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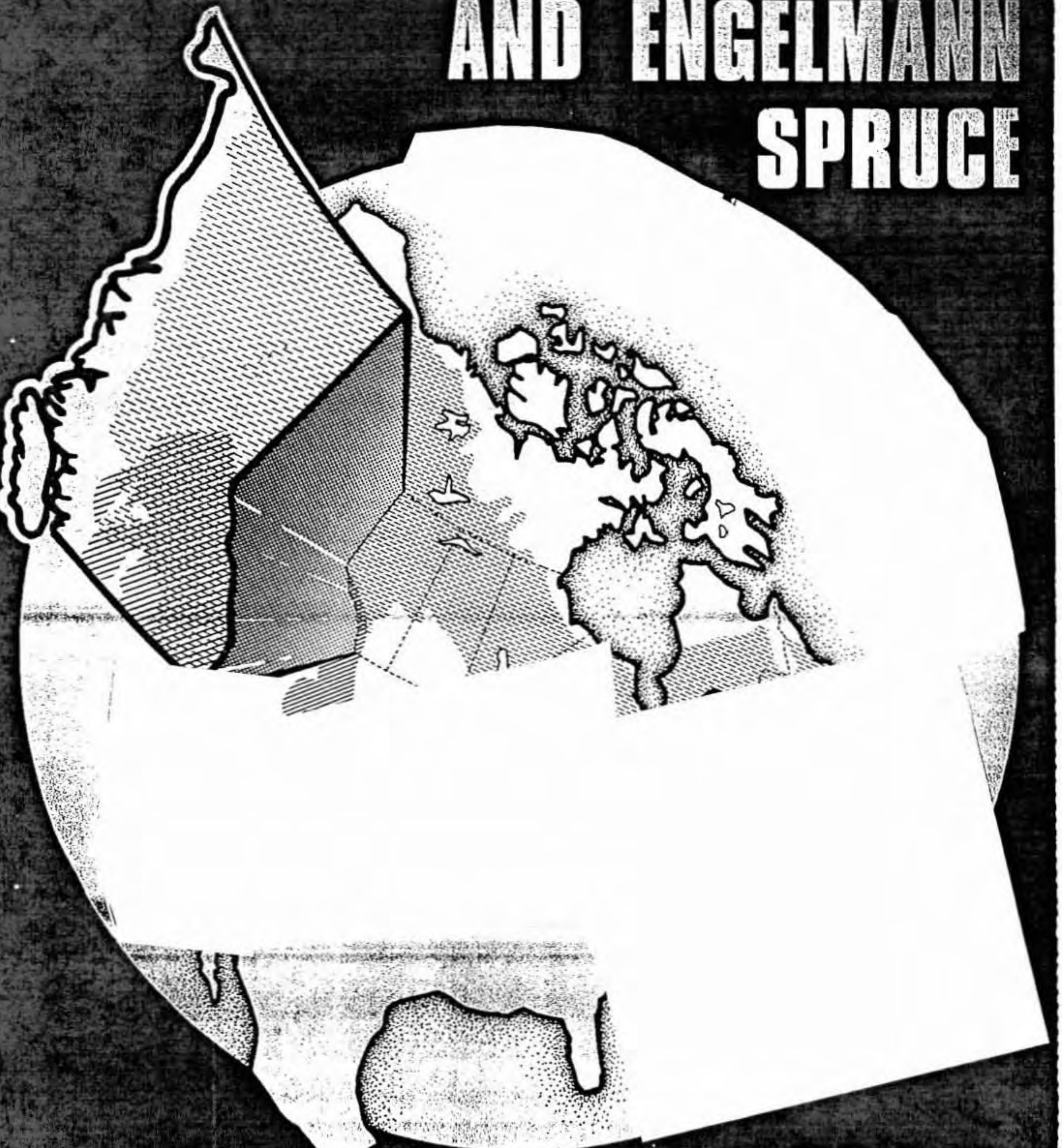
REGENERATION OF WHITE AND ENGELMANN SPRUCE



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Canadian Forestry Service

A LITERATURE REVIEW WITH SPECIAL REFERENCE TO THE BRITISH COLUMBIA INTERIOR

REGENERATION OF WHITE AND ENGELMANN SPRUCE:

A Literature Review with Special Reference to the British Columbia Interior

by

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FOREWORD

This review was prepared as background for a research program on regeneration of white spruce/alpine fir types in the British Columbia Interior. White spruce (Picea glauca (Moench) Voss) will undoubtedly continue to be the major species used in reforestation programs within this type although lodgepole pine is heavily utilized as well. Engelmann spruce (P. engelmannii Parry) is a closely related sympatric species which also occurs naturally in the British Columbia Interior. Indeed, the gene pools of the two species are intermixed within the general area where the research is to be undertaken (119). For these reasons, and because the two species apparently are similar in regeneration ecology, this review is concerned with both.

Essentially the review is presented in two parts. The first part, SILVICAL AND ENVIRONMENTAL FACTORS AFFECTING REGENERATION, is based on reports of observations and studies conducted throughout the ranges of the two species. The second part, REGENERATION SILVICULTURE IN THE BRITISH COLUMBIA INTERIOR, is based principally on reports emanating from within British Columbia.

TABLE OF CONTENTS

INTRODUCTION

The botanical range of white spruce (Picea glauca (Moench) Voss) is transcontinental, extending from eastern Newfoundland to western ~~Alberta~~ ALASKA (148). The species extends northward to the tundra and southward into Minnesota, Wisconsin, Michigan and the New England States (see cover). Engelmann spruce (P. engelmannii Parry) extends from central British Columbia to Colorado with high elevation outliers almost reaching Mexico (6). The ranges of the two species overlap in the British Columbia Interior and the Alberta Rockies where substantial introgressive hybridization is evident (119). There appears to be some degree of altitudinal zonation, with white spruce predominating in the lower valleys, Engelmann on the upper slopes and hybrid swarms in between (70, 119).

