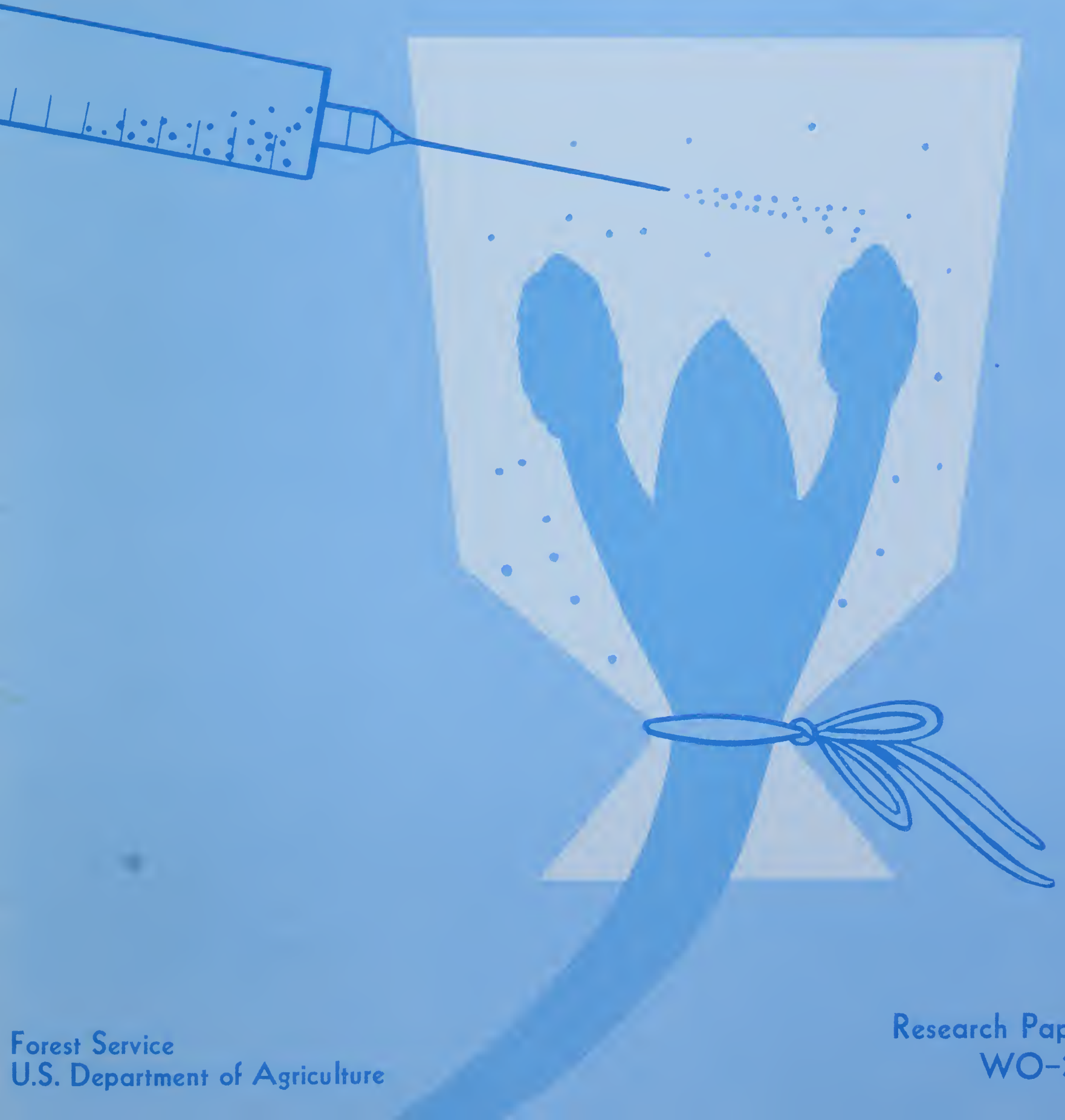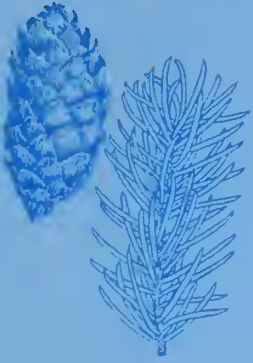# GENETICS

of ENGELMANN SPRUCE

This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D.C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

CONTENTS

RESEARCH SUMMARY

Engelmann spruce is widely distributed in northwestern North America. It hypbridizes extensively with white spruce, occasionally with blue spruce, and possibly with Sitka spruce in regions of natural sympatry. Artificial crosses to date of Engelmann spruce with these and other spruce species are summarized. The evolutionary history of Engelmann spruce from its Asian ancestors is traced, and its relationships to other modern spruces are discussed. Particularly important are its Pleistocene distribution in refugia, and its more recent contact and hybridization with white spruce.

The reproductive biology of Engelmann spruce is not well studied, but it appears to be consistent with that of most other spruces. Experience to date with controlled pollination techniques is reviewed.

Natural layering has been observed in Wyoming, and vegetative propagation appears possible via either rooted cuttings or grafts. Engelmann spruce tissue has also been successfully grown as a callus culture.

Considerable genetic variation occurs within Engelmann spruce. A combination of introgressive hybridization and habitat-correlated selection has led to clinal patterns of morphological variation, as well as possibly of terpene variation, of variation in juvenile growth and in dormancy. Analyses of genetic variation within stands, based on two open-pollinated progeny studies, are to date equivocal.

Nature reserves of various sorts are abundant within the native range of Engelmann spruce. Thus, the species is in good condition relative to *in situ* gene conservation, and base-line ecological studies. Tree improvement programs are beginning in British Columbia, Michigan, and the Inland Empire.

GENETICS OF ENGELMANN SPRUCE

D. P. Fowler [1] and L. Roche [2]

INTRODUCTION

Engelmann spruce (*Picea engelmannii* Parry) was named in commemoration of Dr. George Engelmann, a noted German-American physician and botanist of the mid-19th century (Harlow and Harrar 1950). Other names for this species include Columbian spruce, mountain spruce, silver spruce, and white spruce (McSwain, Alexander, and Markstrom 1970).

