatic climax forest throughout the transition region; but, when growing in pure stands, it probably represents either a temporary association or else an edaphic climax. Not only does it appear unwarranted, from the standpoint of ecological plant geography, to recognize such subdivisions as distinct, but, as elsewhere suggested (p. 261), from this point of view the vegetation of the transition region itself is best regarded merely as a part of the great deciduous forest climatic formation of eastern North America.

II. THE EDAPHIC FORMATION-COMPLEX OF THE REGION

A. Primary Formations of the Xerarch Series

1. The Formation-types of Ordinary Uplands

a. INTRODUCTORY

In attempting to formulate the successful series which lead toward and, under favorable circumstances, culminate in the climax association-type of the region, there are three possible sources of evidence: (*1*) areas in which succession is actually taking place at the present time (or has taken place within comparatively recent times), as indicated more particularly by the presence of (*a*) relicts of more primitive associations, or (*b*) pioneers of more advanced associations than the present ones;

(*2*) areas in which, owing to the limiting influence of certain local factors, the succession has culminated in an edaphic climax which is less mesophytic than the regional climax association-type; and (*3*) areas which have been denuded of their original vegetation, and where secondary succession is taking place. Secondary successions are discussed in a separate section, but they obviously possess many points in common with primary successions.

Aside from the views of the regional climax forest (Figs. 10–11), the primary formation-types of ordinary uplands are pictured only by Figs. 14–16; but see in this connection the figures illustrating secondary formations (Figs. 33–40).

b. THE ASSOCIATION-COMPLEXES OF ROCK OUTCROPS

Rock surface association-types.—The first forms of life to grow on a bare rock surface are usually the lichens. Commonly the crustose lichens appear first: species of *Buellia, Lecanora, Lecidia, Rhizocarpon,* etc. These are closely followed and often accompanied by foliose lichens: species of *Parmelia, Gyrophora,* etc. Associated with these may be the fruticose lichen, *Stereocaulon* sp., and certain lithophytic mosses, such as *Hedwigia ciliata* and *Grimmia apocarpa*. Where the rock slopes steeply, other plants may be entirely absent, owing to their inability to secure a foothold on the bare rock surface, and the succession may become arrested at this early stage.

But on gentle slopes the conditions are different, for here plants are able to maintain their positions even when entirely unattached to the substratum. Situations of this sort are favorable to the development of the fruticose lichens, notably species of *Cladonia* (e. g., *C. rangiferina, C. sylvatica*). These usually establish themselves first in shallow depressions of the rock surface, where moisture conditions are relatively favorable, and from here they may spread laterally in all directions until the surface of the rock becomes completely covered with a loose, essentially unattached mat of vegetation. In company here with the fruticose lichens very commonly grow certain mosses: these may include any of the species mentioned below as characteristic of crevices, but particularly *Racomitrium canescens* and species of *Polytrichum.*

Crevice association-types.—Contemporaneously with the rock surface "subsuccession" (Cooper '13, p. 118) occurs the crevice "subsuccession." In the crevices, and also, to some extent, in hollows of the rock surface, a soil is usually present, and this enables plants to grow which are unable to secure a foothold on a rock surface or to maintain themselves in such an environment. The pioneer crevice vegetation may include the fruticose lichens already mentioned as growing on rock surfaces. It may also include various mosses, such as *Ceratodon purpureus, Leucobryum glaucum, Dicranum scoparium* and *D. Bonjeanii,* and *Polytrichum piliferum.* But more important than these, in the light of subsequent events, are the ferns and seed plants. Of the ferns, *Pteris aquilina* is the most frequent crevice form, although *Polypodium vulgare* often grows here, in sheltered situations. Among the more important herbaceous seed plants which inhabit crevices may be cited *Potentilla tridentata,* which seldom grows anywhere else, *Deschampsia flexuosa* and *Danthonia spicata, Cornus canadensis,* and *Solidago bicolor.* Of the shrubby and semi-shrubby seed plants, *Vaccinium pennsylvanicum, V. canadense,* and *Gaultheria procumbens* are rarely absent, while *Vaccinium Vitis-Idaea* is especially characteristic of such habitats. Almost any of the trees to be mentioned presently as occurring on the heath mat may be found in crevices. In a sense there may appear to be a succession of growth forms in crevices, herbs preceding shrubs, etc., but succession of this sort, on the whole, is probably more apparent than real.

The heath association-type.—Up to a certain point, the rock surface and the crevice "subsuccessions" are distinct from one another. But with the formation of the lichen–moss mat over the rock surface, and the gradual accumulation of soil which accompanies the process, the two tend to merge into one. The various seed plants, particularly the shrubs, which hitherto have been largely confined to the crevices, become increasingly abundant over the rock surface, and ultimately there may arise what Cooper has aptly termed a "heath mat" ('13, p. 125). Here the ground is still covered by a mat of fruticose lichens and mosses, but these are no longer the dominant plants. As such they have been superseded by ferns and seed plants, whose roots tend to bind together the hitherto loose mat and to consolidate it into a more or less compact turf. The predominant plants of the heath association-type are low shrubs, particularly Ericaceae. A list of species characteristic of this phase in the succession is given below.

Herbaceous Plants

Pteris aquilina	*Cornus canadensis*
Deschampsia flexuosa	*Melampyrum lineare*
Danthonia spicata	*Solidago bicolor*

Shrubby and Semi-shrubby Plants

Juniperus communis depressa	*Kalmia angustifolia*
Juniperus horizontalis	*Gaultheria procumbens*
Salix humilis	*Epigaea repens*
Alnus crispa	*Gaylussacia baccata*
Amelanchier sp.	*Vaccinium pennsylvanicum*
Empetrum nigrum	*Vaccinium canadense*
Nemopanthus mucronata	*Vaccinium Vitis-Idaea*
Rhododendron canadense	*Viburnum cassinoides*

Trees

Pinus Strobus	*Betula alba papyrifera*
Abies balsamea	*Pyrus americana*
Picea canadensis	*Prunus pennsylvanica*
Picea mariana	*Acer rubrum*

As a rule the dominant shrub of the heath mat is *Vaccinium pennsylvanicum.* But *Vaccinium canadense* may be equally abundant; while in some places the *Kalmia* forms an almost pure growth, or may grow mixed with *Rhododendron. Gaultheria* and *Epigaea* usually form a lower story of vegetation; and the same, locally, is true of *Vaccinium Vitis-Idaea. Empetrum* is particularly characteristic of exposed bluffs along the seacoast, and will be referred to again in that connection. Occasionally the grasses, *Danthonia spicata* and *Deschampsia flexuosa,* are dominant forms.

The coniferous forest association-type.—As already pointed out, trees may inhabit the crevices at an early stage in the succession. With the improvement of soil relations which results from the mantling of the rock surface by a mat of vegetation, they cease to be confined to crevices and invade the areas between. At first few and scattered, they gradually increase in number and size and come to occupy the ground more completely. In the course of time, groups of trees in the more favorable situations form patches of embryonic woodland, and, as these spread and unite with one another, a more or less continuous forest may be evolved. Not infrequently trees come in so rapidly and in such force at the outset that the heath stage in the succession is virtually eliminated. The succession does not proceed with equal rapidity everywhere, even within a given physiographic unit area. For, owing to locally unfavorable edaphic conditions, succession in some situations lags behind that in others, with the result that there commonly arises a complex of associations, in which various stages in the developmental series are represented. This promiscuous intermingling of primitive and advanced associations becomes less pronounced as time goes on, but even in the midst of a climax forest there may be situations in which succession has never progressed beyond the rock face–crevice stage.

During the early phases of forest development, the white spruce commonly stands out as the predominant tree: the balsam fir, as a rule, is second in importance. Common associates in the rising forest are the paper birch, conspicuous by reason of its light color and large size; the black spruce, red maple, and mountain ash; and, less commonly, the white pine. As the forest matures, the relative importance of the two dominant trees undergoes certain changes, due very largely to the differing degree to which the two are tolerant of shade. The white spruce is a relatively intolerant species. Its seedlings thrive only in situations where there is abundant light. While it reproduces prolifically in the open, young trees are rarely encountered in the forest. The balsam fir, on the other hand, is relatively tolerant of shade. Like the white spruce, it reproduces best in well lighted situations, but unlike the white spruce its seedlings are also capable of thriving in moderate shade. The result is obvious. With the diminished illumination of the forest floor which accompanies the growth of the forest, there is a marked decrease in the rate of reproduction of the white spruce, while the balsam fir is much less affected. It follows that, as the forest matures, the white spruce tends to become relatively less abundant, the balsam fir relatively more so.

Contemporaneously with the ever-increasing amount of shade produced by the canopy of foliage overhead, the vegetation of the forest floor also changes. The cladonias of the heath stage are largely superseded by bryophytes. Of the mosses, *Hypnum Schreberi* is the pioneer forest species and often appears on the heath mat well in advance of the forest itself. Along with this, but much less common, may grow *Rhytidiadelphus triquetrus.* As the shade and moisture conditions on the forest floor become more favorable, two relatively mesophytic mosses, *Hylocomium splendens* and *Ptilium crista-castrensis,* together with the liverwort, *Bazzania trilobata,* come to play an important part in the formation of the moss carpet, by which the ground sooner or later becomes almost completely covered over.[9] Of the shrubs and herbaceous vascular plants which are characteristic of the heath mat, certain species, such as *Pteris aquilina, Cornus canadensis, Epigaea repens, Vaccinium pennsylvanicum* and *V. canadense,* are equally characteristic of the coniferous forest, particularly during the early phases of its development. Coincident with the formation of the moss carpet, however, other species begin to appear which, while they may have been represented to some extent in the earlier stages of the succession, are more typical of the forest. The forerunners include *Maianthemum canadense, Aralia nudicaulis, Pyrola secunda, Trientalis americana, Chiogenes hispidula,* and *Linnaea borealis americana.* Later on, as the forest matures, these relatively xero-mesophytic forms are followed by other species which are more truly mesophytic, such as *Clintonia borealis, Coptis trifolia, Oxalis Acetosella, Moneses uniflora, Pyrola minor,* and *Aster acuminatus.*

Very often, during the early development of a coniferous forest there is a considerable period when the ground underneath the trees is almost barren of a plant cover. The probable explanation of this frequently observed phenomenon is suggested later in connection with the discussion of succession in abandoned pastures.

The edaphic climax association-type.—Theoretically, at least,

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[9] Cooper ('11) has described a similar succession of lichens and mosses as accompanying the development of the climax forest on Isle Royale.

it is conceivable that even on a bare rock surface, through the gradual amelioration of the habitat by biotic factors, the succession of plant associations might progress still further, and that the vegetation here might ultimately attain the condition which characterizes the climax association-type of the region. But, as a matter of fact, on bare rock outcrops the succession seldom proceeds further than the coniferous forest stage. In other words, the coniferous forest can be regarded as representing the edaphic climax association-type of the rock outcrop successional series: it is a permanent association-type, though ordinarily less mesophytic than the regional climax association-type (in this connection, see Nichols '17, pp. 310-317). In its optimum development, the coniferous forest association-type of the rock outcrop series in the lowland may resemble very closely the climatic climax of the mountains, and indeed it may be quite as mesophytic as the regional climax type. Balsam fir is the predominant tree, while white spruce, paper birch, black spruce, white pine, red maple, yellow birch, and mountain ash are more or less abundantly represented. But, as has already been suggested, such may be the effect of the limiting edaphic factors that in many places the succession halts at a much earlier stage than this.

c. THE ASSOCIATION COMPLEXES OF GLACIAL DRIFT

Extensive outcrops of bare rock are seldom encountered in the lowland. The most widespread type of substratum here is glacial drift. The drift, to perhaps a greater degree than any other type of substratum, is well adapted to rapid colonization by plants. So favorable, indeed, were the original conditions here, and so rapidly has the succession of plant associations ensued, that the drift everywhere has long since become covered by forests. It is only where the original plant cover has been destroyed, either through the agency of stream or wave erosion, or else as the result of human activity or fire, that the earlier phases of the succession become apparent. The early stages of primary successional series on drift can be reconstructed by analogy, after a fashion, from the study of primary successions on other substrata and of secondary successions on the drift.

Coniferous forest locally an edaphic climax.—Disregarding for the present the earlier phases of the succession, suffice it to state that eventually there may arise on the drift a type of forest essentially similar to what has been described above as constituting the ultimate phase in the rock outcrop series: a forest of balsam fir, white spruce, paper birch, etc. And it is of interest to note that, locally, such a forest may also constitute an edaphic climax, even on the drift. In the vicinity of Baddeck, for example, over most of the country succession has never progressed beyond the coniferous forest stage. This circumstance, without much question, is correlated with the heavy, clayey nature of the drift here, which has acted as a limiting factor to prevent the attainment of the regional climax. It is of further interest in this connection that around Baddeck, and in certain other localities where the soil is heavy, the tamarack (*Larix laricina*) is an important arborescent pioneer and a constituent of the coniferous forest. Throughout much of northern Cape Breton the tamarack is a rarity. Its ecological status will be referred to again in another connection (p. 412).

Development of the regional climax.—The yellow birch may be regarded as the forerunner of the deciduous trees which characterize the regional climax forests. This tree is usually represented in coniferous forests in the lowland, but there it occupies a position of prominence only in forests which are well advanced in their development. As the pioneer among the deciduous climax trees, it seems not unlikely that this tree, together with the red maple and paper birch, may help to pave the way for the beech and sugar maple. The effect on the moss carpet of the periodic accumulation of fallen leaves has been referred to elsewhere; and it is at least conceivable that the deciduous advance-guard in the coniferous forest, through the medium of leaf-fall, may in some way exert an ameliorating influence on the substratum, which facilitates the invasion of the forest by beech and sugar maple.

At any rate, wherever the soil conditions are favorable, coniferous forests are superseded by forests of the regional climax type. The trees of the coniferous forest stage in the succession may persist in varying degree, as earlier suggested, but they relinquish their position of dominance. All stages of transition may be found between forests of the coniferous type and those which are purely deciduous. During the transition from one type to another the undergrowth undergoes various changes. Certain species of the coniferous forest stage, such as *Coptis* *trifolia* and *Chiogenes hispidula,* vanish almost completely; others, such as *Pteris aquilina, Cornus canadensis, Epigaea repens,* and *Moneses uniflora,* become much less common; while still other species, such as *Polystichum acrostichoides, Smilacina racemosa,* and *Sanicula marilandica,* which were poorly or not at all represented in the coniferous forest stage, come to occupy a more or less prominent position.

FIGURE 14.—Granitic talus of the prevailing type; north of Cheticamp.

d. THE ASSOCIATION-COMPLEXES OF TALUS

With reference to the size of the component rock fragments and the consequent degree of stability of the rock mass, talus slopes (FIG. 14) vary greatly. Two extreme types may be distinguished: the *Boulder Talus* and the *Gravel Slide.* Boulder talus consists essentially of large rock fragments (sometimes many feet in diameter), which tend to lodge together and interlock with one another on the slope in such a way as to produce a relatively stable rock mass. A gravel slide, on the other hand, consists primarily of fine, loose rock débris, which is not held together in any way but is constantly tending to slip further down the slope, and thus produces a very unstable rock mass. Between the two extremes are all degrees of intergradation.

The association-types of boulder talus.—As in the rock outcrop series, two types of habitat are available to plants here, the rock surfaces and the crannies between the fragments. The surfaces of the boulders are usually overgrown with crustose and foliose lichens. Any of the rock face species previously cited may grow here. These, however, play little or no active part in the talus succession as a whole: the latter is instituted almost entirely by the plants which grow in the crannies. Here, through the further disintegration of the larger rock fragments, and also to some extent from other sources, a soil accumulates. Toward the base of a talus slope soil gathers faster and soil moisture is more abundant than higher up, so that as a rule succession progresses much more rapidly here than elsewhere on the slope. Very commonly the base of a talus slope will be clothed by a mesophytic forest while above there are only scattered trees and shrubs.

The shade and protection from exposure afforded by the blocks which surround the crannies create here conditions which are congenial to mesophytes as well as to many xerophytes. The pioneer plants may include various species of *Cladonia* and any of the bryophytes which have been cited as characteristic of crevices in the rock outcrop series. It also commonly includes certain more mesophytic species, such as *Ptilidium ciliare, Hypnum Schreberi,* and *Hylocomium splendens.* The lichen-bryophyte element may perform an important function in the succession by forming cushions and mats which often spread away from the crannies over the adjoining rock surfaces, creating a substratum favorable for the germination of the spores and seeds of higher plants. The presence in the crannies of a soil, however, permits the growth at the outset, not only of lichens and bryophytes, but of vascular plants as well. Herbaceous plants are sparingly represented by *Polypodium vulgare* and a few other species, while the two shrubs, *Sambucus racemosa* and *Rubus idaeus canadensis,* usually occupy a prominent position. But both herbs and shrubs are subordinate in importance to trees. These gain a foothold early and may predominate the succession from start to finish. For a long time, at least as long as the intermittent bombardment of the slope continues by rocks dislodged from above, the trees remain scattered, and, at this stage, paper birch commonly is the most conspicuous tree. The reason for this frequently observed predominance of paper birch over conifers at this time, as pointed out by Cooper ('13, pp. 218, 219), is undoubtedly due to the ability of the former to sprout from the stump and thereby recover from the injuries inflicted by falling boulders. Ultimately, a coniferous forest of the type already described may become established, in which the predominant trees include the balsam fir and white spruce, the paper birch and yellow birch, the white pine, the black spruce and mountain ash. On north-facing slopes, coniferous forests, while attaining a high degree of mesophytism, frequently represent the culminating phase of the succession: in other words, they constitute an edaphic climax. But, under favorable conditions, the regional climax association-type is capable of attainment on boulder talus, as on the glacial drift.

The association-types of gravel slides.—In extreme cases, as, for example, on gypsum slides[10] (Fig. 15), the instability of the rock mass may be so great that plant life is almost excluded. Largely on account of this instability, lichens and mosses usually play but little part in gravel slide successions: only plants with roots are capable of maintaining a foothold here. The most important pioneers are xerophytic ferns and seed plants, especially herbaceous forms which perennate by means of roots and rhizomes: such species, for example, as *Pteris aquilina, Dicksonia punctilobula, Danthonia spicata, Campanula rotundi-*

[10] In this connection it is worthy of note that floristically the vegetation of gypsum outcrops commonly differs to a marked degree from that of other rock outcrops which may be physically similar. On the gypsum the vegetation includes a pronounced calciphilous element which elsewhere is mostly absent. Prominent among the seed plants are *Carex eburnea, Shepherdia canadensis, Cornus circinata,* and *Erigeron hyssopifolius.* The bryophytes include *Swartzia inclinata, Gymnostomum rupestre, Tortula mucronifolia, Encalypta contorta, Myurella Careyana,* and *Thuidium abietinum.* Generally speaking, however, while there are frequent other evidences throughout this region of a similar correlation between the chemical nature of the underlying rock and the character of the vegetation, the writer has been unable to distinguish any broad relationships of general ecological significance. Aside from the influence of topography, the general aspect of the vegetation appears to be correlated more with the physical character of the substratum than with its chemical character.

folia, Anaphalis margaritacea, and *Solidago bicolor.* Most of the weeds found in pastures and along roadsides thrive on gravel slides. Of the herbaceous plants, the grasses, particularly *Danthonia spicata,* commonly play an essential rôle, contributing to bring about increased stability in the substratum through the formation of a more or less continuous sod. Shrubs, notably *Rubus idaeus canadensis,* and trees, especially the white spruce, are also important in this respect.

FIGURE 15.—Gypsum ("plaster") outcrop along shore of Ingonish Harbor.

Sometimes a xerophytic weed stage in the succession, in which the plants are scattered and the vegetation open, is followed by a definite grass stage, in which the ground is completely carpeted by vegetation. But more commonly trees are present from the outset, and the first continuous plant cover is dominated by trees, which form an open grove, the ground between the trees being grassed over or else occupied by colonial herbaceous species, such as *Dicksonia* and *Anaphalis,* or by *Rubus.* The white spruce invariably stands preëminent among the trees, but there is a scattered representation of balsam fir, paper birch, balsam poplar, bird cherry (*Prunus pennsylvanica*), etc. In the course of time a closed coniferous forest may be developed, and, under favorable conditions, this may be superseded eventually by a forest of the regional climax type.

One of the commonest types of talus in northern Cape Breton is shown in Fig. 16. The rock fragments are relatively small and the rock mass is much less stable than the large-bouldered talus, though more so than the gravel slide. The common

Figure 16.—Pioneer association of white spruce, etc., on granitic talus; Barrasois.

pioneers here are the white spruce, the raspberry, *Dicksonia,* and *Anaphalis.*

2. The Formation-types of Uplands along Streams

a. introductory

In a general way, two topographic features are intimately associated with streams: valleys and flood plains. In northern Cape Breton the valleys range from deep, narrow ravines and gorges in which the stream occupies entirely the narrow floor, on the one hand, to wide, open valleys with broad, flat floor, on the other. All of the larger streams, in their passage from the interior toward the coast, flow during at least part of their course through deep valleys (FIG. 17), while on a lesser scale ravines are well developed along many of the small brooks. In general, so far as the larger streams are concerned, narrow ravines (FIG. 19) are more characteristic of the higher, crystalline areas, broad valleys of the lower Carboniferous regions. Broad, open

FIGURE 17.—Valley of Barrasois River, just above contact between crystalline and Carboniferous areas; *Pinus Strobus* in right and left foreground. Compare with FIG. 18, photographed but a short distance downstream.

valleys (FIGS. 7, 20) are especially well developed in the zone of contact between the lowland and the highland, where very frequently the Carboniferous lowland extends as a finger-like depression for several miles into the heart of the higher crystalline formation. The floor of such a valley, as a rule, is relatively flat and is referred to locally as an *Intervale*.

The glacial débris, which at one time must have buried the floor of every valley to a considerable depth, has been very largely scoured out from the narrow-floored ravines through stream activity; but in the broad-floored valleys, as throughout the Carboniferous lowland in general, it may still form, at least locally, deposits many feet thick. Wherever these heterogeneous deposits are exposed to the erosive action of the current, the finer materials tend to be carried away, the coarser constituents being left behind and forming what are here designated as *Boulder Plains*—areas covered with stones, mostly rounded, but

FIGURE 18.—Boulder plain along lower course of Barrasois River.

of all shapes and sizes (FIGS. 18, 21). Where the stones are uniformly small, they may well be referred to as *Cobble Plains.* These stony plains commonly border the larger streams wherever they flow through deposits of glacial drift. In flood time they are submerged, but ordinarily, except for the small channel permanently occupied by the stream, they are uncovered.

In contrast to boulder plains, which are a result of degradation, flood plains are a product of aggradation. They are best developed along sluggish, old-age rivers, and at first thought might not be expected to occur at all along swift, young streams, like the majority of those in northern Cape Breton. But, on the contrary, even in narrow ravines incipient flood plains may be commonly observed in situations which in some way are protected from the swift current (foreground in FIG. 17), while in wider valleys (FIG. 20) the stream is usually bordered by an interrupted series of low, terrace-like flood plains, which have been built up along the less exposed banks. The flood plains of rapid streams, however, not only in Cape Breton, but elsewhere as well, differ markedly from the familiar type of sluggish streams. There the alluvial deposits consist largely of fine-grained sediments. Flood plains of this latter sort, in northern Cape Breton, have been developed to a considerable extent locally, particularly toward the mouths of some of the larger rivers. Along rapid water courses, however, the deposits are much coarser, the swiftness of the current in times of flood being so great that most of the finer material is washed away. Even where the conditions for deposit are most favorable, the alluvial material along a rapid stream is made up largely of coarse sand and gravel, while miniature flood plains built up almost wholly of cobbles and pebbles are frequent in less favorable situations. Incidentally, it should be remarked that while, in a sense, a boulder plain might be regarded as a flood plain, for obvious reasons it is best treated separately. Typical flood plains commonly overlie former boulder plains.

b. THE ASSOCIATION-COMPLEXES OF ROCK RAVINES

This is the only type of ravine which need be considered. The associations here may be divided roughly into four groups, as follows. (*1*) The stream bed association-types: comprising the vegetation in areas where the bottom is submerged at all seasons. (*2*) The stream bank association-types: comprising the vegetation of areas, mostly along the margin of the stream, which are flooded at times of high water but at other times, of variable duration, are exposed to the air. (*3*) The association-types of cliffs: comprising the vegetation of areas above the flood zone which are too steep or unstable to support a forest. (*4*) The ravine forest. With reference to their water relations, some of these association-types are naturally classed under the xerarch series, others under the hydrarch series, but this classification is not always easy to apply. In the hydrarch category should of course be classed the stream bed association-types, and here also it seems most appropriate to include those stream bank and cliff association-types whose ecological aspect is obviously correlated with the more or less constant presence of an abundant water supply. Similarly, in the xerarch category should be classed the ravine forest and such of the association-types of stream banks and cliffs as are exposed for considerable periods of time to more or less xerophytic conditions. In the present connection

FIGURE 19.—Gorge along Indian Brook; the upper edge of the flood zone is indicated by the lower margin of the forest.

attention is directed primarily to ravine associations of the xerarch series. Apropos, it may be remarked that, for reasons which the author has pointed out elsewhere ('16[b], pp. 237, 249, 250), in considering the vegetation of rock ravines from the dynamic point of view, the question of an actual succession of plant associations, in so far as it is correlated with the physiographic development of the ravine itself, may be virtually disregarded.

Stream bank association-types.—Largely owing to the narrowness of the channel to which the rushing flood water ordinarily is confined, the character of the vegetation within the flood zone in ravines is influenced to a marked degree by the abrading action of the current at times of high water. Particularly is this true along the larger streams (FIGS. 17, 19), to which the following remarks primarily apply. Woody plants, for the most part, are either absent or sparsely developed and even the herbaceous plants are scattered. The characteristic vascular plants of rocky banks between high and low water levels are herbaceous perennials, and these are mostly restricted to crevices and similar situations where their perennating roots and rhizomes can maintain a foothold. Common species are *Equisetum sylvaticum, Deschampsia flexuosa, Sagina procumbens, Campanula rotundifolia, Erigeron hyssopifolius,* and *Solidago bicolor,* together with various weeds, such as *Prunella vulgaris, Achillea Millefolium,* and *Chrysanthemum Leucanthemum.* In addition to these, a prominent position is frequently occupied by various bryophytes, such species as *Preissia quadrata, Fossombronia foveolata, Marsupella emarginata, Nardia obovata, Hygrobiella laxifolia, Grimmia apocarpa, G. conferta,* and *Racomitrium aciculare.* Toward the upper margin of the flood zone, skirting the lower edge of the ravine forest, there is commonly a narrow fringe of shrubs which constitutes a more or less distinct association-type. The characteristic species here is *Alnus mollis,* with which may be associated *Salix humilis, Rubus pubescens, Acer spicatum, Diervilla Lonicera,* and other shrubs, together with such herbaceous mesophytes as *Osmunda Claytoniana, Phegopteris polypodioides, Streptopus amplexifolius,* and *Solidago latifolia.*

Conditions similar to those just outlined may prevail in ravines along small streams, but here the stream bank vegetation commonly is such that it has seemed best to treat it under the hydrarch series (see p. 368).

Cliff association-types.—Certain pteridophytes are especially characteristic of crevices in cliffs, well above the level of the stream, notably *Polypodium vulgare, Aspidium fragrans, Cystopteris fragilis, Woodsia ilvensis,* and *Lycopodium Selago.* With the exception of perhaps the last-named species, these grow best in moist, somewhat shaded habitats. Various of the herbaceous perennials of the flood zone are equally common here, particularly *Deschampsia* and *Campanula,* while the crevice plants mentioned earlier in connection with the rock outcrop series of ordinary uplands may likewise be well represented. Of special interest, however, is the conspicuous position commonly occupied by the mosses and liverworts, which, in favorable situations, may develop luxuriantly, growing either in crevices or on sloping or perpendicular rock surfaces. Representative species are listed below, and, in addition to these, various of the species of wet cliffs (p. 370) may grow here.

Bazzania tricrenata	*Tortella tortuosa*
Diplophyllum taxifolium	*Racomitrium fasciculare*
Porella platyphylloidea	*Ulota americana*
Radula complanata	*Pohlia cruda*
Lejeunea cavifolia	*Bartramia pomiformis*
Andreaea petrophila	*Hedwigia albicans*
Swartzia montana	*Drepanocladus aduncus*
Fissidens osmundoides	*Polytrichum alpinum*

The ravine forest.—Nowhere in the lowland of northern Cape Breton are forests of the coniferous type more luxuriantly developed than in ravines. In general, these forests conform closely with the regional climax type of the mountains, and need not be described in detail at this point. Such forests here represent an edaphic climax association-type, and as such their development is correlated very largely with local peculiarities of temperature and soil moisture. They are best developed on north-facing slopes, where the failure of the succession to proceed beyond the coniferous forest stage may be attributed to the slowness with which the snow melts and the ground thaws out in spring and to the relatively low temperatures which obtain throughout the season. Quite commonly the north-facing slope of a ravine supports a coniferous forest while the opposite, south-facing slope is clad with a forest of the regional climax type. On north-facing slopes, coniferous climax forests are by no means confined to ravines: one of the most distinctly boreal examples of upland forest which has come to the writer's attention in the lowland is situated along the lower slopes of a steep mountain side, where ice frequently lingers as late as August, notwithstanding the fact that it faces an open intervale which was formerly occupied by a deciduous forest. In ravines which run north-and-south, and where both flanks are thus equally well exposed to the sun, on the other hand, the ravine forest may be wholly of the deciduous type.

One feature of coniferous ravine forests worthy of special mention is their great mesophytism, as evinced more particularly by the wonderful development of the bryophytic ground cover. Commonly the ground beneath the trees is literally buried beneath a thick bed of liverworts and mosses. The sphagnums in particular—such species as *Sphagnum capillaceum tenellum, S. Girgensohnii, S. quinquefarium,* and *S. subsecundum*—commonly form wide, deep cushions, flourishing here as in no other upland habitat in this region.

The summer evaporating power of the air in coniferous ravine forests, as compared with other habitats.—During the summer of 1915 a series of porous cup atmometers was operated, for a period of a little more than two weeks, in various habitats, with the object, primarily, of ascertaining the relative evaporating power of the air in coniferous ravine forests as compared with the deciduous climax forests. The habitats selected were as follows:

Station 1 ("Open—Shore"): Open hillside, east exposure, half a mile from seacoast.

Station 2 ("Open—Intervale"): Open hillside, east exposure, four miles from coast at head of intervale.

Stations 3 and *4* ("Hardwood"): Hardwood (climax) virgin forest; east exposure; near station *2*.

Station 5 ("Ravine Conifer—High"): Coniferous forest; steep north-facing slope of ravine, about 250 feet above river; near station *1*.

Station 6 ("Ravine Conifer—Low"): Dense coniferous forest; steep north-facing slope of ravine, about 150 feet above river; near station *1*.

Station 7 ("Ravine—Bed"): Gravel bar in bed of stream; exposed to sun about six hours daily; stream bed about 75 feet wide at this point; near station *1*.

The readings obtained are given in Table VI. During much of the period that the cups were in operation the weather was intermittently rainy, foggy, and clear. From August 3 to August 7, however, it was uninterruptedly clear, so that for pur-

TABLE VI

Rate of Evaporation in Various Habitats, as Indicated by the Porous Cup Atmometer

	July 22–July 27	July 27–August 3	August 3–August 7	Total
Station 1: Open—shore	28.8 cc.	45.0 cc.	84.2 cc.	158.0 cc.
Station 2: Open—intervale	39.4 cc.	53.3 cc.	91.9 cc.	184.6 cc.
Station 3: Hardwood A	16.0 cc.	19.6 cc.	42.1 cc.	77.7 cc.
Station 4: Hardwood B	15.3 cc.	16.3 cc.	37.8 cc.	69.4 cc.
Station 5: Ravine Conifer—high	14.4 cc.	20.6 cc.	52.5 cc.	87.5 cc.
Station 6: Ravine Conifer—low	11.0 cc.	14.0 cc.	43.3 cc.	68.3 cc.
Station 7: Ravine—bed	24.1 cc.	31.1 cc.	63.0 cc.	118.2 cc.

pose of comparison the third column of figures is the most reliable. From an examination of these figures various facts are obvious, but only one of these need be emphasized, namely, that the evaporating power of the air in the coniferous ravine forest differs little from that in the climax deciduous forest. Greater humidity, then, will not explain the luxuriant development of the moss carpet in a ravine forest. Other explanations have already been suggested.

c. THE ASSOCIATION-COMPLEXES OF OPEN VALLEYS

Chiefly by reason of the protection which they afford from cold winds in spring and fall, open valleys (Fig. 20), in general, present edaphic conditions which are more congenial to plants of southward distribution than those of any other type of habitat-complex. Robinson ('03) has already called attention to the relative abundance in the intervales of eastern Nova Scotia of early spring-flowering plants, and the writer (16[b], pp. 252, 253) has commented on parallel conditions in Connecticut. Nowhere in northern Cape Breton are forests of the deciduous-hemlock climax type more luxuriantly developed than on the floors of broad, sunny valleys, i. e., in the intervales. Here, more abundantly than anywhere else, grow the hemlock, red oak, white ash, and elm (*Ulmus americana*), among the trees, together with various herbaceous plants of pronounced southward range. Of the latter, many forms, such as *Anemone virginiana, Sanguinaria canadensis,* and *Dicentra Cucullaria* (*fide* Robinson '03), *Actaea alba, Epifagus virginiana,* and *Triosteum aurantiacum,* are practically restricted to the intervales or to the adjoining slopes. From the standpoint of their physiographic origin, the intervales are largely the result of stream activity, and their vegetation in part is that of the boulder plains and flood plains which are still in the course of formation. But in large part, so far as the vegetation is concerned, the influence of the stream is of merely historical significance. In the case of boulder plains and flood plains, local soil as well as local atmospheric factors have to be taken into account.