Where both species and their hybrids occur, some distinction may be made on the basis of cone scale morphology. The cone scales of white spruce are "stiff, smooth-margined, often indented, roundish, close-fitting (and) light-brown" while those of Engelmann spruce are "finely-toothed, often notched, flexible, yellowish-brown, loosely fitting, ...tapered at both ends and have rather prominent bracts" (71). McKinnon (100) observed that white spruce cone scales are broader than they are long, with the broad part of the scale lying above the center, while Engelmann spruce scales are longer than they are broad, with the widest part generally below the center of the scale. Roche (24) further pointed out that the impression of the seed wing extended almost the full length of the white spruce cone scale and little more than half the length of the Engelmann spruce cone scale. Cone scales having intermediate morphological characteristics infer hybridization.

SILVICAL AND ENVIRONMENTAL FACTORS AFFECTING REGENERATION

The Phenology of Flowering and Seed Maturation

Cone-bearing age. Cones have been observed on white spruce trees as young as 10 years old and viable seed have been obtained from a 13-year-old tree (170). Excellent seed crops have been observed on 20-year-old plantation-grown white spruce (104), although normally substantial seed production starts at approximately 30 years of age and reaches an optimum when the trees are 60 years or older (154). In the Mixedwood Forest Section, white spruce begins to flower abundantly at 45 to 60 years of age (133). At more northern latitudes, seed production is apparently much delayed and infrequent (133). In Alaska, good cone crops have been observed on trees up to 170 years of age (170).

Engelmann spruce apparently begins commercial seed production at an earlier age (16-25 years) and produces most abundant crops at 150-200 years (154).

Cone crop periodicity. Both species exhibit periodicity in cone production and considerable variation in the interval between good crops. The Woody Plant Seed Manual indicates good Engelmann spruce seed crops every 2-3 years with intervening light crops, and good white spruce every 2-6 years with intervening light crops (154). A study in Montana revealed 5 good, 8 fair and 9 poor Engelmann spruce seed crops west of the Continental Divide compared to 2 good, 4 fair and 15 poor crops for a 21-year period east of the Divide (21). Studies on white spruce in the Duck and Porcupine Mountains in Manitoba between 1911 and 1951 indicated good cone crops for 12 of the 40 years, or once every 3 or 4 years (133).

In the North Central Interior of British Columbia, a record of white spruce cone production was maintained between 1954 and 1961 (11). During this period, heavy crops occurred twice, a moderate crop once, and light or nil crops five times. According to Eis (personal communication), the following 10-year period (1962 to 1971) produced only one heavy crop and one moderate crop; the others were all light or nil crops.

Flowering phenology. White spruce flower buds form in the growing season prior to flowering and can usually be distinguished from vegetative buds in late summer (51, 54, 105). Primordia of reproductive strobili continue to grow in the fall and even into the winter, long after vegetative meristems have ceased growing (51). Male strobili overwinter in the pollen mother-cell stage, and female strobili apparently pass the winter in the megaspore mother-cell stage (104).

Microsporogenesis and megasporogenesis occur early the next spring. Winton (168) presented evidence that a minimum number of consecutive warm days in the spring are required for the initiation of meiosis. In St. Paul, Minnesota, two white spruce trees began meiosis on April 22, 1961 and April 21, 1962, after five days in which the average daily temperature rose to 50 F. On another tree located about 100 miles farther north, meiosis began two days later, in both years, after 7-8 consecutive warm days averaging 43 F. In 1963, the same tree began meiosis about two weeks earlier, after 10 days averaging about 40 F.

Pollen dispersal. The number of days by which pollen dispersal follows meiosis may also be temperature-controlled. In 1961, the two white spruce trees at St. Paul shed their pollen in mid-May, 21 days after the onset of meiosis (168). The average daily temperature during this period was 51 F. In 1962, the interval between meiosis and pollen dispersal was 19-24 days at an average temperature of 58 F. The longest interval, 37 days, occurred in 1963, when the average daily temperature was only 47 F.

Flowering of white spruce near Ely, Minnesota, occurred between May 25 and May 30 over a 4-year period, and in Marquette County, Michigan, the average date of flowering was May 25 (155). Further north, in the Mixedwood Forest Section (135), pollen was shed from mid-May to mid-June (134). The earliest date of pollen dispersal at Riding Mountain, Manitoba, was May 25; the latest recorded date was June 13 (134). Near Fairbanks, about 65°N latitude, pollen was dispersed between the last few days of May through early June in 1958 (170). In 1962, pollen dispersal began on June 4 and was essentially completed by June 21, with peak activity between June 6 and 12.

Engelmann spruce pollen is disseminated in June at lower elevations and in July at higher elevations (6).

Pollination and Fertilization. Nienstaedt (105) studied the period of receptivity of the female strobili of white spruce trees in northeastern Wisconsin. His results indicated that bagged strobili are receptive for a period of 3 to 5 days. He found some variation from tree to tree but on a single tree, development was fairly well synchronized. Pollen shedding appeared to coincide fairly well with female receptivity. In Connecticut, controlled pollinations were carried out between May 9 and 16, 1961 (90); fertilization occurred in early June, rapid differentiation occurred in July, and the embryos were mature by mid-August. Fertilization, the union of male and female nuclei within the ovule, takes place about 3 weeks after pollination in the genus Picea compared to a 13-month interval in the genus Pinus (117).

Incomplete pollination is a principal cause of empty seed, although some empty seed will occur in spite of sufficient pollination (170). Pollination of spruce strobili is generally less effective during years of low strobili production (170). Nekrasov (103) reported that supplementary pollination of white spruce cones produced 49% sound seed; naturally pollinated controls yielded 12%.

Cone maturation and seed dissemination. White and Engelmann spruce cones generally ripen in late August or September and seed is shed soon thereafter. Hot, dry weather tends to hasten seed dissemination while cool, moist, cloudy weather retards it (76). Over a period of years, first white spruce cones opened between September 5 and 17 in northeastern Minnesota, and the average date of cone opening in Marquette County, Michigan, was September 17 (155). At Indian Head, Saskatchewan, natural seed dispersal began, on the average, 98 days after pollen dispersal (37). Near Fairbanks, Alaska, from 1958 to 1962, cones appeared to ripen about August 20, followed shortly by seed dispersal (170). Zasada and Gregory (170) suggested that pollen dispersal occurs later in interior Alaska than farther south but that seed maturation and dispersal occur at about the same time over the species range, indicating a more rapid development of white spruce seed in subarctic forests.