Although never planted on a large scale, at one time Engelmann spruce was the third most widely planted spruce species in the United States (USDA Forest Service 1948). Interest in planting this species waned because of the mediocre results obtained in plantations which were almost invariably established outside its native habitat at low elevations and in relatively warm climates.

In the past, the Engelmann spruce forests of Western North America were largely ignored from the standpoint of forest management and planting (Roe and James 1959). More recently, the vast potential of these forests and the desirability of formulating suitable management policies has been recognized. Associated with this recognition is a resurgence of interest in planting Engelmann spruce, especially in interior British Columbia (Kiss 1971), and interest in the genetics of the species is also increasing.

For detailed bibliographies of the literature pertaining to many aspects of Engelmann spruce, the reader is referred to Ronco (1961) and Christensen and Hunt (1965).

NATURAL DISTRIBUTION AND HABITAT

Engelmann spruce is widely distributed in the Western United States and Canada, where it occurs from British Columbia and Alberta in the north to New Mexico and Arizona in the south (fig. 1).

R. R. Alexander (1958), in "Silvical characteristics of Engelmann spruce," presented a detailed account of the climatic, edaphic, physiographic, and biotic characteristics of the habitat of this species. In summary, Engelmann spruce's habitat is characteristically cold and humid. The mean annual temperatures of this habitat are near freezing and the mean precipitation exceeds 25 inches (63 cm) with only moderate or no seasonal deficiency. Summer temperatures average 45 to 60° F (7 to 16° C) and winter temperatures 10 to 20° F (−12 to −7° C).

Engelmann spruce can be found on a wide variety of soils but attains its best development on alluvial soils or on moderately deep, well drained silt and clay loam soils developed from basalt, andesite,

rhyolite, shale, or limestone. The species is seldom found below 2,000 feet (610 m) elevation even in the northern part of its range, and there it occupies only relatively moist sites. It attains its greatest elevational distribution in the southern Rocky Mountains, where it can be found at timberline at over 11,000 feet (3250 m) and occasionally below 9,000 feet (2750 m).

Engelmann spruce may form pure stands, but more often it is found in association with other tree species. The species occurs as part of 15 cover types (Soc. Am. For. 1954), the most important of which is the Engelmann spruce—subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) (fig. 2).

White spruce (*Picea glauca* (Moench) Voss) and blue spruce (*Picea pungens* Engelm.) are the only other spruces with which Engelmann spruce is associated. The association with white spruce occurs in Alberta, British Columbia, and northwestern Montana, while that with blue spruce occurs in scattered locations throughout much of the central Rocky Mountains in Montana, Idaho, Wyoming, Utah, Colorado, Arizona, and New Mexico (fig. 1).

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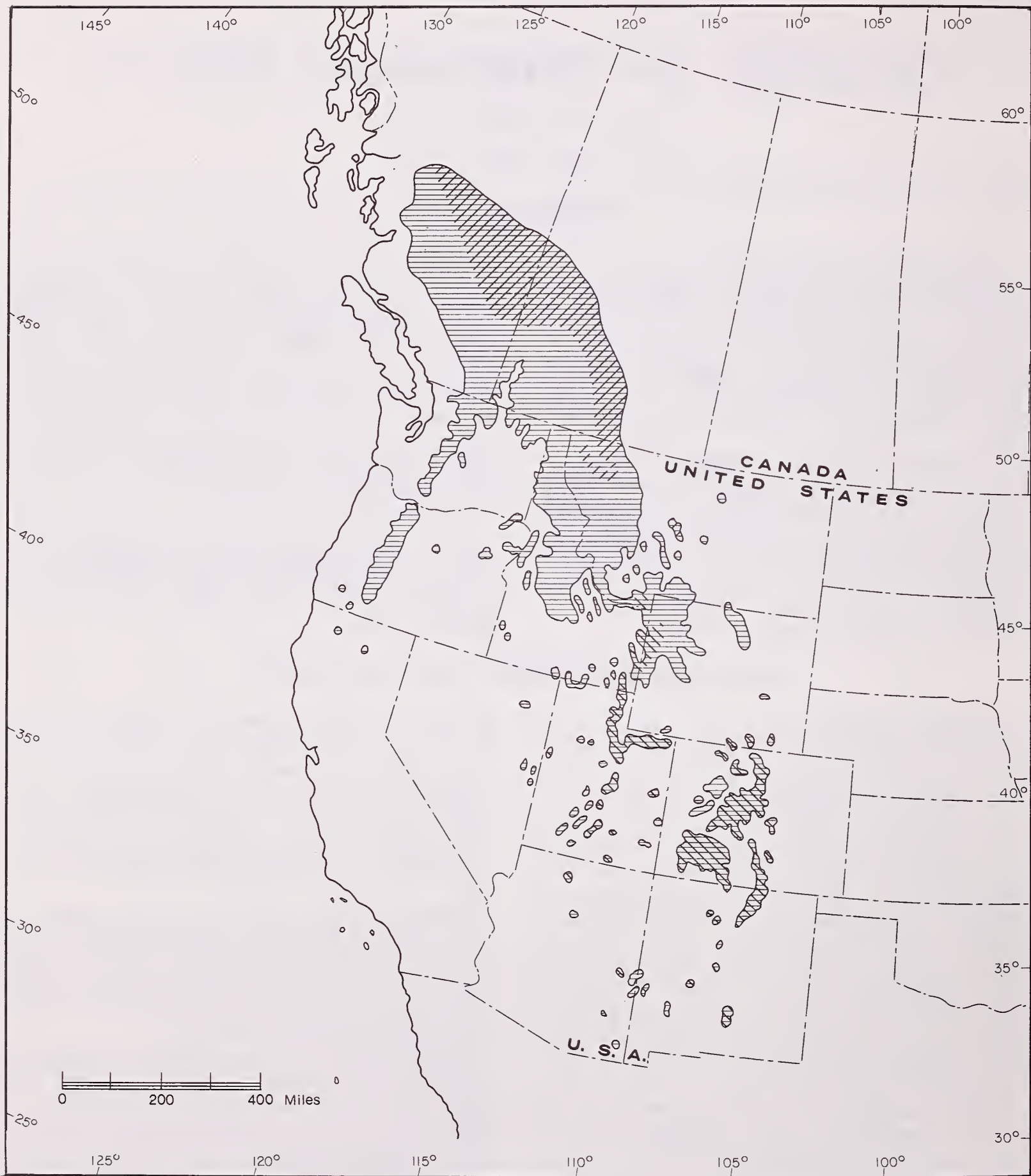
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Figure 1.—Natural range of Engelmann spruce, showing overlapping range of white spruce and blue spruce (Little 1971).