FIGURE 20.—The Big Intervale along North Aspy River: floor of valley at this point largely under cultivation; in background, talus slopes in various stages of forestation; view taken toward upper end of intervale; compare FIG. 7.

d. THE ASSOCIATION-COMPLEXES OF BOULDER PLAINS

In extreme cases, vegetation may be almost wholly lacking on boulder plains (FIG. 18). But such cases are not common. While from a distance the lower and more frequently flooded portions of a boulder plain may have almost the aspect of a desert, closer inspection usually reveals, even here, a goodly representation of shrubs and herbaceous plants, which maintain a precarious foothold in the interstices between the cobbles and boulders, rooting in the sand and gravel which have accumulated in the shelter afforded by the larger rocks. The pioneers are preëminently herbaceous perennials: species which are able to tide over the unfavorable periods by means of underground organs. Except for shrubby willows (such species as *Salix cordata, S. lucida,* and *S. humilis*), which are able to survive considerable battering and

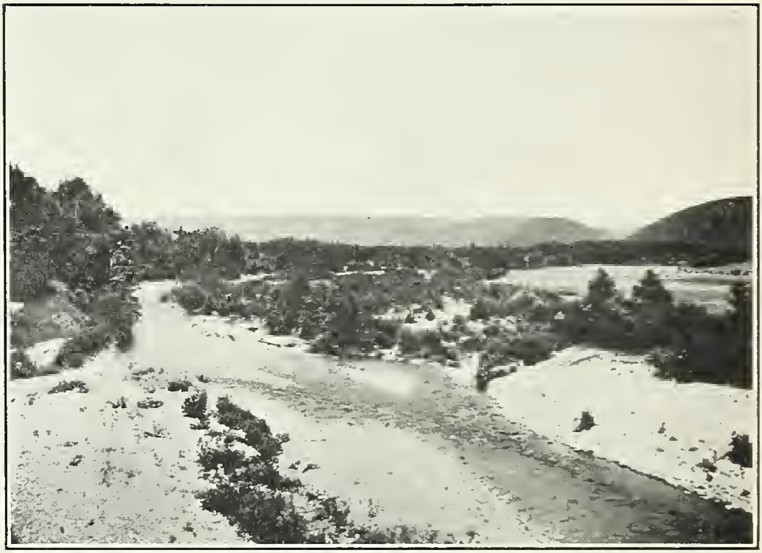

FIGURE 21.—View along Middle River, showing boulder plain with scrubby willows, etc. (left foreground), young flood plain with pioneer tree stage (center, mid-distance), and mature flood plain, now under cultivation (right, mid-distance).

locally may form dense, low thickets (FIG. 21), woody plants are scarce.

On the higher parts of a boulder plain, the vegetation is much more abundant, but always open. In addition to the willows, species of alder, particularly *Alnus incana,* are ordinarily conspicuous here, together with such other woody plants as *Rubus idaeus canadensis, R. pubescens,* and *Spiraea latifolia.* A list of some of the more characteristic herbaceous plants of boulder plains is given below. This list does not include weeds, many of which occupy a very prominent position here.

Equisetum arvense
Calamagrostis canadensis
Agropyron repens
Poa pratensis
Carex torta
Ranunculus repens
Fragaria virginiana
Viola cucullata
Viola pallens
Epilobium angustifolium
Epilobium adenocaulon
Apocynum cannabinum
Eupatorium purpureum
Solidago canadensis
Aster radula
Aster puniceus

e. THE ASSOCIATION-COMPLEXES OF FLOOD PLAINS

Transition from boulder plain to flood plain.—It commonly happens, sooner or later, that the stream shifts its course or that the current is deflected by some sort of an obstruction, so that an area occupied by a boulder plain becomes protected in a measure from the erosive activity of the stream. If the protection is sufficient, degradation may become largely superseded by aggradation, and a flood plain may gradually be built up on top of the former boulder plain (FIG. 21). Eventually, even along swift stretches of the stream, such flood plains may attain a height of five or six feet above low water level. At first composed of coarse gravel and cobbles, as the surface is raised higher the successive deposits become finer, and finally the soil comes to consist of coarse sand. Only in exceptionally favorable situations, however, does the soil approximate the fine alluvium of old-age rivers.

The succession of plant associations outlined.—In the familiar type of flood-plain succession (to be discussed later), the pioneer stages of the series are usually hydrophytic: in other words, the succession is hydrarch. In the boulder plain–flood plain succession, on the other hand, the pioneer stages, as a rule, are relatively xerophytic: that is, the succession is xerarch. Three more or less distinct stages in the succession may be distinguished: the gravel bar stage, the pioneer tree stage, and the edaphic climax forest.

The gravel bar association-type.—The pioneer association-type of gravel bars consists largely of the shrubs and herbaceous perennials listed as characteristic of boulder plains, most of which grow in greater profusion here than there. It also may include many species which are not prominent on boulder plains: such, for example, as *Alnus mollis* and *Diervilla Lonicera; Campanula* *rotundifolia, Anaphalis margaritacea,* and *Centaurea nigra.* The mosses, *Racomitrium canescens* and *Polytrichum piliferum,* frequently form a loose, discontinuous ground cover in protected spots; while species of *Cladonia* may also be present. Locally, wherever the soil is fairly moist, the early vegetation may include mesophytic species, such as *Clematis virginiana, Thalictrum polygamum,* and *Heracleum lanatum*—forerunners of subsequent stages in the succession.

The pioneer tree association-type.—Although the vegetation in the gravel bar stage of the succession is predominated by shrubby and herbaceous species, trees may be present from the outset. The balsam poplar, more than any other species, is preëminently the distinctive pioneer tree of gravelly or sandy flood plains, although it often shares this honor with the paper birch and white spruce (Fig. 21). The balsam poplar owes its prominence to its copious root system and exceptional ability to maintain itself on shifting alluvial soils, its tendency to reproduce and spread by means of root suckers, and its rapid rate of growth, which enables it to outstrip any chance competitors. In these respects it resembles its southern relative, the cottonwood (*Populus deltoides*), of which it may be regarded as an ecological counterpart. One frequently encounters on flood plains groves of good-sized balsam poplars, beneath which the more characteristic trees of the climax forest apparently are just beginning to establish themselves. But any of the climax trees may appear simultaneously with the poplar. On one small, treeless stretch of gravelly flood plain, for example, the writer noted seedlings of nearly every tree (all except white pine, hemlock, and red oak), which has been cited earlier as growing in the climax forest; also seedlings of bird cherry and choke cherry (*Prunus virginiana*). For the reasons suggested above, however, the poplar usually gains a temporary ascendancy over its competitors, thereby giving rise to a more or less distinct phase in the succession.

The edaphic climax forest.—Flood plain forests of the sort ordinarily associated with old-age rivers have been developed along some of the larger lowland streams, and in some cases the physiographic history of the areas which these occupy has probably been similar to that of flood plains as described in the preceding paragraphs. But in the most typical instances observed, such forests represent the culmination of hydrarch rather than xerarch successional series, and they will therefore be discussed later (p. 371), in connection with hydrarch successions.

The average climax forest of sandy flood plains along swift streams approximates closely the climatic climax forest-type of the region, differing from this chiefly in the presence, or more luxuriant development, of such species as *Ulmus americana* and *Fraxinus americana,* among the trees, and of various herbaceous plants, such as the following:

Osmunda Claytoniana	*Streptopus amplexifolius*
Polystichum Braunii	*Thalictrum polygamum*
Cinna latifolia	*Sanicula marilandica*
Trillium cernuum	*Osmorhiza divaricata*
Smilacina racemosa	*Pyrola asarifolia*
Listera convallarioides	*Solidago latifolia*

3. The Formation-types of Uplands along the Seacoast

a. INTRODUCTORY

Under this heading are included only those upland associations which are peculiar to habitats in the immediate proximity of the shore and whose ecological aspect is obviously correlated with this fact. The character of vegetation along the seacoast is influenced to a greater or less degree by wind, salt water, and physiographic agencies. The plant associations are best classified with reference to physiographic factors, as (*1*) Associations along Eroding Shores, and (*2*) Associations along Depositing Shores. As eroding shores are classed the sea bluffs and headlands which form such a striking topographic feature along much of the coastline. Depositing shores include the commonly encountered shingle beaches and the less frequently encountered sandy beaches and dunes.

In addition to the figures that accompany the description which follows, attention may be called in this connection to FIGS. 3, 6, 8, 15, 33, 38, 41.

b. THE ASSOCIATION-COMPLEXES OF SEA BLUFFS AND HEADLANDS

Association-types of rocky sea bluffs.—The application of the term sea bluff is here restricted to the more or less precipitous slopes which face directly on the shore and therefore are most exposed to the action of waves and spray (Fig. 3). Along such bluffs there is usually a pronounced zonational arrangement of plant associations. Between low and high tide levels, wherever the base of the bluffs is submerged, the rocks are usually plastered with sea-weeds, prominent among which are species of *Fucus* and *Ascophyllum*. Above high tide level is a zone of varying width in which, owing largely to the mechanical action of waves

Figure 22.—*Juniperus horizontalis* on sea bluff; Middle Head, Ingonish.

and ice, vegetation is absent. Higher up, and sometimes reaching to a height of thirty-five or forty feet, is a zone in which the vegetation consists largely of scattered halophytic crevice plants. The upper limits of this zone are presumably determined by the height of the waves in winter storms. The most abundant plant here is *Plantago decipiens,* along with which commonly grow *Solidago sempervirens* and *Sagina procumbens*—the latter, of course, hardly to be considered a typical halophyte. Other halophytic species which may inhabit crevices or ledges toward the upper edge of this zone and which, like the preceding, may also occur on low headlands far beyond the actual reach of the waves, are *Potentilla pacifica, Atriplex patula hastata,* and *Lathyrus maritimus.* The most characteristic plant on that part of a bluff which lies beyond the usual reach of the waves is the trailing juniper (*Juniperus horizontalis*), which commonly sprawls out here in great profusion (FIG. 22), and is only occasionally found in any other habitat. Commonly associated with this shrub is the crowberry (*Empetrum nigrum*) and frequently the low juniper (*Juniperus communis depressa*), while any of the other species to be cited presently as occurring on headlands may also grow in the crevices of precipitous, rocky sea bluffs.

FIGURE 23.—*Alnus mollis* and *Picea canadensis* on sea bluff of clayey drift; Cape North.

Association-types of sea bluffs in uncompacted rock.—So long as a sea bluff of clay or glacial drift continues to be acted on, from time to time, by the waves, vegetation is scantily developed. Just as along the shores of the Great Lakes (see Cowles '01, pp. 164–167), about the only plants present here are xerophytic annuals and "slump plants" (i. e., plants which have slid down from the crest of the bluff). As soon, however, as there is a cessation or diminution in the erosive activity of the waves, which may be brought about by the formation of a shingle beach between the bluff and the sea or through the accumulation along the base of the bluff of boulders derived by erosion from the bluff itself, a plant cover is rapidly developed. *Equisetum arvense* and *Agrostis alba maritima* frequently, and *Elymus arenarius* occasionally are conspicuous pioneers, but for the most part the pioneer species here are largely weeds and slump plants. Sometimes a grassy sod is formed, but more commonly *Alnus mollis* (Fig. 23) comes in along with the grasses and forms a dense thicket. Sooner or later, trees appear, mostly white spruce and paper birch, and these may supersede the alders, forming a low, scrubby forest along the bluff. The trees often exhibit the same one-sided habit as those on headlands.

Figure 24.—Exposed rocky headland at White Point; scrubby forests, mostly white spruce; in right foreground a characteristically one-sided spruce. Photograph by Dr. L. H. Harvey.

Owing to the abundance of seepage water, soil conditions locally, especially along clay bluffs, may be unusually favorable for plants, and in such places it is a common thing to find the vegetation made up in large part of species which are ordinarily associated with swamps or flood plains: such, for example, as *Alnus incana, Calamagrostis canadensis, Juncus effusus* and various sedges, *Heracleum lanatum, Eupatorum purpureum,* and *Aster puniceus.* Associations of this sort, though mentioned here for convenience, should naturally be classed under the hydrarch series.

Association-types of exposed headlands.—Bleak headlands like the one pictured in Fig. 24 are a prominent feature of the coast, especially northward. In the vicinity of Cape North and in other very exposed situations the mountain sides in some places are devoid of forest from sea level to a height of fully a thousand feet. Without doubt many of these areas were formerly wooded and their barren aspect has been induced primarily through the action of fire or human activity; but the continuance of this condition is attributable very largely to the retarding effect on succession of exposure to strong winds, frequently laden with

FIGURE 25.—Detail view of vegetation on exposed headland shown in FIG. 24; see text. Photograph by Dr. L. H. Harvey.

salt spray. Wherever, on headlands of the sort pictured, there is a depression which affords shelter, scrubby forests are encountered, while scattered trees are commonly present in the barren area itself. These latter, as well as many of the trees which fringe the lower margin of the forest farther up the slope, are usually unsymmetrical in shape and dwarfed in size. Frequently the living part of the crown is wholly on the landward side of the tree.

In some cases the predominant type of vegetation on these headlands is grass: species such as *Danthonia spicata, Festuca rubra,* and *Deschampsia flexuosa.* But more often (FIG. 25) the ground is covered very largely with a dense tangle of low, sprawling shrubs which are seldom more than a foot high. Perhaps the most characteristic, and commonly the predominant shrub is the crowberry, but associated with this and often equally abundant may be *Juniperus communis depressa, Vaccinium Vitis-Idaea, V. pennsylvanicum,* and occasionally *Juniperus horizontalis.* Other species commonly encountered on bleak, exposed headlands, but not yet mentioned in this connection, are listed below.

Botrychium ramosum	*Cornus canadensis*
Smilacina stellata	*Gaultheria procumbens*
Iris setosa canadensis	*Halenia deflexa*
Myrica carolinensis	*Euphrasia Randii*
Arenaria lateriflora	*Euphrasia Randii Farlowii*
Fragaria virginiana	*Campanula rotundifolia*
Potentilla tridentata	*Solidago puberula*
Lathyrus palustris	*Aster novi-belgii*
Ligusticum scothicum	

To these should be added *Cladonia* sp., *Polytrichum piliferum,* and *Polytrichum juniperinum,* which frequently carpet the bare soil where other vegetation is absent.

c. THE ASSOCIATION-COMPLEXES OF BEACHES AND DUNES

Association-types of shingle beaches.—Even along parts of the coast which are exposed to active erosion, at least where the eroding land mass consists of glacial drift, a rocky, beach-like strip commonly intervenes between the foot of the bluff and the water's edge. Such deposits may be composed in part of wave-washed material, but as a rule they are largely made up of boulders and cobbles of all sizes which have been washed out of the bluff itself. The analogy with the boulder plain is obvious. All degrees of transition exist between such deposits, which may be virtually destitute of vegetation, and the typical shingle beaches, which constitute a familiar feature along the shore. These latter commonly form a narrow fringe along the seaward edge of the land, but wherever there are reëntrants in the coast line, barriers and spits tend to be developed. St. Ann's Bay and Ingonish Harbor are nearly closed in by narrow, rocky spits, and there are similar spits at the mouth of the Barrasois River and Indian Brook. Near the Barrasois and at South Bay, Ingonish (Fig. 42), lakes of considerable size have been cut off from the sea by barriers, the one at the latter place being fresh and several feet higher than high tide level. Small ponds and lagoons, cut off by barriers, are of frequent occurrence (Fig. 26).

In a general way, a shingle beach, like a sandy beach, is subdivided into three more or less distinct zones which, following the classification of Cowles ('01, p. 170), may be termed respectively the lower, middle, and upper beaches (Fig. 27). The lower

Figure 26.—Shingle beach enclosing small fresh pond; scrubby spruces, etc. in foreground, habit largely the result of grazing; in background, second growth spruce, etc.; Wreck Cove. Photograph by Dr. L. H. Harvey.

beach is the part submerged by ordinary high tides. It ranges in width from a few yards to more than a hundred feet. The deposit here (at least in summer) is usually gravelly or sandy toward its lower limit, becoming pebbly above and gradually merging with the shingle. Except for the occasional presence near low tide level of *Zostera marina* and brown algae such as *Fucus,* vegetation is absent. The middle beach comprises that part of the beach immediately above the lower beach which is swept by the waves of winter storms or is covered over by ice in winter. Like the lower beach, it varies greatly in width. The deposit here consists almost wholly of water-rounded cobbles and pebbles, ranging from the size of hens' eggs up to six inches or more in diameter—the type of accumulation commonly referred to as *Shingle.* Vegetation is sparse and xerophytic, practically the only plants ordinarily present being the annual, *Cakile edentula,* and the herbaceous perennials, *Lathyrus maritimus* and *Mertensia maritima.* The last-named species, the so-called sea lungwort, with its glaucous foliage and rose-pink or blue flowers, and growing in depressed, circular patches two or

FIGURE 27.—Shingle beach near mouth of Barrasois River; forest of white spruce, etc. along landward edge.

three feet in diameter, is by far the most striking of the beach plants. The upper beach includes that part of the beach which, except during unusual storms, when parts or all of it may be wave swept, lies beyond the reach of the waves at all seasons of the year. Its crest is commonly more than three and occasionally as much as six or eight feet higher than ordinary high tide level. Stones are cast up on these higher beaches only by exceptionally severe storms, perhaps years apart. Like the middle beach, the upper beach, especially in its more exposed parts, may be little more than a great stone heap on which, except for a frequently luxuriant growth of lithophytic lichens, vegetation is scantily developed. Common lichens on the shingle are *Rhizocarpon geographicum* (crustose), a form which is very conspicuous by reason of its bright, greenish yellow color, and *Lecidea tenebrosa* Flot. (crustose) and *Gyrophora hyperborea* (foliose), both of which are blackish in color. As a rule, however, even in such places, there is more or less gravel and coarse sand underneath the stony surface layer, while in the older parts of the upper beach the shingle in some cases (FIG. 28) has been covered over

FIGURE 28.—Spit near mouth of Barrasois River; to right, a typical shingle beach; to left, a mixture of sand and shingle, overgrown with *Ammophila*, white spruce, etc.

by sand to such an extent as to produce conditions approximating those to be described presently as characteristic of sandy beaches. All intergradations may be found on lea slopes between rocky shingle at one extreme and sandy beach at the other.

On the upper beach, soil conditions usually favor the development of vegetation, and there may be a succession of plant associations leading to the formation of a scrubby forest. The pioneer plants here are predominantly herbaceous, and various introduced weeds figure prominently. Indeed, almost no other natural habitat supports a greater variety of weeds than shingle beaches. In this connection it may perhaps be remarked that there seems little question that in former days, in so far as they were then represented in this region, the majority of the plants popularly classed as weeds, and which to-day thrive in a variety of open situations created by man's activity, were restricted to situations such as gravel slides; boulder plains, sandy flood plains and rocky banks along streams; and sea beaches. Excluded through competition from situations edaphically more favorable to them, the weeds, which as a group are essentially pioneers, have always flourished in these open situations.

In addition to the weeds, the grasses are well represented on the upper beach by such species as *Ammophila arenaria, Danthonia spicata, Poa compressa, Poa pratensis, Festuca rubra,* and occasionally *Elymus arenarius,* while the sedge, *Carex silicea,* is seldom absent. Other common herbaceous species here are *Fragaria virginiana, Potentilla tridentata, Geranium Robertianum, Oenothera muricata, Ligusticum scothicum, Campanula rotundifolia,* and *Anaphalis margaritacea.* Various xerophytic mosses, notably *Ceratodon purpureus, Racomitrium canescens, Brachythecium albicans, Polytrichum juniperinum,* and *Polytrichum piliferum,* thrive in open, gravelly soils, while the foliose lichens, *Cladonia rangiferina, C. sylvatica,* and *Stereocaulon coralloides* may also be represented. But the vascular vegetation is by no means restricted to herbaceous forms, for even on rocky and quite exposed parts of the beach there usually are scattered shrubs and trees. In stony situations the plants may secure a foothold in patches of gravel between the cobbles, but very frequently a favorable substratum is created by the decomposition of logs which have been cast up by storms. Of the shrubs, *Juniperus communis depressa, Myrica carolinensis, Rubus idaeus canadensis, Empetrum nigrum, Gaylussacia baccata,* and *Vaccinium pennsylvanicum* are quite characteristic of shingle beaches, and *Vaccinium Vitis-Idaea* grows well in grassy, gravelly or sandy areas. The commonest tree is the white spruce, though the balsam fir is scarcely less frequent. Both of these trees often exhibit a weather-beaten aspect, but this is especially true of the balsam fir. On the beach at Englishtown (Fig. 29) grow specimens of the latter which measure less than two feet in height but sprawl out on the ground over a radius of more than six feet. Their low stature is due to the repeated killing off of the leader, and this in turn is probably attributable to the erosive effect of wind-driven snow in winter, a phenomenon which will be referred to again in connection with the vegetation of the barrens.

Wherever a shingle beach borders on the mainland, there is a tendency for the forests of the adjoining upland to encroach on the beach (FIG. 27), and even on barriers and spits scrubby forests are frequently developed on the older parts of the upper beach (FIG. 29), usually on lea slopes where there is optimum

FIGURE 29.—Stunted balsam firs (foreground) and scrubby forest (left background) on shingle beach; St. Ann's Bay; compare FIG. 33.

protection from wind and wave. Such forests are quite open, and are composed almost wholly of white spruce and balsam fir, which seldom reach here a height of more than twenty-five feet. In the open spaces between the trees grow in more or less profusion various of the shrubs and herbaceous plants which have been listed as occurring on the upper beach, while certain less xerophytic species, which have been cited earlier as characteristic of the pioneer forest stage in the ordinary upland series, are found here also. Common bryophytes in the shade of the trees are *Ptilidium ciliare, Dicranum Bonjeanii, Dicranum undulatum,* and *Hypnum Schreberi.* On the whole, the aspect of such a forest is quite xerophytic.

Association-types of sandy beaches and dunes.—Aside from their frequent association with shingle beaches, to which reference has been made above, broad strips of sandy beach fringe the mainland here and there in somewhat protected situations along the coast, as at North Bay and South Bay, Ingonish. Frequently such beaches overlie deposits of shingle and during

FIGURE 30.—Sand spit at North Pond, Aspy Bay; *Ammophila,* etc.; in the distance, Cape North.

heavy storms the sand may be completely swept away from the more exposed parts of the beach. The finest display of sandy beach along the coast of northern Cape Breton is seen at Aspy Bay, where North Pond is nearly cut off from the ocean by a sand spit (FIG. 30), which is fully three miles long and averages perhaps a hundred yards in width. South Pond similarly is almost shut in by a shorter but much broader spit, on which have been built up a fine series of sand dunes.

As in the case of shingle beaches, the lower beach here is practically plantless, while the middle beach is populated by a scattered growth of annual and perennial herbaceous plants which maintain a precarious foothold on the shifting sand. The number of species in this latter zone is small, the only forms noted here being *Ammophila arenaria, Salsola Kali, Arenaria peploides, Cakile edentula, Lathyrus maritimus, Euphorbia polygonifolia,* and *Mertensia maritima.* The lower and middle beaches vary in width. On the South Pond spit, each is about 150 feet wide; but ordinarily they are much narrower. The

FIGURE 31.—Sand dunes with forest of white spruce, etc.; South Pond, Aspy Bay.

upper beach likewise varies in width; at South Pond it is fully 250 feet wide, but this is exceptional. At both North and South Ponds the crest of the beach proper is perhaps four feet above high water mark. At North Pond the upper beach is covered by a broad, low dune which in places rises to a height of eight or ten feet above high water mark. The plant cover here consists mainly of a rank, open growth of *Ammophila,* with which are associated *Lathyrus maritimus* and, locally, *Elymus arenarius.* Over limited areas on the lea slope, the shrubs, *Myrica carolinensis* and *Rosa virginiana,* have replaced the *Ammophila* association. In one place a scrubby forest has been buried by the sand, but at the present time trees are scarce and of merely sporadic occurrence.

The South Bay spit with its dunes (Fig. 31), from the standpoint of physiographic ecology, affords in itself a study of exceptional interest, and has already been written up in some detail by Dr. Harvey ('18). In crossing the spit from the seaward margin on the east to the "pond," which is between one and two miles wide, one encounters in order (*1*) the lower beach, (*2*) the middle beach, (*3*) the upper beach, and (*4*) the salt meadows and marshes which border the spit on its western side. Along the seaward edge of the broad upper beach is a row, sometimes double but mainly single, of sand-dunes, mostly less than six feet in height, but in one locality rising to fully fifteen feet. Some at least of the dunes have originated in moist depressions, or "pans," in which grow *Juncus balticus littoralis* and *Iris versicolor*. On many of the lower dunes, as might be expected, the sand-reed (*Ammophila*) is the predominant plant, fulfilling in connection with dune-formation the twofold function of (*1*) breaking the force of the wind and causing it to drop part of its burden of sand, and (*2*) binding together and holding, by means of its copious, slender roots, the sand which thus accumulates. More often than not, however (Fig. 32), the sand-reed is absent and in its place occurs a luxuriant growth of wire-grass (*Poa compressa*), which seems fully competent to carry out the functions elsewhere performed by the sand-reed.

Figure 32.—Low dunes at South Pond, Aspy Bay; in foreground, *Poa compressa* acting as a sand-binder.

On the lea slopes of these low dunes, trees germinate, predominantly white spruce, but some balsam fir. The reciprocal relation between these trees and the dunes is rather striking. Germinating in the first place in the shelter of the low dunes, as the trees increase in size they afford an effective wind-break, which in turn is largely responsible for the further increase in the height of the dunes. The bases of the trees may be covered to a depth of six feet or more by sand, but both the spruce and the balsam are able to accommodate themselves to the changed conditions through the development of adventitious roots from the buried part of the trunk. The highest dunes are covered at the crest with good-sized trees which have thus been partially buried.

The dunes very likely would attain a greater height here, were it not for the fact that they are exposed to winds from two directions; the westerly winds which sweep across the pond tend to check the growth of the dunes, which is due mainly to the easterly winds from off the ocean.

In the lea of the dunes, between them and the salt meadows, is a broad stretch of low, sandy "back beach," the surface of which is rolling, and is covered partly by an open coniferous forest, partly by grassy areas with scattered trees. Below is given a list of the vascular plants, exclusive of certain weeds, which occur more or less abundantly in these open tracts.

Juniperus communis depressa
Panicum implicatum
Agrostis alba maritima
Danthonia spicata
Festuca rubra
Arenaria lateriflora
Fragaria virginiana
Potentilla tridentata
Lechea intermedia juniperina
Vaccinium Vitis-Idaea
Campanula rotundifolia
Leontodon autumnalis

The grassy sward is nowhere very close, but the sand is nearly everywhere hidden by the two mosses, *Tortula ruralis* and *Dicranum spurium,* and species of *Cladonia.* In among the trees occur a number of species which were not noted in the more open situations, or only rarely so, such as *Maianthemum canadense, Trientalis americana, Rhus Toxicodendron, Ribes lacustre,* and the mosses, *Dicranum undulatum* and *Hypnum Schreberi.* The branches of some of the white spruces support the most luxuriant growth of the dwarf mistletoe (*Arceuthobium pusillum*) that the writer has ever seen.

B. Secondary Formations of the Xerarch Series

Formation-types Resulting Primarily from Human Activity

a. association-complexes due to cultivation

Notwithstanding the comparative recency with which this country was settled, deserted farms are a familiar sight, and abandoned farmlands in all stages of revegetation are encountered. It is only through constant grazing and cutting, or repeated mowing, that pastures and meadows can be kept

Figure 33.—Cultivated fields, abandoned pastures, and coniferous second growth forests along St. Ann's Bay; in the left background, the shingle beach which nearly encloses St. Ann's Harbor (compare Fig. 29).

open, for the rapidity with which a neglected field reverts to woodland is even greater here than in southern New England. The association-types which arise in the course of secondary successions subsequent upon cultivation may be considered under two heads: (*1*) the association-types of fallow fields, and (*2*) the association-types of abandoned pastures.

The following figures, in addition to those introduced herewith, illustrate secondary formations: Figs. 3, 9, 15, 24, 41, 42, 46.

The association-types of fallow fields.—For several years after a plowed field has been abandoned its vegetation may consist largely of weeds. Common species in such a habitat are:

Rumex Acetosella	*Solidago graminifolia*
Spergula arvensis	*Achillea Millefolium*
Raphanus Raphanistrum	*Chrysanthemum Leucanthemum*
Prunella vulgaris	*Leontodon autumnalis*
Galeopsis Tetrahit	*Taraxacum officinale*
Plantago major	*Cirsium arvense*

In the early stages of reclamation, so long as the plants are scattered and the vegetation relatively open, both annual and perennial species may be about equally well represented. But as the ground comes to be more densely populated, most of the annuals are crowded out and the plant cover comes to consist almost entirely of species which are perennial. Various grasses, especially *Danthonia spicata* and *Poa pratensis,* appear rather early in the succession, and as time goes on these come to comprise a more and more important element. Sooner or later a continuous mat of vegetation is developed, in which the grasses are usually the predominant plants, and the formerly bare soil becomes covered over by a thin turf. Species of *Cladonia* and *Polytrichum* also commonly play an important part in the development of the turf. With the formation of a grassy sward, the conditions come to approximate those of pastures. A few shrubs and trees may have appeared, but on the whole the succession beyond this point is essentially the same as that in abandoned fields, which is discussed in the following paragraphs.

The association-types of abandoned fields.—The predominant plants in open fields are the grasses. In dry pastures *Danthonia spicata* and *Poa pratensis* are ordinarily the most abundant species, but growing along with these and contributing to the formation of the thin sward may be various perennial weeds, particularly any of those mentioned in the second column of the preceding list as characteristic of fallow fields, together with other herbaceous perennials such as *Fragaria virginiana, Trifolium repens,* and *Antennaria neodioica.* Species of *Cladonia* and *Polytrichum* also are usually present here; sometimes the ground cover consists almost wholly of *Polytrichum* and *Leontodon.*

The general aspect of the vegetation, as just described, is xerophytic. Under favorable edaphic conditions, however, it may be much more mesophytic. In moist meadows the grass forms a denser growth and is made up largely of species such as *Poa pratensis, Agrostis alba,* and *Anthoxanthum odoratum.* Common associates of the grasses here are *Euphrasia purpurea* Reeks and *Rhinanthus Crista-galli.* The *Euphrasia* occupies much the same ecological position in the fields of northern Cape Breton as does *Houstonia caerulea* in those of southern New

FIGURE 34.—Abandoned field with white spruce and *Dicksonia;* Barrasois.

England. Any of the perennial herbs referred to above may grow in moist meadows, but here, in addition, pronounced mesophytes, such as the orchids, *Habenaria clavellata, H. lacera,* and *H. psycodes,* are also frequent.

Whenever a field is permitted to run wild, *Dicksonia punctilobula* (FIG. 34), *Pteris aquilina, Anaphalis margaritacea,* and other herbaceous perennials which grazing or haying have held in check tend to assert themselves, while various shrubs may also become conspicuous. Among the latter, *Juniperus communis depressa, Rubus idaeus canadensis* and *Vaccinium pennsyl-*

vanicum are common in neglected pastures, while *Salix humilis, Alnus mollis* and *Spiraea latifolia* are frequently prominent. But while *Dicksonia* and other herbs often develop luxuriantly, and while shrubs may sometimes come to predominate over considerable areas, on the whole there is no sharply defined intermediate successional stage between grassland and coniferous forest. As a matter of fact, trees are present from the outset.

FIGURE 35.—Reproduction of balsam fir and spruce in abandoned field, Barrasois.

A close examination of almost any grassy field will usually reveal the presence of numerous young seedling coniferous trees (FIG. 35). In the face of repeated mowing these trees will persist for several years and are ready, whenever the opportunity offers, to grow up and to more or less completely occupy the ground. Grazing may check tree reproduction but seldom prohibits it entirely. In one field where sheep are pastured much of the year, the writer counted as many as twelve seedling white spruces to the square yard. The browsing of cattle may check their growth and is responsible for various grotesque tree shapes, but only frequent cutting will prevent trees from eventually gaining supremacy. The speed with which grassland may become superseded by woodland is suggested by the conditions observed in two quadrats (10 meters, 32.8 feet square), which were located in fields that had been neglected for twelve or fifteen years. In one case, counting only specimens which were more than a foot high, there were ninety trees in the quadrat, ranging up to twelve feet in height and thirteen years in age. Of these trees, thirty-four were white spruce, twenty-seven balsam fir, twenty-seven paper birch, and two white pine. In another similar quadrat there were fully five hundred trees, dead or alive, ranging up to fifteen feet in height and averaging between eight and fifteen years in age. In this case, the trees without exception were white spruce. These quadrats illustrate the varying composition which an old field woodland may possess. In some cases there will be nearly pure stands of white spruce, in others intimate admixtures of this tree with black spruce, balsam fir, and paper birch. In the vicinity of Baddeck, and in a few other localities noted, the tamarack, in many cases, rivals the white spruce for the position of prominence in abandoned pastures. The local frequency of the tamarack, as already suggested, is attributable, without much question, to soil conditions: indeed, it seems quite possible that the local distribution of this tree might prove of value as an indicator of the capabilities of land for crop production. It seems quite probable that variations in the composition of old field woodlands can be correlated still further with local differences in soil, etc., although, so far as the observations of the writer have extended, the variations might well be explained, in large measure at any rate, by the proximity of seed trees and the fortuitous distribution of seed.

The changes which accompany the development of woodlands in old fields can best be brought out by a specific illustration: a series of pastures along the Barrasois River which have been abandoned at different dates. The vegetation of the pastures themselves is essentially as described above. The pioneer trees are mostly white spruce. These germinate prolifically, especially in places where there is a carpet of *Polytrichum*. The moss carpet apparently furnishes an ideal seed bed, since in situations where it is absent reproduction is noticeably sparser. As the spruces mature, forming first a rather open grove (Fig. 36) and later a closed forest, a sequence of changes may ensue similar to what has been described in connection with the later phases of the rock outcrop succession. By the time the grove phase has been attained, much of the pasture vegetation has vanished. In its place, in the semi-shaded, narrow lanes (or spaces) between the trees (or groups of trees), is a more or less continuous bed of moss, growing on which may be found the pioneer representatives of various woodland species of plants. The moss carpet at first may consist of *Polytrichum commune,* but soon this is

FIGURE 36.—Grove of white spruce in former pasture; Barrasois. Photograph by Dr. L. H. Harvey.

largely superseded by *Hypnum Schreberi.* Among the herbaceous woodland pioneers noted here are *Lycopodium complanatum, L. clavatum, Maianthemum canadense, Cornus canadensis, Viola incognita, Epigaea repens, Linnaea borealis americana,* and *Trientalis americana.* Small white spruce seedlings grow scattered over the moss carpet, but, practically speaking, white spruce reproduction has come to a standstill, for few of these seedlings are destined to mature.

In this connection, there is one feature of a young spruce forest that demands special comment. On the ground beneath the trees in such a forest there may be no vegetation whatever, but only a dry layer of dead spruce needles, comprising what the forester familiarly refers to as "duff." The absence here of plants does not seem to be attributable directly to insufficient light. In remarking recently on this same phenomenon, Moore ('17, pp. 156, 157) has concluded that the lack of vegetation is due to the dryness of the soil which results from the interception of the precipitation by the crowns of the trees. The writer had already arrived at a conclusion somewhat as follows. During the development of a group of young spruces in the open, at first there is ample light for all. But later on, in the competition for light which ensues as they become larger, many of the trees are killed. The accumulation on the ground beneath, both of the needles which fall from these dead trees and of needles derived from the shaded branches of the living trees, may take place so rapidly that the ground vegetation is buried. The formation of this thick, loose layer of dry needles not only wipes out the original ground cover, but, because of its dryness, prevents any new vegetation from getting a start. This process, initiated while the tree growth is still open, continues during the transition from the grove to the forest stage in the succession. A layer of needles several inches thick may collect on the forest floor, and all the mosses and herbaceous plants, as well as the seedling trees described in the preceding paragraph, may be exterminated. The extreme paucity of vegetation on the forest floor which results in this manner is a very characteristic feature of young coniferous forests. Later on, as the forest matures, the trees becoming greatly decreased in number by the constant competition for light, and in consequence becoming more widely spaced, the rate of leaf-fall gradually slackens so that a certain degree of equilibrium is brought about on the forest floor. It then becomes possible for a new ground cover to establish itself: *Polytrichum commune* and *Hypnum Schreberi* reappear, followed shortly by *Hylocomium splendens,* and a moss carpet is gradually reëstablished, on which woodland herbs and shrubs, together with seedlings of balsam fir and other trees of the coniferous forest association-type become increasingly abundant. The history of the forest beyond the grove stage of the succession is practically identical with what has been described in connection with primary successions.

b. ASSOCIATION-COMPLEXES DUE TO FIRE

Fire, like cultivation, destroys the original vegetation and causes the institution of new successional series. According to the completeness of the devastation, particularly as it affects the humus layer with its subterranean plant organs and its micro-organisms, broadly speaking, two lines of succession may be distinguished: one where the humus has escaped serious injury, the other where the humus has been destroyed. Between these there of course are intermediate possibilities.