Peak white spruce seed dispersal at Riding Mountain varied from late August to early October over a 10-year period (165). In northern Minnesota, 22% of the seed had fallen within a month after the beginning of dispersal and 87% had fallen by the end of the second month (124).

Crossley (42) reported that during a good seed year in the Subalpine Region of Alberta, about 88% of total seedfall occurred in the first month of dispersal; however, seed continued to fall during the winter and as late as May. Some viable seed had been found in white spruce cones the summer following maturation (124, 132). At Verdun Mountain, in the Prince Rupert Forest District of British Columbia, 85 to 90% of the total 1968 seedfall occurred between August 20 and October 15, with the peak in mid-September (27). Most Engelmann spruce seed is shed by the end of October but some falls throughout the winter (6).

Seed maturity as measured by the occurrence of peak germinability occurs before seed dispersal begins. Crossley (40) reported that white spruce seed could be collected in Manitoba after the second week of August without sacrificing much viability. Seed dispersal began on September 17. At Indian Head, Sask., the highest germination percentages occurred in seeds collected five weeks before seedfall in one tree and in seeds collected one week prior to seedfall in another tree (37).

Cram and Worden (37) found that a cone moisture content of about 48% and a specific gravity of about 0.74 are good indications of seed ripeness. Crossley (40) suggested that the firmness of cone, color of testa and brittleness of seed are reliable indices of seed maturity. He stressed that cone color is unreliable.

Cone crop predictability. The ability to predict well in advance the size of the cone crop would be an important asset to the forest manager in that it would provide a firm basis for seedbed preparation for natural regeneration and for organizing seed collection programs. Several workers have suggested that estimates of floral bud production, which may be made as much as a year in advance of the seed crop, might provide an indication of its potential.

Fraser (54) demonstrated that white spruce floral bud primordia were laid down during July and August. In the British Columbia Interior, white spruce reproductive buds were set in late July, and by late August they were macroscopically distinguishable from vegetative buds (51). Several workers (10, 51, 124) have suggested that an early determination of the abundance of reproductive buds would permit the accurate prediction of a cone crop failure as well as an early estimate of potential crop size. To what extent the potential crop is realized depends on the operation of several inimical factors from bud set to the time of seed maturity. Eis (51) lists late frost, unfavorable weather during pollination, summer drought, seed and cone destroying insects, cone rusts, and abortion of buds, flowers or developing cones. Zasada (169) presented evidence that a late-May frost occurring during the period of maximum pollen dispersal substantially reduced the percentage of sound white spruce seed yielded by the 1969 cone crop in interior Alaska. An estimate of the following year's potential seed crop may be made in the fall (51); then, by assessing the modifying factors, the estimate may be progressively reduced and refined as the various stages in flower, cone and seed development progress. The initial estimate is relatively simple and clear-cut; the modifications applied to it are quite complex.

The best initial estimate of potential cone crop size is based on the production of ovulate buds (10, 51, 124). Allen (10) used the ratio of ovulate buds to vegetative buds, which he termed "cone intensity", as the basis for predicting Douglas-fir cone crops. There may, however, be difficulties in this approach. Eis (51) pointed out that staminate and ovulate buds are difficult to differentiate in white spruce.

Estimating numbers of floral buds presents problems, too. Binocular counts and twig sampling are possibilities. Telephotography as a method of cone counting is being studied (26) and may have applicability.

Revel (27) made a prediction of the 1968 white spruce seed crop in the Prince George Forest District of British Columbia in the early spring, based on the percentage of trees having viable reproductive buds which he determined by forcing twig samples for 18 days in tap water at room temperature. His prediction of a moderate to heavy cone crop was confirmed by cone crop surveys in July and cone collections in the fall.

A method of forecasting seed crops not based on bud counts was suggested by Uskov (156). He based his prediction of Norway spruce seed crops on the relationship between climatic variables and seed production. Unfortunately, the required amount of data on seed crops from many stands for many years and weather conditions at the time of reproductive bud formation, flowering, pollination and seed formation is a prerequisite which is often lacking.

Seed Production and Dispersal

Seed production. White and Engelmann spruce seed production varies considerably from year to year. A mature white spruce stand at Riding Mountain, containing 190 square feet of basal area per acre, dispersed seed for eight consecutive years in amounts varying from a low of 10,000 seeds per acre to a high of over 5,000,000 seeds per acre (76). In three of the eight years, production was over 1,000,000 seeds per acre. Engelmann spruce stands produce 570,000 to 760,000 seeds per acre in an average good year (89); 950,000 seeds per acre were dispersed during a bumper seed year (144). Engelmann spruce seeds are larger than white spruce seed, yielding an average of 135,000 cleaned seeds per pound compared to 240,000 for white spruce (154).

Dominant and codominant trees bear cones more often and produce heavier crops than intermediates; cone crops on intermediates are more frequent and larger than on suppressed trees (76). An open-grown 75-year-old white spruce tree in northern Minnesota produced 11,900 cones with a total of 271,000 viable seeds in a heavy crop year (125). Twenty-five study trees in Ontario bore an average of 8,000 cones per tree containing a total of 184,000 good seeds during a heavy seed year (152).

Tripp and Hedlin (152) observed that white spruce cones have an easily recognizable central zone containing the potentially sound seeds and two unproductive zones, one at the base and the other at the apex. One hundred and thirty cones, collected randomly from 5 mature trees, had an average of 140 seeds, of which 92 (66%) were in the productive zone (152). Some 44 to 53% of these were hollow, leaving a possible 40 to 50 filled seeds per cone. This potential will invariably be further reduced by insect depredation. In a good seed year, Tripp and Hedlin obtained an average of 23 good seeds per cone. Nienstaedt (105) found an average of 28.3 sound seeds per cone in a sample of cones which were pollinated in bags. During an excellent seed year (1968) in the Nelson Forest District of British Columbia, Engelmann spruce cones yielded from 119 to 132 seeds with a viability ranging from 52 to 75% (27).