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The conifers originated around the periphery of the north Pacific Basin (Li 1953), probably in eastern Asia (Wright 1955). Many of the modern conifer families were differentiated during the Mesozoic Era (Delevoryas 1962). The present-day spruces retain the basic spruce type, which evolved at least as early as the Cretaceous Period. The genus is of monophyletic origin, and it would appear that speciation is the result of mutation at many loci rather than by chromosomal change (Wright 1955). The haploid chromosome number of Engelmann spruce is 12 (Santamour 1960), and no readily recognizable differences from the general spruce karyotype have been reported.

Intergeneric Relationships

Van Campo-Duplan and Gaussen (1948) advanced the hypothesis that *Tsuga mertensiana* (Bong.) Sarg. is an intergeneric hybrid of *Picea sitchensis* (Bong.) Carr. and *T. heterophylla* (Raf.) Sarg. They further suggested that *T. crassifolia* Flous is a hybrid of Engelmann spruce and *T. mertensiana* and proposed the name *Tsugo-Piceo-Picea crassifolia* comb. nov. This hypothesis has received the support of other authors of the Toulouse school (Ferré 1952; Vabre-Durrieu 1954a, b; Chopinet 1962) at least in respect to *T. mertensiana*.

Duffield (1950), in discussing the Van Campo-Duplan and Gaussen hypothesis, concluded that the crossability of *Tsuga* and *Picea* will have to be further tested before this hypothesis can be accepted. The nomenclature as proposed by the Toulouse school has not found wide acceptance.

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Figure 2.—Virgin stand of Engelmann spruce and subalpine fir, northeast of Cranbrook, British Columbia, latitude 49°47′, longitude o15°27′, elevation 4,600 feet (1400 m).

Interspecific Crossability

There is abundant evidence that natural hybridization between Engelmann and white spruces occurs in sympatric populations of these species (Wright 1955; Garman 1957; Horton 1959; Taylor 1959; Weaver 1965; von Schantz and Juvonen 1966; von Rudloff 1967; La Roi and Dugle 1968; Ogilvie and von Rudloff 1968; Habeck and Weaver 1969; Roche 1969; Hanover and Wilkinson 1970). Hybrid populations also occur, as outliers, at low elevations on moist sites in British Columbia (Roche 1969). Taylor (1959) considered Engelmann and white spruce to represent extremes in a continuum of variation exhibited by a single, wide-ranging, highly variable species. However, most authorities consider Engelmann and white spruce to be closely related but distinct species (see La Roi and Dugle 1968).

There is also evidence that blue spruce occasionally crosses with Engelmann spruce in sympatric areas in Wyoming (Weaver 1965; Habeck and Weaver 1969). Garman (1957) suggested that Engelmann and Sitka spruces cross in northwestern British Columbia. However, Daubenmire (1968) and Roche (1969) considered it more probable that hybridization in this area is between Sitka and white spruces.

Engelmann spruce has been crossed artificially with several other spruce species with varying degrees of success. The results of this work are summarized in table 1. On the basis of crossability, Engelmann spruce is closely related to *P. glauca* and *P. sitchensis*, and somewhat less closely related to *P. pungens*. Data from the other crosses are too limited to suggest relationships.

Wright (1955), using 32 morphological characters, compiled a list of the numbers of characters (weighted) by which spruce species differ. Those figures pertinent to Engelmann spruce are included in table 1 and show only moderate agreement with the crossability data.

Assuming that the spruces originated in eastern Asia, then Engelmann spruce or an ancestor of Engelmann very likely reached North America via a land bridge between northeastern Asia and Alaska. The high crossability of white, Engelmann, and Sitka spruces suggests that speciation occurred after their establishment in North America. Wright (1955) considered *P. jezoensis* (Siebold and Zuccarini) Carrier to be the most probable connecting link between the Old World and western American spruces because of its taxonomic similarity to Sitka spruce. Fowler (1966) questioned this theory and suggested *P. glauca* as a more probable line because of the ease with which it crossed with the Asiatic *P.*

Table 1—Interspecific crosses of *Picea engelmannii* arranged in order of probable crossability

Other Parent	Cross-ability	Authority [1,2]	Morphological differences [3]	Remarks	Authorities
glauca	High	H–2, 7, 9, 11: 3, 5, 9, 10, 11, 12	17	Closely related, natural hybrids, good seed yields	1. Cheng 1939
sitchensis	Probably high	H–1, 5:5	14	Closely related, poor data on crossability	2. Fechner & Clark 1969 3. Habeck & Weaver 1969
pungens	Moderate	H–2, 8:6 U–4:3 F–:2	12	Fairly closely related seed yields moderate to low	4. Johnson, A.G. (in Wright 1955)
					5. Johnson, L.P.V. 1939
omorika	Low?	F–:11	19	More crossing required to determine relationship	6. Kossuth and Fechner 1973
orientalis	Low	F–11	22	No successful crosses	7. Larsen 1948
abies	Low	F–11	19	No successful crosses	8. Richens 1945 (in Fechner & Clark 1969)
asperata	Low	F–11	22	No successful crosses	9. Santamour 1967
retroflexa	Low	F–11	22	No successful crosses	10. Taylor 1959
maximowiczii	Low	F–11	22	No successful crosses	11. Wright 1955
montigena	Low	F–11	19	No successful crosses	12. Wright 1962

[1] Numbers in front of the colon (:) refer to crosses where *P. engelmannii* is used as female cross, numbers after the colon refer to the reciprocal cross.