Humus little injured.—Let it be assumed that previous to the conflagration a burned area has supported a forest of the climax type. Aside from the annihilation of much of the antecedent vegetation, the most obvious immediate effect of fire is the removal of the forest cover and the consequent increased illumination of the forest floor. The revegetation of such an area is destined to be accomplished partly through the agency of plants which in various ways have survived the fire, partly through the invasion of plants from other sources. Almost the first after-effect of the fire is seen in the rapid spread of certain herbaceous species which were only sparingly represented in the original forest, but which are able to flourish in the new environment. *Cornus canadensis* perhaps nowhere develops more luxuriantly than in burned areas, while *Linnaea borealis americana* and *Maianthemum canadense* also thrive here. Of the shrubs and small trees in the burned forest, *Corylus rostrata, Acer spicatum* and *Viburnum cassinoides* frequently survive. The local herbaceous element in the flora may predominate for a longer or shorter period, but it is soon augmented by an extraneous element in which the following species are usually conspicuous: *Lycopodium clavatum* and *Gaultheria procumbens; Solidago bicolor* and *S. macrophylla; Pteris aquilina* and the "fire-weeds," *Epilobium angustifolium* and *Anaphalis margaritacea,* which frequently form a rank growth; and *Rubus idaeus canadensis,* which within a few years may produce an almost impenetrable tangle over the entire area.

In the reëstablishment of forests in burned areas of this sort, the paper birch, as elsewhere in the northwoods, is everywhere the conspicuous pioneer. This tree, it will be recalled, is sparingly represented in the regional climax forest. After a burn it reproduces rapidly, partly by means of coppice shoots from stumps which have survived the fire, partly from seed, and with its rapid rate of growth it quickly gains the ascendancy over other trees in the rising forest. Red maple also frequently plays an active rôle in reforestation, reproducing in much the same manner as the birch; while the bird cherry and any of the poplars may be present in greater or less abundance. A point of interest, to be emphasized in this connection, is that the balsam fir, with the spruces, may appear at a very early stage

FIGURE 37.—Succession after a burn; balsam fir coming in under paper birch; northwestern Maine.

in the succession: in fact, their seedlings may be present from the outset. But, on account of their relatively slow growth in the shade cast by the birch canopy, the conifers continue to occupy a position of subordinate importance for many years (FIG. 37). By the time a hundred years has elapsed, however, a marked change in the character of the forest has taken place; for by this time the balsam fir has usually become the predominant tree. This latter phase in the succession is well illustrated by an old burn forest near Indian Brook. Here the bulk of the mature stand consists of balsam fir intermixed with frequent white spruces, scarcely any of the balsams being more than ten inches in diameter. Paper birch is rarely present in the younger growth, but is represented abundantly by scattered older specimens ranging up to a foot and a half in diameter, while the ground beneath is strewn with the remains of fallen trees. Large red maples are frequent and one large hemlock with a healed fire scar was noted, obviously a relict of the former forest.

The ultimate association-type of the burn succession is a forest of the regional climax type, provided edaphic conditions

FIGURE 38.—View along coast north of Neil's Harbor: barrens and second growth forest, mostly white spruce; aspect largely the result of repeated burning. Photograph by Dr. L. H. Harvey.

are favorable to its development. Indeed, very often the beech and others of the climax trees beside those already mentioned may appear early in the series, arising either from coppice sprouts or from seed. It seems hardly necessary to describe the changes in the undergrowth which accompany the development of the forest.

Humus destroyed.—There are extensive tracts of land along the eastern coast of northern Cape Breton, particularly between North Bay, Ingonish and Aspy Bay (FIG. 38), which it is presumed were formerly covered, very largely at any rate, with deciduous forests, but which have suffered so severely from fires that at one time or another not only the greater part of the vegetation, but most of the humus as well has been consumed. In areas of this sort succession must start all over again from near the bottom and a sequence of stages similar to what has been described in primary successional series may be observed. To be sure, succession in an area which has been denuded by fire differs in certain respects from a primary succession, owing chiefly to the fact that even repeated fires fail to completely annihilate all the previously existing humus and plant life, and

Figure 39.—White spruce reproduction in an area which has been repeatedly cut and burned; South Bay, Ingonish.

that the relicts which have thus survived may play an important part in the succession. But it is hardly worth while to attempt to depict the stages in detail. In general it may be stated that, just as in the case of primary successions, there is a marked variation in the nature of the primitive associations, due to local differences in the nature of the substratum, etc., but that all successional series tend to merge in the formation of forest.

Abundance of white spruce the result of fire and cultivation.— At the present day, throughout the region of deciduous forests, wherever tracts of land have been cultivated and then abandoned or have been ravaged by repeated fires, white spruce, with local exceptions, is everywhere the most abundant tree of second growth forests. The explanation of this fact is obvious. The white spruce is essentially a pioneer. It seeds prolifically and rapidly colonizes open grounds of almost any description (Fig. 39). The effect of cultivation and fire in destroying the seedlings of balsam fir and other trees, which otherwise might have dominated, enables the spruce, with its capacity for rapid reproduction in the open, to establish itself and to make head-

Figure 40.—Blueberry barren near Frizzleton.

way which otherwise would be impossible. The common practice of burning over woodlots in order to keep them open for pasturage or for some other reason, naturally favors the spruce. In brief, the combined effect of cultivation and fire is to arrest the succession, so that it rarely progresses beyond the pioneer forest stage.

Blueberry barrens.—Among the most unique features of the interior plateau of northern Cape Breton are the Barrens. These natural barrens, which will be described later, should not be confused with the barrens of the lowlands (Fig. 40), which are the result of repeated fires, usually set intentionally every few years in the interest of the blueberry crop. Extensive blueberry barrens of this sort are found in the Margaree district, where they may occupy hundreds of acres. The predominant plants in such tracts are the blueberries, *Vaccinium pennsylvanicum* and *V. canadense,* with which, though far less abundant, are associated other ericaceous shrubs, such as *Kalmia angustifolia, Vaccinium Vitis-Idaea, Gaultheria procumbens,* and *Ledum groenlandicum.* Various herbaceous plants occupy a prominent position, notably *Pteris aquilina, Danthonia spicata* and *Aster multiflorus,* while *Cladonia rangiferina* and the mosses, *Polytrichum commune, P. juniperinum,* and *Hypnum Schreberi,* are common. The ecological aspect is that of a heath, though there are scattered trees, mainly tamarack and white spruce. The balsam fir is virtually absent.

Left to itself, such an area becomes forested within a few years. The process of reclamation is graphically illustrated by one area examined, which adjoins a large heath, but is separated from it by a highway that has acted as a "fire line." This area is now occupied by an open forest of tamarack and white spruce. The balsam fir is absent from among the larger trees, but is abundantly represented in the young growth. The heaths are present in greatly reduced abundance, as compared with the barren area across the road, and the moss carpet has become correspondingly more luxuriant.

c. ASSOCIATION-COMPLEXES DUE TO LOGGING

The indiscriminate removal of the merchantable timber in a climax forest by logging usually has little effect on the future composition of the forest, provided the area escapes being burned over. Some trees, notably the paper birch and balsam fir, tend to become somewhat more abundant here, and frequently pioneer species such as the aspens are able to establish themselves temporarily in cut-over tracts. But, on the whole, the forest may be said to regenerate itself through the younger generation of trees which was present in the original forest. Where a forest is lumbered *discriminately,* as is frequently done for fir and spruce alone, it is of course obvious that the detailed physiognomy of the forest may be quite appreciably altered. Where the removal of the timber is followed by burning, most of the younger trees are destroyed and complete regeneration is impossible. This latter point is well illustrated by conditions near an old settlement along Indian Brook, which has been deserted for many years. The climax forest was cut over in two adjoining tracts, one of which was afterward burned over, the other not. To-day, perhaps forty years after cutting, the unburned area is covered by a forest of yellow birch, sugar maple, and other climax trees, with scattered specimens of paper birch and large-toothed aspen (*Populus grandidentata*). The burned area, on the other hand, supports an almost pure forest of paper birch. In both forests the balsam fir is the most conspicuous undertree.

C. Primary Formations of the Hydrarch Series

1. The Formation-types of Lakes and Ponds Inland

a. introductory

The ecological relationship of lakes and swamps.—For purposes of convenience, lakes and swamps are here treated under separate headings, but, broadly speaking, they belong to the same family and there is no sharp dividing line between them. Through the activity of various agencies a lake or pond may become filled in and converted into a swamp. The manner in which this transformation may be accomplished by plants, together with the changes in vegetation which accompany the process, is outlined in the following paragraphs, quoted, with slight alterations, from an earlier paper by the writer ('15, pp. 175–178):

The important rôle commonly played by plants in the conversion of lakes into swamps has long been recognized. When the plants in a lake die, their remains sink to the bottom where, because of insufficient oxidation, the vegetable débris is only partially decomposed. In this way there collects on the floor of the lake a layer of vegetable muck, or peat; and through the continued addition of fresh layers the deposit is gradually thickened and built upward. This constructive process may go on until ultimately the surface of the deposit reaches the level of the water, when the lake gives way to a swamp. But the rate at which the substratum is built up and the length of time which elapses before it reaches the water level varies greatly in different parts of a lake. Plants grow most luxuriantly in shallow water; they may be practically absent from the deeper areas. It follows, therefore, that the accumulation of muck or peat proceeds much more rapidly in shallow than in deep water—so much so, in fact, that the shoreward parts of a lake may have become completely filled in before any appreciable accumulation has taken place in the deeper areas. The filling in of deep lakes usually proceeds centripetally. This is due to the fact that the shoreward zones of vegetation, in consequence of their more vigorous growth, exhibit a tendency to push outward into deeper water. Where this tendency is pronounced, the shoal water zones may completely override the deeper water zones, at the same time causing the lakeward slope of the deposit to become much steeper. The filling in of the deeper parts of a lake may also be effected to a varying degree by the accumulation of loose débris from the adjoining shallows or by the deposition of sediment in flood time, while various plankton forms may contribute in a small measure to the deposit.

Coincident with the upbuilding of the substratum through the deposition of muck or peat, as outlined in the preceding paragraph, transformations occur in the character of the vegetation growing on the lake's bottom. For, as the depth of the water diminishes, it becomes possible for plants to develop which were unable to grow in the deeper water. And as these shallow water plants increase in number and abundance, they may crowd out and eventually replace the deeper water species. Thus there may follow one another a series of plant associations, each one of which, by helping to raise the bottom of the lake to a higher level, prepares the way for less hydrophytic associations, but at the same time, by so doing, brings about its own extermination.

It is a familiar fact that the plants which fringe the edges of so many lakes are commonly massed in more or less definite bands or zones that tend to be concentric with respect to the deeper parts of the lake. The floristic composition of these zones in any given lake is determined largely by the ecological requirements of the various species of plants which happen to be present, in relation to the depth and clearness of the water . . . Reference has already been made to the succession of plant associations which accompanies the building up of the lake bottom. It has been found that this dynamic Vertical Succession corresponds closely with the apparently static Horizontal Zonation just outlined . . . . . This general coördination between the contemporaneous horizontal sequence of zones and the historical or vertical order of succession has been verified repeatedly by the stratification of plant remains observed in peat deposits, and is of great assistance in reconstructing the past or predicting the future course of events in any specific locality.

Of course, not all swamps have originated in the manner just described (see further under head of swamps) ; neither, on the other hand, do all lakes exhibit any pronounced tendency to become converted into swamps. For reasons which are not always clear, there is the greatest variation in the speed at which the transformation is brought about, and in many lakes, not only does there seem to be scarcely any tendency toward swamp formation, but little change would appear to have taken place at any time since their formation.

Geological and other factors influencing the distribution and vegetation of inland lakes.—The majority of the lakes and ponds in the lowland of northern Cape Breton are glacial: they occupy depressions which have resulted from glacial activity (see further discussion in Nichols '15, pp. 170–171). In calcareous districts, however, particularly in localities where there are

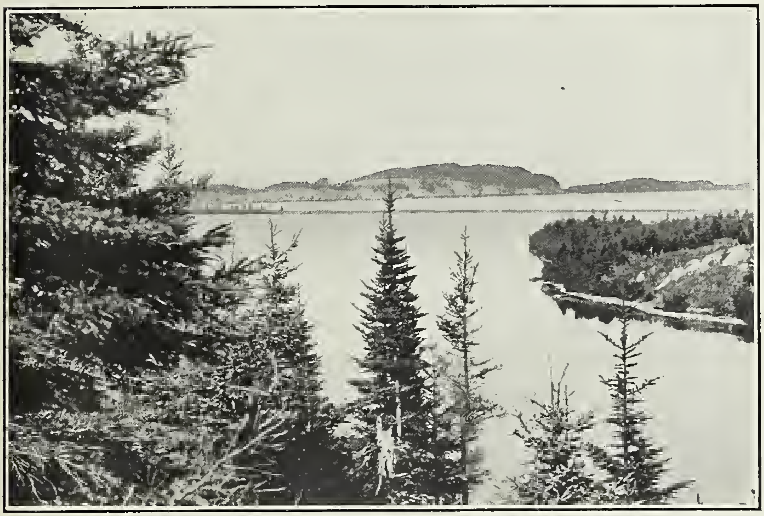

FIGURE 41.—Freshwater Lake, South Bay, Ingonish; cut off from ocean by a shingle beach; in distance, Middle Head, mostly granitic; in right foreground, a gypsum outcrop; second growth forests of white spruce and balsam fir. Photograph by Dr. L. H. Harvey.

extensive deposits of gypsum, "sink holes" due to subterranean erosion are common, and these frequently are occupied by ponds. Still a third type of water basin, due entirely to vegetative activity, is encountered on the plateau, and will be described in some detail later.

In their influence on the vegetation of lakes and ponds, drainage and permanency are factors of considerable significance. The effect of drainage will be discussed presently in connection with the formation-types of swamps. The effect of permanency is seen in comparing the vegetation of permanent, with that of periodic, lakes or swamps. Permanent and periodic lakes and swamps, as related to topography and ground water level, have been fully discussed in the writer's paper referred to above ('15, pp. 172–175).

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED LAKES AND PONDS

The association-types of permanent lakes.—Freshwater Lake (FIG. 41) and Warren Lake, at Ingonish, may be taken as representative examples of fairly large, well-drained lakes. Except for *Chara* and various algae there is little vegetation below a depth of six feet. The majority of aquatic plants grow best in water less than three feet deep. Along sandy shores, which are the prevailing type in both ponds, the following aquatic species are more or less abundant.

Chara sp.	*Eleocharis palustris vigens*
Fontinalis sp.	*Scirpus americanus*
Isoëtes echinospora Braunii	*Juncus militaris*
Sparganium angustifolium	*Nymphaea advena*
Potamogeton Oakesianus	*Ranunculus Flammula reptans*
Potamogeton heterophyllus	*Myriophyllum humilis*
Potamogeton bupleuroides	*Nymphoides lacunosum*
Glyceria borealis	*Eriocaulon septangulare*
Scirpus subterminalis	*Lobelia Dortmanna*

Nymphaea and *Nymphoides* are the commoner forms in the deeper shallows. *Eriocaulon* often forms a bright green carpet on the bottom in water three or more feet deep, but seldom flowers where it is more than a foot deep: *Ranunculus* forms similar carpets in shallow water, but flowers only on the shore. In places *Juncus* and *Isoëtes* grow in profusion. But for the most part the sandy bottom is only sparsely covered by vegetation. It might be added that *Carex aquatilis,* not noted in either of these lakes, is a frequent form along the shores of lowland lakes, locally giving rise to marshy marginal swamps similar to those to be described later in connection with lakes in the highlands.

The narrow sandy beach, between high and low water marks, supports a scanty growth of herbaceous species, among them

Equisetum arvense, Juncus articulatus, and *Ranunculus Flammula reptans.* Above high water mark there is ordinarily a fringe of *Myrica Gale* (nearest the water) and *Alnus incana.*

Muddy shores are developed to some extent in sheltered situations. Here the aquatic vegetation includes most of the species already listed, and in addition *Utricularia intermedia* and *U. vulgaris.* Certain other species, mostly amphibious, grow in

FIGURE 42.—Fresh pond behind shingle beach, well drained by seepage through barrier; *Typha latifolia* in left foreground; Barrasois.

shallow water or on the mucky shore, which is swampy at low water. These latter include: *Sphagnum* sp., *Drepanocladus fluitans, Dulichium arundinaceum, Iris versicolor, Potentilla palustris, Hypericum virginicum, Sium cicutaefolium,* and *Lysimachia terrestris.* As along sandy shores, the sweet gale and alder fringe the shore at high water mark. Along sandy shores there is little evidence of succession, but along muddy shores there is a tendency for swamps to develop.

The association-types of permanent ponds.—Small ponds (FIGS. 26, 42) may differ little from lakes in the character of their vegetation. But, on the whole, aquatic plants are apt to be relatively more abundant here by reason of the lesser depth of the water, its comparative quietness, etc. Largely because of the absence of any appreciable amount of wave action, the shores of small ponds tend to be more muddy than those of the larger bodies of water. The vegetation of sandy shores is similar to what has been described above, and the same is true in general of muddy shores. Here, however, there is often a rank growth of cat-tails (*Typha latifolia*) and bulrushes (*Scirpus occidentalis, S. cyperinus, S. atrocinctus,* etc.), through the activity of which the pond tends to become filled in and converted into a swamp.

Sink-hole ponds frequently exhibit the phenomenon of marl-formation (see Nichols '15, pp. 194–196). In such ponds there is usually a luxuriant growth of *Chara,* one of the most important marl-forming plants, and of various algae. Among the prominent aquatic seed plants here may be *Potamogeton pectinatus* and *P. pusillus.* Leaves and stems of all submersed forms are usually incrusted with a thin, whitish, flaky deposit of marl.

The association-types of periodic ponds.—Periodic ponds are not sharply delimited from permanent ponds on the one hand or from periodic swamps on the other. Very shallow depressions, which during the growing season contain water for only a brief period, are commonly occupied by a rank growth of such species as *Scirpus cyperinus* and *S. atrocinctus, Juncus effusus* and *J. brevicaudatus,* and *Iris versicolor.* In the case of ponds which disappear completely only for a short period during the summer, there may be a striking concentric zonation of plant associations. In one instance, for example, the wetter central area is largely occupied by the moss, *Amblystegium riparium.* Proceeding from here toward high water level there are encountered (*1*) a zone of more or less amphibious species such as *Sparganium americanum, Juncus effusus, Ranunculus Flammula reptans, Hypericum canadense, Lysimachia terrestris,* and *Sium cicutaefolium;* (*2*) a zone of *Iris versicolor;* (3) a zone of *Alnus incana.* Elsewhere *Eleocharis palustris* and the species cited earlier in this paragraph may be prominent as marginal plants, while in some cases the liverwort, *Marchantia polymorpha,* develops profusely on the muddy shores of periodic ponds.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED LAKES AND PONDS

The association-types of permanent ponds.—Sink-hole ponds commonly have no visible outlet and are practically undrained. Aquatic vegetation as a rule is luxuriantly developed here, but varies greatly in its floristic composition, even in neighboring ponds. In one small pond, for example, *Potamogeton natans* is practically the only species present; in another, *Chara;* in another, *Fontinalis gigantea;* while in still another, *Chara, Fontinalis gigantea,* and *Potamageton pusillus* grow intermixed. Such ponds fluctuate more or less in level from season to season and the marginal vegetation resembles that of periodic ponds.

Of particular interest, in view of their subsequent history, are the undrained ponds in which originate peat bogs. The water in these fluctuates very little in level from season to season, and while the ponds may be small in area they are usually fifteen or more feet in depth. Depressions of this sort are by no means common near the coast, and most of those which were discovered had already attained the bog stage in their development. It is of interest to note, however, that the pioneer vegetation in and about these ponds is similar in most respects to that of other ponds. The aquatic vegetation includes *Nymphaea advena,* species of *Potamogeton,* and various aquatic mosses and algae. *Chara,* however, seems to be rare or absent. In the shallow water near the margin may grow *Sparganium americanum, Eriocaulon septangulare, Carex Pseudo-Cyperus, Potentilla palustris,* and *Lobelia Dortmanna.* Along the more or less mucky shores may occur herbaceous species, such as *Onoclea sensibilis,* various sedges, *Iris versicolor, Lysimachia terrestris, Hypericum virginicum,* and *Lycopus americanus;* and shrubs, such as *Myrica Gale, Alnus incana, Rosa nitida,* and *Ilex verticillata.* The most striking difference between these and ordinary ponds is seen in the frequently luxuriant development of various species of *Sphagnum,* the significance of which will be pointed out later. The marginal shrubs here also commonly include *Chamaedaphne calyculata* and *Kalmia angustifolia,* both of which are typical bog forms.

The association-types of periodic ponds.—Periodic undrained ponds scarcely differ in their vegetation from periodic well-drained ponds, since essentially the same end is accomplished through the periodic drying up of the pond as might be attained through drainage. They therefore require no special comment.

2. The Formation-types of Lake- and Spring-swamps Inland

a. INTRODUCTORY

Lake-, spring-, and precipitation-swamps.—Swamps which have originated in the manner described earlier, through the filling in of lakes by vegetation, may be designated *Lake-swamps.* Many swamps, however, probably the majority of those in the lowland, owe their existence to the relation between topography and ground water level, i. e., to the presence of spring or seepage water. Such swamps may be designated *Spring-swamps* (see Nichols '15, pp. 184, 192). Lake- and spring-swamps are widespread in their distribution throughout most regions. In regions like the one under consideration, where precipitation is high and the evaporating power of the air low, there is still a third type of swamp whose existence is dependent very largely on direct atmospheric precipitation. Swamps of this sort, well exemplified by the raised bogs of the high interior plateau, may be designated *Precipitation-swamps.*

The ecological significance of drainage.—In his study of the geographical distribution and ecological relations of bog associations in eastern North America, Transeau ('03, p. 420) arrived at the conclusion that "the 'drained swamp' and 'undrained swamp' classification will not hold over any great area." Drainage, however, has been employed as a basis of classification by Cowles ('01, pp. 145–156) and others, and it is the conviction of the writer that, from the standpoint of physiographic ecology, this factor affords by far the most fundamental criterion yet conceived, at least for the classification of the lakes and swamps in the inland group. The relationship between cause and effect may often be obscure, since the influence of drainage is commonly expressed indirectly through other, more direct factors; but, in the last analysis, drainage, more than any other single factor or set of factors, seems to have a vital influence on the vegetation, through its effect on the aeration of the soil and on the accumulation therein or removal therefrom of various deleterious substances, as well as on other peculiarities of the substratum with which the character of the vegetation may be more directly correlated (in this connection, see Rigg '16; also Harper '18, pp. 27–31).

Drainage as a basis of classification.—In treating the lakes and swamps of the inland group in northern Cape Breton, drainage has been selected as the most fundamental basis of classification. On this basis the lakes and ponds have been divided into two groups, well-drained and undrained, and the swamps into three, well-drained, poorly drained, and undrained. The practical application of any scheme of classification of course has its limits, owing to the difficulty, if not the impossibility, of adequately correlating cause and effect, and whatever factors are selected as criteria, all sorts of intergrading conditions are encountered. Particularly in the case of swamps is the complexity of the situation enhanced in a cool, humid region such as this by the fact that atmospheric factors may react on the vegetation in such a manner as to neutralize to a greater or less degree the influence of dissimilar edaphic conditions.

During the course of the present investigations in northern Cape Breton, the writer has examined several hundred different lakes and swamps. In a number of the swamps, in addition to observations on the surface conditions, soundings were taken with a fifteen foot iron rod (summer of 1915). By this means it was possible (*1*) to ascertain the depth of the underlying vegetable deposit; (*2*) by the attachment of a Davis peat-sampler (see Bastin & Davis '09, p. 61), to determine the character of the deposit at different depths; and (*3*) with the aid of a hand-level, to figure out the topography of the underlying terrain, with particular reference to its bearing on the drainage problem and also its general relation to the surface of the swamp.

Well-drained and undrained swamps compared.—In their typical development, well-drained and undrained swamps differ from one another in several important respects. (*1*) Well-drained swamps are best developed on springy slopes, where the gradiant is sufficiently steep to insure adequate drainage. They also commonly occur along the banks of streams (many such swamps, more especially along small brooks, are better included with the swamps of the inland group than with those of the river group). Undrained swamps, as exemplified by bogs, ordinarily are best developed in relatively deep, undrained or poorly drained, water filled depressions. For reasons which will be apparent later, however, in humid regions, like the one under discussion, swamps of the undrained type are by no means confined to depressions. (*2*) Both well-drained and undrained swamps may be underlain by peat; but in the former the deposit usually is quite shallow and sometimes it is entirely absent. Moreover, in well-drained swamps the peat as a rule is mucky, the plant remains being pretty thoroughly decomposed. Undrained swamps invariably are underlain by peat deposits, which often exceed fifteen feet in thickness; the peat is more or less spongy, and the plant remains for the most part are well preserved. (*3*) The soil in practically all swamps in northern Cape Breton is acid to litmus, but it is appreciably more so in swamps of the undrained type than in others. (*4*) The vegetation of well-drained swamps is characterized by the moderate abundance of the sphagnums; by the great variety of herbaceous seed-plants, which in large part are hydrophytes; by the scarcity of ericaceous shrubs; and by the presence of several deciduous trees of southward distribution. The vegetation of undrained swamps, on the other hand, is characterized by the luxuriant development of the sphagnums; by the comparatively small number of species of herbaceous seed-plants, which in large part are bog xerophytes; by the abundance of ericaceous shrubs; and by the absence of practically all trees except the black spruce and tamarack.

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED SWAMPS

Pioneer association-types.—Among the important pioneers in the development of vegetation on springy or wet slopes are the bryophytes, notably the following species:

*Marchantia polymorpha**	*Sphagnum squarrosum*
*Pellia epiphylla**	*Philonotis fontana**
*Pallavicinia Lyellii**	*Mnium punctatum**
*Scapania nemorosa**	*Brachythecium novae-angliae*

Of the herbaceous vascular plants, almost any of the species to be listed later as characteristic of wet meadows may appear at a very early stage in the succession, but the following list includes the forms which, on the whole, are more prominent as pioneers:

*Onoclea sensibilis**	*Juncus effusus*
Equisetum sylvaticum	*Iris versicolor**
Glyceria canadensis	*Sagina procumbens**
Glyceria laxa	*Cardamine pennsylvanica**
Scirpus atrocinctus	*Drosera rotundifolia*
Scirpus rubrotinctus	*Chrysosplenium americanum**
Carex crinita	*Hypericum canadense*
*Carex scabrata**	*Epilobium palustre*
Carex stipata	*Lysimachia terrestris*
*Juncus articulatus**	*Lycopus americanus*
Juncus brevicaudatus	*Mentha arvensis**

Association-types of open swamps.—The luxuriant growth of the grasses, sedges, and rushes may result in the development of a wet meadow association-type, characterized by the predominance of grass-like growth-forms and the relative absence of woody plants. During the evolution of the wet meadow, the plant cover gradually becomes denser, while the nature of the substratum may become modified through the formation of a layer of mucky peat. Contemporaneously with these changes, many of the pioneer species (notably those starred [*] in the above lists), either disappear or else become restricted in their distribution to the more open, wetter habitats. Others become more abundant, and at the same time still other species not before represented may make their appearance. The following list includes various herbaceous plants, which, in addition to those already mentioned, and together, less frequently, with those to be given in a subsequent list, commonly are more or less abundantly represented in open, well-drained swamps.

Aspidium Thelypteris	*Habenaria dilatata*
Aspidium cristatum	*Habenaria psycodes*
Osmunda cinnamomea	*Thalictrum polygamum*
Osmunda regalis	*Fragaria virginiana*
Agrostis hyemalis	*Geum rivale*
Calamagrostis canadensis	*Sanguisorba canadensis*
Eriophorum virginicum	*Chelone glabra*
Carex canescens disjuncta	*Galium palustre*

Carex flava
Carex intumescens
Carex pallescens
Carex paupercula
Carex stellulata
Habenaria clavellata
Eupatorum purpureum
Aster nemoralis
Aster puniceus
Aster radula
Aster umbellatus

The bryophytes, as a rule, are well represented in open swamps, usually forming a more or less conspicuous understory of vegetation. The following additional species may be mentioned as characteristic:

Sphagnum palustre
Sphagnum imbricatum
Sphagnum magellanicum
Sphagnum Girgensohnii
Camptothecium nitens
Rhytidiadelphus squarrosus
Chrysohypnum stellatum
Acrocladium cuspidatum

More often than not, shrubs put in their appearance so early that the wet-meadow stage in the succession is of very brief duration. Frequently it is eliminated as a distinct phase. Instead, there may arise a mixed growth of shrubs and herbaceous plants: these with scattered trees constitute the most familiar type of vegetation in open swamps. The common pioneer shrub is the alder (*Alnus incana*). Associated with this may grow any (or all) of the following species:

Salix humilis
Myrica Gale
Ribes hirtellum
Spiraea latifolia
Rubus pubescens
Rubus canadensis
Rosa nitida
Ilex verticillata
Viburnum Opulus americanum
Viburnum cassinoides

On the whole, ericaceous shrubs (or semi-shrubs) are scarce in well-drained swamps, but *Chiogenes hispidula* commonly, *Kalmia angustifolia* frequently, and *Chamaedaphne calyculata* and *Vaccinium macrocarpon* occasionally are present.

The edaphic climax association-type.—Ultimately the entire swamp may become wooded, but, as a rule, much of it remains fairly open, with trees scattered, but more abundant toward the margin, and with the shrubs and herbaceous plants of open swamps occupying the spaces between them. The predominant trees, as a rule, are balsam fir, black spruce, white spruce, and red maple; but associated with these, in varying abundance, may grow paper birch and yellow birch, white ash and black ash (*Fraxinus nigra*), and occasionally white pine.

The vegetation of wooded swamps may include various of the herbaceous and shrubby species already listed, but in addition to these a number of forms occur here which have not yet been mentioned, although some of them may likewise grow in open swamps. Such, for example, are the following:

Phegopteris polypodioides	*Maianthemum canadense*
Aspidium noveboracense	*Coptis trifolia*
Osmunda Claytoniana	*Mitella nuda*
Taxus canadensis	*Oxalis Acetosella*
Carex trisperma	*Viola renifolia*
Carex tenella	*Circaea alpina*
Carex leptalea	*Cornus canadensis*
Carex folliculata	*Linnaea borealis americana*
Clintonia borealis	*Aster acuminatus*

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED SWAMPS

Occurrence of bogs along the coast.—In the vicinity of Baddeck and in other localities where the clayey nature of the soil retards drainage, bogs may develop in shallow depressions of any description. They develop best, however, here as in regions farther south, in fairly deep, closed, water-filled depressions. Raised bogs, such as occur along the coast in New Brunswick (see Ganong '98), and which are extensively developed on the interior plateau in northern Cape Breton, are apparently absent along the coast. The finest series of bogs discovered in the lowland is situated near the mouth of the Barrasois River, where in a tract of woodland less than a square mile in area there are six or eight fine examples. All of these occupy closed basins, presumably kettle holes in the drift, but possibly drift-covered sink holes, range in size from less than one to more than three acres, and bear a remarkable resemblance to certain Connecticut bogs (see Nichols '15, pp. 202–217). The following observations relate more particularly to this collection of bogs, which can be regarded as representative.

The floating mat and its association-types.—The early stages of bog development are best exhibited in the largest of these bogs, where, at the south end, there still remains a pond some sixty feet long by twenty-five feet wide (Fig. 43). The filling in of such a pond is accomplished through the intervention of a floating mat, and the general features of mat formation are quite similar to what the writer has described for Connecticut bogs ('15, pp. 196–202). Its formation is brought about through the combined activity of shrubs, sedges, and sphagnums. Very

Figure 43.—Bog near mouth of Barrasois River; *Nymphaea* in foreground; sedge-shrub-sphagnum mat in middle distance; bog forest in center background.

commonly the forerunner of mat formation is the cassandra (*Chamaedaphne calyculata*). This shrub occurs both along the shore and along the edge of the advancing mat and frequently grows out several feet into the open water. Its relation to the mat is similar to that of the steel framework to a concrete building: it forms a skeleton upon which the sphagnum may be supported. The necessity for such support will be pointed out in the next section. Where, as is commonly the case, the cassandra is followed by a dense growth of sphagnum, a mat is developed. Where, however, as along the south shores of several of these bogs, shade conditions preclude the growth of the sphagnums, no mat is developed (see further on p. 363). So luxuriant, as a rule, is the development of the sphagnums that the important rôle played by the cassandra is liable to be overlooked; but if a newly formed "sphagnum mat" be dug into, the woody ribs formed by this shrub will usually be found.

In some instances, certain sedges play a rôle similar to that just ascribed to the cassandra. Certain of these, e. g., *Carex filiformis,* in contrast to the shrubs, are quite capable of forming a mat themselves, independently of any assistance from the sphagnums. But, as a rule, the sphagnums make their appearance at an early stage in the history of the mat and thereafter play an important part in its development: ordinarily they spread so rapidly and grow with such luxuriance as to quickly become the predominant element of the plant cover. Various features associated with the formation and growth of floating mats are discussed further in the following paragraphs and in later pages, in connection with the swamps of the highland.

On the "sphagnum mat" thus formed, in greater or less abundance, grow various sedges and shrubs which, by their roots, rhizomes and trailing stems, tend to bind together and consolidate the otherwise loose structure. Characteristic species are the following:

Eriophorum callitrix
Eriophorum virginicum
Rynchospora alba
Carex canescens disjuncta
Carex paupercula irrigua
Carex stellulata
Kalmia polifolia
Ledum groenlandicum
Vaccinium macrocarpon
Vaccinium Oxycoccus
Menyanthes trifoliolata

Along the wet margin of the mat, where it borders on the marginal ditch (see further below), and in the ditch itself where this is swampy, commonly grow various forms which one ordinarily associates with well-drained swamps; among them: *Sparganium americanum, Iris versicolor, Alnus incana, Myrica Gale, Rosa nitida, Ilex verticillata, Hypericum virginicum, Lysimachia terrestris,* and *Lycopus americanus.* These plants seldom occur in the older parts of the bog.