Seed quality. Seed quality or the proportion of sound seed is generally better in years of heavy production than in years of light production. At Riding Mountain, cutting tests revealed that 59 and 71% of the seeds were sound during the successive good seed years of 1960 and 1961, whereas during the poor 1958 seed year, only 15% were sound (164). A random sample of 180 cones taken from trees near Fairbanks during an excellent seed year had 60.5 sound seeds per cone (170). During a fair seed year, there were 11.4 sound seeds per cone and in two poor years, cones yielded only an average of 6.5 sound seeds. According to the Woody Plant Seed Manual (154), Engelmann spruce seed has both a higher germinative energy and germinative capacity than white spruce seed; germinative energies are respectively 58-76% and 37% while germinative capacities are 69% and 49%. Curtis (43) obtained values between 50 and 70% for the germinative capacity of Engelmann spruce seed. Seed quality also varies with time of dispersal, with early- and late-falling seed being less sound than seed falling during the peak dispersal period (76).

Seed dispersal. Patterns and distances of seed dispersal are functions of tree height, seed weight, and wind velocity at the time of dissemination. On this basis, we would expect white spruce seed to be dispersed further than Engelmann spruce seed because of the former's slightly greater average height (155) and lighter seed (154). However, this expectation is not upheld by the literature. Current reviews report that the greatest accurately determined distance of white spruce seed dispersal is 330 feet (5 chains) (76, 133, 170) although Rowe (133) suggested that wind turbulence and convection currents may carry seed 1,000 feet or more and that, with the right conditions, late-falling seed may be whisked over the snow for long distances.

A bumper Engelmann spruce crop dispersed seeds from a clear-cut edge in decreasing amounts to a distance of 9 chains, beyond which very low catches were obtained (144). Alexander (8) reported that nearly half of the Engelmann spruce seeds dispersed into a clear-cut fell within 1.5 chains of the windward timber edge. Less than 10% was dispersed beyond 4.5 chains. Roe (120) stressed the importance of effective dispersal distance, which depends on the size of the seed source as well as on aerodynamic considerations.

Factors Influencing Field Germination and Early Survival and Growth

"Poor seed production is rarely a silvicultural bottleneck of itself" (16; p.182). Over a 10-year period at Riding Mountain, 11.7 million white spruce seeds fell per acre; the smallest annual catch during this period was 10,000 seeds per acre (165). We could quite economically apply 50,000 or more seeds per acre if it would ensure successful regeneration of logged-over stands. Unfortunately, the many factors bringing about seed losses and seedling mortality can prevent successful regeneration even with the heaviest inoculum of seed.

Losses of seed. Since the vast majority of white and Engelmann spruce seeds are naturally dispersed in the fall and early winter, most of the seeds will overwinter under or within the snowpack. Animals, particularly rodents, are by far the most important sources of overwintering seed losses (16).

Practically any site supporting a forest also supports a substantial population of small mammals, the most ubiquitous and most voracious consumers of forest tree seeds being mice (138). Logging, which precipitates the need for regeneration, also initiates plant succession which favors the rapid expansion of mouse populations. Tevis (151), reporting on trapping results in the Douglas-fir region of northwestern California, indicated that within two or three years following logging, as the cutover passes into the weedbrush stage, there is a veritable eruption of mice. From the fourth to the tenth year after logging, mice are three to four times more numerous on the cutover than in the surrounding forest. The local tendency for mouse populations to expand following logging is undoubtedly complicated by wide cyclic fluctuations in their population about which little is known (16).

Several studies have shown that mice and other rodents are important depredators of white spruce seed (20, 34, 42, 114, 116, 140, 161, 162). Wagg (161) studied the food habits of caged deer mice (Peromyscus maniculatus) and red-backed mice (Clethrionomys gapperi). Although the mice preferred lodgepole pine seed, their daily maximum consumption of white spruce seed was about 2,000. The author stressed that it was not possible to interpret his results in terms of seed consumption in the field, where factors such as mammal density, mammal activity, seed density and variety of alternative foods complicate the matter. Radvanyi (116) followed the fate of radio-tagged white spruce seed in the field. From recovered seed hulls, he determined that 49% had been destroyed; 35% by mice, 9% by chipmunks, 3% by shrews and 2% by insects. These results are made more startling by the fact that the seeds were treated with the rodent repellent endrin.

Crossley (42), working in Alberta, concluded that over 90% of white spruce seed broadcast on unprotected plots was destroyed by birds, rodents and insects before they had a chance to germinate. Prochnau (114) carried out a seeding study on white spruce, alpine fir, Douglas-fir and lodgepole pine in the central interior of British Columbia. For all species combined, he found five times the third-year survival on screened seed spots as on unprotected spots. Smith (140) examined regeneration of Engelmann spruce and alpine fir in the southern interior of British Columbia and concluded that, other than drought, rodents were the most important cause of seed and seedling losses.

Potential losses to rodents may vary considerably from year to year. In an interim report on an Engelmann spruce direct seeding trial (27) in the southern interior of British Columbia, Clark observed in 1966 that "...the treatment of seed for protection from birds and rodents, covering of seed with soil, and a mineral seedbed are absolute necessities for spot-seeding success in the Interior Wet Belt". In reference to another direct seeding experiment, Clark indicated that "...loss of seed after treatment with Endrin as a protection from mice will not be a major problem" (25). Contrarily, Armit, in reporting on a direct seeding experiment on a prescribed burn, stated that "...pine and (white) spruce seed losses, presumed due to rodents, might be as high as 60-75 per cent for fall sowing and 45-55 per cent for spring sowing" (26).

In some instances, squirrels may also bring about heavy seed losses through their cone-caching activities. Red squirrels (Tamiasciurus hudsonicus), indigenous to most of the Boreal Forest Region of North America, can thrive on a diet of white spruce seed (170). Streubel (cited by Zasada and Gregory (170)) reported (cone) caches containing as many as 14,000 cones.

Neither insects nor fungi are important sources of loss of coniferous seed after they have fallen, although the former may bring about substantial losses of seed in the cone and the latter may attack seeds upon germination, bringing about damping-off losses (16).

High surface temperatures, usually considered a factor in seedling mortality, may, in some instances, result in pre-germination losses of white spruce and, probably, Engelmann spruce seeds. Tests have indicated that white spruce seeds are much more sensitive to high temperatures than seeds of black spruce, jack pine or red pine (32). Exposure of white spruce seeds to a temperature of 120 F for 50 to 70 hours or to 150 F for a short period was lethal. The higher the humidity, the more damaging was the effect of a given temperature. During a hot, dry period in the Crowsnest Forest of Alberta, surface temperatures above 122 F prevailed on all seedbeds for several hours, and temperatures of 167 F were reached for short periods on the more heat-prone seedbeds (44).