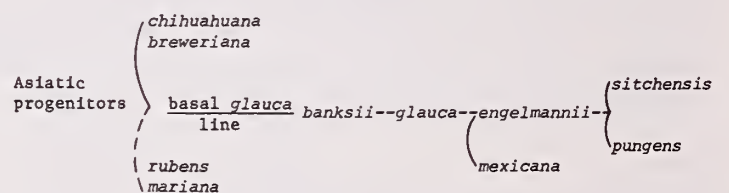[2] H = hybrids reported; U = undetermined, possible hybrids; F = failure reported.

[3] From weighted analysis of 32 characteristics (Wright 1955). The higher the number, the greater the morphological difference between *P. engelmannii* and the listed species.

schrenkiana Fischer and Meyer and the poor success of the cross *P. schrenkiana* x *P. jezoensis*. Subsequently, Hills and Ogilvie (1970) reported finding fossil cones of a *P. glauca*-like spruce, *P. banksii*, in the Beaufort formation on northwestern Banks Island, Arctic Canada. They considered the formation to be of late Miocene or early Pleiocene origin (11 million years ago). They suggested *P. banksii* as an ancestor of *all* the North American spruces. While *P. banksii* could well be ancestral to the western American spruces, the difficulty encountered in crossing *P. mariana* (Miller) B.SP. and *P. rubens* (Sargent) and *P. glauca*, and the ease with which these species can be crossed with the European *P. ormorika* (Panic) Parkyne, opposes this hypothesis. The presence of *Picea* pollen, possibly representing 2 or 3 species, in sediments deposited during the Eocene (60–40 million years ago) (Wodehouse 1933) suggests a much earlier presence of spruce in North America.

Nienstaedt and Teich (1972) have taken these factors into account in suggesting an alternate phylogenetic pathway:

Roche and Fowler (1974), while not disagreeing with the phylogeny as proposed by Nienstaedt and Teich (1972), suggested that *P. mariana* and *P. rubens* reached North America from the East during the Jurassic (180–135 million years ago), before continent separation.

The Possible Phylogeny of North American *Picea* Species (from Nienstaedt and Teich 1972)

The fossil history of *Picea* during the Pleistocene is incomplete. It is most probable that Engelmann spruce survived Pleistocene glaciation in mountainous areas south of the ice sheet. At that time, its range probably extended to lower elevations (it was certainly forced by mountain glaciers from some of the areas it now occupies) and possibly to lower latitudes. It is not known if Engelmann spruce was separated from white spruce during all or part of the Pleistocene. Wright (1955) considered the spruce populations found along the east slope of the Canadian Rocky Mountains, where Engelmann and white spruce are sympatric, to be unstable introgression products. This would indicate that contact, and consequently gene exchange, is a fairly recent

phenomenon. This is compatible with Garman's (1957) conclusion that the two species occupied separate refugia during the glacial periods. Horton (1959) also considered the Engelmann-white spruce complex unstable and did not recognize *P. glauca* var *albertiana* as a distinct entity. However, Weaver (1965) reported that a more stable situation exists in parts of Montana and suggested that both white and Engelmann spruces survived glaciation in the South. He also suggested that *P. columbiana* (*P. glauca* var *albertiana*) is the product of hybridization between white and Engelmann spruces and that *P. columbiana* is a taxonomically valid species. Most of the evidence seems to indicate that white and Engelmann spruce were spearated, at least during the later stages of the Pleistocene, and that contact between the two species and the resulting hybridization is a fairly recent phenomenon.

SEXUAL REPRODUCTION

Reproductive Development

Relatively little has been written on the flowering and fruiting of Engelmann spruce. The species is monoecious with ovulate and staminate strobili generally borne in separate parts of the crown. Under natural conditions, Engelmann spruce begins to bear cones at age 16 to 25 (USDA Forest Service 1948). Cone production increases with age at least for 200 to 250 years (Alexander 1958). No information is available concerning the success or failure of techniques to reduce "age to flowering" in this species. It is probable that treatments that stimulate growth and development of a large crown will reduce the time required to begin flowering.

Seed production is usually not a serious problem with Engelmann spruce. Good cone crops are produced every 2 to 5 years (USDA Forest Service 1948; Franklin 1968) with moderate to light crops in intervening years. Evidently cone production is somewhat less reliable east of the Continental Divide in Montana (Alexander 1958).

The early stages of cone morphology have not been described for this species. It is probable that initiation and development follow a similar pattern to that of the closely related white spruce. If this is correct, initiation would occur during the growing season preceding the emergence of the reproductive structures. Ovulate and staminate strobili can be identified microscopically in the fall. In the spring or early summer of the next year, the strobili emerge and pollination takes place. Time of "flowering" is strongly related to elevation (Alexander 1958) and probably to latitude. The "Woody Plant Seed Manual" (USDA Forest Service 1948) listed June to July as the flowering time for this species. In the Prince George area of British Columbia, pollination occurs from May 30 to June 15. Pollination of white spruce, which grows at lower elevations in this same area, occurs between May 15 and 25.[3] The frequency of hybridization between these species indicates that flowering is more nearly synchronized at mid-

elevations. In eastern Canada, planted Engelmann spruce flowers in mid-May at almost the same time as nearby white spruce. As in other spruces, the staminate strobili are located in terminal positions on branchlets in the less vigorous portion of the crown. They are about 1.3 cm long at maturity. The erect ovulate strobili are about 2.5 cm long when receptive and appear on the previous year's internode in the position of lateral buds. These strobili, although generally concentrated in the upper portion of the crown, may also occur on the ends of branches distributed throughout the crown.

Shortly after pollination, the developing ovulate strobili turn down and, during the next 2 months, mature into cones which are 2.5 to 6.4 cm long. No published information is available on the embryology of Engelmann spruce. Presumably it is similar to that of white spruce, which has been described by Mergen et al. (1965) and Rauter and Farar (1969).

In the native range, Engelmann spruce cones ripen during August and September (USDA Forest Service 1948), and the cones begin to open in September. Most of the seed has been shed by the end of October, but some fall throughout the winter (Alexander 1958). In the Prince George area of British Columbia, the cones ripen from August 15 to September 1, and the most of the seed are dispersed from September 1 to 15. The seeds are small, with an average of 660,000/kg (USDA Forest Service 1948) to over 1,090,000/kg.[3] One litre of cones will yield 5 to 14 grams of seed (USDA Forest Service 1948).