The sphagnums in relation to the formation of floating mats.—The relatively subordinate rôle played by the sphagnums in initiating the formation of floating mats was suggested by Ganong ('03, pp. 440–441) and Transeau ('05-'06, p. 363), and has been emphasized by Davis ('07), Cooper ('13) and others. From these and the writer's observations it seems certain that in general the appearance of the sphagnum is subsequent rather than antecedent with reference to that of the vascular plants. The inability of the sphagnums of themselves to form a mat may be attributed largely to the lack of coherence and buoyancy in the mass of floating vegetation which they sometimes form. But added to this is the fact that comparatively few species of sphagnum are capable of flourishing with their foliage completely submerged. Of course there are certain sphagnums which are distinctly aquatic in their mode of growth, but among the twenty species which have been recorded from Cape Breton, only two definitely belong in this category, namely, *S. Pylaisei* and *S. cuspidatum* (see in this connection the ecological classification of bog sphagnums on p. 422). In many mountain ponds these two species grow in great profusion, floating at or just below the surface of the water, and their ecological relations there will be discussed in some detail later (see especially pp. 424, 429), Neither of these two species, however, occurs in any abundance along the coast: in fact, the writer has never seen *S. Pylaisei* except in the mountains, while *S. cuspidatum,* though frequently represented in lowland ponds by the var. *Torreyi,* is seldom of ecological importance here. The important mat pioneers among the sphagnums in the Barrasois bogs, which may be regarded as representative of lowland bogs in general, are *S. papillosum, S. magellanicum,* and *S. recurvum.* These three species grow best in very wet situations, but they will flourish only where the nature of the substratum is such that, at least throughout most of the growing season, their shoots remain partially raised above water level. The maintenance of this position they are not sufficiently buoyant to accomplish themselves, so that the preexistence of some sort of a support to prevent their sinking below the surface is essential. Hence the importance of shrubs and sedges as pioneers in the development of a "sphagnum mat."

The marginal ditch and its significance.—The formerly water-filled depressions now occupied by the Barrasois bogs have become almost completely filled in through the activity of vegetation. All that remains in most cases to remind one of the pond stage in the succession is a moat-like marginal ditch or fosse, which averages perhaps ten feet in width and up to two or more feet in depth, which may be open and filled with water or occupied by a wet sphagnous swamp, and which, as a rule, more or less completely encircles the area occupied by the bog proper. The significance of this marginal ditch is not wholly clear. Elsewhere ('15, pp. 207, 208), the writer has been inclined to uphold the explanation first suggested by Davis ('07, pp. 150, 151), which attempts to correlate it with fluctuations in water level. But conditions here in northern Cape Breton are even better explained by Atkinson's theory ('05, pp. 615, 616) that the formation of the ditch is due to the shade produced by the forest along the shore, which hinders or prevents the growth of the mat-forming plants. In several of the forest-encircled Barrasois bogs the ditch is open along the southern shore, i. e., along the shore where the effect of the shade produced by the fringing forest naturally would be most pronounced, while along the northern, least shaded shore it has become completely filled in by vegetation. This condition obviously cannot be explained by the fluctuation theory; and for that matter, as already mentioned, there is very little seasonal fluctuation in water level in these basins.

Development of the edaphic climax association-type.—Beyond the wet bog stage, further development is largely dependent on two species of *Sphagnum* which have not as yet been mentioned: *S. fuscum* and *S. capillaceum tenellum,* particularly the former. Where the hydrophytic (or relatively mesophytic) pioneer sphagnums are superseded by these relatively xerophytic forms, the surface of the bog may become built up a foot or more above water level. In a mature bog the sphagnums almost everywhere are the predominant plants underfoot. They cover the ground with a continuous, hummocky, mattress-like carpet, which consists for the most part of the russet-green *S. fuscum,* interspersed with occasional more or less extensive patches of the reddish *S. capillaceum tenellum.* Commonly growing along with the sphagnums, in the older parts of the bog, are two mosses: *Polytrichum commune* and *P. juniperinum,* while in some of the higher, drier areas the sphagnums may have become superseded by cladonias or by such bryophytes as *Ptilidium ciliare* and

Hypnum Schreberi. Here and there, even in an old bog, there are moist or wet depressions in which may occur the more hydrophytic species of *Sphagnum*, together with liverworts such as *Cephalozia fluitans* and *Mylia anomala* and mosses such as *Calliergon stramineum* and *Drepanocladus fluitans*.

Scattered about over the sphagnum substratum, and varying greatly in abundance locally, are diverse trees, shrubs, and herbaceous plants. The characteristic and omnipresent tree of bogs is the black spruce. Invariably dwarfed in size, it commonly forms low, scraggly clumps, the result of layering followed by the death of the parent tree or of the original trunk.[11]

The predominant bog shrubs are ericads: *Chamaedaphne calyculata, Gaylussacia baccata, Kalmia angustifolia, K. polifolia*, and *Ledum groenlandicum*, to which should be added the semi-shrubby forms, *Chiogenes hispidula* and *Vaccinium Oxycoccus*. Three non-ericaceous shrubs also are usually well represented: *Amelanchier* sp., *Nemopanthus mucronata*, and *Viburnum cassinoides*. The most important herbaceous species are *Osmunda cinnamomea, Eriophorum callitrix, E. virginicum, Rynchospora alba, Carex trisperma Billingsii*, and *Cornus canadensis*. Three orchids, *Habenaria blephariglottis, Pogonia ophioglossoides*, and *Calopogon pulchellus*, are conspicuous when in flower; *Drosera rotundifolia* is common, and *Lycopodium inundatum* occasional in moist depressions; *Smilacina trifolia* occurs locally in wet places; *Empetrum nigrum* grows abundantly in the drier portions of one bog; while *Arceuthobium pusillum* is a frequent parasite on the black spruce.

d. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED SWAMPS

Under the head of poorly-drained swamps are classed swamps of an intermediate character: swamps whose vegetation resembles in some respects that of well-drained swamps, in other respects that of undrained swamps. Boggy swamps of this character are of far more general occurrence than are those of the more extreme types, such as have been described in the foregoing paragraphs.

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[11] Ganong ('97: see quotation on p. 447 of the present paper) has called attention to layering as a means of reproduction in *Picea mariana*, and the phenomenon has been discussed in some detail by Cooper ('11) and Fuller ('13).

Illustrative examples.—The general situation in poorly drained swamps is unusually well illustrated by a group of small swamps on Broadcove Mountain, which were studied in some detail. These swamps occupy a series of very shallow, trough-like depressions, which cross approximately at right angles the road from Ingonish to Neil's Harbor. Three of them, which may be designated respectively as swamps *A, B,* and *C,* are roughly represented in longitudinal section in FIG. 44. The surface slope, depth of peat, etc., were determined by means of sounding-rod and level. All three swamps have outlets at the lower end, and swamp *A* has a small brooklet traversing perhaps half its length. At the time they were studied (August, 1916), the out-

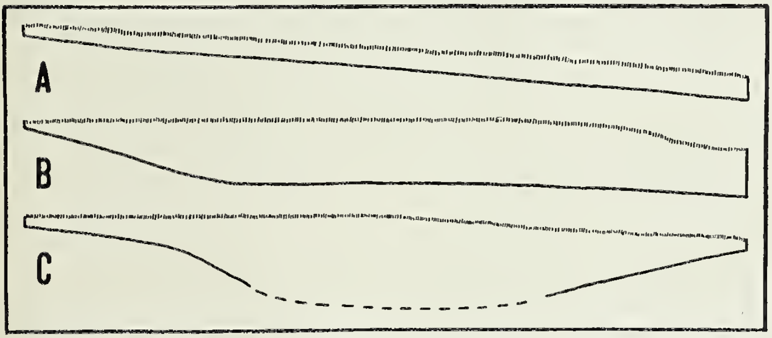

FIGURE 44.—Diagrammatic longi-sections of poorly drained swamps on Broadcove Mountain, north of Ingonish: see text.

lets in swamps *B* and *C* were dry, but a small amount of water was trickling out of *A.*

Swamp *A.*—This swamp is the least boggy of the three. Genetically it represents a condition which presumably obtained at an earlier period in the development of swamp *B.* In area it is about 300 feet long by 100 feet wide. In proceeding from its upper to its lower end, the ground slopes gently, dropping at the rate of about 1 : 50. Over almost the entire tract a layer of peat from two to two and a half feet in thickness has been formed. The aspect of the vegetation over much of the area is that of a meadow: *Scirpus hudsonianus* and *S. caespitosus* with species of *Sphagnum* form the bulk of the plant cover. Scattered over the meadow are various herbaceous plants, shrubs, and trees, *Osmunda regalis* in particular of the herbs forming considerable patches locally. Along the margin of the swamp is a fringe of swamp forest. Floristically the vegetation of this swamp resembles in many respects that of an ordinary well-drained swamp. The majority of the vascular plants present there are also represented here, but they are relatively much less abundant. *Myrica Gale* is perhaps the commonest shrub in the open part of the swamp, and there are present here three shrubs not previously listed: *Pyrus arbutifolia atropurpurea, Rhamnus alnifolia,* and *Lonicera caerulea.* The boggy nature of the swamp is suggested by the presence of such plants as the two species of *Scirpus* mentioned, *Rynchospora alba, Smilacina trifolia, Sarracenia purpurea, Vaccinium Oxycoccus,* and *Lobelia Kalmii,* as well as by the luxuriant growth of the sphagnums. The dissimilarity between this swamp and a bog is emphasized, among other things, by the presence among the marginal woody forms of *Taxus canadensis, Acer rubrum, Fraxinus americana* and *F. nigra.*

Viewed from a genetic standpoint, it seems apparent that the area formerly occupied by the swamp vegetation was much more restricted than that which it occupies to-day. Originally long and narrow, as the surface has become built up through the accumulation of peat the swamp has spread out laterally, encroaching on the adjoining forested areas. Evidences of quite recent encroachment were noted just above where the swamp crosses the road. Among the pioneer seed plants, to judge from a relict colony near the lower end of the swamp, were *Calamagrostis canadensis, Juncus brevicaudatus,* and *Iris versicolor;* but the upbuilding of the surface and the lateral expansion of the swamp have been largely attributable to the luxuriant growth of the sphagnums and of the two sedges, *Scirpus hudsonianus* and *S. caespitosus.* It may well be said that the nature, and indeed the very existence, of the swamp as it is to-day is closely correlated with the activity of the compact mass of peat thus formed and of the superimposed plant cover in obstructing the drainage and thereby conserving the water supply.

Swamps *B* and *C*.—Swamp *B,* from a genetic standpoint, may be regarded as representing a later stage in the developmental series than swamp *A*. Conditions in swamp *B* have been more favorable to peat accumulation than in swamp *A,* owing to the more level nature of the terrain, and over much of the area the deposit of peat is more than six feet thick. It will be noted (toward the right in FIG. 44) that where the rock floor is slightly inclined the layer of peat becomes thinner. Swamp *C* differs from both swamps *A* and *B* in having originated in and around a shallow, poorly drained pond, the extreme depth of which was not ascertained. In its larger aspects, the vegetation in both these swamps is similar to that of swamp *A:* the two species of *Scirpus* and the *Sphagna* predominate, and various species characteristic of both well-drained and undrained swamps are represented. But the still more boggy nature of the habitat is evidenced particularly by the frequency here of the ericaceous shrubs, *Chamaedaphne calyculata* and *Ledum groenlandicum,* neither of which occur in swamp *A*. The relatively xerophytic nature of the habitat is further suggested by the presence of *Pteris aquilina* and *Juniperus communis depressa.*

The following list of species characteristic of one or all of the Broadcove Mountain swamps, but mostly not heretofore mentioned in any connection, is of interest.

Selaginella selaginoides
Larix laricina
Muhlenbergia racemosa
Eriophorum tenellum
Eriophorum viride-carinatum
Carex Michauxiana
Carex oligosperma
Spiranthes Romanzoffiana
Potentilla fruticosa
Viola conspersa
Conioselinum chinense
Solidago rugosa
Solidago uliginosa
Cirsium muticum

General observations.—In general, bogginess seems to be correlated with poor drainage; and this may be either occasioned by the nature of the terrain or brought about through the influence of vegetation. Topography favors the development of boggy swamps where the surface is flat, fairly level, and so situated that the ground becomes covered with a thin sheet of water in wet weather. Boggy swamps are frequently encountered, for example, on low, flat areas, bordering lakes and ponds, which are subject to periodic inundation (see in this connection p. 419). A heavy soil which dries out slowly favors the development of boggy swamps. But many of the tracts, which in northern Cape Breton are occupied by swamps of this type, in a warmer, less humid climate would be merely periodic swamps of the ordinary, well-drained type. The general prevalence here of boggy swamps may be attributed in large measure, indirectly, to the influence of the cool, humid climate of the region. The climate favors the luxuriant development of the sphagnums and other peat-forming plants, and it seems to be very largely through the direct influence of the layer of peat to which these give rise, in retaining the water and thereby extending the swampy condition throughout the season, that the boggy condition is brought about. Very often, in this way, through the obstruction of the drainage which results from the activity of the vegetation, a swamp which, during the early stages of its development, would be classed as well-drained, in the course of time becomes increasingly boggy. This is well illustrated by the examples just described.

It has been mentioned earlier that peat accumulation may occur in connection with well-drained swamps; but there, as already suggested, the deposit is mucky and invariably shallow. Again, the bog has been cited as the characteristic swamp-type of undrained depressions; but not infrequently shallow, undrained depressions are occupied by swamps of the poorly drained type. Sink hole swamps are often of this character. Fluctuations in water level, underground drainage, alkalinity of the soil water, or some such factors may perhaps explain the discrepancy here. But, after all, the whole swamp situation is an extremely complex one, and it is candidly admitted that there are any number of questions which must be left unanswered.

4. The formation-types in and along Rivers and Streams

a. INTRODUCTORY

Under this head are included fundamentally those association-complexes of hydrarch origin whose ecological aspect manifestly is correlated with the activity of rivers and streams. In so far as it affects associations of the hydrarch series, the influence of a stream on the vegetation in and along its course is expressed primarily at times of high water, and then in two ways: first, through the deposition of sediment, which leads to the development of flood plains; second, through the erosive activity of the current, which may affect the vegetation directly, particularly through the abrading action of ice, or indirectly, as seen in the formation of oxbows. Under this head have also been included the association-complexes of wet or dripping rock outcrops, since these are especially characteristic of, though by no means confined to, ravines.

b. THE ASSOCIATION-COMPLEXES OF RAVINES

The stream bed association-types.—The predominant plants in the rocky stream beds which prevail in ravines, and to a large extent elsewhere, are bryophytes. Characteristic species are the following:

Marsupella aquatica
Jungermannia cordifolia
Scapania undulata
Porella pinnata
Fontinalis dalecarlica
Oxyrrhynchium rusciforme
Hygrohypnum dilatatum
Hygrophynum eugyrium
Hygrophynum ochraceum

The degree of luxuriance exhibited by the submersed bryophytic vegetation varies greatly in different streams. The aquatic mosses and liverworts are best developed in small brooks; in large streams they may be conspicuous by their absence. This latter fact may be explained somewhat as follows. The instability of the substratum might account for their absence on small boulders and cobbles, but even where there is a firm rock substratum, bryophytes are scarce. There seems little question that, in general, the scarcity is attributable to mechanical factors —to the erosive action of the sediment-laden water in flood time, or, more likely, of ice-laden water in spring. Were the phenomenon restricted to northern Cape Breton, one might feel tempted to correlate it with the acidity of the water, which in most streams commonly contains so much organic matter that it is colored yellow or brownish (see, in this connection, Ganong '98); but the same conditions can be observed in other regions, e. g., in Connecticut streams, where the water is clear and colorless. Often the rocky bottom in swift streams is utterly devoid of plants of any description, but sometimes, in the absence of mosses, there may be a considerable growth of *Nitella* sp.

Stream bank association-types.—Along small ravine brooks the banks, as a rule, are well shaded by overhanging foliage, the air is always cool and moist, and the substratum continuously damp or wet. It is doubtful whether the plant cover in many such habitats ever has been xerophytic, and for this reason it has seemed best to treat it under the head of hydrarch successions. The outstanding feature of such a ravine is the intense mesophytism, commonly verging on hydrophytism, of its vegetation. In the periodically inundated zone along the edge of the stream there is a profuse development of mosses and liverworts, which commonly include, among others, the following species:

Conocephalum conicum	*Philonotis fontana*
Plagiochila asplenioides	*Thuidium delicatulum*
Sphagnum squarrosum	*Brachythecium rivulare*
Fissidens adiantoides	*Hylocomium brevirostre*
Mnium hornum	*Climacium dendroides*
Mnium punctatum	*Catharinaea undulata*

Vascular plants are more or less numerous, particularly toward the upper limit of the flood zone. Here the ferns are represented by a wealth of species, among which *Polystichum Braunii* is especially characteristic, while the seed plants include some of the most pronounced shade- and moisture-loving mesophytes. A list of some of the more representative ferns and seed plants follows:

Phegopteris polypodioides	*Aspidium spinulosum* var.
Phegopteris Dryopteris	*Streptopus amplexifolius*
Asplenium Filix-femina	*Geum macrophyllum*
Polystichum acrostichoides	*Circaea alpina*
Polystichum Braunii	*Galium kamtschaticum*
Aspidium noveboracense	*Aster acuminatus*

Along the larger ravine streams the banks are more exposed to sun and wind than along the smaller ones, and the vegetation tends to be less mesophytic, with shade plants in particular much less prominent. The character of the vegetation between low and high water levels is influenced to a more marked degree by the abrading action of the current in flood time. Even here, however, associations of the sort just described are frequently encountered.

Cliff association-types.—Many cliffs and steep rock outcrops are kept wet to such a degree with dripping water that their vegetation differs quite perceptibly from that of the drier cliffs described earlier under the xerarch series. It is of course difficult to draw sharp lines, since there are all degrees of intergradation. Here, as there, the most distinctive plants are the bryophytes, which thrive in crevices and frequently plaster over even precipitous rock surfaces. But in addition to various of the species cited earlier as characteristic of relatively dry cliffs, there occur here, usually as the predominant forms, various more or less hydrophytic species. Prominent among these are the sphagnums, the species mainly those mentioned elsewhere in connection with the ravine forest, and the liverworts and mosses enumerated in the subjoined list.

Marsupella emarginata	*Didymodon rubellus*
Sphenolobus Michauxii	*Hymenostylium curvirostre*
Mylia Taylori	*Anoectangium Mougeotii*
Plagiochila asplenioides	*Plagiothecium denticulatum*
Diplophyllum albicans	*Hylocomium brevirostre*
Scapania nemorosa	*Plagiopus Oederi*
Blindia acuta	

c. THE ASSOCIATION-COMPLEXES OF FLOOD PLAINS

Here should be included the strips of swale which not infrequently border even rapid streams and which obviously represent incipient flood plains. In valleys, for example, and locally even in ravines, a narrow, marshy strip frequently intervenes between ordinary summer water level and the lower edge of the upland forest. The vegetation in such a tract is essentially that of a well-drained swamp, with sedges, such species as *Carex torta* and *C. aquatilis,* and the grass, *Calamagrostis canadensis,* usually the predominant forms. Swampy flood plains of this particular sort are much more extensively developed on the plateau (see p. 456) than in the lowland, where they are of minor consequence.

Of much more importance here, though somewhat restricted in their occurrence, are the flood plain formations which have been developed in particular at the mouths of some of the larger streams, as at the heads of Ingonish Harbor, Middle Harbor (Aspy Bay), and Margaree Harbor. The earlier phases of the hydrarch series of association-types, which reaches its culmination in the flood plain forests that have been developed on the higher portions of flood plains, are well illustrated by the conditions about the head of Margaree Harbor, which will be briefly described.

Pioneer association-types.—Owing to the intermittent backing up of the outflowing river water by the inflowing tide water, the depth of the water over the submerged portion of the flood plain here fluctuates daily. On parts which are permanently submerged, vegetation, where present, consists largely of submersed aquatics, notably *Potamogeton bupleuroides.* Areas which are bared at low tide, but which may be inundated to a depth of from perhaps six inches to two feet at high tide, are occupied by a wet marsh association-type, in which the following are the more prominent species:

Equisetum fluviatile
Scirpus occidentalis
Dulichium arundinaceum
Typha latifolia
Sagittaria latifolia
Acorus Calamus
Castalia odorata
Nymphaea advena
Cicuta bulbifera
Sium cicutaefolium

Fringing the shoreward margin of this marshy area is a more or less well defined transition zone, in which the predominant plants are species of generally recognized amphibious proclivities. Here, to a greater extent than in the areas of deeper water, grow, among others, the following species:

Leerzia oryzoides
Juncus brevicaudatus
Iris versicolor
Caltha palustris
Rumex Britannica
Potentilla palustris
Proserpinaca palustris
Lysimachia terrestris
Menyanthes trifoliolata
Myosotis laxa
Mentha arvensis

On portions of the flood plain where the water at high tide ordinarily is very shallow, or which are flooded only in time of spring tides, the general aspect of the association-type is that of wet meadow, although various of the marsh species may grow here also. Below is a list of some of the species noted as characteristic:

Acrocladium cuspidatum
Onoclea sensibilis
Aspidium Thelypteris
Glyceria grandis
Calamagrostis canadensis
Carex crinita
Habenaria dilatata
Sanguisorba canadensis
Impatiens fulva
Viola cucullata
Scutellaria galericulata
Chelone glabra
Eupatorium purpureum
Aster novi-belgii

The edaphic climax association-type.—The condition of the vegetation on parts of flood plains which lie above ordinary high tide level has been greatly modified by human activity, owing to the suitability of such areas for raising hay, and the original character of the vegetation here must be judged from the fragmentary evidence which has survived.

In wet meadows of the sort above described, the common occurrence of scattered shrubs, such as *Alnus incana* and *Myrica Gale,* suggests that the present day meadow association-type is of secondary origin; and it is certain, from the conditions observed at Margaree Harbor, Ingonish, and Aspy Bay, that in former days the higher parts of flood-plains of the sort under consideration were occupied by forests made up largely of elm, white ash, black ash, and white spruce. Specimens of elm more than six feet in diameter are occasionally encountered on flood plains. The characteristic shrubs here include *Salix* sp., *Alnus incana, Cornus stolonifera, Viburnum Opulus americanum,* and *Sambucus canadensis.* Below is a list of the more distinctive herbaceous species of the higher parts of flood plains, most of them being noted in all three localities cited.

Onoclea Struthiopteris
Onoclea sensibilis
Asplenium Filix-femina
Calamagrostis canadensis
Laportea canadensis
Thalictrum polygamum
Clematis virginiana
Agrimonia striata
Sanguisorba canadensis
Impatiens biflora
Circaea intermedia
Heracleum lanatum
Galium asprellum
Eupatorium purpureum
Solidago canadensis
Solidago rugosa
Aster novi-belgii
Aster puniceus
Aster umbellatus

The association-types of oxbow ponds.—Oxbow ponds have been observed in a few places, as at Margaree Harbor and Pleasant Bay. Such ponds usually support a luxuriant aquatic vegetation, notably such species as the following:

Sparganium angustifolium	*Ranunculus aquatilis capillaceus*
Potamogeton bupleuroides	*Callitriche palustris*
Potamogeton epihydrus	*Ludvigia palustris*
Scirpus subterminalis	*Myriophyllum verticillatum*
Nymphaea advena	*Utricularia intermedia*
Nymphaea microphylla	*Utricularia vulgaris*
Castalia odorata	

The marginal vegetation here requires no particular comment. It may include any of the wet marsh species of the flood plain series, in addition to various of the herbaceous plants and shrubs elsewhere listed as characteristic of well-drained swamps.

4. The Formation-types along the Seacoast

a. INTRODUCTORY

In this group may be included all association-complexes of hydrarch origin whose ecological aspect is influenced directly by the proximity of the sea. This influence is seen most obviously in the effect of salt water on the character of the vegetation. But beside this, from the standpoint of physiographic ecology, the dynamic agencies which are associated with the activity of waves and currents are of prime importance, either directly or indirectly: the formation and destruction of barrier beaches, which may result in the development of coastal ponds of all degrees of salinity—from completely salt to completely fresh; the deposition of sediment, which under favorable conditions may lead to the development of coastal swamps, etc. With reference to these physiographic agencies, just as was pointed out in discussing the vegetation of uplands along the seacoast, it is possible to divide the associations of lakes and swamps here into two groups: associations along eroding shores, and associations along depositing shores. Little attention has been given, however, to the associations of the first group, which comprise primarily the formation (or formation-complex) of seaweeds concerning which brief mention has already been made in discussing the vegetation of rocky sea bluffs. In the remarks which follow, attention is restricted to the associations along depositing shores. These are conveniently treated under three heads: the association-complexes of salt and brackish lakes and ponds, the association-complexes of salt marshes, and the association-complexes of brackish marshes.

b. THE ASSOCIATION-COMPLEXES OF SALT AND BRACKISH LAKES AND PONDS

The most prominent constituent of the aquatic flora in salt lakes and ponds is the eel grass (*Zostera marina*) which commonly grows in great luxuriance, covering large areas of bottom between approximately mean low water mark and a depth of several feet below. Ecologically the eel grass fulfils an important function in that, by its interference with tidal currents, it stimulates the deposition of silt and the consequent upbuilding of the bottom. Associated with the eel grass, but seldom attaining any great prominence, usually grow the sea lettuce (*Ulva* sp.) and other algae, which may either form a loose covering over the sandy or muddy bottom or grow attached to the eel grass. Another seed plant found here is *Ruppia maritima*. In Middle Harbor (Aspy Bay), to select a concrete example, this plant is not at all conspicuous toward the outlet, but in the shallow water about the head of the harbor, in company with *Potamogeton pectinatus,* it completely covers the muddy bottom with a prolific growth. The presence here at the head of a sizeable stream may account for the abundance of the *Ruppia* in this vicinity, although this plant is by no means confined to brackish water. In Cold Spring Harbor, Johnson ('15, p. 26) says that *Ruppia* is most abundant in areas of "soft bottom, bare of *Ulva,* and usually protected from currents and waves." It is worthy of note, however, that in brackish ponds, in northern Cape Breton, the bulk of the aquatic vegetation consists of *Ruppia* and *Potamogeton pectinatus.*

The shores of salt and brackish ponds may be occupied by the salt or brackish marshes which will be described presently, or they may be merely muddy or gravelly. Gravelly shores ordinarily occur in more exposed situations than muddy shores. The conditions which prevail on gravelly shores may be illustrated by a specific example, a spot just inside the entrance of a salt pond. A luxuriant growth of *Plantago decipiens, Spergularia leiosperma,* and *Salicornia europaea* covers much of the shore between mean high and low water levels. Attached to scattered cobbles in this zone are *Fucus, Ascophyllum,* and other algae. In the vicinity of high water mark grow *Puccinellia maritima, Suaeda maritima, Solidago sempervirens* and other halophytes. Such a shore may be regarded as an incipient marsh.

The vegetation of muddy shores is essentially that of the marshes. The conditions here are well exemplified by a small brackish pond near the Barrasois, which has become completely barricaded off from the ocean but is still influenced by tide water filtering through the barrier. The pond itself is densely populated by *Ruppia* and *Potamogeton pectinatus,* together with various algae. Surrounding the pond is a low, muddy border from two to five feet wide, which is ordinarily submerged at high tide. The predominant plant here is *Scirpus nanus,* which forms a low, soft sward. Associated with it grow *Triglochin maritima, Ranunculus Cymbalaria, Spergularia canadensis,* and *Salicornia.* At a slightly higher level, barely covered at ordinary high water, is a narrow zone of *Spartina patens,* together with *Agrostis alba maritima, Carex norvegica,* and *Triglochin;* while at a still higher level, not submerged by ordinary tides, is a zone occupied almost exclusively by *Juncus balticus littoralis.* Such an association-complex, like the preceding, might equally well, if not better, be considered in connection with salt and brackish marshes.

c. THE ASSOCIATION-COMPLEXES OF SALT MARSHES

As might be anticipated, in view of its exposed coastline, coastal swamps are nowhere extensively developed in northern Cape Breton. The finest area of this sort which has come to the writer's attention is situated along the oceanward shore of South Pond (Aspy Bay), bordering the pondward side of the sand-spit elsewhere described, and extending out into the salt pond nearly a quarter of a mile (Fig. 45). This particular salt marsh is of unique interest because of the presence here *in situ* of a number of large white pine stumps. These occur scattered throughout the landward half of the marsh and their roots are well exposed above its surface. The explanation for this unusual condition seems to be this. The pines formerly grew on a low, sandy, pondward extension of the present spit. Through some shifting in the tidal currents the sand was eroded away from around the bases of the trees, and subsequently, presumably as the result of further shifting in the current, deposition has succeeded erosion and the salt marsh has been built up. The active erosion of the sand spit which is now taking place along

FIGURE 45.—Salt marsh at South Pond, Aspy Bay; scattered stumps in marsh; see text.

certain other sections of the shore upholds the plausibility of the explanation just given, and excavation of the muddy deposit about the stumps shows beach-sand at a depth of scarcely a foot below mean low tide level (in this connection, see also Harvey '18).

The pioneer association-type.—The mechanics of salt marsh formation need not be detailed here: suffice it to say that it is accomplished through the combined activity of plants and physiographic agencies (see in this connection, Davis '10). In northern Cape Breton, as in salt marshes along the New England coast, the pioneer stage in the salt marsh successional series is dominated by the rank-smelling salt thatch (*Spartina glabra alterniflora*). In typical cases this grass forms a fringe along the outer edge of the marsh. It predominates from about a foot above mean low tide level upward to within a few inches of mean high water mark, its actual vertical range being scarcely two feet. Except for *Vaucheria* and certain other filamentous algae, which commonly thrive on the muddy substratum, the salt thatch is ordinarily the only plant present in this outermost zone (*Spartina glabra* association-type).

The salt meadow association-types.—By the time the surface of a marsh has been built up to such a height that it is submerged for only a few hours daily, the pioneer association-type has given way to salt meadow: the rank, but open growth of tall, coarse salt-thatch has become superseded by a sward of lower, finer grasses, predominantly the salt meadow grass (*Spartina patens*). Along with the salt meadow grass in this association (*Spartina patens* association-type) commonly grow in greater or less abundance: *Distichlis spicata, Triglochin maritima, Plantago decipiens,* and *Limonium carolinianum.*

At this point there is one feature which is almost universally associated with salt marsh building and which demands a few words of comment. During the elevation of the substratum there may arise in various ways, which will not be discussed in detail here (but see in this connection, Yapp and Johns '17; Johnson and York '15, pp. 22, 25, etc.; Harshberger '16), sloughs and depressions which become generally distributed throughout the higher parts of the marsh. Here the depressions may be deep or shallow; they may be filled much of the time with more or less stagnant water or may be merely muddy. In the majority of these so-called "pans" the difference in level between their bottoms and the higher surfaces of the surrounding meadow is but a matter of inches or even fractions of an inch, yet they present an environment for plants which is quite different from that afforded by the higher, better drained areas. The pans may be quite barren of vegetation or they may be well populated, but their plant cover is usually in marked contrast with that of the surrounding meadow. Especially characteristic of such situations are *Salicornia europaea* and *Spergularia canadensis,* which, one or both, may be the only forms present or which may grow in association with such species as *Scirpus* *nanus, Glaux maritima obtusifolia* and *Puccinellia maritima.* Again, the pans may be colonized almost exclusively by the salt thatch, which in such situations forms a dense but usually depauperate growth, while *Distichlis* frequently skirts the edges.

In proceeding from the outer margin of a salt marsh toward the mainland, the general level of the surface becomes slightly higher and the general character of the vegetation changes correspondingly. But even in the older, higher parts, owing to the local variations in elevation and drainage, the surface vegetation is far from being uniform. The predominant plant on the higher, shoreward reaches of the salt meadow is *Juncus balticus littoralis* (*Juncus balticus* association-type), which in the salt marshes of northern Cape Breton occupies an ecological position quite similar to that held by *Juncus Gerardi* in regions farther south. The latter species is seldom met with here. Associated with the *Juncus,* and locally dominant, may be *Agrostis alba maritima, Hierochloë odorata, Scirpus campestris paludosus,* and *Eleocharis palustris.* The two latter species are especially well developed in the wetter situations, where also *Ranunculus Cymbalaria* and *Potentilla pacifica* are commonly present. Other species characteristic of the shoreward reaches of the salt meadows are *Triglochin palustris, Stellaria humifusa, Atriplex patula hastata, Solidago sempervirens,* and *Aster novi-belgii.* In addition to these, the salt thatch and most of the species of the *Spartina patens* association-type are represented here: *Spartina glabra, Scirpus nanus, Spergularia,* and *Salicornia* in poorly drained depressions; *Spartina patens* and *Plantago decipiens* in low but fairly well-drained situations. *Limonium,* however, apparently is confined to the outermost meadows.

c. THE ASSOCIATION-COMPLEXES OF BRACKISH MARSHES

Brackish marshes are of far more general occurrence than salt marshes. To some extent they are developed toward the mouths of many of the larger streams (FIG. 46), but the finest examples observed are situated at the heads of Ingonish Harbor and of Middle Harbor (Aspy Bay). The vegetation of brackish marshes includes many of the plants which have been listed as characteristic of salt marshes, but it also includes other species which are rarely represented there. The wetter parts of a brackish marsh ordinarily support a rank growth of coarse sedges, notably *Scirpus occidentalis, S. campestris paludosus, Carex maritima,* and *C. salina.* These, singly or collectively, may constitute the pioneer association-type. On the higher parts of the marsh the predominant forms usually are *Juncus balticus littoralis* and *Agrostis alba maritima.* Other forms which may be more or less abundantly represented in brackish marshes are listed below.

Figure 46.—Brackish marsh near mouth of Barrasois.

Triglochin maritima	*Carex Oederi pumila*
Triglochin palustris	*Juncus pelocarpus*
Hierochloë odorata	*Atriplex patula hastata*
Spartina Michauxiana	*Spergularia canadensis*
Eleocharis palustris	*Potentilla pacifica*
Scirpus americanus	*Plantago decipiens*
Scirpus rufus	*Solidago sempervirens*
Eleocharis palustris	*Aster novi-belgii*

Transitions from salt to brackish, from brackish to fresh swamps, etc.—It is impossible to draw a sharp line between brackish and salt swamps, on the one hand, and between brackish and fresh swamps, on the other. In the character of the predominant plants, the vegetation of the higher, shoreward reaches of a well developed salt marsh almost invariably resembles that of a brackish meadow, and it commonly includes various species characteristic of fresh water swamps. Along the shoreward edge of a salt marsh, for example, in places where unquestionably they are subject to partial submergence in salt water, at least by the high, semi-monthly "spring-tides," commonly grow such non-halophytic swamp species as *Iris versicolor, Sanguisorba canadensis,* and *Lysimachia terrestris; Vaccinium macrocarpon, Alnus incana, Myrica Gale,* and *Spiraea latifolia.* By way of further illustration, two specific transitional series will be briefly described.