Field Germination. Those viable seeds that survive the rigors of winter will germinate in spring or summer provided they rest on a suitable medium, and elements of their immediate environment, particularly moisture and temperature, are favorable. Place (112), working with white spruce, obtained field germination percentages from 0 to 89, depending on seedbed and weather conditions.

Given adequate moisture, field germination occurs when seedbed temperatures become favorable. Nienstaedt (104) lists 60 to 90 F as the range of favorable germination temperature for white spruce. Fraser (55) studied the laboratory germination of six provenances of white spruce and reported that germination does not occur below 45 to 50 F or above 85 to 95 F, depending on provenance. Optimum temperature varied from 55 to 75 F.

Field germination of white spruce on mineral soil generally occurs in June or July (104). On mineral soil seedbed plots near Fairbanks, Alaska, 1,300 white spruce seeds germinated between June 1 and September 1, 1968. Of these, 1,100 (about 85%) germinated on or before June 24 (170). At Riding Mountain, Manitoba, more than 90% of germination on mineral soil seedbeds occurred during June and July and of this more than 75% occurred in June (166). In another study at Riding Mountain, 90% of the germinants on undisturbed and mineral soil seedbeds had appeared by mid-August as compared to only 18% on burned seedbeds (166). Rowe (131) also reported a germination delay of over a month and a half on burned ground. Eis (49) studied germination of white spruce and alpine fir in the central interior of British Columbia and noted that both species started and completed germination earliest on light sandy soils and fully exposed plots. Germination of seed sown on June 23 was completed by July 16. Hellum (68) noted that average-size white spruce seed germinates 2 to 3 days earlier than either lighter or heavier seed.

Ronco (126) noted that the time of Engelmann spruce germination in the field is geared to the distribution of summer precipitation in western Colorado. In 1957, adequate rainfall occurred from one week before to 6 weeks after experimental sowing, with the result that germination began the second week after sowing and was mostly completed by the end of the third week. Precipitation in the two following years was less favorably distributed and as a consequence, germination was delayed for 7 or more weeks.

The time of germination is of considerable consequence to the seedling. At Riding Mountain, white spruce seedling mortality during the first summer was greater for June and July germinants than it was for August germinants. However, the over-winter losses of August seedlings were so high that by the following spring their survival rate was well below that of the June and July germinants (166). Survival of four-year-old June germinants was slightly higher than that of July germinants and four times as high as that of August germinants. Place (112) observed that in New Brunswick, white spruce seedlings germinating after the middle of July seldom live through the winter. Similar observations have been made on Engelmann spruce seeds (126).

In some instances, white spruce seeds have been observed to lie over and germinate the second season following dispersal (91, 126, 166). In two cases, Moore (91) recorded no germination the first season, followed by good germination the second season. Ronco (126) reported initial field germination of Engelmann spruce seed of 35%, followed the next season by hold-over germination of 16%. It is probably unusual for seed germination to be delayed until the third growing season. MacGillivray (99) found that prolonged stratification (14 months or more) reduces germinability.

Initial growth of germinant. "The successful establishment of the newly germinated seedling is a member of the forest stand is, without doubt, the weakest link in all the chain of processes that go to make up the regeneration of the forest" (16; p.247). The initial growth of the germinant, particularly its rate of root penetration, is an important determinant of its chance for survival. The further the primary root penetrates the soil, the more stable its moisture supply and the less its chance of succumbing to drought (16). The critical depth is a variable which depends on several factors, most notable of which are the physical properties of the seedbed and the surficial layers of soil and the dependability of well-distributed precipitation.

The root of the first-year seedling rarely penetrates more than three inches (6, 104). First-year white spruce seedlings are up to one-inch tall with six cotyledons; their root systems are thin, sparsely branched and about two inches long (133). The root penetration of one-year-old Engelmann spruce seedlings in the northern Rockies averages about 1½ inches (6). Place (111) investigated initial root elongation in white, black and red spruce and balsam fir in sandflats. He noted that balsam fir is a much more robust seedling after one year than any of the spruces. The average total dry weight of balsam fir seedlings was 18.1 mg compared to 9.2 mg for white spruce. Balsam fir's average total length was 3.5 inches; white spruce's was 2.7 inches. Perhaps the most significant comparison was root elongation in the first 10 days: 1.87 inches for balsam fir and 1.26 inches for white spruce. Undoubtedly such comparative data as these relate to balsam fir's (and probably alpine fir's) ability to establish on organic seedbeds which preclude spruce regeneration.

Eis (49), working in the central interior of British Columbia, compared the root lengths of white spruce and alpine fir seedlings, which succumbed to drought, with those of seedlings that survived. The average root length of those seedlings that died was 18 mm; of those that survived, 37 mm. He further noted that under all habitat conditions, mortality was greatest among seedlings with the shortest roots. The shoot growth of both species ended in early August but root growth continued until late fall. At the end of the season, white spruce root lengths averaged 52 mm (2.1 inches) and alpine fir roots averaged 69 mm (2.7 inches).

Several factors determine the growth rate and ultimate stature of the first-year seedling. Perhaps the most obvious intrinsic factor is seed size. Hellum (68) reported that white spruce seeds lighter than 0.00145 gram produce germinants less than 20 mm tall while those heavier than 0.00405 gram produce germinants taller than 28 mm under laboratory conditions. He also indicated that white spruce germinants have from three to eight cotyledons and that this is correlated with seed weight. Burgar (29) divided a sample of white spruce seeds into three size classes: small (<1.41 mm), medium (1.41 - 1.59 mm), and large (>1.59 mm). He reported that resultant seedlings after one season's growth were 5.8 mg, 7.7 mg and 9.8 mg, respectively. He concluded that "....the larger the white spruce seed the larger will be resultant seedling after the first season's growth, bud seed size affects neither the germination nor the survival rate in this species." This is a dubious extension of his results inasmuch as his seedlings were grown in a greenhouse where initial root elongation would not likely be a survival factor. Ackerman and Gorman (2) studied the effect of seed weight on the size of white spruce container-planting stock. They also found a statistically significant increase in seedling size with increasing seed weight. However, they noted that relatively small part of the total variation in seedling size could be explained by seed weight. Place (111, 112) attributed the more rapid initial development of balsam fir over white spruce to the difference in the size of their seeds. (Balsam fir has 60,000 seeds per pound; white spruce has 240,000 (154)).