Controlled Pollination

The techniques for controlled pollination of Engelmann spruce are basically the same as those reported by Wright (1962) but have been modified to suit local conditions. Most modifications have involved isolation bags, pollen extraction, and pollen application. The ovulate strobili can be recognized with certainty a few days or a week before they emerge from the bud scales. Isolation bags are usually placed over the branches bearing the female strobili soon after they are distinguishable from vegetative buds. Many different types of isolation

[3]C.K. Kiss Correspondence. B.C. For. Serv., Prince George, B.C., March 14, 1972, on file at Maritimes For. Res. Cent., Can. For. Serv., Frederiction, New Brunswick.

bags have been used, including shaded and un-shaded sausage casing, kraft paper, parchment paper, and terylene. We have used several of these types of bags for controlled pollinations of a number of spruce species. We prefer the terylene bags, with or without windows, because they are light, durable, readily available in suitable sizes for spruce, and do not interfere with normal cone development. Fechner and Clark (1969) obtained high seed sets from controlled pollinations of Engelmann spruce when they used kraft paper isolation bags.

The ovulate strobili are most receptive when the scales are perpendicular to the strobilus axis. Pollen should be introduced into the bags when most of the female strobili are in this condition. As it is not unusual for some strobili to be in slightly different stages of development, and as all ovules of a strobilus do not reach maximum receptivity at the same time, seed set can be increased by pollinating once when most of the strobili are fully receptive and again 2 to 4 days later.

The isolation bags should be left in place for 10 to 20 days to assure that all strobili are closed and that there is no chance of contamination. If the bags are removed, it is usually desirable to rebag the cones later in the season (August) to prevent premature seed-shedding, or cone-cutting by rodents. Fiber glass screen or cloth bags have been used for this purpose. We have found it desirable to leave the isolation bags (terylene) in place until the cones are harvested. This procedure saves time, simplifies relocation of the cones, prevents premature seed loss, and does not reduce sound seed set. Although this technique has not been adequately tested on Engelmann spruce, it will probably be satisfactory.

Staminate strobili of Engelmann spruce can be collected a few days before pollen shed begins, when strobili are fully developed and beginning to dry. When the male strobili are squeezed between the thumb and forefinger, the exudate should be granular in appearance and almost free of clear fluid. Pollen can be obtained somewhat earlier by "forcing" branches bearing staminate strobili. Almost any drying method that prevents contamination and does not subject the pollen to extremes of temperature is satisfactory. The dry pollen can be separated from the strobili by passing it through a 25- to 30-mesh/cm screen. Fresh pollen is generally preferred for controlled pollination, but pollen can be stored with little loss of viability at -18° C in a desiccator over silica gel for at least 1 year.

Engelmann spruce pollen will germinate in distilled water. Pollen viability tests using agar or hanging-drop techniques (Wright 1962) are satisfactory. Viability estimates also can be made from pollen germinated on the surface of distilled water in sterile, cotton-stopped vials. Germination counts can be made after 48 to 72 hours at 24°C. It does not necessarily follow that pollen that is viable *in vitro* will function *in vivo*.

Loss of developing strobili and cones to insects can be a serious problem in any controlled pollination program. Control of cone insects with insecticides has generally been expensive and only partially satisfactory. We have found that a small piece (1 × 1 × 0.5 cm) of polyvinylchloride impregnated with Vapona[4] insecticide, placed in the bag at the time of isolation, is inexpensive and provides good control of several insect pests (Fowler 1971).

## Seed Germination and Establishment

Seeds of Engelmann spruce generally do not require any pretreatment before germination (USDA Forest Service 1948). For optimum germination, Heit (1961) recommended that seeds be placed on a moist substratum subjected to alternating periods of 16 hours of darkness at 20° C and 8 hours of low intensity light (at least 500 lux) at 30°C. Seeds of this species are sensitive to excessive moisture during the germination period, at least in the laboratory (Heit 1961). Although they do not require stratification, it is advisable to sow nursery beds in the fall or very early spring. If it is necessary to sow during the suboptimum conditions of late spring, the seed should be stratified. Nursery practices suitable for other spruce species (USDA Forest Service 1948) are satisfactory for Engelmann spruce.

X-ray photography techniques have been used successfully to assess seed quality in this species (Roche 1965a; fig. 3). Engelmann spruce seed will germinate, and the seedlings will become established, in almost any soil where adequate moisture is available, but under natural conditions mineral soil is most satisfactory. Shade (less than 50 percent full sunlight), adequate soil moisture, and cool temperatures are important for subsequent survival (Alexander 1958). Maximum photosynthesis of Engelmann spruce seedlings occurs at light intensities of about 40,000 to 50,000 lux (Ronco 1970). Exposure to full sunlight, especially at elevations over 3,000 m, can result in chlorosis and mortality of seedlings (Ronco 1970).

Engelmann spruce, like most trees of the North Temperate Zone, requires a period of chilling to maintain a normal growth rhythm. When grown in a controlled environment, 6 to 8 weeks of chilling at 4 to 5°C before return to normal growing conditions is required to break dormancy (Nienstaedt 1967). Night temperature also appears to be an important environmental factor in controlling many phases of growth and development (Hellmers et al. 1970) and may influence survival under natural conditions (Wardle 1968).