MacDonald's Pond, near the mouth of the Barrasois, affords an unusually interesting illustration of this sort. At the present time the pond, which is perhaps half a mile long, is completely shut in by a barrier beach and its water is brackish; but within twelve years it communicated with the sea by a narrow outlet. Around much of the margin the vegetation is similar to that described in preceding paragraphs. The area of particular interest is a sheltered cove, connected with the main pond by a shallow open channel a dozen feet wide, presumably fed by springs, and occasionally (probably every spring) the recipient of the flood waters of the Barrasois, which reach it through a channel ordinarily dry. This cove has been for the most part filled in to a depth of more than a dozen feet with a mixture of peat and silt. From a small but deep pool near the center of the swamp thus formed to the outlet of the cove runs the open channel already referred to. Toward the outlet of the swamp, the vegetation is predominantly that of a slightly brackish marsh, consisting largely of *Spartina Michauxiana, Agrostis alba maritima, Scirpus americanus,* and *Eleocharis palustris,* together with *Potentilla pacifica, Triglochin palustris,* and *Carex maritima.* In the open water of the channel grow *Ruppia maritima* and *Potamogeton pectinatus.* Bordering the pool is a zone of *Typha latifolia,* followed by a zone of *Juncus balticus littoralis.* But throughout the remainder of the area the vegetation is predominantly that of a fresh swamp, the more prominent herbs including *Calamagrostis canadensis, Scirpus cyperinus, S.*

rubrotinctus, Carex canescens disjuncta, C. crinita, C. paupercula irrigua, Juncus filiformis, Sium cicutaefolium and *Galium palustre.* Considerable patches have been preëmpted by *Myrica Gale,* while *Sphagnum imbricatum* is locally abundant. From a superficial study it would appear that at the present time the fresh swamp, presumably as a result of the comparatively recent complete cutting off of MacDonald Pond from the sea and the consequently decreased salinity of the water, is gradually encroaching on a former brackish marsh whose vegetation over most of the swamp is now represented only by scattered relicts. But, as a matter of fact, the situation is much more complicated. This is merely suggested here, without attempt at explanation, by the facts (*1*) that while there are no living trees in the swamp there are numerous dead spruces, and (*2*) that a sample of the peat taken near the margin of the central pond showed abundant sphagnum remains at a depth of twelve feet below the surface.

Another interesting transitional series, in this case from salt pond to boggy swamp, was observed along the shores of North Pond, Aspy Bay. Here, starting from low water mark and proceeding inland, within a distance horizontally of scarcely a hundred feet one passes through the following associations: (*a*) *Sparitina glabra alterniflora* and *Spergularia canadensis;* (*b*) *Spartina patens;* (*c*) *Juncus balticus littoralis, Agrostis alba maritima,* and *Ranunculus Cymbalaria;* (*d*) *Scirpus occidentalis;* (*e*) various species of *Carex, Alnus incana, Myrica Gale, Vaccinium macrocarpon, Chrysophynum stellatum,* etc.; (*f*) boggy swamp with *Carex trisperma, Rynchospora alba, Sarracenia, Drosera rotundifolia, Vaccinium Oxycoccus, Chamaedaphne, Ledum,* various *Sphagna,* etc. Area *a-c* are below mean high tide level, area *d* is partly above and partly below, area *e* is barely out of reach of ordinary high tides, and area *f* extends down to within less than a foot (vertically) of mean high water mark.

In discussing the occurrence along the shore of Cold Spring Harbor of non-halophytic vascular plants, in places where the soil is often covered by salt water, sometimes for as much as three or four hours daily, Johnson ('15, p. 110, etc) explains the situation somewhat as follows. The ground in such places is usually springy, and the soil is saturated with fresh water, the abundance of which "prevents the salt water from really penetrating it." In such situations, therefore, many upland and fresh swamp plants which can stand more or less inundation of their shoots with salt water but which cannot endure salt water around their roots are enabled to push down to much lower levels than usual, even growing below mean high tide level. This explanation is doubtless the correct one, and the line of demarcation between halophytic and non-halophytic associations is always sharper along dry than along wet shores, although even here non-halophytic plants frequently invade areas which are subject to tidal overflow.

Of peculiar interest in this connection is the occurrence of bryophytes in situations where they must necessarily be more or less exposed to the influence of salt water. In northern Cape Breton, for example, *Chrysohypnum stellatum* commonly grows quite abundantly on the wet soil of brackish meadows, in company with such vascular species as *Triglochin palustris* and *Ranunculus Cymbalaria,* and the sphagnums sometimes occur in similar situations. *Sphagnum palustre* and *Bryum inclinatum* have been collected on exposed sea cliffs well within reach of storm waves, while *Bryum fallax* thrives around the edges of salt ponds. From these and similar observations elsewhere, there seems little question that while as a class the bryophytes may be regarded as halophobous, many of them are capable of existence in habitats where, periodically at any rate, they are bathed in brackish or salt water.

D. Secondary Formations of the Hydrarch Series

Formation-types resulting primarily from Human Activity

Association-complexes due to various agencies

In so far as the association-types of lakes and ponds are concerned, the effect of human activity has been negligible. The vegetation of swamps has been variously modified, but it is only occasionally that it has suffered as severely as that of uplands. This state of affairs, in the main, is easily explained by the fact that in this climate, with its abundant atmospheric precipitation, the swamps, for the most part, are of comparatively little value from the cultural standpoint. Instances of a more or less pronounced change in swamp vegetation from its original character are afforded by well-drained swampy areas which have been converted into meadow-land. Here sedges and grasses predominate and the vegetation approximates more or less closely that elsewhere described as characteristic of open, well-drained swamps. Grazing cattle and sheep may bring about the introduction into a swampy area of plants not previously present and they may appreciably retard succession, but otherwise they do not seriously modify the conditions. Aside from instances such as those just outlined, any changes in the vegetation and succession in the swamps which are attributable to human activity have been largely due to logging and fire. The former agency may have resulted in the removal of the original forest cover, where one was present, but beyond this has had little retrogressive effect on the vegetation in the areas concerned. The influence of fire is much less in swamps than on uplands, since the very wetness of the substratum may prevent the complete destruction of subterranean plant organs. In general, the association-types of secondary hydrarch series appear to differ little from those of the primary series as described elsewhere.

THE NORTHEASTERN EVERGREEN CONIFEROUS FOREST CLIMATIC FORMATION IN NORTHERN CAPE BRETON

I. GENERAL CONSIDERATIONS

Distribution and general character.—By far the greater part of northern Cape Breton, indeed nearly all the country above an elevation of approximately seven hundred feet, is occupied by this formation. With reference to the general ecological aspect of the vegetation, however, the area thus defined can be subdivided into two regions: (*1*) the forest region proper, which hereafter will be referred to simply as the Forested Region; and (*2*) the Barrens. The extent of these regions is roughly indicated on the map (Fig. 2). In a general way, the forested region can be said to include the upper mountain slopes, together with the outer and lower, less exposed parts of the plateau. Here the country is covered by an almost unbroken forest of balsam fir, spruce, and paper birch (Figs. 4, 47, 49). The barrens (Figs. 48, 51, etc.) include primarily the higher, more exposed portions of the plateau, being especially well developed toward the interior, and occupying altogether an area estimated by Fernow ('12, p. 20) at about 375 square miles. Here forests of the usual description are largely confined to the "gulches," while the country at large is covered mainly by heath and scrubby forests, swamps and bogs ("muskeag").

Evergreen coniferous forest in the highlands a climatic, not an edaphic climax.—In a brief summary report of field work in Cape Breton, Macoun ('98, p. 199A), records the following observations: "Before going to Cape Breton, I had, like many others, a very mistaken notion of the 'barrens'[12] in the northern part of the island. After spending some time in the north and on the plateau, the conditions producing these barrens became evident. Along the base of the escarpment bordering the plateau, the subsoil is generally impervious, and here spruce and fir occupy the ground. The broken face of the escarpment is

[12] Macoun here seems to use this term in a much more comprehensive sense than that in which it is employed by the writer.

usually covered with broad-leaved trees, such as maple, beech and birch, because it is well drained." In other words, Macoun would seem to intimate that in the mountains, as the writer has shown to be locally the case in the lowland, the evergreen coniferous forest is to be regarded as an edaphic rather than

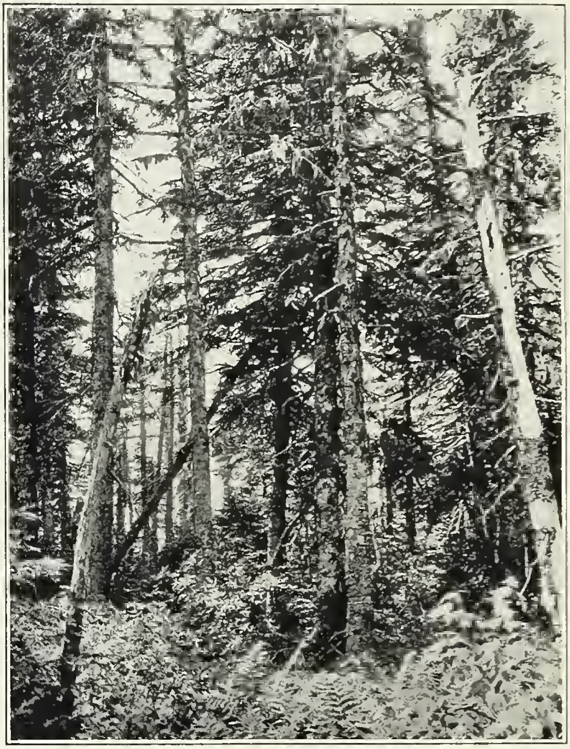

FIGURE 47.—Primeval coniferous forest of the regional climax type; mountains near Cape North.

a climatic climax association-type. With this opinion the writer emphatically disagrees for reasons which are briefly outlined below.

In ascending the mountain slopes which flank the plateau, there is a gradual transition from the forests of the lowland climax type to those of the highland, a transition which has been repeatedly traced out and verified. In passing upward, the character trees of the deciduous climax formation disappear in approximately the following order: beech; hemlock; oak and sugar maple; white pine; red maple; yellow birch. Except for the two species last named, none of these are represented in the evergreen coniferous climax forests of the highland. The yellow birch, however, is frequently encountered here in edaphically favorable situations, while the red maple is commonly represented by shrubby specimens, which, however, seldom attain the dignity of trees. It is also significant that for some distance above the level where it ceases to occupy a prominent position in the forest, the sugar maple still maintains an important place in the undergrowth, being represented here by more or less abundant, scraggly, shrubby specimens, which exhibit unmistakable evidence of having been repeatedly killed back. It is further significant that there is a marked correlation between the vertical distribution of most of these trees in northern Cape Breton and their north-and-south geographic range; and it is of interest to observe that toward its upper limits the deciduous-mixed forest commonly is dominated by the yellow birch.

The facts just presented, and particularly the complete absence on the plateau, even in the many situations which are edaphically favorable, of beech, sugar maple and oak, hemlock and white pine, would seem to indicate conclusively that the factors responsible for the character of the climax association-type here are climatic and not edaphic. The controlling factor in determining the upward extension of the deciduous forest climatic formation is probably temperature (see discussion elsewhere under head of climate). But atmospheric humidity may also be a decisive factor, since the upper limit of the deciduous climax forest coincides approximately with the lower limit of the low-lying cloud belt in dull weather, a feature which has been commented on earlier (p. 274).

The status of the barrens, from the standpoint of ecological plant geography.—The barrens are of peculiar interest, since they present essentially the same type of vegetation that prevails over vast areas on the Labrador Peninsula and throughout northern Canada, regions concerning which almost nothing is known ecologically. So distinct in its general aspect from that of the forest region proper is the vegetation of the barrens that it was at first thought to constitute a distinct climatic formation.

Further investigations, however, have indicated beyond question that this remarkable formation-complex, in northern Cape Breton, is the result of edaphic rather than climatic factors. The climax association-type of uplands in the barrens bears much the same relation to the coniferous forest climax of the highlands that the climax association-type of exposed headlands along the seacoast bears to the deciduous forest climax of the lowland. The relation between the edaphic formation-complex here and

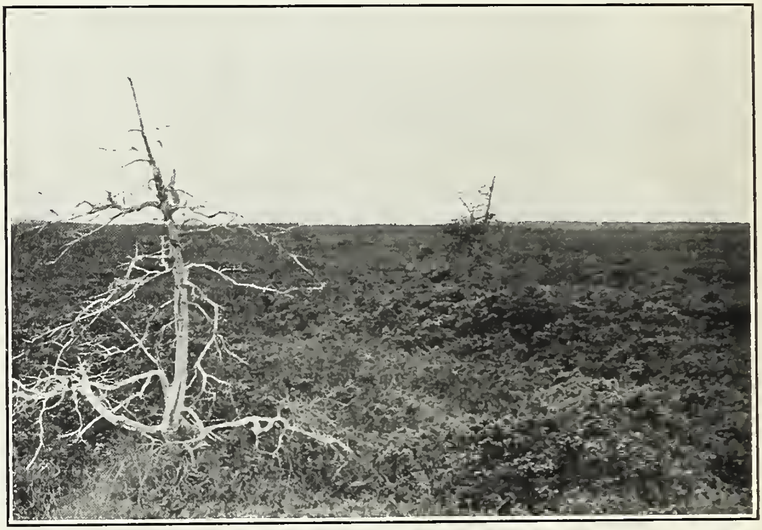

Figure 48.—Barrens in mountains north of Barrasois River (Scotchman's Barren); vegetation closely approximating heath; tamaracks in left foreground and mid-distance.

that of the highlands as a whole is somewhat analogous to the relation between the edaphic formation-complex of the New Jersey pine barrens and that of the whole state of New Jersey. The character of the vegetation in the barrens is attributable very largely, directly or indirectly, to conditions of exposure, topography, and soil. Along the streams the climax forests of the forested area extend into the heart of the barrens, while, conversely, in high, exposed situations the vegetation of the barrens reaches well toward the coast.

Forest resources of the region.—In summing up the results of a timber survey of this region, made a number of years ago, Fernow ('12, pp. 20, 24) estimated the commercially productive forest area of the "1200 square miles of plateau" at about 780 square miles, the unproductive area being largely occupied by barrens. He describes the forest as "an almost unbroken pure balsam fir forest, with only 15 per cent. to 25 per cent. of spruce, except in the black spruce swamps, and about three per cent. of birch," in which "the trees run from 6 to 14 inches in diameter, occasionally up to 18 inches, with 36 feet log length, and ten trees to the cord." Among the sample plots measured in connection with this survey, some 180 in all, many ran from fifty to sixty cords per acre, with an average of at least twenty. The forest is of value chiefly for pulpwood; saw timber is scarce. On a basis of the figures obtained, Fernow estimates that the area contains twelve million cords of pulpwood, or an amount equal to that which is computed to be present in the entire province of Nova Scotia outside of northern Cape Breton, an area more than sixteen times as large. And while these facts are primarily of economic import, they are also of ecological interest, since they serve to emphasize the dissimilarity between the forests of this region and those in other parts of Nova Scotia.

Apropos, it may well be suggested here that while, as has been shown in preceding pages, conditions over much of the lowland are favorable to the development of forests of the deciduous climax type, they are even more so to the growth of coniferous forests. It is only through their inability, in the long run and under natural conditions, to cope successfully with their southern competitors that the northern conifers do not today constitute the predominating element in the primeval, as well as in the second growth forests of this region. Both climate and soil are more favorable here than in the highland. It is the conviction of the writer that the commercial production of spruce and balsam fir in the lowland of northern Cape Breton offers large possibilities for the future.

II. THE REGIONAL CLIMAX ASSOCIATION-TYPE: THE CLIMAX FOREST

The trees of the climax forest.—The general aspect of these forests is well portrayed by FIGS. 47, 49. The balsam fir is by far the most abundant species, comprising ordinarily more than

75 per cent. and sometimes fully 85 per cent. of the stand. Individual trees may attain a trunk diameter in excess of sixteen inches with a height approaching seventy feet, but such specimens are exceptional: the bulk of the balsams which go to make up the mature forest run from eight to twelve inches in

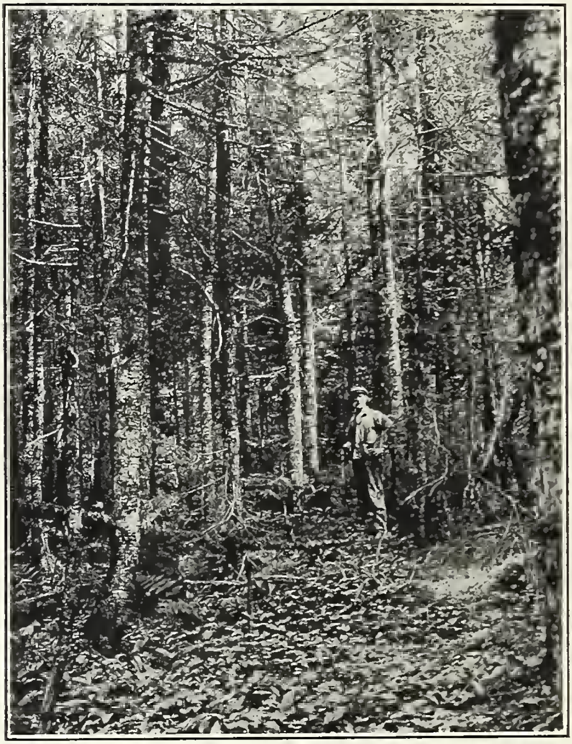

FIGURE 49.—Primeval coniferous forest of the regional climax type; mainly balsam fir; mountains north of Barrasois River.

diameter, mostly about ten, and range around fifty feet in height. The average age of such trees, as ascertained in many cases with the aid of an increment borer, would scarcely exceed seventy years. Occasional specimens are encountered which must be 125 or more years of age, but the exact age of these larger specimens it is seldom possible to determine accurately, owing to the fact that almost invariably they are heart rotted. It is a noteworthy fact, as Cooper ('13, pp. 17–21) has pointed out, that while the balsam fir far outnumbers all other trees in the forest, yet, owing to its susceptibility to fungus attack and consequent liability to windfall, its relative abundance decreases greatly with age. In other words, "its high birth-rate is balanced by a high rate of mortality."

Second in importance to the balsam fir in the climax forest is the white spruce, which is well distributed throughout, common, yet nowhere approaching the balsam in abundance, and conspicuous by reason of its relatively large size. It ordinarily attains a diameter of sixteen inches, sometimes of more than two feet, and as a rule is correspondingly taller than the balsam. Black spruce is also an important constituent, locally quite common, and in size about equal to the balsam. It never attains here the proportions which it exhibits in the Adirondacks where, in virgin forests, trees three feet in diameter and more than a hundred feet high are frequent. These three trees comprise the evergreen coniferous element in the climax forest. The deciduous element is represented primarily by two species, the paper birch and the mountain ash. The paper birch is well scattered through the forest, somewhat less abundant, perhaps, than the white spruce, but prominent by reason of its showy bark and spreading, broad-leaved crown. In height it seldom exceeds the average for the forest as a whole, and its trunk is rarely as much as a foot in diameter. The mountain ash is a very characteristic and omnipresent constituent, usually a small undertree, but sometimes fully fifty feet high with a trunk a foot in diameter. The yellow birch, though frequently represented in favorable situations, never reaches anywhere near the size which it attains in the lowland. Red maple is more or less scattered throughout, but as a rule is little more than an undershrub. The small-toothed aspen (*Populus tremuloides*) also is occasionally present.

The undergrowth in the climax forest.—Below is given a list of the characteristic shrubs and herbaceous vascular plants in the coniferous climax forest. Their general occurrence and local abundance when present is indicated by symbols, as explained elsewhere (p. 283).

Shrubs

Taxus canadensis	*cc*	*Acer spicatum*	*cc*
Corylus rostrata	*cf*	*Acer pennsylvanicum*	*cf*
Ribes prostratum	*cf*	*Lonicera canadensis*	*cf*
Amelanchier sp.	*co*	*Viburnum cassinoides*	*cf*
Nemopanthus mucronata	*cf*	*Viburnum pauciflorum*	*fo*

Herbaceous Vascular Plants

Phegopteris Dryopteris	*fl*	*Oxalis Acetosella*	*cc*
Phegopteris polypodioides	*cf*	*Aralia nudicaulis*	*cc*
Pteris aquilina	*cf*	*Cornus canadensis*	*cc*
Aspidium spinulosum var.	*fo*	*Moneses uniflora*	*cf*
Osmunda cinnamomea	*cf*	*Pyrola secunda*	*co*
Osmunda Claytoniana	*ff*	*Monotropa uniflora*	*co*
Clintonia borealis	*cc*	*Monotropa Hypopitys*	*co*
Maianthemum canadense	*cc*	*Epigaea repens*	*cf*
Streptopus roseus	*co*	*Chiogenes hispidula*	*cc*
Habenaria obtusata	*cf*	*Trientalis americana*	*cc*
Epipactis sp.	*co*	*Linnaea borealis americana*	*cc*
Listera cordata	*fo*	*Solidago macrophylla*	*ff*
Coptis trifolia	*cc*	*Aster acuminatus*	*cl*
Mitella nuda	*cl*		

Except for occasional colonies of the yew, the shrubs and herbaceous vascular plants in the undergrowth seldom form dense masses of vegetation. The ground is usually occupied by a continuous but rather open growth of the various species mentioned above. As on Isle Royale, the most conspicuous element in the herbaceous ground-cover is the bryophyte contingent, whose profuse development here in these coniferous forests is in striking contrast to its paucity in the deciduous climax forests of the lowland. Almost everywhere the ground is overlain by a soft, verdant carpet of *Bazzania trilobata, Hypnum Schreberi,* and *Hylocomium splendens,* with which are associated *Dicranum undulatum, Rhytidiadelphus loreus, R. triquetrus, Ptilium crista-castrensis* and species of *Sphagnum.* In the drier places the hypnum alone may predominate, in moist situations the sphagnums. Ordinarily all the species mentioned, except perhaps the sphagnums, are well represented. The ecological significance of this bryophyte ground cover in hindering evaporation and impeding drainage, thereby influencing not only the moisture of the substratum, but also its temperature, aeration, and toxicity, can hardly be questioned. Usually the surface layer of living plants is underlain by a more or less spongy mass of incompletely decomposed vegetable remains (the duff), which commonly is six inches or more in thickness. Corticolous liverworts and mosses in general are much more poorly developed in coniferous than in deciduous climax forests, although the lichens occupy a prominent position, particularly the beard lichen (*Usnea barbata*), which in well-lighted situations commonly drapes itself in graceful festoons from the branches of the trees.

Reproduction of the climax trees.—In his ecological investigation of the northeastern evergreen-coniferous climax forest, as developed on Isle Royale, Cooper ('13, pp. 42, 43) arrived at the following conclusions, which were based in large part on the intensive study of carefully selected quadrats. For successful reproduction the balsam fir requires abundant light, given which it will germinate and thrive in any sort of situation. In the forest, reproduction is practically confined to the openings caused by windfall. "The forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little young growth beneath. The history of a windfall area is as follows. After the débris has disintegrated sufficiently to allow abundant light to reach the ground, a new generation of trees springs up, approximately even-aged, composed of the three dominant species [balsam fir, white spruce, and paper birch], *Abies* always greatly preponderant. During the continued development of this group most of the individuals are at various times eliminated, . . . Because of the dense shade no new individuals can start beneath them and the final outcome is a group composed of a few large trees, approximately even-aged, in which *Abies* has nearly or quite lost its position of dominance to *Betula*." The resultant forest is thus "a mosaic or patchwork which is in a state of continual change." Yet "the forest as a whole remains the same, the changes in various parts balancing each other."

Turning now to northern Cape Breton, it would seem that the ecological relations of the balsam fir here are somewhat different from those just described for Isle Royale. Here, as there, openings due to windfall are a characteristic feature of the forest; and the immediate sequel to windfall is a commonly prolific crop of balsam. Some of the young trees may originate from seeds shed previously to the windfall, but which have been lain dormant on the ground for want of conditions suitable to germination. Others doubtless arise from seeds shed only a short time before the windfall, or else contemporaneously with or subsequent to it. But many of the young trees represent specimens which were already present in the forest previous to the windfall. For while the reproduction of the balsam is most prolific in the windfall areas, it is by no means confined to them. It is seldom that the shade on the forest floor is sufficiently dense to prevent reproduction, and almost everywhere the undergrowth in a forest of the climax type includes numerous small, scattered balsams, mostly suppressed but ready to take advantage of any chance opening which may occur in the canopy overhead. Such openings, to be sure, are commonly due to windfall, since except in protected situations the balsam seldom dies a natural death. It is a not infrequent occurrence for groups of trees to be overthrown by the wind, thus giving rise to openings of considerable extent, but more commonly it is only scattered individuals which are blown down at one time. The influence of the openings thus created is probably twofold: (*1*) more light is introduced into the lower layers of vegetation, and (*2*) wherever sunlight reaches the forest floor the moss carpet, together with the more or less spongy underlying layers of duff and humus, tend to become somewhat dried out and in consequence warmer and better aerated. This latter indirect influence, the possible significance of which is suggested by Cooper ('13, p. 20), it seems to the writer, is of fully as great importance here in northern Cape Breton, at least so far as the balsam is concerned, as is the direct influence of increased illumination. The understory of balsams in a deciduous forest is much more thrifty than that in a coniferous forest, a circumstance which might be explained by the more favorable soil conditions there: so far as shade is concerned, this is generally greater in a deciduous than in a coniferous forest, at least during the growing season. But without question increased illumination is a very important direct factor, and perhaps the most important one, affecting the growth of the balsam. In this connection attention may be called to earlier remarks (p. 285) regarding the ecological relations of the balsam.

The white spruce and paper birch are much more dependent on an adequate light supply for successful reproduction than is the balsam fir. This is demonstrated by the relative abundance of the young growth of these two species in a windfall area or clearing, as contrasted with the great scarcity of any but large trees in the forest. In the case of the paper birch, to quote Cooper ('13, p. 22), "low birth-rate is compensated by a very low mortality and it is thus able to maintain itself in making a good proportion of the mature stand." The same observation may apply equally well to the white spruce, which apparently is relatively more abundant here than on Isle Royale. The black spruce grows best in well lighted situations, but, like the balsam, it is capable of maintaining itself for years in moderate shade.

With reference to their tolerance of shade in this climate, the writer would arrange the climax trees of the northeastern coniferous forest climatic formation in northern Cape Breton in about the following order: paper birch and aspen (very intolerant), white spruce (intolerant), balsam fir, black spruce, and mountain ash (tolerant), and yellow birch (very tolerant).

III. THE EDAPHIC FORMATION-COMPLEX OF THE REGION

A. Preliminary Observations

One of the most perplexing features of this region, when it comes to the exact analysis and delimitation of the various formation-types, is the manner in which these overlap and intergrade. This condition is attributable primarily to the abundance of atmospheric moisture. In less humid climates soil moisture plays an all important rôle in determining the character and distribution of vegetation, and as a result differences in soil and topography are associated with corresponding differences in plant cover. In general it can be stated that the influence of soil and topography on the character and distribution of plant associations is least pronounced in humid climates; most pronounced in arid climates: or, in other words, that this influence is inversely proportional to the dryness of the climate. This tendency toward uniformity in a humid region is of course due in part to the fact that here many soils, which in a less humid region would be too dry to permit the development of the types of association which characterize the better soils, are kept constantly moist. It may also be due to the fact that bare rock outcrops, which in themselves are unable to retain water except in crevices, become rapidly overgrown, except where they are too steep, by a layer of lichens and bryophytes which create a water-retaining substratum and thus tend to produce ground conditions similar to those found in soils which naturally would be more favorable to plant growth. In the coniferous forest region of northern Cape Breton, and probably in other similar regions as well, this tendency toward uniformity is accentuated by the fact that in the upland forests, owing largely to the prolific development of mosses and liverworts and the copious accumulation of humus, not only is the substratum kept constantly moist, but it is invariably acid to litmus, thus approximating the conditions which prevail in bogs and in the majority of the swamps. In less humid climates, many of the species which here are characteristic of uplands, or which grow both on uplands and in bogs and swamps, are restricted to situations of the latter sort. The tendency for different edaphic formation-types to merge into one another is exhibited to some degree in the lowland region of northern Cape Breton; it is quite pronounced in the forested portion of the highlands; but it reaches its culmination in the barrens, where it is almost impossible to draw a sharp line between the vegetation of uplands and that of the swamps.

B. Formations of the Xerarch Series

1. The Formation-types of Ordinary Uplands in the Forested Region

a. the association-complexes of well-drained uplands

In comparing xerarch successions on ordinary, well-drained uplands here with those of the lowland, the most striking difference is seen in the character of the climax association-type. There, a balsam fir–spruce–paper birch forest may represent merely a passing stage in the succession: in all edaphically favorable situations it is a temporary association-type, destined in the course of time to be superseded by a forest of the deciduous type. Here, however, a forest of this sort represents the culminating stage in the succession: it is a permanent association-type. Throughout most of the forested region in the highland this coniferous forest climax has been attained, and it is only in edaphically unfavorable situations or in places where the original forest has been destroyed by fire that the more primitive stages in the succession are encountered. The association-types of exposed hilltops may resemble those of similar situations in the barrens, but, on the whole, the sequence

FIGURE 50.—Low coniferous woodland on plateau west of Ingonish.

and general character of the preliminary successional stages in the highland is essentially similar to what has been described for the lowland and therefore need not be discussed further. As a rule the succession takes place rapidly, the trees of the climax forest being present from the outset, and the various stages are more or less telescoped.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED UPLANDS

Forests of the regional climax type attain their optimum development on well-drained slopes. But over a considerable portion of the forested region the country is flat or rolling, with a tendency to be poorly drained, and the prevailing type of vegetation here is low, more or less swampy woodland (FIG. 50). No sharp line can be drawn between woodlands of this description, which constitute an edaphic climax association-type, and forests of the regional climax type. Essentially the same species may be present in both cases. Here, however, the trees average scarcely twenty-five feet in height, and black spruce may be quite as abundant as balsam, while swamp species, notably *Osmunda cinnamomea* and the sphagnums, commonly predominate in the undergrowth. Associations of this sort may originate through a

FIGURE 51.—Summit of low hill in barrens; mountains west of Ingonish; vegetation in immediate foreground, dwarf shrub heath; in mid-distance (vicinity of figure and beyond), mainly dwarf shrub–spruce heath. The low, bushy spruce in center foreground was about 150 years old.

hydrarch successional series, but more commonly the pioneer stages are xerophytic, the swampy condition being induced very largely through the activity of vegetation in retarding drainage. Parts of the plateau occupied by barrens are commonly skirted on all sides by low woodland, which forms a transition zone between these areas and those congenial to forests of a more mesophytic character. Raised bogs have been developed locally on uplands in the forested region, but these are especially characteristic of the barrens and will be discussed under that head.

2. The Formation-types of Ordinary Uplands in the Barrens

a. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED UPLANDS

The rock face–crevice complex.—Over most of the plateau the bed rock is covered by a thin soil which may be residual or extraneous in its origin. Here and there, however, rounded knolls or blocks of granite and syenite rise conspicuously, and on these may be found rock-face and crevice associations essentially similar to those which have been described as characteristic of rock outcrops in the lowland.

But the prevailing pioneer type of vegetation on uplands in the barrens is some sort of a heath. In the heath the lichens, notably the cladonias, are invariably conspicuous, while sedges and grasses, shrubs and scrubby trees occupy a position of varying importance.

The dwarf shrub heath association-type.—This is characteristically developed on exposed hill tops, where the soil may support only the scantiest kind of a plant cover (foreground of FIG. 51). In such situations the ground in places is bare; elsewhere it is overlain by a sparse mat of cladonias and *Racomitrium lanuginosum,* or maintains a stubby growth of *Polytrichum juniperinum, P. piliferum,* and *Ceratodon purpureus.* Of the seed plants peculiar to such habitats, *Potentilla tridentata* is worthy of note, but particularly characteristic are the four shrubs: *Empetrum nigrum,* which forms low, sprawling mats; *Vaccinium uliginosum,* which occurs in depressed circular patches; *Vaccinium Vitis-Idaea,* which scrambles over the ground and frequently is intricately interwoven in the lichen mat; and *Vaccinium pennsylvanicum angustifolium,* a form of blueberry only a few inches high. In addition to these, there is usually a scattering of other plants, particularly ericaceous shrubs, all of which are noticeably impoverished.

Typical dwarf shrub heath occurs locally throughout the barrens, but in a pure state is nowhere extensively developed. In exposed situations it may constitute a permanent association-type, i. e., an edaphic climax. But more commonly it seems to represent a temporary stage, destined to be superseded by dwarf shrub–spruce heath, into which it nearly everywhere merges. In places dwarf shrub heath very evidently is a retrogressive type which has arisen subsequent to the destruction of dwarf shrub–

spruce heath; but more commonly it represents a primitive phase. Characteristic plants here, in addition to those already specifically mentioned, are the following:

Lichens

Cladonia alpestris	*Cladonia rangifernia*
Cladonia coccifera	*Cladonia sylvatica*
Cladonia crispata	*Cetraria islandica*
Cladonia pyxidata	*Sphaeophorus coralloides* Pers.

Seed Plants

Juniperus communis montana	*Kalmia angustifolia*
Ledum groenlandicum	*Kalmia polifolia*
Rhododendron canadense	*Melampyrum lineare*

The sedge–grass heath association-type.—This occurs in somewhat moister, less exposed situations than the dwarf shrub heath, as for example, or rather dry slopes. The ground is usually covered by a luxuriant growth of cladonias, which may be replaced locally by *Racomitrium lanuginosum* or occasionally by xerophytic species of *Sphagnum,* such as *S. capillaceum tenellum* and *S. tenerum.* The predominant vascular plants are the sedge, *Scirpus caespitosus,* and the grass, *Calamagrostis Pickeringii.* Other herbaceous plants generally present are as follows:

Lycopodium sitchense	*Cornus canadensis*
Lycopodium annotinum pungens	*Prenanthes trifoliolata*
Deschampsia flexuosa	*Solidago uliginosa*
Melampyrum lineare	*Aster nemoralis*

In addition to these, the woody species characteristic of the dwarf shrub–spruce heath are well represented, but for the most part by small specimens, scattered and relatively inconspicuous. Like the preceding association-type, the sedge–grass heath is nowhere extensively developed, and it displays a constant tendency to pass over into dwarf shrub–spruce heath.