Seedbed types. White and Engelmann spruce seeds falling in the forest or into cut-over or burned-over areas come to rest on a variety of seedbed types. In the undisturbed forest, most seedbeds are organic: fresh litter, partially decomposed humus, moss, lichen or decaying wood.

Occasionally, mineral soil seedbeds are provided when trees are blown over. Following logging, the same seedbeds are available as well as some additional mineral soil which may be exposed by logging machinery. Seedbed microclimate will, of course, be modified by the removal of trees and deposition of slash. Either before or after logging, mineral soil or mixed mineral soil and humus seedbeds may be created by machine scarification. Fire will provide various kinds of burned organic seedbeds or, where burning is intense, burned mineral soil seedbeds.

An overwhelming number of studies have indicated that mineral soil seedbeds are superior to organic seedbeds and are often requisite to the establishment of white or Engelmann spruce seedlings (1,6,7,17,20, 34,38,39,41,42,49,59,62,69,72,75,83,85,91,101,104,106,107,108,109,112, 114,115,121,122,133,141,148,155,163,166,170). In the undisturbed forest, decaying wood is the major seedbed supporting white spruce seedlings (17,19,31,44,45,46,62,78,84,98,104,107,110,112,141,155,170). Engelmann spruce is apparently not quite so constrained in that it becomes established on landslide areas on steep slopes and under a cover of Vaccinium on light, gravelly soils (6, 84).

The microenvironment provided by the seedbed is determined by several intrinsic and extrinsic factors, operating primarily through their effects on moisture and temperature. The intrinsic factors are essentially the physical properties of the seedbed such as texture, compactness, organic content and color. These properties determine such thermal parameters as conductivity and damping depth (36), and such moisture parameters as water retention capacity, field moisture capacity and permanent wilting point. Surface roughness also affects the microenvironment encountered by the seed.

The most important extrinsic influence determining seedbed environment is weather. Such factors as insolation, air temperature, relative humidity, wind, and amount and distribution of precipitation all have important and obvious effects. These are modified by macro- and microslope aspect, the presence of a canopy, the size of an opening, shade, depth of the water table and competing vegetation.

Moisture relations. "The moisture condition of the seedbed is the most important factor determining germination and early survival of spruce seedlings" (155). Mineral soil provides a much more stable moisture source than most organic seedbeds (104, 139). Most organic seedbeds readily dry out after only a few rainless days, particularly when they are exposed to direct solar radiation (104, 139).

Mortality through drought occurs when the rate of transpiration exceeds the rate of water uptake by the roots over a sufficient time period. The result is wilting, shrivelling, loss of color, and eventual death by dessication of the tissues. No mechanical injuries are associated with drought-caused mortality (44). Drought losses may be cumulative throughout the growing season, or they may occur suddenly (22).

Place (110) compared the moisture content of humus and rotten wood seedbeds over a 3-month period beneath a dense 60-70-year-old white spruce-balsam fir stand at the Acadia Forest Experiment Station. Despite an abnormally dry summer, the moisture content of the rotten wood remained just slightly below field capacity; only after a 30-day drought did it approach the wilting point. The moisture content of the humus was below the wilting point four times during the measurement period, once for 20 consecutive days.

Jarvis and Tucker (77) related the moisture contents of L- and F- layers in Mixedwood Forest cutovers in Riding Mountain Park, Manitoba, to drought index (essentially days since measurable precipitation). They reported that saturated L- layers dried very fast as drought progressed but that the moisture content of the F- layer remained relatively high except after prolonged drought. The rate of drying of both horizons was fastest in the open, intermediate under dense hazel, and slowest under slash piles.

Eis (49) ~~(40)~~ measured the available water in raw humus at 5 cm and in mineral soil at 5, 15 and 45 cm from July through early September on three sites -- alluvium, Aralia-Dryopteris and Cornus-Moss (73)-- in the central interior of British Columbia. Available water was lowest in the humus throughout the measurement period and it went below the wilting point for several days on each site. Available water in mineral soil remained above the wilt-ng point; it was consistently highest at 45 cm, intermediate at 15 cm, and lowest (although substantially higher than in the humus) at 5 cm.

Height above the water table, although only indirectly related to seedbed, can have an important effect on seedling establishment, survival and growth. Studies have shown that there is an optimum height above the water table that depends on soil texture, species, size of seedling and local environmental factors such as overhead shade (48, 93). The optimum height above the water table increases with seedling age (size) and with increasing clay content in the soil (93).

The amount and distribution of precipitation interacts with seedbed and site in determining the moisture supplied to the seedling. Waldron (166) noted that fresh, moderately moist and moist sites were generally better for white spruce germination than very moist or wet sites. During dry summers, however, the wetter sites were more favorable. Many workers (e.g. 9, 112, 114, 121, 126) have stressed the importance of precipitation throughout the growing season. Moisture is particularly critical during germination and the immediate post-germination period. Prochnau (114) reported that when spring and early summer were slightly drier than usual, eight viable white spruce seeds (protected against rodents) were needed to establish one seedling on scarified seedbeds in a cutover. When the spring and early summer were wetter than usual, four viable seeds were sufficient.

Alexander and Noble (9) studied the effects of amount and distribution of watering on the germination, survival and growth of Engelmann spruce in the greenhouse. They noted that total germination on field soil increased with amount of applied water up to 1.5 inches per month, and that distribution of water influenced total germination only when the amount received each month was 1.0 inch or less. There was no significant survival after 24 weeks unless at least 1.0 inch of water was received at intervals through the month, and few seedlings survived when a single watering was applied each month unless the amount exceeded 2.0 inches. Growth parameters were not significantly related to watering treatments.

Well-distributed summer rainfall would seem to enhance the establishment and survival of spruce. However, Roe et al. (121) pointed out that summer storms may not be an unmitigated benefit. In the central Rocky Mountain and Intermountain regions, summer storms may be so intense that much of the moisture runs off, especially from bare soils. Moreover, soil movement on unprotected seedbeds buries some seedlings and washes out the roots of others.