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[4] Registered trademark; Shell Canada Ltd. 2, 2-dichlorovinyl dimethylphosphate.
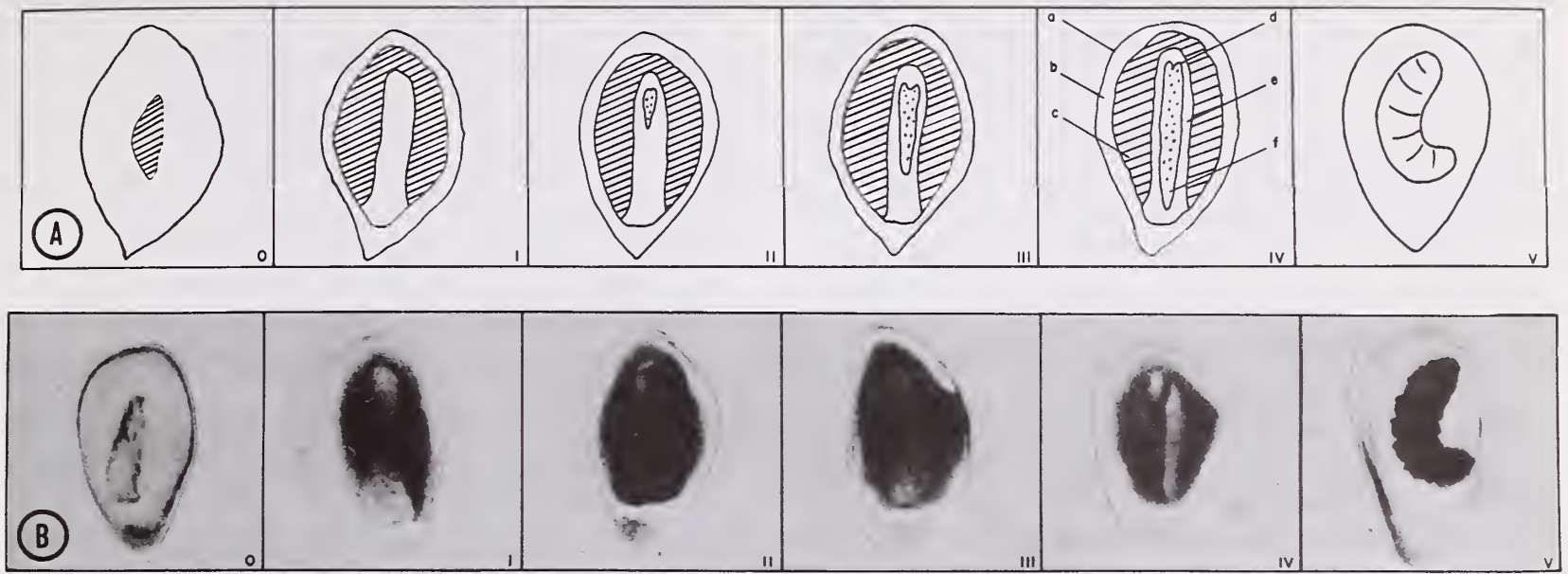
Figure 3.—A, Diagrammatic; and B, photographic representation obtained from radiographs of five Engelmann spruce embryo classes and an insect infested seed. Embryo development and germination capacity of Engelmann spruce seed varies with date of harvesting. For instance, seed harvested from a single tree on September 1, 8, 15, and 22 contained, respectively, 38, 47, 65, and 71 percent of embryo class IV (embryo fills embryo cavity), and produced germination of 60, 66, 76, and 81 percent. A (IV), a—seed coat; b—cavity between seed coat and endosperm; c—female gametophyte; d—cotyledons; e—embryo cavity; f—radicle (Roche 1965a).

ASEXUAL REPRODUCTION

Hansen (1938) observed that, after destruction of an Engelmann spruce stand by fire, residual surviving trees may reproduce by layering. The original stand studied occurred at 3,000 m in the Medicine Bow National Forest, Wyo. Although not far below the timberline, some of the trees reached diameters of 46 cm. Two isolated populations of 23 and 24 trees were studied. These populations gradually increased in size through layering, as the conditions for growth and survival improved within the immediate vicinity.

There is little published information on rooting or grafting which deals specifically with Engelmann spruce. Althrough our experience with the vegetative propagation of this species is limited, we have found that the methods suggested for white spruce by Nienstaedt and Teich (1972) are, in general, effective for Engelmann spruce. Kiss (1970, 1971) did not distinguish between white and Engelmann spruces for purposes of vegetative propagation. He (Kiss 1970) reported that fall grafting (side veneer grafts) of white and Engelmann spruces in a greenhouse was far superior to field or greenhouse grafting in the spring. Although actual grafting success was not given, Kiss (1971) reported successfully grafting 172 clones out of the 176 attempted. Four clones "resisted" grafting.

Stewart (1948) presented information on callus formation on cuttings of blue and Engelmann spruces. He treated cuttings of 1 and 2 years' growth from 30-year-old blue and Engelmann spruces with a number of hormone solutions. Soil, sand, and distilled water were used as the "rooting" media. He concluded that the use of hormones did not result in greater callus development. Leaving twigs in distilled water or hormone solution gave better callusing than was obtained in sand, and 2-year-old twigs callused as readily as 1-year-old twigs. Stewart (1948) did not present information on rooting success.

Harvey and Grasham (1969) presented procedures and media for obtaining tissue cultures of a number of coniferous species including Engelmann spruce. The tissue used in these studies was obtained from the cortex of current-year stems of 3- to 7-year-old nursery stock. The cortex of current-year growth from mature trees was found to respond more slowly than that of seedlings. Good callus proliferation was obtained and growth maintained for a minimum of 120 days. The authors concluded that the techniques described provided a means by which cultures of conifer tissue, including that of Engelmann spruce, can be established and studied under completely controlled conditions.

GENETICS

Almost all the available information on genetic variation in Engelmann spruce has been derived from studies of the Engelmann-white spruce complex rather than from studies dealing exclusively with Engelmann spruce. Variation resulting from hybridization and introgression with white spruce,

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and to a lesser degree with blue spruce, makes it difficult to deal separately with variation in Engelmann spruce. A detailed study of geographic variation, dealing exclusively with Engelmann spruce, would make an important contribution to our understanding of this species. The often overriding effects of species hybridization on genetic variation patterns will be evident in the following sections.

Morphological Variation

Natural populations of Engelmann spruce (fig. 2) when not in contact with other indigenous spruce species may be easily identified on the basis of a number of morphological characteristics. White and blue spruces may be similarly identified. When Engelmann spruce occurs sympatrically with either white or blue spruce, however, particularly with white spruce, gradations in these morphological characteristics are found between the pure forms of each species. Most students of the phenomenon have concluded that introgressive hybridization occurs when Engelmann spruce is in contact with either white or blue spruce (Wright 1955; Garman 1957; Horton 1959; Taylor 1959; Weaver 1965; La Roi and Dugle 1968; Roche 1969).