The dwarf shrub–spruce heath association-type.—This is one of the most widely distributed and most distinctive types of vegetation in the barrens. It commonly occupies the upper slopes of hills (Figs. 51, 52), and in general prevails on well-drained uplands wherever the conditions of exposure are such as to prevent the development of a more mesophytic type of vegetation. At first sight an area occupied by this association-type appears as a crowded, labyrinthine series of low mounds or hummocks, irregular in size and shape, but averaging perhaps from three to ten feet in diameter by from one to two feet in height. The hummocks are densely overgrown with cladonias and support a thick growth of low shrubs, mostly ericads. Depressed, bushy trees, mainly black spruce, scarcely two feet high but spreading

Figure 52.—Dwarf shrub-spruce heath; barrens in mountains west of Ingonish.

out laterally over a radius of several feet, constitute an important element in the vegetation, growing on or alongside the hummocks. Here and there, scattered tamaracks may be conspicuous by reason of the fact that they project somewhat above the general surface level of the surrounding vegetation, which otherwise maintains a nearly uniform height at from two to two and a half feet above the floor of the depressions which separate the hummocks. In typical dwarf shrub–spruce heath, the depressions between the hummocks are open and, aside from the cladonia mat which nearly everywhere covers the ground, their vegetation is scanty.

The following list includes the more characteristic plants of dwarf shrub–spruce heath:

Lichens

Cladonia alpestris	*Cladonia rangiferina*
Cladonia sylvatica	*Cetraria islandica*

Bryophytes

Sphagnum capillaceum tenellum	*Leucobryum glaucum*
Sphagnum tenerum	*Racomitrium lanuginosum*
Ptilidium ciliare	*Hypnum Schreberi*

Vascular Plants

Pteris aquilina	*Cornus canadensis*
Abies balsamea	*Andromeda glaucophylla*
Picea mariana	*Chamaedaphne calyculata*
Larix laricina	*Epigaea repens*
Juniperus communis montana	*Kalmia angustifolia*
Maianthemum canadense	*Kalmia polifolia*
Myrica Gale	*Ledum groenlandicum*
Pyrus melanocarpa	*Rhododendron canadense*
Amelanchier sp.	*Vaccinium canadense*
Empetrum nigrum	*Vaccinium pennsylvanicum*
Nemopanthus mucronata	*Viburnum cassinoides*

Any of the other species mentioned earlier as characteristic of sedge–grass heath may grow here also, but these, for the most part, are confined to the depressions between the hummocks.

The structure of the hummocks (Fig. 53) is extremely interesting. Examination shows them to be due entirely to plant activity. Internally they consist of an intricate mass of incompletely decomposed vegetable débris: the sort of structure commonly referred to as "raw humus." Ordinarily the bulk of the material has been derived from the lichens and from the leaves of the various shrubs which inhabit the surface of the hummock, the whole being bound together by the stems and roots of the surface vegetation. In some cases the sphagnum has contributed very largely to the formation of the hummocks: in one instance the excavation of a hummock two feet high, whose surface vegetation, aside from various shrubs, consisted entirely of *Sphagnum capillaceum tenellum,* showed the whole hummock to have been built up by this moss, whose remains, still in a fine state of preservation, extended nearly to the bottom, where, at the very base of the hummock and overlying the gravelly substratum, was a thin layer of *Leucobryum* remains. It is evident that for the most part the formation of these hummocks is a result of the combined activity of the lichens, particularly the cladonias, and the ericaceous shrubs. They have arisen somewhat as follows. Previous to their formation the ground was covered by a thin mat of mosses and lichens in which grew vari-

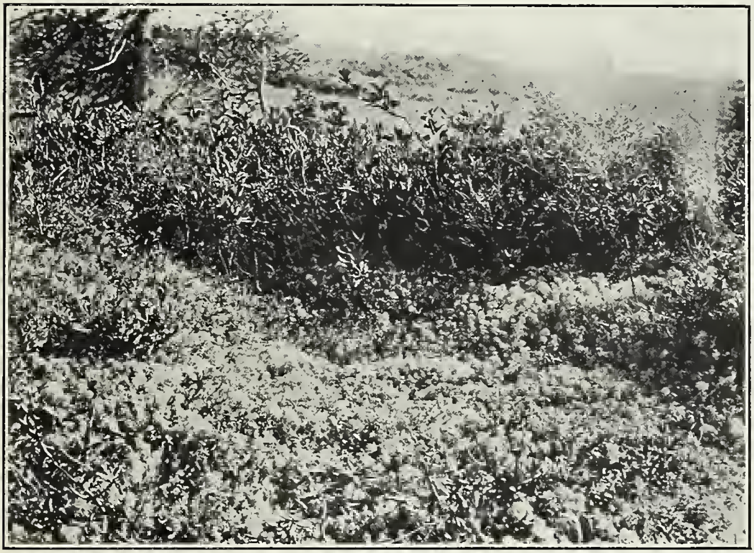

FIGURE 53.—Detail view of hummock in dwarf shrub heath association-type; *Cladonia alpestris, Chamaedaphne, Ledum,* etc.; barrens in mountains west of Ingonish.

ous herbaceous plants and shrubs: essentially the same condition which prevails in sedge–grass heath and which still persists in the open depressions between the hummocks. Where edaphic conditions are favorable the cladonias exhibit a marked tendency to grow upward, but they are unable to do so to any extent without some sort of support. The needed support is furnished by the shrubs which, where they grow close enough together, afford a sort of scaffolding upon or around which the lichens are able to push upward. As the shrubs gradually become buried below they grow above, at the same time branching more or less profusely. And as the branches become covered over they produce copious adventitious roots, with the result that the original number of physiologically independent individuals, as viewed at the surface of the hummock, becomes multiplied many times. The shrubs, therefore, which cover the surface of a hummock have been derived directly, in large part at least, from pre-existing shrubs: they antedate the hummock itself.[13]

The genetic relationship between dwarf shrub and sedge–grass heath, on the one hand, and dwarf shrub–spruce heath, on the other, has already been suggested. During the evolution of the present association-type, various of the herbaceous vascular plants characteristic of the more primitive stages either disappear or else become in large part or wholly confined to the depressions: to situations where there is no great depth of humus and where the soil relations presumably are more favorable than on the hummocks. This is true, for example, of both *Scirpus* and *Calamagrostis,* and of such forms as *Lycopodium, Potentilla, Solidago,* and *Aster.* At the same time, scrubby trees become increasingly conspicuous.

In its ecological aspect, an association of the sort just depicted certainly approximates very closely dwarf shrub heath, as defined by Warming ('09, pp. 210–214). It agrees in the nature of the underlying soil, in the dominance of lichens and ericaceous shrubs, in the low stature of the vegetation, and in the copious production of raw humus: this latter a phenomenon which, according to Warming, "must be regarded as the most characteristic peculiarity of heath." It would seem to differ from typical heath primarily in the presence of various arborescent species which, in more favorable situations, attain much larger dimensions than here. But while any of the trees of the climax coniferous forest (with the exception of yellow birch and red maple) may be represented here, it is significant that black spruce is invariably predominant; that tamarack, which is practically absent from the climax forest, is usually a prominent constituent; and that, on the other hand, balsam fir, the predominant tree in forests of the regional climax type, is of very subordinate

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[13] In this connection, see observations by Ganong, quoted on p. 447.

importance. In its typical development, then, the writer would regard this type of association as a true heath.[14]

Transition from heath to Krummholz.—All intergradations are found between typical dwarf shrub–spruce heath and *Krummholz,* the association-type to be treated next, and in this connection the behavior and ecological relations of the spruce and other evergreen conifers has an important bearing. As the principal species concerned, the black spruce will serve to illustrate the points in question. Like the ericaceous shrubs, this species appears at an early stage in the development of the heath: it is antecedent with reference to the hummocks. Through the death of the primary leader, the extensive development and copious branching of the lateral shoots, and commonly also through vegetative reproduction by layering, it characteristically assumes a low, compact, rounded, shrub-like habit. So closely may one of these bushy spruces conform with the contour of the hummock alongside which it grows that on superficial examination it appears to be growing on the hummock itself; but ordinarily the relationship is very different. For the shade produced by these clumps of spruce has an important local effect on the nature of the vegetation, in that it inhibits the growth of lichens and thereby prevents or checks hummock formation. In some areas the depressions between adjacent hummocks are completely filled in by a dense snarl of scrubby spruces which rise to about the same general level as the low vegetation which tops the hummocks. From a distance the surface contour of

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[14] Warming ('09, p. 210) defines heath as "A treeless tract that is mainly occupied by evergreen, slow-growing, small-leaved dwarf-shrubs and creeping shrubs which are largely Ericaceae." But the use of the term is not wholly restricted to such areas. Warming himself recognizes lichen-heath and moss-heath (op. c., pp. 205, 208), and Graebner ('01, pp. 26, 27), while distinguishing as most representative areas of the sort specified by Warming, extends the term to include "not only areas dominated by ericaceous shrubs, but open tracts in which there is neither a good tree growth nor a close grass turf; [in which] ligneous plants dominate, especially low shrubs. [Thus,] what we call pine or oak barrens would probably be included in Graebner's heath" (quotation from Cowles' review of Graebner's book). Applying the term in this latter sense, Harshberger ('11, pp. 165-168) regards the "plains" of the New Jersey pine-barrens as heath. Rübel ('14, p. 237) would restrict the use of the term heath to "ericoid-leaved bushland."

such an area appears quite flat and easy to travel, but one soon learns to steer clear of these "tanglefoot" barrens, as an old trapper who served as guide for the writer aptly termed them, whenever possible. Barrens of this sort obviously represent a transition stage between the dwarf shrub–spruce heath association-type and the *Krummholz* association-type. Not only is the arborescent element in the vegetation present in increased abundance, but the character of the undergrowth is different.

FIGURE 54.—*Krummholz* in immediate foreground, passing into low woodland or forest scrub behind the figure; barrens in mountains west of Ingonish.

For the presence of the spruce not only causes the exclusion of certain species, but favors the introduction of others. Underneath these dwarf evergreen trees, wherever they occur, may be found any or all of the liverworts and mosses characteristic of the climax forest of the region (e. g., *Bazzania, Dicranum undulatum, Hylocomium splendens, Ptilium*), together with various of the herbaceous plants (e. g., *Clintonia, Coptis, Linnaea*).

The Krummholz association-type.—This differs from heath in the following important respects: (*1*) Dwarf, bushy trees

(*Krummholz*) predominate and form a relatively closed stand. (*2*) The lichens which characterize the heath (together with the hummocks which they form) are either absent or else poorly developed, while ericaceous shrubs occur here mainly as an understory and are of subordinate importance to arborescent species. (*3*) The undergrowth approximates that of the climax coniferous forests of the region, essentially the same list of bryophytes, herbaceous vascular plants, and shrubs being characteristic of each. (*4*) The ecological aspect is much more

FIGURE 55.—Low *Krummholz* association-type with scattered tamaracks, many of them dead, projecting up above general level of surrounding vegetation; barrens in mountains west of Ingonish.

mesophytic. In typical *Krummholz* (FIGS. 54, 55) the trees range around three and four feet in height and commonly produce a dense tangle through which it is exceedingly difficult to force one's way. It is a type of association characteristic of situations in the open barrens which are somewhat sheltered from wind. In the opinion of Dr. Harvey, who accompanied the writer in 1916, the *Krummholz* of the barrens in northern Cape Breton is a close ecological counterpart of the *Krummholz* on Mount Ktaadn, concerning which he has written ('03, p. 34): "It seems then that the *Krummholz* forest is almost as mesophytic as the *Picea-Abies* combination . . . . which very evidently is the climatic mesophytic forest of this district." *Krummholz* differs from forest scrub not only in the lesser height of the trees, and in their more pronounced tendency to approximate the *Krummholz* growth form, but in the lesser abundance of the balsam fir.

Factors responsible for failure of forests to develop.—True alpine conditions are found nowhere in northern Cape Breton. This is evidenced by the complete absence of an arctic-alpine flora. On Mount Franey, the highest measured mountain in Nova Scotia, for example, no species were observed which are not equally abundant at lower elevations, while with the exception of perhaps a few forms such as *Betula pumila, Vaccinium uliginosum,* and *V. pennsylvanicum angustifolium,* the flora of the interior plateau scarcely differs in its composition from that of the upper mountain slopes. The general failure of forests to develop in the barrens can be ascribed very largely if not wholly to edaphic factors, especially to the combined influence of snow and wind during the winter months. Heavy winds prevail on the barrens intermittently at all seasons, but particularly in winter. The primary effect of the wind at this season is to sweep the snow from the more exposed sites and pile it up in the more sheltered situations. Exposed hill crests may be swept entirely bare, while in some of the ravines great drifts fully fifty feet in depth may accumulate. In general, it is apparent that the height of the trees, with the possible exception of the tamarack, is closely correlated with the depth of the snow in winter. In exposed situations any branches which project above the surface of the snow are liable to be killed by excessive transpiration or through the sand-blast-like action of the wind-driven snow. Individual shoots may survive a few mild winters, but then comes a severe winter and they too are killed. In the case of forest scrub, an association-type to be described presently, it is evident that, in spite of the apparently exposed position of the low hills on which it is commonly developed, local conditions favor the accumulation of snow drifts in much the same manner that sand dunes are built up along the seacoast.

Age of dwarf trees.—In this connection, a few observations regarding the ages of some of the dwarf trees may be of interest. The tamarack shown in Fig. 56, situated near the crest of the hill pictured in Fig. 51, was found to have more than 150 annual rings; and about the same number was counted in a cross section of the trunk of a balsam fir, scarcely three feet high, but with a trunk seven inches in diameter. Knee-high spruces more than fifty years old are common in exposed situations, one of those in the foreground of FIG. 51, scarcely a foot in height, having more than a hundred annual rings.

The forest scrub association-type.—From a distance, many of the low hills in the barrens appear to be well wooded, but closer

FIGURE 56.—Gnarled tamaracks, aged about 150 years, at summit of low hill shown in FIG. 51; barrens in mountains west of Ingonish.

inspection commonly reveals a most remarkable type of association. Because of the size of the trees, many of which may be as much as twenty feet high, it should be classed as forest; yet it is an abortive attempt at forest development rather than true forest. Three trees predominate: the balsam fir, the black spruce, and the tamarack, and one and all are battered and weather-beaten, betraying unmistakably the severity of the atmospheric forces to which they have been subjected. In this connection the dissimilar behavior of the three constituent trees under these adverse conditions is of much interest.

The balsam fir commonly possesses a short, stocky trunk from three to six feet high, according to the depth of the snow blanket. This trunk ranges in diameter up to more than a foot (in one case sixteen inches), and some of the trees must be well over two hundred years old (one six inch trunk showed more than 150 annual rings), an unusual age for the balsam in northern Cape Breton. The total height of the tree may be little greater than that of its stubby trunk: the lateral branches, usually borne in

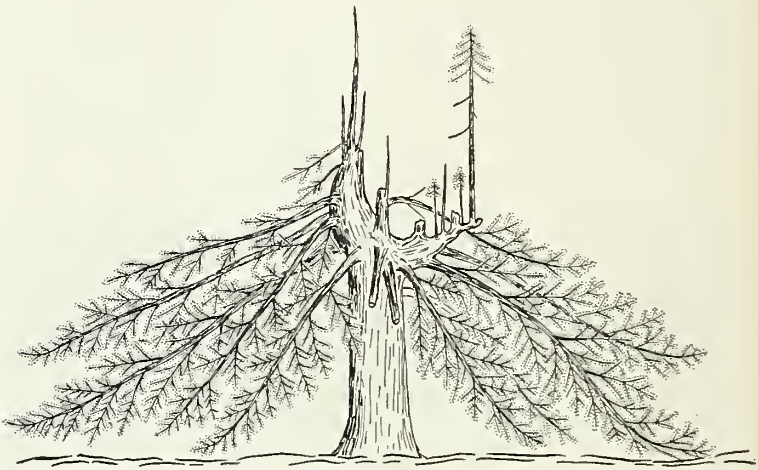

FIGURE 57.—Habit sketch of balsam fir growing in forest scrub association-type; barrens in mountains west of Ingonish. This particular tree is ten feet high (overall) and has a spread of more than a dozen feet with a trunk diameter of nearly a foot.

profusion near its summit, spread out widely, giving rise to a dense, flat-topped crown, low but commonly ten or a dozen feet broad and drooping nearly to the ground. But as a rule, upon the death of the primary leader, a new leader is developed which tends to continue the upward growth of the trunk. After a few years, the length of the interval depending on the severity of the winters, this leader may be killed and replaced by a third, and so on. More than twenty dead leaders have frequently been counted on a single tree. Often several leaders may be active at the same time, but usually one of them soon gains a marked ascendancy over the others. Very often a leader which rises six or eight feet above the main body of the tree will have had all its foliage blasted away by the wind-driven snow except for a small, pyramidal crown at the very tip.[15] The general aspect of these trees is suggested by the accompanying sketch (FIG. 57).

Usually quite different in its behavior from the balsam fir is the black spruce. In the balsam, while the lateral branches may be capable of assuming the functions of the leader, it would appear that they are able to do so only when very young, and more often than not the leader seems to originate adventitiously from either the main axis of the tree or a lateral branch. In the spruce, on the other hand, the potential capacity for radial growth in the normally dorsiventral lateral branches is much more pronounced, and this capacity is less restricted to the younger branches. Upon the death of the primary leader, a number, often nearly all, of the lateral branches tend to assume the radial habit, thus producing a clump of leaders, all of approximately equivalent rank. As a result, while one leader may sometimes become more prominent than the rest, the spruce commonly acquires a bushy habit quite different from that of the balsam. This dissimilarity of habit in the two trees is often strikingly exhibited in the *Krummholz* association-type: the balsam here is constantly tending to send a vigorous leader up above the general level of the surrounding vegetation and invariably possesses a short, sturdy trunk (FIG. 58); while the spruce adapts itself readily to the prostrate *Krummholz* habit and is virtually devoid of a distinct trunk.

The tamarack behaves differently from either the balsam or the spruce, being apparently better able than these species to withstand the rigorous winter climate. The trees exhibit a gnarled, scraggly aspect, but seldom are killed back to any extent.

Sometimes a forest of the sort under consideration is well nigh impenetrable, and the undergrowth is essentially that of the coniferous climax forest of the region. But more often the trees occur singly or in groups, with open spaces between in which the vegetation is made up largely of the species characteristic of

[15] A different explanation for a similar phenomenon in the spruce has been offered by Ganong ('04, pp. 188, 189).

heath. In general, this association-type is intermediate in character between heath and typical forest.

The ecological status of the tamarack in northern Cape Breton. —The status of the tamarack in the lowland has already been referred to. In the barrens it is a common tree, but throughout the forested region of the highlands it is absent or very rare in

FIGURE 58.—Weather-beaten balsam fir; barrens in mountains west of Ingonish. This tree measured eight feet high (overall) and had a trunk less than three feet high (in position indicated by arrow) but seven inches in diameter and with more than 150 annual rings. The present leader, to left of trunk, shows well the effect of heavy westerly winds (from right in picture) and wind-driven snow.

upland forests, being confined mainly to open swamps. The evident scarcity of this tree in all but open situations is correlated with the fact that it is primarily a pioneer species: it is notoriously intolerant of shade. As a result, except in barrens, swamps, or other open situations, it has almost everywhere been crowded out in competition with the more tolerant climax trees.

The low woodland association-type.—This is essentially similar to the low woodland type of poorly drained uplands described for the forested region. It may occupy like situations in the barrens, but here it also is a frequent type on moist, fairly well drained hillsides which are protected from the wind.

Summary of successional relations.—It will be seen that in a general way the association-types of well-drained uplands in the barrens have been arranged in an ascending series; that there are all gradations between dwarf shrub heath and sedge–grass heath at the one extreme and typical forest at the other. Incident to the special discussion of the association-types, various successional relationships have been pointed out. But while it is conceivable that in the course of time the associations of relatively primitive types are everywhere destined to become superseded by associations of more advanced types, as a matter of fact this is not generally the case. For the degree of mesophytism capable of attainment in the majority of sites is limited by edaphic factors, and any of the association-types described above may constitute locally an edaphic climax.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED UPLANDS

Although a distinction may be made between well-drained and poorly drained uplands in the barrens, as a matter of fact, as has been intimated earlier, it is practically impossible to draw sharp lines of demarcation. Owing to the character of the vegetation, especially to the influence of the almost universally developed lichen–bryophyte ground cover in retarding drainage, an area which originally may have been well-drained rapidly becomes less so, and there are few areas in which water cannot be squeezed out of a peaty substratum at almost any time of the year.

In protected situations, wet, poorly drained uplands may support low, swampy forests of (mainly) black spruce, with an undergrowth of *Alnus incana, Osmunda cinnamomea,* and the like: forests which might almost equally well be treated under the head of hydrarch successions. Further, the occurrence of sphagnum hummocks in areas occupied by heath has already been mentioned. On flat upland areas from which the water runs off slowly or where it tends to collect locally in shallow rock basins, as well as in various other situations where drainage conditions are such as to favor, at least locally, the development of the sphagnums, bogs and boggy swamps may arise on uplands.

The discussion of these is deferred until later (see under head of raised bogs, p. 433).

3. The Formation-types of Uplands along Streams

THE ASSOCIATION-COMPLEXES OF RAVINES AND VALLEYS

The association-types of ravines.—Streams in the forested region for the most part flow through ravines or broadly V-shaped valleys. The character of the stream-bank and cliff

FIGURE 59.—Low forest in ravine, with barren hill-top above; barrens in mountains west of Ingonish.

vegetation here is essentially similar to that already described for lowland streams. Ravine forests exemplify further the general tendency of the vegetation of uplands in this region toward uniformity, since they differ scarcely, if at all, from the forests of ordinary uplands.

Ravine vegetation in the barrens (FIG. 59), in general, resembles that of the forested region, and the forest-clad slopes here may afford a striking contrast to the barren aspect which prevails on adjoining exposed uplands. In shallow ravines the woodland is low, but in the deeper "gulches" the trees attain considerable size.

The association-types of open valleys.—While practically all the larger streams on their way to the sea run for long distances through deep gorges and ravines, on the plateau itself most of the streams flow through broad, shallow, characteristically flat-floored valleys, but little below the general level of the surrounding country. The slopes which flank these valleys may be covered with low woodland, or in the barrens by *Krummholz*. Their floors are commonly occupied by "hay marshes," alder thickets, and swampy woodland, which will be discussed under hydrarch successions.

C. Formations of the Hydrarch Series

1. The Formation-types of Lakes and Ponds

a. INTRODUCTORY

Small lakes and ponds of all sizes, but mostly quite shallow, are freely interspersed among the countless low hills which go to make up the surface of the plateau and occur scattered here and there along the seaward slopes of the highland. Many of them lie at the sources or along the courses of the innumerable streams which originate in the barrens, but a large proportion are devoid of any definite outlet. Ponds of the latter type are especially common on the plateau where, owing to the abundant precipitation and the impermeable nature of the rock floor, more or less permanent bodies of water tend to collect in basins of any description. On an undulating, rock-floored table-land such as this, the number of depressions suitable to pond formation is naturally very great, but the number of ponds actually present is even greater. This is due to the fact that, in addition to those whose presence is conditioned by the character of the topography, there are numerous ponds which bear no relation whatever to the topography, whose presence is attributable primarily to the activity of vegetation. The manner in which ponds of this latter sort arise will be discussed in some detail in later paragraphs (p. 449 *et seq.*). On the highland, as in the lowland (while there are plenty of apparent exceptions, particularly in the case of well-drained water bodies) there is a general tendency for lakes and ponds to become clogged up through vegetative activity, and in this way many basins formerly occupied by ponds have become more or less completely filled in.

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED LAKES AND PONDS

The plants named in the subjoined list are characteristic of well-drained lakes and ponds in the highland, growing either in the deeper water or in the shallows along the shore. Extended comment seems hardly worth while, since in their local distribution and ecological relations they conform closely with what has been described for similar areas in the lowland.

FIGURE 60.—Shallow pond in mountains north of Barrasois River; aquatic vegetation and narrow marginal fringe of swamp shrubs.

Sphagnum cuspidatum Torreyi
Drepanocladus Sendtneri
Drepanocladus scorpioides
Fontinalis sp.
Isoëtes sp.
Equisetum fluviatile
Sparganium angustifolium
Potamogeton natans
Potamogeton Oakesianus
Carex aquatilis
Carex filiformis
Carex rostrata
Eriocaulon septangulare
Nymphaea variegata
Castalia odorata
Ranunculus Flammula reptans
Nymphoides lacunosum
Lobelia Dortmanna

Dulichium arundinaceum
Eleocharis palustris vigens
Scirpus subterminalis
Utricularia vulgaris
Utricularia intermedia

The character of the marginal vegetation might perhaps more appropriately be considered in connection with swamps, but two phases will be briefly mentioned at this point. Between the water's edge and the adjoining upland vegetation there may occur only a narrow fringe of swamp thicket (FIG. 60), made up of such shrubs as the following:

Myrica Gale
Alnus incana
Spiraea latifolia
Rosa nitida
Ilex verticillata
Nemopanthus mucronata
Chamaedaphne calyculata
Kalmia angustifolia
Rhododendron canadense
Viburnum cassinoides

Elsewhere, however, intervening between this thicket and ordinary summer low water mark there may be a strip of sandy or rocky beach, of varying width, which supports an open swamp association of an essentially pioneer type. Characteristic plants of such a habitat are the following:

Scapania nemorosa
Sphagnum sp.
Lycopodium inundatum
Agrostis hyemalis
Carex filiformis
Carex Michauxiana
Carex Oederi pumila
Carex stellulata
Juncus brevicaudatus
Ranunculus Flammula reptans
Drosera longifolia
Drosera rotundifolia
Hypericum canadense
Hypericum virginicum
Viola cucullata
Viola pallens
Bartonia iodandra
Vaccinium macrocarpon
Lycopus uniflorus
Utricularia cornuta
Aster nemoralis
Aster radula

Very commonly, at least locally, the lake is bordered by swamps of a more advanced type, but these are better considered under the head of swamps.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED PONDS

In the number and abundance of seed plants, the aquatic vegetation of undrained ponds as a rule is inferior to that of well-drained ponds. Of species with submerged or floating leaves the most commonly represented are *Nymphaea variegata* and *Castalia odorata, Eriocaulon septangulare, Ranunculus Flammula reptans* and *Utricularia intermedia.* In addition to these, various sedges may grow in the shallow water around the margin or elsewhere, such species as *Eleocharis palustris vigens, Carex oligosperma* and *Scheuchzeria palustris,* together with the buck-bean, *Menyanthes trifoliolata.* Of particular importance, however, because of their frequently prolific growth, are the aquatic sphagnums, notably *Sphagnum Pylaisei* and *S. cuspidatum* (including the var. *Torreyi*), and certain filamentous algae. But there is the greatest variation in the vegetation even of closely adjacent and seemingly quite similar ponds. One may be quite choked up with aquatic sphagnums, while in the next there is scarcely any vegetation save a dense growth of algae on the bottom. One may contain a rank growth of *Eleocharis,* its neighbor a similar growth of *Menyanthes,* or neither of these species may be present; and so on. Practically all undrained ponds are mucky at the bottom and along the shores. The dynamics of the vegetation in lakes and ponds are discussed in later paragraphs.

2. The Formation-types of Lake-, Spring-, and Precipitation-swamps

a. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED SWAMPS

As elsewhere suggested, throughout the region of coniferous forests, wherever the ground is sufficiently wet, there is a tendency for the substratum, through the influence of vegetation in obstructing the drainage, to become boggy. In view of this fact, it would not have been at all surprising to find that swamps similar to the undrained type of the lowlands were entirely lacking here. But this is not the case. While the majority of the swamps belong to the undrained or poorly drained types, swamps are frequently encountered which unmistakably are of the well-drained type. The following list of plants, from an open swamp situated on a fairly steep, springy hillside in the forested region, scarcely a mile from the edge of the barrens, is quite characteristic of well-drained swamps in this region: it has been practically duplicated in other similar areas.

Taxus canadensis
Calamagrostis canadensis
Cinna latifolia
Glyceria canadensis
Scirpus caespitosus
Scirpus hudsonianus
Eriophorum virginicum
Rynchospora alba
Carex crinita
Carex flava
Carex stellulata
Juncus brevicaudatus
Smilacina trifolia
Iris versicolor
Habenaria clavellata
Habenaria dilatata
Spiranthes Romanzoffiana
Myrica Gale
Alnus incana
Thalictrum dioicum
Drosera rotundifolia
Spiraea latifolia
Amelanchier sp.
Sanguisorba canadensis
Rosa nitida
Viola blanda
Viola cucullata
Chamaedaphne calyculata
Lonicera caerulea
Viburnum cassinoides
Eupatorium purpureum
Solidago rugosa
Aster acuminatus
Aster nemoralis
Aster puniceus
Aster radula
Aster umbellatus
Cirsium muticum

Aside from relatively steep, springy slopes, swamps of the well-drained type are commonly developed along streams, in places where the ground is subject to occasional inundation (see further under head: formation-types along streams, p. 456). The vegetation in swamps of the well-drained type is apt to include more or less admixture of bog species, as shown by the above list, but these occupy a subordinate position and sometimes even the omnipresent ericad, *Chamaedaphne,* is absent. The only occurrence of *Typha latifolia* noted on the plateau was in a swamp of this description. Well-drained swamps are far less frequent in the barrens than in the forested region, but even here they are by no means absent, particularly along the larger streams.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED SWAMPS

Under this head, here as in the lowland, may be included a large number of swampy areas which, in the character and ecological relations of their vegetation, appear to be intermediate between the well-drained and the undrained types. There is one group of swamps in particular which seems to fit in under this head better than under any other, swamps which are quite commonly encountered along the shores of well-drained lakes. Locally along the margins of these lakes (Fig. 61) there have been formed broad, nearly level beaches, sometimes twenty-five or fifty feet in width, which lie somewhat above the level of the lake in summer, but are submerged during winter and early spring, at times when the outlet is blocked up by the ice.

At an early period in its development the vegetation in such an area is essentially as described for the beach in connection

Figure 61.—Small, well-drained lake with border of marshy swamp; mountains north of Barrasois River.

with the vegetation of well-drained lakes and ponds (p. 417): an open swamp association of a pioneer type. In the course of time, under favorable conditions, the more or less discontinuous plant cover characteristic of this early stage may become continuous. Largely through the activity of the sedges, *Carex filiformis, Carex oligosperma,* and *Rynchospora alba,* a shallow layer of peat is formed and the level of the swamp's surface is gradually raised higher. It is worthy of special note that the sphagnums play a relatively insignificant part in the building up process: the cushion-forming species so conspicuous in bog formation are usually absent or poorly developed. About the only form at all abundant is *S. Pylaisei,* a rather delicate species which, with the liverwort, *Cephalozia fluitans,* commonly covers the peaty substratum in among the sedges with a thin, felty mat. At an early stage in its development, in addition to the sedges already mentioned, the vegetation of such an association-type includes, among others, the following species:

Schizaea pusilla	*Rynchospora fusca*
Lycopodium inundatum	*Bartonia iodandra*
Scheuchzeria palustris	*Drosera longifolia*
Scirpus caespitosus	*Vaccinium macrocarpon*
Rynchospora alba	*Utricularia cornuta*

As time goes on, *Scirpus caespitosus,* at first scattered, comes to occupy the ground more and more completely, forming a rather dense sward and crowding out most of the species listed above, except such as are able to persist in local depressions. The *Scirpus* is responsible for a still further elevation of the substratum, but the peat in such a swamp is almost invariably shallow, seldom exceeding two feet in thickness. Commonly associated with the *Scirpus* in this association-type are the following:

Calamagrostis canadensis	*Epilobium palustre*
Carex Michauxiana	*Drosera rotundifolia*
Carex pauciflora	*Sarracenia purpurea*
Habenaria blephariglottis	*Aster nemoralis*

The vegetation is predominantly herbaceous, with *Scirpus* as the character plant. As a rule, however, there is a scattering of low shrubs, such forms as *Myrica, Spiraea, Andromeda, Chamaedaphne, Kalmia polifolia, Rhododendron,* and *Lonicera caerulea,* which, along the shoreward margin, commonly form a thicket. An association of this sort bears a marked resemblance to bog-meadow, as described later in connection with raised bogs. In many situations it seems without question to represent an edaphic climax. Failure for succession to proceed further is probably correlated with an inability on the part of the cushion-forming sphagnums to gain control, an inability for which the periodic inundation seems in some way to be responsible.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED SWAMPS

Ecological characteristics of the more important bog species of Sphagnum.—Emphasis has been laid earlier on the prominence in bogs of the sphagnum mosses. Allusion has also been made to differences in the ecological relations of various species, in their manner of growth, and in the rôle which they play in bog development. It seems appropriate at this point to sum up briefly, with reference primarily to their ecological relations, the essential features of the more important species of *Sphagnum* which grow in the bogs of this region. These may be divided more or less definitely into five groups, as follows.

Group 1. Plants primarily aquatic, floating at or near the surface of the water. *S. cuspidatum:* commonly yellowish green in color, limp and flaccid, with a delicate, feathery appearance; when growing emersed, stems usually prostrate and trailing or creeping. The var. *Torreyi* is very robust, more rigid than the typical form, and ordinarily a dirty brownish green in color. *S. Pylaisei:* dark purple to nearly black in color; soft and delicate, but as a rule scarcely flaccid; slender, with sparsely developed, short branches; when growing emersed, stems prostrate and trailing or semi-erect; perhaps the most easily recognized of any native sphagnum.

Group 2. Plants semi-aquatic, amphibious; occasionally completely submerged and with a habit similar to that of *S. cuspidatum,* but more commonly with the tips of the shoots projecting well above the surface of the water; quite robust, fairly rigid, erect. *S. Dusenii:* in color, usually green, more or less tinged with yellow-brown. *S. pulchrum:* in color, olive-green to brownish green; commonly grows emersed, forming dense but rather loose, soft cushions (see further under group 4).

Group 3. Plants primarily non-aquatic, commonly growing in low, wet, boggy grounds. *S. tenellum:* erect, slender, fragile, usually occurring in dense, loose masses and forming beautiful, soft, low mats; in color, ordinarily yellowish green; one of the most delicately lovely of all the sphagnums.

Group 4. Plants mainly non-aquatic, though commonly growing in very wet places and occasionally submersed; usually very robust, erect and rather rigid; when emersed, forming dense, rather compact masses and building up fairly firm cushions; submersed forms quite flaccid. *S. papillosum:* in color, generally brownish to nearly black. *S. magellanicum:* in color, pale greenish white, or usually strongly tinged with pink or purple-red. *S. pulchrum* might perhaps also be classed here. It may be noted, as of contemporaneous interest, that in the selection of sphagnums suitable for making surgical dressings the full-leaved forms of *S. papillosum* and, to a lesser extent, *S. magellanicum* have been found to furnish the best material (in this connection, see Porter '17).

Group 5. Plants strictly non-aquatic, growing in moist or relatively dry situations; erect and mostly slender; forming dense, compact masses and building up firm cushions. *S. capillaceum tenellum:* color commonly a vivid red. *S. fuscum:* color commonly russet-green. *S. tenerum:* color commonly yellowish, or more or less tinged with pink or red.