Winter drying is a special case of drought damage that may occur during the dormant season (22). It occurs when sudden warm weather brings about foliar water losses at a time when water absorption is prevented by frozen ground. Winter drying is not generally a problem for very young seedlings because they are usually protected by a covering of snow. It may be most severe in openings and during years of light snowfall. There is little in the literature to suggest that this is an important cause of mortality of very young seedlings, although problems have been encountered in western forest nurseries (22). Nevertheless, losses of first-year seedlings to winter drying would be difficult to detect and the possibility of it being important in certain instances should not be overlooked.

Excess moisture can be an important cause of seedling mortality on some sites. Seedling roots in saturated soils or standing water are deprived of oxygen and may be subject to root rot. Seedlings suffering from excessive soil moisture generally develop hypertrophied lenticels, or "root warts" (22). Lees (86) studied the tolerance of one- and two-year-old white spruce seedlings to flooding under laboratory conditions. He totally immersed seedlings for periods of 3½, 7, 10½ and 14 days. The 14-day immersion resulted in total mortality and only a small percentage of seedlings survived immersion for shorter periods. Two-year-old seedlings were more tolerant of flooding than one-year-old seedlings. In the Peace and Slave River lowlands, one- and two-year-old white spruce seedlings survived a flood of unspecified duration provided that they were not buried deeper than their cotyledons by the accompanying alluvial deposits

(163). Wagg (163) suggested that floodplain ecotypes of white spruce may occur and that this should perhaps be a consideration in the selection of seed for artificial regeneration programs. A study in Minnesota listed balsam fir, black spruce, white spruce, white pine and red pine in order of decreasing tolerance to flooding (4). Gilmour and Konishi (59) indicated that "....excessive soil moisture probably is the most significant factor inhibiting adequate regeneration on alluvial and 'black muck' soil...." in the central interior of British Columbia.

Temperature relations. Tree seedlings in the succulent stage following germination may be particularly susceptible to stem girdling caused by excessive heat at the soil surface. The cortex is killed by a temperature of about 130 F, although a prolonged tissue temperature of 120 F may also be lethal (15). Species vary in their ability to maintain temperatures in the hypocotyl that are lower than the soil surface temperature. Baker (15) has measured hypocotyl temperatures 12 to 30 F below those of the surrounding soil surface. The factors involved in this phenomenon are apparently the diameter of the hypocotyl, the shading effect of the cotyledons, and the cooling effect of the transpiration stream. In order to develop lethal tissue temperatures, the surrounding soil surface would therefore have to reach temperatures of 140 to 150 F (16).

The temperature of the soil surface can rise considerably above the air temperature. Because of friction in the boundary layer, the air near the soil surface is generally quite still, virtually eliminating the turbulent transfer of heat away from the surface. Also, thermal conductivity, the ability of soils to conduct heat downward, is limited (57).

The amount of heat energy received by the soil surface depends on factors such as the angle of the sun, the slope and aspect of the surface, and the presence of clouds, haze or shade. Several variables determine the ability of the surface to dissipate heat.

Surface color affects the amount of heat that may be reflected. Isaac (74) reported that with an air temperature of 100 F, a soil surface blackened by burning reached 165 F, while a yellow mineral soil surface reached 145 F. Cochran (36) suggested that the influence of color on surface temperature has probably been overemphasized. He pointed out that other thermal properties may override the effect of color.

The thermal conductivity of the surface layer markedly affects its temperature. Soils with a higher thermal conductivity will conduct heat downward at a greater rate and will thus attain lower surface temperatures. Organic layers have relatively low thermal conductivities and are subject to excessive surface temperatures (36). Eis (49) recorded surface temperatures of 135 F on humus and 120 F on mineral soil at maximum air temperatures of about 100 F. Baker (16) observed temperatures exceeding 135 F on 62 days per season on duff, 18 days on mineral soil, and 34 days on burned mineral soil. The maximum temperature reached on the duff was 161 F compared to 150 and 152 on the mineral soils. Compaction increases thermal conductivity, thus reducing surface temperature (16, 36).

Soil moisture moderates surface temperature through the cooling effect of evaporation and by increasing thermal conductivity (57). Baker (16) reported that a moist soil heated only to about 100 F on a day when the same soil, thoroughly dry, reached 145 F.

Wind tends to reduce surface heating by stimulating turbulent transfer of heat (57). This effect is enhanced by surface roughness (36). Even small amounts of shade can markedly reduce the chance of developing lethal surface temperatures (16, 36, 44). As forest openings increase in size, the mitigating effect of side shade disappears; at the same time, the chance of beneficial air flow increases. Geiger (57) presented evidence based on these facts that an opening with a diameter of 1½ to 2 times the height of the surrounding trees exhibits the greatest extremes in temperature in its center. Cochran (36) stated that surface temperature extremes increase with size of clear-cut.

The seedling suffering the effects of high surface temperatures develops bark necrosis at the base of its stem. If the injury circumscribes the stem, the condition is fatal. Baker (16) lists the following field conditions as leading to heavy seedling losses from heat injury:

1. Lack of shade during the middle of the day - by far the most important factor.
2. A dark-colored soil with poor conductivity of heat and water.
3. A dry soil.

Bates (18) studied the physiological requirements of Rocky Mountain trees and concluded that Engelmann spruce is most efficient in the use of water and possesses the lowest tolerance to high temperatures. In fact, he contended that spruce is restricted to high elevation by this limitation. Recent work by Hellmers et al. (67) support Bates' contention.

Day (44) studied heat and drought mortality in hybrid spruce (Picea engelmannii Parry X P. glauca (Moench) Voss) seedlings in the Subalpine Region of southern Alberta. Seeds were sown on four seedbed types in flats which were then subjected to either full insolation or 40% shade. After germination and a brief growth period, watering was discontinued and rainfall was excluded. Shade significantly reduced mortality on all seedbed types. Three-quarters of the mortality in the shaded flats was due to drought, while three-quarters of the mortality in the exposed flats was due to stem girdling. Surface temperatures as low as 113 F caused stem girdle. Temperatures above 122 F caused severe mortality even when the soil was moist at one-inch depth. Mortality was reduced where root extension kept ahead of the drying front.

Germinants and young seedlings may be adversely affected by low temperatures. Unseasonal frosts, soil heaving, and poor performance in cold soils may all be problems.