Comparative studies on the morphology and anatomy of the needles of a number of spruce species, including Engelmann spruce, have been completed by Marco (1931, 1939); Reed and Freytag (1949); and Colleau (1968). Marco (1931) suggested that the absence of resin canals in the upper half of Engelmann spruce needles is a useful diagnostic feature in distinguishing this species from blue spruce, the needles of which invariably contain one or more resin canals. In general, the work of Reed and Freytag (1949) confirmed Marco's findings though these authors concluded that the relative length of the resin canals, rather than their frequency, may have greater diagnostic value in distinguishing between these two species. Colleau's (1968) study was similar to that of Marco's (1939) in that needle anatomy was examined in detail. Colleau (1968) also presented detailed descriptions by species, including Engelmann spruce, of morphological characteristics of diagnostic value.

Of the various morphological characteristics studied in relation to the Engelmann-white spruce complex, the one with the greatest diagnostic value in delineating hybrid zones appears to be cone scale form (Garman 1957; Horton 1959; Taylor 1959; Roche 1964, 1969). Throughout the Engelmann-white spruce complex in British Columbia, cone scale morphology varies progressively from typical low elevation white spruce of the Montane Forest Region to typical Engelmann spruce of the Subalpine Forest Region (Roche 1969) (Forest regions defined by Rowe 1959). In British Columbia east of

the Rocky Mountains, the hybrid zone, determined by cone scale morphology, lies between 825 and 1050 m (Roche 1969). In the Canadian Rocky Mountains, the hybrid zone lies approximately between 1375 and 1825 m (Horton 1959; Roche 1969). Outliers of apparently hybrid populations, however, do occur in British Columbia at low elevations on moist sites, particularly along riverbanks (Roche 1969).

On the basis of cone scale morphology, Horton (1959) grouped spruce stands in the Rocky Mountains of western Alberta into three classes: pure white spruce, the intermediate form, and pure Engelmann spruce. Easily definable extremes of site were recognized for each of these three taxonomic groups, and were classified as hot and dry, normal and fresh, and cool and moist. The data presented for stand composition and natural reproduction in stands of the parental and hybrid forms clearly illustrate the adaptive success of the hybrid in the ecological niche intermediate between those occupied by the parental forms.

Several authors have discussed variation in crown form within the Engelmann-white spruce complex in western Canada (Garman 1957; Horton 1959; Roche 1965b). Variation in this characteristic in Engelmann spruce does exist (Roche 1965b; Roche et al. 1969) and is probably genetically controlled. There is no evidence, however, that it is habitat-correlated or that it is related to introgressive hybridization between Engelmann and white spruces.

The results of studies of morphological variation lead to the conclusions that the clinal pattern of morphological variation in the Engelmann-white spruce complex in western Canada is the result of introgressive hybridization, followed by habitat-correlated selection.

Variation in Growth and Phenology

The available information on genetic variation in growth and phenology of Engelmann spruce is derived primarily from three studies of the Engelmann-white spruce complex. Roche (1969, 1970a) grew 162 population samples, including Sitka and Sitka-white spruce hybrids, in a coastal nursery in British Columbia at latitude 49°00'. Thirteen of these populations were also grown in a more northern (lat. 55°00') interior nursery in British Columbia. Dietrichson (1971), at Blackstad in southern Norway, studied juvenile growth differences in 48 spruce populations from the Engelmann-white spruce complex of western Canada and 18 white spruce populations from eastern Canada. Forty of the western populations were the same as those studied by Roche (1969). Nienstaedt et al. (1971) reported on an Engelmann spruce seed source study in Wisconsin involving 35 population samples, 15 from British Columbia, and 20 from the United

States. The 15 British Columbia populations were also included in Roche's (1969) study.

The results from the three studies were similar. There was a significant correlation (r = .79) between 2-year height growth in British Columbia and 5-year height growth in Wisconsin. High-elevation Engelmann spruce populations were the first to break dormancy in the spring (Dietrichson 1971), the first to become dormant in the fall (Roche 1969; Dietrichson 1971), and the slowest growing (Roche 1969; Dietrichson 1971; Nienstaedt et al. 1971). Seedling dry weight was correlated with percentage of seedlings dormant at the end of July (r = −.80); those seedlings which became dormant first were usually the smallest (Roche 1970a). No discrete differences in growth and phenology were determined between populations, and the variation observed was considered to be clinal and habitat-correlated (Roche 1969).

In British Columbia, Quebec,[5] Wisconsin, and Norway, low elevation populations from southern British Columbia exhibited exceptional vigor in the nursery and appeared to hold considerable promise for field planting. Dietrichson (1971) reported that low elevation British Columbia populations were more vigorous in growth and more resistant to spring frosts than the fastest growing white spruce populations from eastern Canada. He attributed this vigor to heterosis resulting from introgression of white and Engelmann spruces. Nienstaedt et al. (1971) found the three lowest elevation British Columbia populations to be 72 percent taller than the 15-provenance mean in Wisconsin. These three populations were 25 percent taller than the mean of the same 15 provenances grown in British Columbia (Neinstaedt et al. 1971). More recent information[6] indicates that these low elevation populations from British Columbia are not winter hardy in Wisconsin. They continue to be promising for the climatically less rigorous parts of Norway and British Columbia.

Dietrichson (1971) also demonstrated a close association between total nitrogen content of needles, at a given date in the fall, and the data of flushing the following spring for 13 populations from the Engelmann-white spruce complex. High elevation Engelmann spruce populations, which had the greatest nitrogen content in the fall, were the first to flush the next spring. Variation in nitrogen content was clinal.

Twelve of the population samples studied by Nienstaedt et al. (1971) included enough open-pollinated, single-tree collections for evaluation of between-and within-population variation. An analysis of height data from 102 open-pollinated progenies from these 12 populations showed significant differences in 5-year height among populations, but no differences between individual mother trees within populations. On the basis of these results Nienstaedt et al. (1971) suggested that, in future studies of Engelmann spruce provenance variation, only three or four trees per stand need be used as seed parents. Kiss's (1971) report of "striking differences" in germination, growth rate, and phenology between open-pollinated progenies from selected Engelmann spruce trees does not support this suggestion. We believe it would be unwise to reduce population samples to 3 or 4 trees, in the absence of supporting evidence from tests which include samples from a wide geographic range.