As grouped above, the species are arranged approximately in the order of decreasing hydrophytism. For purposes of convenience, the species of group 1 may be referred to as aquatic or hydrophytic; those of group 2 as semi-aquatic; those of group 4 as *mesophytic;* and those of group 5 as *xerophytic.* In view of their tendency, of exceeding importance from an ecological standpoint, to form more or less compact cushions, the species in groups 4 and 5 may be distinguished further as "cushion-forming species." The significance of the above classification will be seen presently.

Outline of methods by which bogs arise in water-filled depressions.—Bog formation in water-filled depressions is due largely, if not wholly, to plant activity. In general, as has been indicated elsewhere (see discussion of lowland swamps), there are two methods by which the conversion of a pond into a swamp may be accomplished. These may be designated: (*1*) *filling from within,* and (*2*) *encroachment from without.* By the first method the bottom of the pond is built upward toward the surface through the gradual accumulation thereon of successive layers of organic débris, derived mainly from the incompletely decomposed remains of various aquatic plants. By the second a mat of swamp vegetation, originating on the banks or in the shallow water near the shore, pushes outward over the surface of the water, roughly speaking, into the deeper parts of the pond. In typical instances these two lines of development are quite distinct from one another, and the filling in of a pond may be accomplished entirely through one or the other. But both processes may commonly be observed in one and the same pond and, as will be shown later, the filling in and obliteration of the pond may frequently be achieved through the combination of the two.

Filling from within, with particular reference to the rôle of various sphagnums.—The commonly active participation in this process of various aquatic seed plants and algae calls for no special comment. Of more interest here is the conspicuous part often taken by certain species of sphagnum. These are particularly important in the barrens where, in the small, undrained ponds which are so abundantly developed and which constitute such a characteristic feature of the plateau, various sphagnums commonly predominate the successive stages of bog evolution from start to finish. It is to the conditions observed in and about these ponds that the following remarks apply. Here, while a subordinate part may frequently be played by various other plants, the bulk of the organic débris by which the pond becomes filled in up to water level is contributed by the two aquatic sphagnums, *S. Pylaisei* and *S. cuspidatum,* associated with which, but in lesser abundance, usually grows the liverwort *Cephalozia fluitans.* During the summer months these two species of *Sphagnum,* either or both, may be present in such profusion as to completely clog the pond to a depth of several inches below the surface with a loose, floating mass of vegetation. One is tempted to regard such a structure as a true floating mat, but such is hardly the case (see, however, in this connection, p. 429). For while the "mat" does float during the growing season, so long as there is open water underneath it sinks to the bottom in winter. It is indeed extremely doubtful whether under any circumstances sphagnum of itself is capable of forming a permanent floating mat, i. e., a raft-like growth sufficiently firm and stable to permit the establishment and maintenance on its surface of a non-aquatic type of vegetation.

Eventually, however, the bottom of the pond may become built up to such a level that, except during periods of high water, the substratum is exposed to the air, and here, in addition to the bryophytes which have been largely responsible for its development and which still cover its surface with a thin, more or less continuous mat, the soft, mucky ground usually becomes populated by a very characteristic group of vascular plants, among which the following are almost invariably present:

Lycopodium inundatum	*Drosera longifolia*
Rynchospora alba	*Vaccinium macrocarpon*
Eriophorum angustifolium	*Vaccinium Oxycoccus*
Carex oligosperma	*Bartonia iodandra*
Ranunculus Flammula reptans	*Utricularia cornuta*

To this list might be added the curly grass fern (*Schizaea*), which sometimes, and the bog rosemary (*Andromeda*), which frequently is met with in situations of this sort. An important ecological function is fulfilled by the sedges and the cranberries, since through the medium of their roots and stems they reinforce and bind together the mucky deposit, thereby producing a semblance to floating mat formation. For convenience, a mat of this sort, formed over a soft, mucky deposit, may be referred to as a *muck mat*.

Sphagnums of the semi-aquatic group, particularly *S. pulchrum*, frequently put in an appearance while the rising substratum is still covered by some depth of water. In such cases the succession may be modified to such a degree that the muck mat stage is omitted. For these semi-aquatic species, growing in fairly dense masses, their stems erect and projecting slightly above water level, are able to eliminate, probably through the influence of shade, the lower, more truly aquatic sphagnums. Associated with the sphagnums in such a habitat may grow, locally in abundance, *Scheuchzeria, Eleocharis, Carex limosa, Smilacina trifolia* and *Menyanthes*. These may fulfill here a function similar to that performed by sedges and cranberry in the case of the muck mat, where also they are not infrequently represented.

Returning to the consideration of the muck mat: the sphagnums of the aquatic group are incapable of building up the surface to any appreciable height above ordinary summer water level, although to a limited extent this may be accomplished by the sedges. Further elevation is dependent primarily on the advent of the more mesophytic sphagnums. For some reason, the prostrate, felty tangle of aquatic sphagnums and *Cephalozia*, which commonly covers the surface of the muck mat, seems to hinder the rapid establishment of other bryophytes, and in consequence this stage may be protracted for a long time. But sooner or later other sphagnums may secure a foothold and eventually gain the upper hand.

In general, the elevation of the bog surface above water level is accomplished very largely through the activity of species of *Sphagnum* which possess to a more or less marked degree the cushion-forming habit, but the process is greatly facilitated by the concurrent activity of the vascular plants growing on the sphagnous substratum, since these, in the manner already suggested, bind together and consolidate the sphagnum cushions, and in addition may form a sort of scaffolding which expedites the upward growth of the mosses. *Sphagnum pulchrum* with its semi-aquatic habit is a common pioneer on the muck mat, and with its erect habit of growth and tendency to form loose cushions is able to build up the surface to some height. Fully as important at this stage, and subsequently much more so, are *S. papillosum* and *S. magellanicum,* species with a generally more robust habit and a tendency to form denser cushions than *S. pulchrum.* Any of these three species may act as pioneers, and frequently all of them grow intermixed.

Once the cushion-forming sphagnums have firmly established themselves, the bog surface may be built up quite rapidly. A measure of the rate at which this takes place is sometimes afforded by shrubs which have been buried by the rising substratum. To cite a specific example, in an erect stem of *Myrica Gale* which had been partially buried to a depth of eight inches a discrepancy of seven years was found in its age near the bottom of the deposit (ten years), and at the surface (three years), a fact which would seem to indicate that here the sphagnums had grown upward at the rate of about an inch a year.

As the surface rises higher, the mesophytic sphagnums (*S. papillosum, S. magellanicum*) may gradually crowd out their more hydrophytic competitor (*S. pulchrum*). The height to which these two species are able to build up the substratum varies, being apparently conditioned in part directly by soil moisture relations, but largely by competition on the part of other species. For with its increasing elevation the substratum naturally becomes somewhat drier and consequently less congenial to the mesophytic species, while at the same time conditions become more favorable for relatively xerophytic species, such as

S. fuscum and *S. capillaceum tenellum,* which, while they may frequently be present, do not thrive in the wetter situations. These xerophytic sphagnums, at first growing intermixed with the mesophytic species, gradually become more abundant, overgrowing and eventually eliminating their less xerophytic competitors. The mesophytic cushion-forming sphagnums may be largely responsible for the elevation of the bog surface to a height of a foot or two above the original water level, but any

FIGURE 62.—Margin of small undrained pond near crest of raised bog; barrens in mountains west of Ingonish; in foreground, *Andromeda* and other shrubs advancing into the pool.

further upward growth is dependent very largely on the xerophytic cushion-forming sphagnums, which invariably are the predominant species in a mature bog.

Encroachment from without, with particular reference to the formation of floating mats.—In its essential features, floating mat formation in the highlands differs little from what has been described for the lowlands. The pioneers may be either shrubs or sedges. In the former case (FIG. 62), here as there, unless the framework created by the shrubs becomes overgrown by sphagnums, mat formation proceeds no farther than this incipient stage. The important sphagnums in this connection are *S. pulchrum* and the more mesophytic cushion-forming species, but particularly the latter. As a rule these are present in abundance, and so favorable are the conditions for their growth here in the highlands that they commonly give rise to a thick mat which rises steeply from the water's edge to a height of one or two feet. *Myrica Gale, Chamaedaphne,* and *Andromeda* are all important as pioneer shrubs, now one, now another playing the leading rôle.

Locally certain sedges are more important as pioneers in mat formation than are the shrubs. *Carex limosa* frequently extends out into the open water from along the shore, growing in length as much as a foot in a single season, and sometimes it is present in sufficient abundance to form the basis of a mat. More commonly *Carex filiformis* is the pioneer sedge. The behavior of this species in mat formation has been described by Ganong ('03, pp. 440–441), Transeau ('05-'06, p. 363), Davis ('07, 135–138), the writer ('15, pp. 198–199), and others. Commonly the sedges are followed by the sphagnums, which build up the surface in the manner already described. On the whole, sedges are much less prominent in the rôle of mat pioneers than are shrubs. Moreover, the latter, because of the framework afforded by their strong, woody stems, favor much more the growth of the cushion-forming sphagnums and the consequent thickening and solidifying of the mat.

As the mat grows outward into the pond, the open water beneath gradually becomes filled in, partly by the sinking of the mat as it becomes thicker and heavier through the continued upward growth at its surface, partly by the dropping down of vegetable débris from the under surface of the mat. Where the outward growth is rapid, the mat may be underlain for some distance shoreward from its outer margin by open water; where outward growth is slow the filling in beneath may keep pace with it, so that very little of the mat is actually floating. But in either case, wherever the filling in is being accomplished primarily through the intervention of a floating mat, the water in the pond is deep right up to the edge of the mat, and in cases where the mat has become "grounded" clear to its margin, in the manner indicated above, the bank usually sheers precipitously to the bottom.

A somewhat puzzling modification in floating mat formation is exhibited in particular by many of the small ponds in the barrens. Commonly the encroaching banks advance at a more or less uniform rate into the pond from one or several sides, but frequently the rate of advance varies locally, and to such an extent that the marginal bog comes to project out into the pond in triangular or tongue-shaped masses (FIG. 64). Through the continued spread or coalescence of such masses a relatively large pond may become subdivided into several smaller ones: in one case noted a group of nine small ponds had thus originated. This singular behavior is not correlated with any differences in the depth of the water, and for a long time the author was at a loss for an explanation. The solution, however, appears to be somewhat as follows. Attention has already been called to the fact that in the small, undrained ponds of the barrens, the surface during summer is commonly occupied by a floating mass of aquatic sphagnums. In winter this mass sinks to the bottom. Here the loose tangle may become intergrown with various filamentous algae to such an extent as to render it impervious to gases, and the following spring it may be floated toward the surface as a result of gas accumulation underneath or within the mass. Cases of this sort have been frequently noted. As a rule, only portions of the mass actually reach the surface, and on the substratum thus presented sedges or shrubs may gain a foothold, thus inaugurating what essentially is a floating mat. Very often, as might be expected if this explanation is correct, peninsulas and islands of bog are encountered in these ponds. In this connection, see Powers' paper on "Floating Islands" ('14).

Encroachment from without in combination with filling from within.—It commonly happens that the conversion of a pond into a swamp is accomplished through a combination of the two methods of filling just described. The filling in up to the surface level may be due largely to the activity of aquatic vegetation, and it is on the substratum thus formed that the mat advances. In this connection the conditions observed around a small, nameless lake, near the upper limits of the forested region, and studied with some care will serve as an illustration. The lake covers an area of perhaps two acres, has roughly the shape of a rounded equilateral triangle, and is drained by a small, sluggish stream.

Its original size has been reduced about one-half by the centripetal encroachment of the bogs which now surround it to a variable width on all three sides. In the still open part of the pond, the bottom seems to be completely covered by a soft, mucky deposit which in places must be many feet thick. This deposit without question has been formed almost wholly through the accumulation on the floor of the pond of vegetable débris, which in large part has been derived from the remains of aquatic seed plants, mosses, and algae. In proceeding from the middle of the lake toward the shore, the depth of the water gradually diminishes, the mucky bottom sloping gently upward until, just before the lakeward margin of the bog is reached, it nearly or actually reaches water level. On the substratum thus produced a mat has been formed, which has advanced from the shore out into the lake as rapidly as the filling in process has permitted. And in this connection considerable interest attaches itself to the divergent courses of development which have ensued on two of the three sides of the lake.

Along one side a sedge mat has pushed its way out for a distance of a dozen or fifteen feet from the original shore. For the development of this mat three plants have been primarily responsible, namely *Carex filiformis, Rynchospora alba* and *R. fusca,* and these are still the predominant forms, practically the only other species present being *Utricularia cornuta, Drosera longifolia,* and *Sphagnum Pylaisei.* The mat is flat and firm, and, although it is but a few inches above ordinary summer water level, one can walk dry-shod almost to its edge.

Along the other shore the behavior is somewhat different. The shoal water along the margin of the advancing bog is occupied by an association made up very largely of the mosses, *Sphagnum pulchrum* and *Drepanocladus Sendtneri.* These are present in sufficient abundance to form a low, wet substratum upon which the sedges, *Carex filiformis* and *Rynchospora alba,* together locally with *Andromeda,* gain a foothold. Thus there is formed a low mat which paves the way for further progress. But subsequent development is not always the same. It may follow one of two courses, and which of these it shall be seems to depend very largely on which species of *Sphagnum* gains control over the situation. Along much of the shore *S. papillosum* establishes itself and with *S. pulchrum,* which is already present, rapidly builds up the surface to a height of a foot or more above water, at which level *S. fuscum* begins to assert itself. In this way there arises a typical bog (FIG. 63), in which the cushion-forming sphagnums and their customary vascular associates prevail. Locally, however, the low mat is usurped by *Sphagnum Pylaisei.* This sphagnum, it should be remarked, while it grows profusely in many small undrained ponds, is seldom a conspicu-

FIGURE 63.—A characteristic bog in the mountains west of Ingonish: sedges, ericads, and sphagnums predominant, with scattered clumps of black spruce.

ous element of the aquatic vegetation in ponds of any size, like the present one, especially where they are well drained. But it frequently occurs in the swamps which border them. Along with *S. Pylaisei* commonly grows the liverwort, *Cephalozia fluitans.* These two bryophytes, as elsewhere suggested, tend to form a rather compact, felty growth over the substratum, which seems in some inexplicable manner to hinder the invasion of these areas by the cushion-forming sphagnums. So tenaciously, indeed, may they hold their own that, as the contiguous higher portions of the bog push out into the pond, these lower areas commonly become completely engulfed. The vegetation of the hollows thus formed is strikingly different from that in the surrounding bog, being essentially similar to that of the muck mat described in earlier paragraphs. In addition to the two sedges, *Carex filiformis* and *Rynchospora,* the following vascular plants are characteristic: *Schizaea pusilla, Lycopodium inundatum, Carex oligosperma, Ranunculus Flammula reptans, Drosera longifolia,* and *Utricularia cornuta.* Ultimately these depressions seem destined to become incorporated with the rest of the bog, but they may persist virtually unaltered for a long time. The usual forerunner of the typical bog vegetation is *Scirpus caespitosus,* and this sedge seems to pave the way for the cushion-forming sphagnums which ultimately gain control.

It has already been noted that in the small ponds of the barrens, where the aquatic sphagnums play such an important part in the filling process, the mucky substratum which these form, with its felty cover of *Sphagnum Pylaisei, S. cuspidatum,* and *Cephalozia,* may similarly persist virtually without further change for a very long time. It may be added here that very commonly such areas are gradually being reduced in size and seem destined to extinction through the slow centripetal encroachment of the steep, peripheral banks of sphagnum.

The method of filling which has been described in the preceding paragraphs differs from that previously described as due entirely to "filling from within" mainly in the more obvious centripetal encroachment of the marginal swamp vegetation. As a matter of fact, there is scarcely any real distinction, for, strictly speaking, as soon as the bottom of a pond has been built to the surface through the activity of the aquatic plants, any further changes are invariably due to the invasion of plants from without.

The climax association-type of bogs.—Extended comment is hardly necessary. The character of the climax association-type varies locally, but in general it is marked by the predominance of sphagnums and ericaceous shrubs, with black spruce and tamarack. In many cases the vegetation of ordinary bogs in the highland is scarcely different from that described for lowland bogs, while in others it closely approximates the conditions found in raised bogs which will be described next.

d. THE ASSOCIATION-COMPLEXES OF RAISED BOGS

Geographical distribution of raised bogs in eastern North America.—Bogs of the raised (*"Hochmoor"*) type (Figs. 64, 66) are extensively developed in parts of northern Europe, and there are numerous published accounts dealing with them, both from an economic and a biological standpoint. But concerning their occurrence and distribution in North America little is known, and specific references to them in the literature are scarce.

Figure 64.—Raised bog on Peter's Barren, in the mountains east of Frizzleton; in the foreground, pond and low, wet bog; in the background, the more elevated part of the bog, which rises more than twelve feet above the pond level.

Ganong, more than twenty-five years ago ('91), called attention to the presence in New Brunswick of bogs of this type, and in 1898 he published a rather detailed account of the raised bogs in the southern part of this province. He has also made some brief notes ('06[b]) on the raised bogs of Miscou Island, New Brunswick. In his second paper, Ganong indicates the reported occurrence of raised bogs in Nova Scotia and Anticosti, and the probability of their occurrence in Newfoundland. In a recent publication ('15), the third of a series of papers on the economic aspects of peat bogs of Canada, Anrep, speaking of the Clyde Peat Bog in Nova Scotia, states (p. 55) that "this is the first 'high moor' bog encountered during the last six years of investigation" (a period during which he had studied numerous bogs in Manitoba, Ontario, and Quebec). Davis, in discussing the origin of the Maine peat deposits (Bastin & Davis, '09), gives a short description of the manner in which raised bogs are formed and of the relation between "built-up deposits" and "filled-basin deposits." The former, corresponding to the raised bog, appears to be a not infrequent type of swamp along the Maine coast as far south as the vicinity of Portland, and evidently it is of quite common occurrence northeastward. On the whole, judging from the data at hand, both published and unpublished, it would appear that in eastern North America raised bogs are largely confined to Newfoundland and to those parts of eastern Canada and Maine which are in the proximity of the sea-coast. Their limitation to this region is unquestionably correlated with the character of the climate: the abundant precipitation, relatively low atmospheric humidity, cool summers, and the absence of extreme low winter temperatures such as prevail farther inland. The paucity of literature dealing with raised bogs in this country is doubtless attributable, as Ganong suggests, to their remoteness from botanical centers and their hitherto little appreciated economic value. In Europe, "great bogs occur within easy reach of the botanists of Germany, Switzerland, and Scandinavia, and their great economic value has led to their exhaustive study both by individual workers and by government commissions" ('98, p. 131).

From the brief examination which the author was able to make of the Spruce Lake bog and two neighboring smaller bogs about a dozen miles west of St. John, New Brunswick, it may be stated that the raised bogs of this region, as described by Ganong, are essentially similar to those of northern Cape Breton.

Occurrence of raised bogs in northern Cape Breton.—In this particular region raised bogs apparently are confined to the plateau, but this is very likely due to edaphic rather than atmospheric factors, since in southeastern Cape Breton fine raised bogs occur at but little above sea-level. On the highlands in northern Cape Breton raised bogs are encountered here and there in the forested region, but their greatest display is seen in the barrens. To the study of the origin, development and ecological relations of the raised bogs here the author has devoted considerable time, and it is hoped that the facts set forth in the following pages may contribute materially to the knowledge of this fascinating swamp type, as developed on this continent.

General features of raised bogs and the influence of edaphic factors on their local distribution.—The most bizarre feature of a raised bog is the fact that it is higher toward the center than toward the margin: the surface is convex, and the entire structure frequently presents more or less the form of an inverted saucer or watch-glass. The outline of a typical raised bog, as viewed in cross section, is shown by Fig. 65, *B*. In this connection, it might be remarked that a slight convexity in the contour of the surface is perceptible in some of the lowland bogs of northern Cape Breton, and similar conditions are occasionally noted in southern New England; but in these cases the elevation of the middle portions at most is only a foot or two. In the case of typical raised bogs the difference in height between margin and center may be many feet: viewed from the surface alone, and disregarding the contour of the underlying rock floor, the higher portion may rise to a height of from fifteen to twenty or more feet above the lower marginal portions. But that the actual elevation of the bog surface above the rock substratum in reality is often much less than it appears from superficial examination will be apparent later. As shown by the cross section (Fig. 65, *C, f-h*) the surface rises rather abruptly from near the margin, then more gently, and the top of the bog may be practically flat. The angle of slope along the steeper flanks of a bog varies locally, but ordinarily the surface rises at the rate of about one foot to fifteen or twenty on the level. Sometimes, however, the slope is much steeper: in one extreme instance (foreground of Fig. 64), for example, a rise of three feet in three and six feet in twelve was noted. The bogs vary in size, but commonly they are many acres in extent, and in some cases they stretch out uninterruptedly for more than a mile. On the higher levels of the bog the ground underfoot, for the most part, is quite firm and springy, but locally, particularly in the vicinity of the small ponds which are frequently present, it may be soft and spongy. The character of the surface vegetation will be discussed in detail later: suffice it to state here that in addition to the sphagnums which form the groundwork of the mass, the most prominent plants are low, ericaceous shrubs and the sedge, *Scirpus caespitosus*.

For the development of a raised bog, the fundamental prerequisites are the presence of certain species of sphagnum and of environmental conditions congenial to their growth, since from start to finish in the evolution of such a bog these mosses play an all essential rôle. Of foremost importance is a copious water supply, and this is controlled partly by climatic, partly by edaphic conditions. Of the water which falls on the earth's surface in the form of rain and snow, part enters the ground, forming the ground water supply; part runs off over the surface into streams and lakes; the remainder is evaporated or is absorbed directly by vegetation. In so far as the development of raised bogs is concerned, it is now generally recognized that the chief source of their water supply is meteoric, rather than telluric. In other words, while locally a limited amount of the water needed may be derived from springs, on the whole their distribution and growth is independent of the ground water supply. Surface drainage from neighboring slopes may and frequently does help out, but in the large it is the water precipitated directly upon the surface of the area occupied, in the form of either rain or snow, which is most important. Swamps which thus are dependent directly upon atmospheric precipitation for their water supply have been designated precipitation-swamps, by way of distinction from spring-swamps and lake-swamps (see earlier remarks, p. 354).

The importance of edaphic factors is seen in their influence on water loss through surface runoff and downward percolation. Given a substratum sufficiently impermeable to prevent loss through percolation, a raised bog may originate under quite varied topographic conditions. In general, it may be built up either in and around a water-filled rock basin or over any essentially flat, undulating or irregular surface from which the rain and snow water tend to run off slowly or to accumulate in local depressions. Such surfaces as the latter, considered in their entirety, may be either approximately level or slightly inclined. It is probably the lack of suitable areas of impermeable substratum that is responsible for the observed absence of raised bogs in the lowland. In the highland the substratum underlying the raised bogs is practically impervious granite rock, bare, or thinly covered by a gravelly soil.

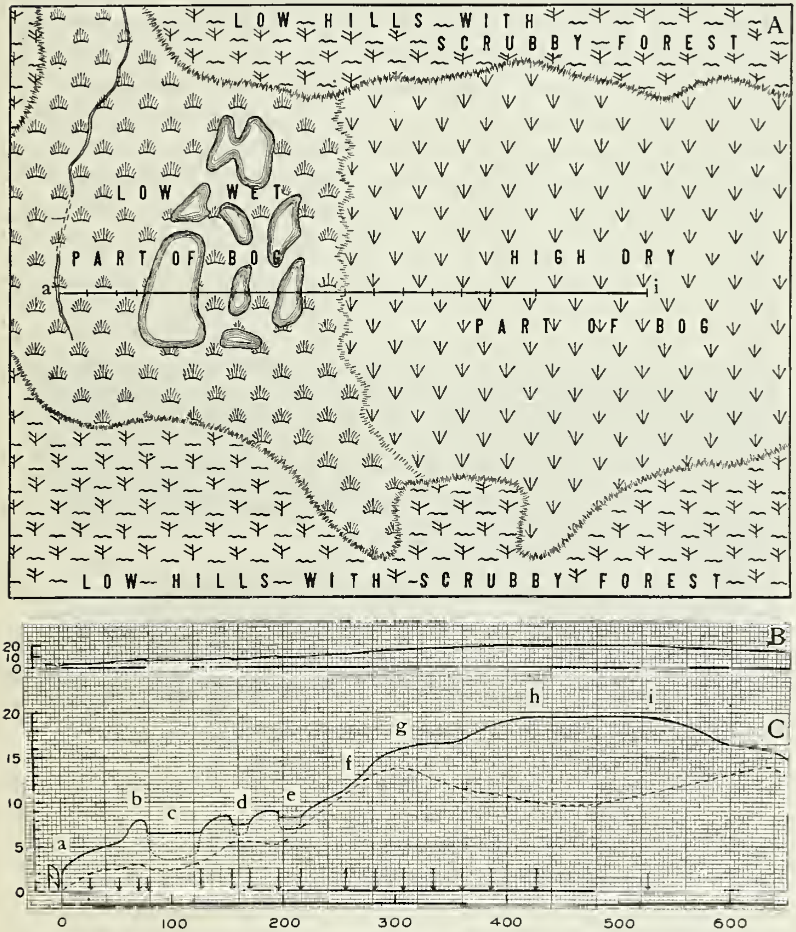

FIGURE 65.—Diagrammatic representation of a bog complex in the barrens; see text. *A.* Sketch map showing relation of area to adjoining upland. *B.* & *C.* Longi-sections along line *a–i* on map. Section *A* drawn to scale; in section *B*, vertical scale eight times the horizontal, and contour of rock floor indicated by dotted line. All measurements in feet. Arrows indicate location of soundings. Mountains west of Ingonish.

a. Development of Raised Bogs in and around Water-filled Rock Basins

An illustrative example.—In Fig. 65 is represented diagrammatically a bog-complex which was studied in some detail. Depth of peat, surface contour, and relations of the underlying topography were determined by means of sounding-rod and level. Section *B,* made along the line *a-i* in map *A,* is drawn to scale and shows the actual contour of the surface. Section *C,* identical with Section *B* but with the vertical scale eight times

Figure 66.—Raised bog in barrens, mountains west of Ingonish; photograph taken from point between *d* and *e* in Fig. 65. In foreground, wet bog; figures standing on dry bog; see text.

the horizontal, brings out the relation between the surface contour and that of the rock floor beneath. It will be seen from this diagram (*f-i,* etc.) that the upper portion of the bog-complex (the portion pictured in Fig. 66) is occupied by a typical raised bog, which has been developed in and around a shallow rock-basin. Through the accumulation of peat, the surface has been built up more than six feet above the rim of the basin and about ten feet above its bottom, and has spread out over the rim. Attention may now be given to the manner in which this bog has been formed, the lower portion of the complex (Fig. 65, *C, a-f*) being neglected for the moment.

The rock basin in question is situated at the summit of a low, rounded hillock which is bounded laterally by slightly higher hills. Partly as the result of direct precipitation, partly perhaps through surface drainage from the adjoining higher ground, this basin originally was kept filled with water, which spilled out over the rim at *g*. The manner in which this pond became obliterated was doubtless similar to what has been described in the general discussion of bogs a few pages back. The open water may have become filled in through the activity of the aquatic sphagnums, or through the encroachment from the margin of a floating mat, or through a combination of both these methods. Assuming the aquatic sphagnums to have been the pioneers, and that through their activity the pond had been more or less completely clogged up, the second stage in the succession was probably dominated by the mesophytic cushion-forming species (*S. papillosum, S. magellanicum, S. pulchrum*), although there may have been an intermediate stage of semi-aquatic species (*S. pulchrum, S. Dusenii*). Largely through the activity of the mesophytic cushion-forming sphagnums the surface may have been raised to a height of one or two feet above the former pond surface, at which point the xerophytic cushion-forming species (*S. fuscum, S. capillaceum tenellum, S. tenerum*) asserted themselves. It is to the species of this latter group that the further elevation of the bog surface to its present height has been largely due. Throughout this series of changes, various seed plants have occupied a more or less prominent position, and have played an important rôle by binding together and strengthening the ground-work formed by the sphagnums. The stages characterized by the predominance of the mesophytic and of the xerophytic sphagnums may be designated respectively the wet bog and the dry bog stages. The character of the surface vegetation in these two stages will be described later.

General observations.—The exact stage at which the central water body becomes obliterated in successions of the sort just described varies. In the present case, the pond has been overwhelmed so completely that there is absolutely nothing on the surface of the bog that even suggests its former presence. In other cases, however, the pond may persist for an indefinite period, and may even be present on the higher parts of the mature bog. The factors concerned may be various, but of particular importance seem to be the depth of the basin to start with and the luxuriance with which the aquatic sphagnums develop. Where these latter are absent or poorly represented, so that the filling in is dependent on encroachment from the margin, the elimination of the pond proceeds slowly. For while the mesophytic, cushion-forming sphagnums may grow luxuriantly, forming great banks of vegetation around the edge of the pond, the centripetal advance into the pond of the fringing banks is usually slow. For this latter fact the commonly sparse development of the pioneer, skeleton-forming shrubs seems primarily responsible, since wherever an adequate shrubby framework is presented the sphagnums tend to push out from the shore quite rapidly. The banks of sphagnum commonly come to form a complete circle about the pond and block up any natural outlet which may have existed. (Of course, in the case of spring-fed ponds or of any ponds with a considerable outflow, the outlet may not become completely dammed, but such ponds are rarely concerned here in the development of raised bogs.) Thereafter drainage must be accomplished entirely by slow seepage through the peaty banks. As these banks are built up higher through the growth of the sphagnums at the surface, the peat underneath becomes more and more compressed by the superimposed weight and in consequence less and less permeable. The result is obvious: as the drainage becomes impeded below, the surface of the pond is forced to a higher level, and in this way, as fast as the surface of the bog is built upward, the pond likewise is shoved higher and higher, until ultimately it may come to lie at the crest of the mature bog. Concurrently with the changes just outlined, the bottom of the pond may likewise be built up through filling from within, but only when this latter process proceeds at a more rapid rate than that at which the surface of the pond rises can it have any immediate visible effect.

Mention has been made earlier of the convex surface which is possessed to a greater or less degree by all raised bogs. This convexity is most pronounced in bogs like the one just described, where there is a central pond which acts as a reservoir and from which water seeps out in all directions. It is self-evident that the areas nearest the pond will be best watered: it is here that the sphagnums thrive most luxuriantly and grow most rapidly and that the surface of the bog tends to be built up the fastest and to the greatest height. Farther away from the pond, at least during dry spells, the water supply is less abundant, so that the rate of upward growth is slower and the height limit lower than in the more favorable central portions. The conditions, however, are not always as simple as are here suggested. Especially are complexities introduced through the development of ponds which are a result rather than a primary cause of bog development. Ponds of this "subsequent" type, as will be shown presently, are even more generally associated with raised bogs than are ponds of the "antecedent" type, like those just described.

β. Development of Raised Bogs over Flat or Irregularly Undulating Rock Surfaces

Perhaps more commonly than not, in northern Cape Breton, the rock floor which underlies a raised bog is essentially flat or else irregularly undulating: at any rate there are no rock basins capable of holding any appreciable amount of water. In the development of raised bogs in situations of this description, three more or less definite stages can frequently be distinguished, which may be designated respectively the *Bog Meadow* stage, the *Wet Bog* stage, and the *Dry Bog* stage. Owing largely to local variations in topography, the rate at which bog formation has progressed and the degree to which the raised bog climax has been approached varies greatly. All stages in the succession, which under favorable conditions culminates in the formation of the typical raised bog association-type, may be found, and, locally, any of the three types just mentioned may constitute an edaphic climax. Through the study and comparison of a large number of such areas, the general course or courses of development and the ecological relations of the association-types involved have been quite satisfactorily worked out. In the following account, attention is first directed to the chief features, vegetational and otherwise, of the respective stages, after which their relation to one another and to bog development will be discussed.

The bog meadow association-type.—As stated earlier, the surface of the tableland comprises a series of low, rounded hills, which rise to a rather uniform height and are separated by valleys of varying depth, but mostly shallow. Many of these valleys (Fig. 67) are quite broad, with a nearly flat or slightly trough-shaped floor, and lie but little below the general level of the surrounding low hills. Lengthwise the floor may be nearly level, but commonly it slopes gently in one direction or another. The ground here for the most part is well watered, not only by direct precipitation but by surface drainage from the higher slopes. It is in situations of this sort that the bog meadow association-type is best developed.

Figure 67.—Broad, shallow valley in barrens; mountains west of Ingonish; occupied mainly by wet bog, but partly by bog meadow. In the background, low hills covered with forest scrub.

The outstanding characteristics of bog meadow are as follows. The predominant vegetation is grass-like, being made up chiefly of *Scirpus caespitosus* and *Calamagrostis Pickeringii,* with *Rynchospora alba* locally prominent. These plants form a thin, more or less continuous sward. Woody plants are relatively inconspicuous, but there is always a scattered growth of low shrubs, mainly *Myrica Gale, Andromeda,* and *Chamaedaphne,* which rise scarcely higher than the sedges, while the tamarack commonly is represented by occasional small stunted specimens.

The cushion-forming species of sphagnum are usually inconspicuous, although the substratum beneath the grasses and sedges is commonly carpeted, at least locally, with *Sphagnum Pylaisei* and *S. tenellum,* together with the liverwort, *Cephalozia fluitans.* The ground is covered by a firm turf, beneath which there usually is a layer of peat from a few inches to a couple of feet in depth. The peat is quite compact, consisting very largely of the remains of sedges and grasses, but usually with a matrix of sphagnum remains. The surface of the swamp is flat or undulating; it is relatively smooth, and not hummocky. Slight depressions in the substratum are frequent, and in some of these water may accumulate temporarily to the depth of a few inches, but there are few if any ponds of the sort to be described as characteristic of wet bogs. In addition to the three shrubs named above, *Kalmia polifolia, Vaccinium macrocarpon,* and *V. Oxycoccus* are commonly present, the two latter, as well as the species starred (*) in the subjoined list, being more characteristic of the depressions, particularly where, as is commonly the case, *Sphagnum Pylaisei* and *Cephalozia* form a more or less continuous, felty ground cover. Additional herbaceous vascular plants commonly met with in bog meadows are as follows:

*Schizaea pusilla**
*Lycopodium inundatum**
Eriophorum virginicum
*Carex oligosperma**
Carex exilis
Habenaria clavellata
Sarracenia purpurea
*Drosera longifolia**
*Drosera rotundifolia**
*Bartonia iodandra**
*Utricularia cornuta**
Solidago uliginosa
Aster nemoralis
Aster radula

The vegetation of the shallow depressions just referred to should perhaps be regarded as constituting a distinct association-type, but for convenience they are included here merely as a type of society.

The wet bog association-type.—This is commonly developed in situations similar to those indicated for the preceding type, but conditions are most favorable where the surface slope is slight and where the presence of shallow depressions or approximately horizontal surfaces affords habitats which are congenial to the local growth of the mesophytic cushion-forming sphagnums. The influence of topography is suggested by diagram *C* of Fig.

65, where area *a-e* is occupied by wet bog, and area *e-f* by bog meadow. Frequently, as here, the two types of swamp alternate on the same slope, while very commonly the wet bog which occupies the floor of a shallow valley (Fig. 67) is separated from the typical upland vegetation on either flank by strips of bog meadow.

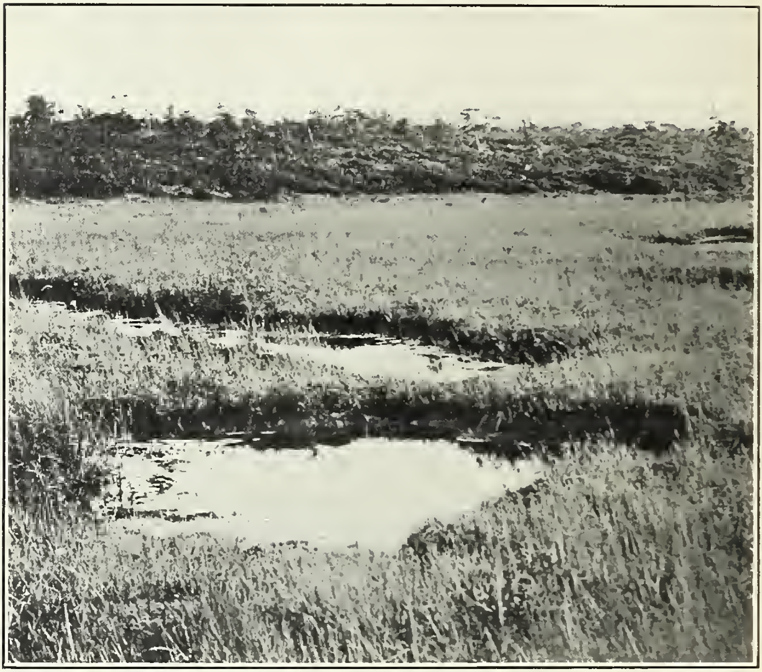

Figure 68.—In foreground, wet bog association-type (same area as that shown by Fig. 67), with pools due to activity of sphagnum (see text); in background, low hill covered with forest scrub; barrens in mountains west of Ingonish.

So far as the vascular element in the vegetation is concerned, the chief difference between this and the preceding association-type is seen in the relatively greater abundance here of the shrubs. Essentially the same list of seed plants is characteristic of each swamp type, and both shrubs (*Andromeda, Myrica, Chamaedaphne, Vaccinium Oxycoccus,* etc.) and herbaceous plants (*Scirpus, Rynchospora, Eriophorum,* etc.) are well represented here. The following additional species might be mentioned as characteristic of wet bogs, although they may also occur to some extent in bog meadows: *Eriophorum callitrix, E. angustifolium, Carex pauciflora, C. paupercula, Smilacina trifolia.* Beside these, various of the species of dry bogs, not yet mentioned, may be sparingly represented. But the vascular plants are of subordinate importance to the sphagnums, and the fundamental dissimilarity between the vegetation of wet bog and that of bog meadow lies in the predominance here of these mosses. Foremost among the sphagnums are the mesophytic cushion-forming species (*S. papillosum, S. magellanicum,* and *S. pulchrum*). Growing in rich profusion, these latter form soft, wet, cushion-like or pillow-like beds which cover the ground almost uninterruptedly over large areas. Other species of *Sphagnum,* however, are by no means absent. Hollows in the bog proper are commonly occupied by societies of *S. tenellum* and *S. Pylaisei,* species which do not form cushions, while on the higher cushions, in greater or less abundance, may grow the relatively xerophytic cushion-forming species. In addition, the small ponds or pools which commonly dot the bog surface (Figs. 62, 64, 66, 68, 69) usually contain various aquatic and semi-aquatic species. These ponds constitute one of the most distinctive features of areas occupied by wet bog, but their vegetation, strictly speaking, belongs in quite a different category from that of the wet bog association-type (see further under discussion of successional relations).

The surface of a wet bog, viewed in its entirety, may be flat or slightly convex; viewed in detail it is more or less uneven and hummocky. It is commonly underlain by an accumulation of peat from two to four feet in thickness, which consists of an intimate admixture of sphagnum, sedge, and shrub remains.

The dry bog association-type.—This, the culminating association-type of the raised bog series, may develop in similar situations to the preceding but particularly or nearly level surfaces, either flat or undulating. In contrast to bog meadow and wet bog, perhaps the most striking features of a dry bog (Figs. 66, 69) are its usually convex shape, the luxuriant development of the xerophytic cushion-forming sphagnums (*S. fuscum, S. capillaceum tenellum* and *S. tenerum*), the presence of such xerophytic seed plants as *Empetrum, Gaultheria,* and *Vaccinium* *pennsylvanicum,* and the predominance among the vascular plants of ericaceous shrubs. The bake apple (*Rubus Chamaemorus*) is one of the most characteristic plants of dry bogs. The surface of such a bog is hummocky, and except in wet weather the springy substratum underfoot is quite dry. The hummocks vary from one to several feet in diameter and from a few inches to more than a foot in height.[16] The depth of peat ranges up to more than six feet over a flat rock floor, while over depressions it may be considerably greater. Pools of the sort characteristic of wet bogs are found here also, but much less abundantly. Except for these and scattered wet depressions, whose vegetation and ecological relations are quite distinct from those of the enveloping area of dry bog (see later), the surface almost everywhere is overgrown by the xerophytic cushion-forming sphagnums, associated with which, and locally predominant, are certain other mosses (such as *Dicranum Bergeri, Racomitrium lanuginosum,* and *Polytrichum juniperinum*) and fruticose lichens (notably *Cladonia alpestris, C. sylvatica,* and *Cetraria islandica*). The moist hollows between the hummocks are commonly colonized very largely by liverworts, such species as *Ptilidium ciliare, Cephalozia media, Lepidozia setacea,* and *Mylia anomala,* which constitute more or less definite societies. The characteristic vascular plants of the dry bog association-type are the following:

Picea mariana	*Cornus canadensis*
Larix laricina	*Andromeda glaucophylla*
Eriophorum callitrix	*Chamaedaphne calyculata*
Scirpus caespitosus	*Gaultheria procumbens*
Carex pauciflora	*Gaylussacia dumosa*
Myrica Gale	*Kalmia angustifolia*
Sarracenia purpurea	*Kalmia polifolia*
Drosera rotundifolia	*Ledum groenlandicum*
Pyrus arbutifolia atropurpurea	*Rhododendron canadense*
Rubus Chamaemorus	*Vaccinium Oxycoccus*
Empetrum nigrum	*Vaccinium pennsylvanicum*
Nemopanthus mucronata	*Solidago uliginosa*

[16] Ganong remarks ('98, pp. 138, 139), that these sphagnum hummocks grow "in such rounded, radiating masses that it reminds one of the *Raoulia* or 'Vegetable Sheep,' and the resemblance is yet closer when, by drying, it assumes a grayish color."

It will be seen from the above list that nearly half the vascular species here are ericaceous shrubs or semi-shrubs, and these also comprise the greater bulk of the vascular plant cover. Herbaceous plants are subordinate in importance to shrubs, although a few forms, such as *Scirpus, Eriophorum* and *Rubus,* commonly occupy quite a prominent position. The various seed plants form a thin upper story of vegetation, but for the most part they rise less than a foot above the mossy substratum and quite commonly their shoots are buried nearly to the tip by the sphagnums. The trees are scattered and dwarfed: specimens of tamarack scarcely a foot high and an inch in trunk diameter may show more than fifty annual rings.[17]

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[17] In this connection certain further observations by Ganong ('98, p. 142), equally applicable to Cape Breton bogs, are of sufficient interest and suggestiveness to warrant quoting at length. "Most of the ericaceous plants on the bog have stems of great length running just beneath the surface, which, as Warming points out, is characteristic of bog plants. In one, *Rubus Chamaemorus,* I followed a stem over seventeen feet without finding an end, and in *Ledum* and *Cassandra* for lesser, though considerable distances, also without finding the ends. These stems run nearly horizontally, branch frequently, and send out roots at intervals. The same stem varies in thickness in different parts; is now thicker, now thinner, showing a more active growth at some times than at others. It is clear, also, that these stems are now alive only at their tips, the under-moss parts being preserved from decay by their position. When one traces what appears to be a clump of young plants of *Ledum latifolium,* he often finds that they are all branches of one plant connected beneath the surface, and he cannot find the end of any one of them; and this is true also of other species. The question now arises, when and how have such plants started, and how do they come to an end? Since the different branches can grow on continuously, and, making their own roots, become independent of one another and of the original plant, and can grow upwards continuously with the growth of the moss, there seems to be no logical limit to their growth, and no cause for death, such as brings most other woody perennials to their end in other situations. Some of them may then be as old as the bog itself, and thus would be amongst the longest lived of phanerogamic vegetation. Yet a comparison between their age and that of a tree, for example, would not be a fair one; physiologically, their longevity should be compared rather with that of those lower organisms, which grow by continuous fission. This continuous life of the bog plants, however, is pure theory; its demonstration is attended with great practical difficulties. To some extent this mode of growth is found also in the trees. In the spruces . . . one may observe how the moss is rising and burying them. As it

Successional relations.—Assuming for the purpose of illustration a nearly level or gently sloping rock floor, approximately flat as a whole but in detail with a more or less irregular surface, with slight elevations and depressions but with no basins capable of retaining any appreciable body of water, the successive steps in the evolution of a raised bog may now be outlined. On an uneven rock surface of the sort under consideration the pioneer aspect of the vegetation varies locally. In the higher, drier situations it is essentially xerophytic. Commonly the vegetation here is that of the sedge–grass heath association-type, as described in connection with xerarch successions: the ground is covered by a carpet of cladonias and *Racomitrium,* and supports a more or less luxuriant growth of *Scirpus caespitosus* and *Calamagrostis Pickeringii,* with a scattering of low shrubs. In the lower situations the vegetation may be quite similar, but here, owing to the generally more favorable moisture relations, the sphagnums commonly establish themselves, either coming in at the outset or later on replacing the cladonias and *Racomitrium.* Subsequent changes in the nature of the substratum and in the ecological aspect of the surface vegetation depend very largely on the sphagnums, not merely on their presence or absence but on the species which come to predominate. Where conditions are such that none of the sphagnums are able to establish themselves in force, any further changes will probably conform closely with what has been described earlier in connection with xerarch successions. Where conditions are such as to favor the growth of the sphagnums and these assert themselves as one of the predominating elements of the plant cover, further changes depend very largely on which particular group of sphagnums gains control over the situation.

For the sake of simplicity there will be described a hypothetical example of what may be regarded as the logical sequence of association-types: a series in which the pioneer stage gives way to a bog meadow, which becomes superseded by a wet bog, which in turn gives way to a dry bog; and, in this connection, various

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buries the lower branches, these put out new roots, turn upwards at their tips, and grow as independent stems. This growth probably, however, does not go on indefinitely, since the trees are ultimately overwhelmed and destroyed by the moss."

other possible lines of development will be pointed out. Let it be assumed, as is very commonly the case, that the low spots have become colonized by *Sphagnum tenellum* and *S. Pylaisei,* species which lack the cushion-forming habit. Under these circumstances the formation of peat and the building up of the substratum may take place very slowly, being due very largely to the accumulation of sedge remains. But, even at that, it takes place much more rapidly in these lower areas than on the higher ones. As the layer of peat in these lower areas becomes gradually thicker and the ground level is raised higher, the surface vegetation spreads out laterally and may override the higher areas; and in this way there may originate what has been described above as a bog meadow.

Further advance beyond the bog meadow stage of the succession is dependent primarily, either directly or indirectly, on the activity of various cushion-forming species of *Sphagnum.* Wherever conditions are congenial to the growth and spread of the mesophytic cushion-forming species (*S. papillosum, S. magellanicum, S. pulchrum*), bog meadow may gradually give way to wet bog. Indeed these species may have been the important ones from the very outset, so much so that the bog meadow stage in the succession may never have been developed. The factors which condition the presence or absence and the relative abundance when present of these species of *Sphagnum* doubtless have to do very largely with the amount of water available throughout the season, but it seems likely also, as suggested elsewhere, that the difficulty with which these and other species are able to invade areas already occupied by *S. Pylaisei* in particular may be a factor of considerable importance as affecting their establishment on the surface of a bog meadow.

The transformation in the character of the habitat accomplished through the agency of the mesophytic cushion-forming sphagnums and the manner in which they bring about the elimination of bog meadow or any other type of vegetation which may be present is exceedingly interesting. Heretofore, in the case of bog meadow, what water has not been absorbed by the compact, peaty substratum has been able to run off quite unobstructed over the comparatively smooth, firm surface, with the result that except during wet periods the ground at the surface may have been relatively dry. One of the essential characteristics of the cushion-forming sphagnums is their great ability to absorb and retain liquids. But while this in itself is a factor of no little significance in hindering the loss of water, even more significant is the manner in which individual clumps of these mosses run together and form banks which may obstruct the drainage to such an extent that in favorable situations, as on gentle slopes, the water may be dammed back to form ponds and pools of various dimensions. The degree to which masses of sphagnums are thus able to hold back the water is remarkable. In the boggy area diagrammatically shown by Fig. 65, *C*, for example, the level of the water in the pond at *e* is nine inches higher than that at *d*, twenty-five feet distant; and the water level in pond *d* is twelve inches above that in pond *c*, equally distant. In another instance a difference in elevation of two feet was measured between two water surfaces thirty-five feet apart; while in two other cases differences in level amounting respectively to nearly ten feet in less than a hundred, and to more than one foot in three were estimated. On the "down-hill" sides of a pond the banks of sphagnum rise steeply from the water's edge to a height of one, two, or more feet above the pond's surface. In one instance a rise of three feet within seven feet of the water's edge (or to a height of about five feet above the mucky bottom of the pond) was noted. It is obvious that these ponds, by retaining much of the water which accumulates in them during wet periods, or which drains into them from higher levels, function as storage reservoirs and insure to adjoining areas a fairly uniform water supply throughout the season.

Incipient ponds of the sort just described are frequently encountered in the bog meadow stage of the succession, but there they are usually shallow and ephemeral. It is in the wet bog stage that they first attain a position of ecological importance. The formation of ponds hastens the elimination of the bog meadow as a distinct association-type, for their spread leads naturally to the extermination of any plants which may have tenanted the areas which they now occupy, except for the few species which are able to adapt themselves to the changed conditions, either by assuming an aquatic habit (e. g., *Sphagnum Pylaisei*) or through their position above the water level (e. g., tussocks of cushion-forming sphagnums).

Sometimes these ponds appear to be distributed quite indiscriminately over the surface of a bog (e. g., see Fig. 65, *A*): particularly is this true on the higher, older bogs. But in other cases their arrangement is very definite. To cite a specific illustration of the latter sort: in one shallow, approximately flat-floored valley (similar to that pictured in Fig. 67) about a hundred feet wide, there are ten of these ponds within a distance of three hundred feet. All are more or less elliptical in outline, twenty to fifty feet long by six to twenty feet wide, and they are arranged, like a flight of steps, at right angles to the long axis of the valley floor. Between the surface of the lower pond in the series and that of the upper there is a vertical difference in elevation of five feet. It may be further noted that the rock floor beneath this bog, as determined by soundings, is quite even and that the peat is uniformly about four feet deep, except around the down-hill margins of the ponds where it is banked up higher. From the study of this and other like cases, there seems little question that a large proportion of the ponds associated not only with wet bogs but also with dry bogs have originated in the manner here described. The absence of any relationship to the character of the underlying topography is exemplified by ponds *d* and *e* in Fig. 65, *C*.

Leaving for the moment the consideration of these ponds, the further history of the bog as a whole may be briefly detailed. Largely through the activity of the mesophytic cushion-forming sphagnums, the general level of the surface has been raised and bog meadow eliminated. These mesophytic sphagnums continue to predominate and to build up the substratum for a locally variable length of time: frequently a wet bog association may represent an edaphic climax. But although the nature of the environment may be considerably modified by the influence of the ponds referred to above, it is apparent that, as a rule, sooner or later, as the surface rises higher, the conditions will become less favorable for the mesophytic sphagnums, while at the same time they will become more favorable for the xerophytic cushion-forming species (*S. fuscum, S. capillaceum tenellum, S. tenerum*). As time goes on, these latter species, which in wet bog constitute merely a subordinate element in the vegetation, gradually become the predominant forms, and wet bog becomes superseded by dry bog. Incidentally it may be remarked that, like the mesophytic forms, the xerophytic cushion-forming sphagnums sometimes predominate from the very outset, so that both the bog meadow and wet bog stages may be eliminated. On the higher, drier parts of a bog, as elsewhere indicated, the xerophytic sphagnums in turn may give way locally to various lichens and mosses, but these never become sufficiently abundant to constitute a distinct association-type.

Throughout the successive steps in bog development, as just outlined, sight must not be lost of the part played by various seed plants. These fulfill a triple rôle in that they facilitate the upward growth of the sphagnums and bind together the spongy, otherwise incoherent matrix of sphagnum remains, beside contributing in varying degree to the bulk of the deposit. Much of the springiness and comparative firmness which characterizes the surface of a mature bog is ascribable to the tangle of stems and roots with which the ground is interwoven. With regard to the rate at which the bog surface is built upward: in general, upward growth is comparatively slow at first, during the bog meadow stage, most rapid during the wet bog stage and during the early part of the dry bog stage, from which point on there is a gradual slowing down until, in the case of the older, higher bogs, growth is practically at a standstill (but see quotation from Weber on p. 456).

From the observations recorded in the preceding pages it is apparent that not only do the sphagnums as a class play an all-important part in the development of raised bogs, but that different groups of sphagnums are responsible for different phases in the development. It is also certain that the formation and upward growth of a bog is not dependent on the presence of any preëxisting water basin from which the required water is raised by capillarity. The view expressed by Ganong ('98, p. 148) that "The raised bogs are formed, as all students of them agree, by the pure Sphagnum growing upward and carrying the water by capillarity with it" has long since been exploded. To quote from Warming ('09, pp. 200–201): "It is erroneous to suppose that Sphagnum sucks up water from the soil; it raises water only for an inconsiderable distance. The movement of water in a Sphagnum-moor is essentially a descending one. The depth at which the water-table lies is dependent on the atmospheric precipitation and upon the permeability of the peat and of the substratum . . . . . [A raised bog (high-moor)] often arises on top of old low-moor; it may also take origin on wet sand, and even on rocks if these be sufficiently wet." Incidentally, it is worthy of note that although he accepted the then current conception as to the origin of raised bogs, Ganong was puzzled by, and commented at some length on, the "presence of much standing water near the surface on the higher parts" of the New Brunswick bogs which he studied ('98, p. 148).

In this connection, it is also of interest that Ganong ('98, p. 151) describes as occurring on the slopes of one of these bogs "a series of remarkable holes . . . . of various sizes, from 30 by 12 feet down to a few inches. They are a foot or two deep, have perfectly level bottoms of black muck, sometimes so dry as to crack in the sun, in others moist, in others covered with water, the latter being at the lower, the former at higher levels." Obviously these are the ponds or pond holes which have been discussed at some length by the author. In northern Cape Breton also, the water in many of them disappears during a dry season, but many of them are several feet deep and apparently always contain water. The ponds on the higher parts of a bog are usually more or less circular in outline (FIG. 69) and ordinarily have steep banks all around. They may be relatively few in number, but commonly there are several or many to the acre. In many of them, save for various algae, vegetation is sparse and any filling in is accomplished through the gradual encroachment of the banks. In others there is a luxuriant growth of aquatic sphagnums (*S. Pylaisei, S. cuspidatum*). As regards the growth of these aquatic sphagnums, the discrepancy between different ponds is hard to account for, unless, as is very likely the case, it be correlated with the abundance of algae (see next paragraph). With the exception of *Nymphaea* and *Eriocaulon,* aquatic seed plants are usually scarce. In general, the ecological relations of the vegetation here approximate what has been described earlier (see: association-complexes of undrained ponds, p. 417; also, development of raised bogs in and around water-filled rock basins, p. 438).

Weber, in his paper on the vegetation and origin of the Augstumal Hochmoor in Prussia ('02, pp. 76–78), has made some important observations regarding the origin of these ponds

(*"Hochmoorteiche"*). Previous investigators for the most part had reasoned either that they represent the remains of lakes which formerly existed in the areas now occupied by bog, or, in view of the common paucity here of sphagnums, that they represent places where springs of lime-carrying water break through, a view which was somewhat doubtfully favored by Ganong. Parenthetically it may be suggested that the luxuriance with which the sphagnums, particularly *S. Pylaisei,* not infrequently occupy such ponds in northern Cape Breton is of relevant interest in this connection. In discussing their origin, Weber points out that while undoubtedly the first explanation mentioned above is sometimes the correct one, the second one is largely based on insufficient investigation. He effectually disposes of this lime theory by making careful analyses of the water in the ponds, which he finds, like that in surrounding parts of the bog, to be extremely poor in inorganic salts. He therefore concludes that the source of water supply cannot come from the ground. He incidentally comments on the universal lack of any positive signs of springiness, an observation which the writer can con-

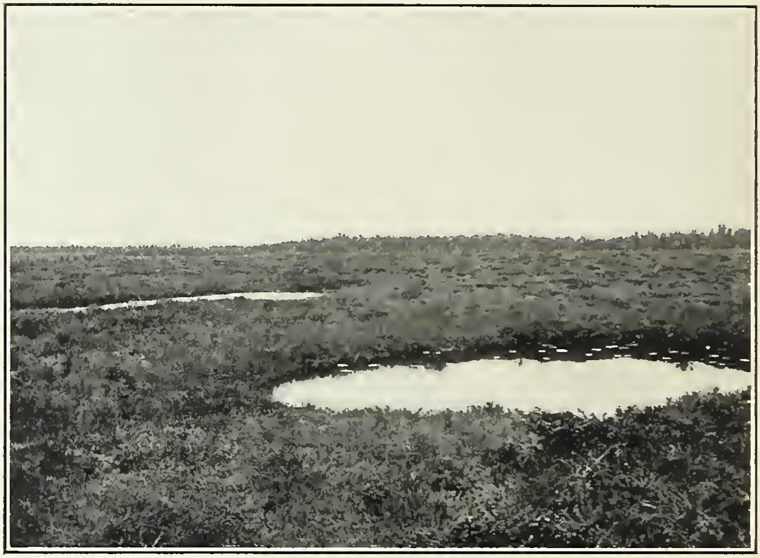

Figure 69.—Pools on surface of mature raised bog; Scotchman's Barren.

firm. Weber's explanation of the manner in which these ponds usually arise is somewhat as follows. They originate in the pools of water which collect in the deeper hollows between the hummocks on the surface, during wet seasons. During the dry season the water collects here only temporarily, but long enough to permit the existence of a number of low algae. The development of algae has a detrimental effect on the growth of any sphagnums which may be present, since (*op. cit.* p. 28) when the water dries up they form a thin parchment-like coat which overgrows the sphagnums and cuts off their light supply. When, in times of increased precipitation, the hollows fill up with water, wave activity brings about the enlargement of the basin, while by its mere weight, which in general is greater than that of an equal volume of water-soaked peat, the water contained in the basin causes the pond to deepen, an end which is also favored through the increasingly active circulation of oxygen through the water. He further remarks that while during subsequent dry periods numerous pools become overgrown again, in other cases the pools persist and become deeper as the surrounding surface of the bog rises higher. He consequently regards the deepest pools, in general, as the oldest ones.

Broadly speaking, Weber's explanation as to the origin of these ponds roughly approximates that arrived at independently by the writer. The essential points of both views are (*1*) the subsequent, rather than antecedent, origin of the ponds with reference to the bog; (*2*) the meteoric, rather than telluric, source of the water supply. The chief point of difference is this. According to the author's explanation, the ponds originate at a rather early stage in the bog's history and by their presence exercise an important influence on its development. Moreover, after their preliminary period of growth, there is little if any subsequent enlargement, but rather the tendency is just the reverse. According to Weber's explanation, the ponds may originate even on the surface of the mature bog. Moreover they are constantly tending to increase in size. So far as the raised bogs of northern Cape Breton are concerned, it is the opinion of the author that the majority of the ponds to be found on mature raised bogs have had a history essentially similar to what he has described. But it also seems very likely that some and quite possible that many of them may have originated in the manner suggested by Weber. At any rate, the writer agrees with Weber that even a mature raised bog is far from being in a condition of permanent equilibrium. To quote Weber (*op. cit.*, pp. 77–78): "Die Teiche sind nach alledem ebenso . . . . Symptome der beständigen Veränderung, die die Oberfläche des Hochmoores unter dem wechselnden Einflusse erfährt, den die Witterung längerer Zeiträume auf die Vegetation und den Boden ausübt. Solange die natürliche Vegetation vorhanden ist, gleicht das Hochmoor gewissermassen einem langsam pulsierenden und auf die äusseren Einflüsse in eigentümlicher Weise reagierenden Organismus."

In brief summary of the successional relations of raised bogs, as developed on essentially flat or undulating surfaces, it may be stated that, in any given area, there may ensue a sequence of stages, starting with a pioneer stage, passing progressively through bog meadow and wet bog, and culminating in dry bog, which latter constitutes the climax stage of the complete series. But the series is not always complete. In an area occupied by dry bog, either or both of the preceding stages may have been omitted; while, on the other hand, either of these two stages may constitute locally an edaphic climax. The course of events is dependent primarily on the activity of certain groups of sphagnums and is conditioned by the presence of environmental conditions suitable to their growth. In the course of a bog's development, through the activity of the cushion-forming sphagnums, ponds are formed which, by conserving the water supply, bear a vital relationship to the bog's growth. It may be added that the growth of a bog is not entirely vertical. As it grows upward it spreads out laterally. A bog originating in an edaphically favorable area may spread out in all directions, eventually covering many areas which of themselves were not favorable to bog development. In this way, as has been repeatedly pointed out, a bog may invade an area occupied by forest and bring about the destruction of the latter. Instances of this sort have been frequently observed in northern Cape Breton.

3. The Formation-types along Streams

THE ASSOCIATION-COMPLEXES OF RAVINES AND FLOOD PLAINS

The ravine associations of the hydrarch series here in the highland, like those of the xerarch series, require no special treatment, since on the whole the vegetation is essentially similar to what has already been described as characteristic of ravines in the lowland. Of special interest, however, are the association-complexes of flood plains.

Attention has elsewhere been called to the fact that on the plateau most of the streams for long distances flow through broad, shallow valleys, but little below the general level of the surrounding country. The floors of these valleys are nearly flat and gently inclined. The surface is only a couple of feet higher

FIGURE 70.—Shallow, flat-floored stream valley with characteristic vegetation; barrens in mountains west of Ingonish.

than the water in the stream in summer, and at times of high water it is subject to overflow. At such times a small amount of sediment is deposited, and this, together with the inundation itself, apparently has a decisive effect on the character of the vegetation. It therefore seems appropriate to regard such areas as flood plains, although they differ in a great many respects from ordinary flood plains. The mineral substratum is commonly overlain by a layer of peat one or more feet in thickness, which is rendered distinctly gritty by the fine sediment which is infiltrated throughout the mass. The surface vegetation is essentially that of a well-drained swamp. Over considerable areas its ecological aspect is that of a meadow, with sedges and grasses predominating. But as a rule these swales or "hay marshes" alternate with equally extensive patches of alder thicket and swampy woodland (FIG. 70). Similar associations are encountered frequently around the small lakes which lie along the courses of the streams. Here all intergradations occur between typical well-drained swamps and bogs. Along the streams themselves it is only occasionally that patches of bog are encountered, even the plants peculiar to bogs commonly being absent. In the barrens, where especially these flat-floored valleys constitute a prominent topographic feature, the flood plain vegetation here contrasts sharply with that of swamps remote from stream activity. In this connection it is worthy of note that the species of *Sphagnum* which play such an important rôle in bog development are scarce or absent here, although certain other species of *Sphagnum,* e. g., *S. Girgensohnii, S. recurvum,* and *S. palustre,* together with such mosses as *Chrysophynum stellatum* and *Drepanocladus fluitans,* are commonly represented, though never developing in any great luxuriance. A list of characteristic vascular plants follows:

Osmunda Claytoniana
Abies balsamea
Picea mariana
Picea canadensis
Larix laricina
Agrostis hyemalis
Calamagrostis canadensis
Glyceria canadensis
Scirpus caespitosus
Carex stellulata
Carex crinita
Carex aquatilis
Carex pauciflora
Carex polygama
Carex oligosperma
Carex folliculata
Juncus sp.
Iris versicolor
Habenaria dilatata
Myrica Gale
Alnus incana
Spiraea latifolia
Pyrus arbutifolia atropurpurea
Amelanchier sp.
Rosa nitida
Viola pallens
Kalmia angustifolia
Chamaedaphne calyculata
Lonicera caerulea
Viburnum cassinoides
Solidago uliginosa
Solidago rugosa
Aster radula
Aster umbellatus

SUMMARY

Cape Breton is situated northeast of the peninsula of Nova Scotia. In northern Cape Breton two topographic regions can be distinguished: the Highland and the Lowland. The highland includes primarily the lofty interior plateau, which rises to an average elevation of more than a thousand feet and is underlain by crystalline rocks of Laurentian age. In places this extends clear to the sea, but along much of the coast there is an intervening border of Carboniferous lowland, of varying width, between the highland and the shore. The entire area has been glaciated, drift being encountered on all sides in the lowland but much less frequently on the plateau.

The climate of the region as a whole may be classed as cool temperate maritime. The climate of the plateau differs from that of the lowland in the lower mean temperatures, greater daily range of temperature, shorter growing season, heavier precipitation, and generally lower humidity, this latter being attributable in large measure to the prevalence of low-lying cloud banks.

Considered from a phytogeographical point of view, Cape Breton lies near the northern border of the Transition Forest Region of eastern North America. In northern Cape Breton, owing chiefly to the differences in climate mentioned above, both the Deciduous Forest Climatic Formation and the Northeastern Evergreen Coniferous Forest Climatic Formation are well represented, the former in the lowland, the latter in the highland. These formations, as developed in northern Cape Breton, are treated separately.

The scheme adopted in classifying the plant associations of these two regions is outlined in the table of contents and has been discussed in some detail in another paper (Nichols '17).

The regional climax association-type in the lowland is a mixed deciduous-evergreen forest, comprising sometimes a dozen different trees, of which the following species are most characteristic: *Fagus grandifolia, Acer saccharum, Betula lutea, Abies balsamea, Tsuga canadensis,* and *Pinus Strobus.* All of these trees grow vigorously and to good size. The woody undergrowth in the forest includes, as the commoner species, *Acer spicatum* and *A. pennsylvanicum, Taxus canadensis* and *Corylus rostrata.*

Thirty-five herbaceous vascular plants are listed as characteristic. Bryophytes are present in profusion, but on the forest floor they are sparsely developed. This latter fact apparently is correlated with the annual accumulation on the ground of a blanket of fallen leaves which prevents the development of a moss-carpet.

The permanency of this type of forest is indicated by the composition of the younger generation of trees, which, in general, conforms with that of the mature stand. In this connection the ecological status in these forests of the balsam fir, character tree of the northeastern evergreen coniferous forest climatic formation, is considered in some detail. The conclusion is reached that the inability of this tree to compete successfully with the trees which characterize the deciduous climax forest formation can be attributed very largely to its shorter tenure of life, coupled with its greater susceptibility to fungus diseases and possibly with its less pronounced tolerance of shade.

The trees which characterize forests of the regional climax type, not only here but elsewhere in the Transition Region, can be divided into five groups: (*A*) Deciduous species whose center of distribution lies south of the transition region; (*B*) Deciduous species whose center of distribution lies within the transition region; (*C*) Evergreen species whose center of distribution lies within the transition region; (*D*) Evergreen species whose center of distribution lies north of the transition region; (*E*) Deciduous species whose center of distribution lies north of the transition region. With reference to the presence or absence of representatives of the first four groups above specified, eleven floristically different types of forest are distinguishable (see p. 292). In general, the trees of groups *B* and *C* are about equally well represented in forests throughout the transition region, those of group *A* are most generally represented southward, those of group *D* northward. In many parts of the transition region black spruce replaces balsam fir as the predominant northern conifer. Black spruce does not appear to be specifically distinct from red spruce. It is very doubtful whether the various floristic subdivisions of the transition region that have been defined should be regarded as ecologically distinct. From the standpoint of ecological plant geography the vegetation of the transition region as a whole is best treated merely as a northward extension of the deciduous forest climatic formation.

The regional climax association-type in the highland is predominantly coniferous, *Abies balsamea* being by far the most abundant tree. Associated with this in the forest, but always of subordinate importance, grow *Picea canadensis, P. mariana, Betula alba papyrifera,* and *Pyrus americana.* Ten shrubs and twenty-seven herbaceous vascular plants are listed as characteristic. Bryophytes develop luxuriantly on the forest floor, forming an almost continuous ground cover.

The permanency of this type of forest is attested by the character of the younger growth which is essentially similar to that of the mature trees. All of the climax trees grow best in the open and reproduction is most prolific in openings of the forest due to windfall. But the reproduction, at least of the balsam fir and black spruce, is by no means confined to windfall areas, which seems to be the case farther inland, as on Isle Royale.

That the coniferous forest climax of the highland is a climatic and not an edaphic climax is evidenced by the gradual transition from deciduous to coniferous forest encountered in ascending the mountains, and by the practically complete absence on the plateau, even in edaphically favorable situations, of the climax trees of the deciduous forest climatic formation.

A detailed review of the character and successional relations of the various association-types which comprise the edaphic formation-complexes of the lowland and highland respectively will not be attempted here. An outline of these is afforded by the table of contents, at the beginning of the paper, and by the paragraph headings which are scattered through the text.

By way of brief general summary it may be stated that: in the lowland, associations of the regional climax type represent the culmination of successional series in all edaphically favorable situations. Elsewhere succession stops at a stage less mesophytic than the regional climax association-type: in other words, in such situations the edaphic climax association-type does not coincide with the regional climax association-type, as it does in the more favorable situations. Due largely to human activity many areas formerly occupied by forests of the regional climax association-type are now occupied by associations of a much more primitive character, notably by forests of white spruce and balsam fir. In the lowland the regional climax forests of the highland are represented in successional series, in favorable situations being destined to give way to forests of the deciduous type but in many unfavorable situations constituting edaphic climaxes.

In the highland the same general relations hold true as in the lowland between associations of the regional climax type and those which are more primitive. But here, owing mainly to the humidity of the climate, the influence of dissimilar edaphic conditions is less pronounced than in the lowland. It can be stated in general that the influence of soil and topography on the character and distribution of plant associations is least pronounced in humid climates, most pronounced in arid climates: that this influence is universally proportional to the dryness of the climate.

The barrens represent an edaphic association-complex, the character of the vegetation being correlated with conditions of exposure, topography and soil. Of especial interest here is the extensive development of heath and of various types of scrubby forest and of raised bogs. Particular attention is called to the important part played in the development of the latter by different species of *Sphagnum.*

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