Chemical Variation

A number of chemosystematic studies have been made of populations from the Engelmann-white spruce complex in western Canada and the United States (von Schantz and Juvonen 1966; von Rudloff 1967; La Roi and Dugle 1968; Ogilvie and von Rudloff 1968; Habeck and Weaver 1969; Hanover and Wilkinson 1970). In general, and apart from certain anomalies which may be the artifacts of inadequate sampling, the pattern of variation determined by these studies closely parallels that delineated by the morphological and physiological studies referred to above. Habeck and Weaver (1969) concluded, on the basis of their results and those of Ogilvie and von Rudloff (1968), that the terpenes may be highly useful in describing and perhaps even measuring hybridization between white and Englemann spruces. Further studies in this field are currently being conducted by Swan and Naylor.[7]

THE CONSERVATION OF GENE RESOURCES

The initiation of breeding programs with the establishment of clone banks and plantations of many diverse provenances, and the storage of massive quantities of seed, have a part of play in gene conservation. However, for many reasons (Roche 1971), one of the most valuable methods of maintaining large, heterogenous gene pools is by establishing a system of natural areas which embrace ecosystems including the species. In this regard, Engelmann spruce is well served (see listing p.10) at least in the United States. In Canada, a system of natural areas has been proposed (Weetman 1970) and, in British

[5] L. Roche. 1971. Unpublished data on file at Laurentian For. Res. Cent., Can. For. Serv., Ste. Foy, Quebec.

[6] H. Nienstaedt. 1973. Unpublished data on file at the Maritimes For. Res. Cent., Can. For. Serv., Fredericton, New Brunswick.

[7] E.P. Swan, and A.F.S. Naylor. Western For. Prod. Lab., Can. For. Serv., Vancouver, B. C. Unpubl. rep. VP-46 (1969).

Columbia and western Alberta, natural areas are being established in Engelmann spruce ecosystems under the auspices of the IBP/CT program.[8]

Natural areas in which Engelmann spruce occurs are: [9]

Research Natural Areas

Idaho	Canyon Creek
Idaho	Game Creek
Montana	Coram
Wyoming	Snowy Range
Wyoming	White-Tern-Fern-Wapiti Lakes
Utah	Elk Knoll
Colorado	Gothic
Colorado	Goliath
Colorado	Mummy Range
Colorado	Paradise Park
Colorado	Saddle Mountain
Colorado	San Cristobal
Colorado	Hurricane Canyon
Arizona	San Francisco Peaks
Arizona	Santa Catalina
Arizona	Oak Creek Canyon

National Parks and Monuments

Montana	Glacier
Wyoming	Yellowstone
Wyoming	Grand Teton
Utah	Cedar Breaks
Colorado	Rocky Mountain
Arizona	Grand Canyon
Arizona	Walnut Canyon

Wilderness and Primitive Areas

Idaho	Selway-Bitterroot
Idaho	Salmon River Breaks
Idaho	Idaho
Idaho	Sawtooth
Montana	Cabinet Mountains
Montana	Bob Marshall
Montana	Selway-Bitterroot
Montana	Anaconda-Pintlar
Montana	Spanish Peaks
Montana	Absaroka
Montana	Beartooth
Montana	Mission Mountain
Wyoming	Teton
Wyoming	North Absaroka
Wyoming	South Absaroka
Wyoming	Bridger
Wyoming	Stratified
Wyoming	Glacier
Wyoming	Popo Agie
Wyoming	Cloud Peak
Utah	High Uintas
Colorado	Mount Zirkel
Colorado	Rawah
Colorado	Flat Tops
Colorado	Gore Range-Eagle Nest
Colorado	Maroon Bells-Snowmass
Colorado	West Elk
Colorado	Uncompahgre
Colorado	Wilson Mountains
Colorado	San Juan
Colorado	La Garita
Colorado	Upper Rio Grande
Arizona	Mount Baldy
Arizona	Chiricahua
Arizona	Blue Range
Arizona	Sycamore Canyon
New Mexico	White Mountain
New Mexico	San Pedro Parks
New Mexico	Wheeler Peak
New Mexico	Pecos
New Mexico	Gila
New Mexico	Black Range

IMPROVEMENT PROGRAMS

An improvement program for Engelmann spruce has been established in British Columbia (Kiss 1970, 1971). The objectives of this program are as follows:

1. Selection of candidate trees within designated areas where the climatic conditions are considered to be relatively uniform. Phenotypic characteristics are used as selection criteria.
2. Establishment of candidate trees by vegetative propagation in seed orchards.
3. Half-sib (i.e. open-pollinated) progeny trials using seed collected from selected trees.
4. Controlled crossing and the establishment of full-sib progeny trials.
5. Selection within the open-pollinated and full-sib progenies for candidates at the next level of improvement.
6. Interspecific hybridization and testing of hybrid progenies.
7. Studies of diverse climatic zones and soil types in order to determine the optimum location for seed orchards.

In 1971 this program had resulted in the selection of 445 candidate trees in three climatic zones. Cones were collected from many of the selected trees and 2- and 3-year-old progenies showed striking differences in germination percentages, growth rates, and certain phenological characteristics (Kiss 1971).

Engelmann spruce is an important component of the Michigan State University blue spruce improvement program (Hanover 1974), which includes a cooperative Engelmann-blue spruce geographic variation project. Engelmann spruce has also been included as one of several species destined for tree improvement work in Region 1 of the USDA Forest Service (Howe 1974).

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PESTICIDES PRECAUTION

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by *appropriate State and/or Federal agencies* before they can be recommended.

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U.S. DEPARTMENT OF AGRICULTURE

Fowler, D.P., and L. Roche.
1975. Genetics of Engelmann Spruce. U.S. Dep. Agric. For. Serv. Res. Pap.
WO–30, —p.

Engelmann spruce is characterized by clinal patterns of genetic variation within a
large natural range, influenced in part by introgressive hybridization with adjacent
species. Tree improvement is just beginning, but a reserve system for *in situ* gene
conservation is well established.

OXFORD: 174.7: *Picea engelmannii:* 181.52, 165.41, 165.52, 165.53.
KEYWORDS: Engelmann spruce, genetics, tree improvement, sexual reproduc-
tion, controlled pollination, geographic variation, racial variation.