Two types of frost are recognized: advective frosts and radiation frosts (16). Advective frosts result from the inflow of subfreezing air from an outside air mass. They generally occur in the winter and only occasionally do serious damage to coniferous seedlings. Radiation frosts are local phenomena resulting from radiation cooling at night. These frosts are likely to occur in early fall or late spring and they may even occur in midsummer (16). Radiation frosts may be a significant cause of seedling mortality.

Early fall frosts may catch seedlings with succulent, unhardened foliage and kill them by the mechanical damage that may result when tissue freezes and thaws. Frost need not be particularly early to destroy late-germinating seedlings (22). In northern areas where the soil usually freezes to a considerable depth, many of the surface roots of trees are killed back each winter (82). Frosts occurring in the late spring may be even more damaging in that recently flushed foliage is particularly susceptible. Baker (16) noted that spruce and true firs are quite susceptible to damage from late frosts. In 1958, a series of frosts between May 26 and June 12 contributed to the death of about 20% of 1-year-old white spruce seedlings at Riding Mountain (76). Rowe (133) had earlier noted that late frosts killed the newly flushed needles of many seedlings in low-lying areas. He pointed out that since regrowth of frost-killed foliage the same year is rare, a succession of frosts could kill the seedlings.

Ronco (126) reported that new growth on planted Engelmann spruce is extremely sensitive to frost. In light frost years, he found that injury was limited to current plantings, but heavy frosts caused damage in plantations that were several years old. Shaded seedlings suffered less damage than those grown in the open. Ronco suggested that frost damage may have greater consequence than just loss of foliage:

> "Until planted seedlings establish new roots and recover from planting shock, photosynthesis and subsequent food production are limited. Since reserve food, already depleted by pre-planting storage, is used to form new shoots, the net result of frost to replace those reserves. When summer foliage losses from frost are preceded or followed by winter-killing of branches by snow mold, a large percentage of the photosynthesis mechanism of a seedling may be lost."

Frost is especially likely to occur in depressions and in clear-cut openings. Cold air drainage increases its likelihood in depressions, and the absence of overhead cover permits maximum radiation cooling in clear-cuts. Slight cloudiness will retard radiation and will usually prevent frost.

Frost heaving is often an important cause of seedling mortality

(101). Baker (16) lists three circumstances that may lead to serious problems:

1. Heavy poorly drained soils deficient in organic matter.
2. Absence of litter.
3. Freezing weather in the absence of snow.

At the Kananaskis Forest Experiment Station in Alberta, frost heaving was the principle cause of mortality on scarified mineral soils and it remained a major problem for the first three years (39, 42). From the fourth year on, seedlings were well enough rooted to resist heaving. Losses from frost heaving in New Brunswick were so severe as to constitute a strong argument against the creation and use of mineral soil seedbeds on sites with heavy soil and high moisture regime (112). In a study on frost heaving of red pine tubelings in Ontario, all tubelings were heaved to some extent by early November (56). The problem ceased when persistent snow fell, but resumed the following spring after the snowpack had melted. The heaving was most pronounced in sandy loam, less so on clay, and least on sand. At Riding Mountain, Manitoba, 11% of one-year-old white spruce seedlings were lost to frost heaving in one study and 23% in another (166). Seedling mortality was most severe on mineral soil seedbeds, but some losses were observed on humus and burned seedbeds.

In the British Columbia Interior, Arlidge (11) observed substantial frost heaving on heavy-textured mineral seedbeds but he did not consider it a serious factor in spruce establishment. He recorded frost heaving on 267 seedbeds; two growing seasons later, 243 of the seedbeds still supported spruce seedlings although many of them had exposed "hockey stick" roots.

Germination and growth may be inhibited on shaded mineral soils that may be excessively wet and cold (104). Low soil temperatures are known to inhibit root growth and absorption and may be one of the more elusive phenomena governing seedling establishment and growth (112, 170).

Light requirements. It is difficult to separate the effects of light intensity on germination, survival and early growth from those of temperature and competition. In many instances, better survival under shade is due to relief from heat and drought losses. Similarly, it is sometimes hard to distinguish between the detrimental effects of shade and the competition of ground vegetation for water and nutrients.

Jones (79) noted that light improves the germination of white spruce seed and Heit (66) classifies white and Engelmann spruce as species requiring light for germination. However, full light is apparently not optimal for field germination, as Eis (52) and Waldron (166) observed that white spruce germination is best in the shade.

Several workers (e.g. 20,49,52,60,112,114,121,123,128,129,140, 166) have reported better establishment of white spruce seedlings on partially shaded sites than in the open. In many instances, the poorer results in the open may be attributed to increased heat and drought mortality. Roe and Schmidt (123) found Engelmann spruce establishment increased with dead shade up to shade levels of over 30%. Le Barron and Jemison (84) noted that Engelmann spruce seedlings could withstand exposure more readily than alpine fir seedlings. However, stocking of both species, determined after three growing seasons, increased with increasing shade up to 60%.

Obviously, too much shade can have a deleterious effect. Waldron

(166) attributed increased survival of white spruce seedlings under a 15% aspen crown cover compared to a 55% cover, partly to increased light; Place (112) noted that seedlings established in deep shade would die within 2 to 3 years if the light intensity was as low as 12%. Eis (52) found that the rate of height growth of white spruce seedlings under 60% sunlight was twice that of seedlings under 20% light. Day (45) reported that the length of the white spruce taproot decreased with increased intensity or duration of shade, although he acknowledged that his observation may have been influenced by vegetational competition. He also observed that shoot length and the length of the longest lateral root was maximum in moderate shade and decreased with deeper shade or full exposure. Eis (53) reported that growth reductions of white spruce seedlings due to undifferentiated shade and competition were expressed most strongly in terms of stem weight, followed by foliage weight and root weight.

Logan (88) grew white spruce, balsam fir and other species for 9 years in 13, 24, 45 and 100% of full light. White spruce and balsam fir were tallest when grown in 45 or 100% of full light. Balsam fir suffered the least dry weight reduction at lower light intensities. The increased growth of all species at higher light intensities resulted from increased amounts of foliage per seedling rather than from any increased photosynthesis per foliage unit. In a similar study, Gustafson (63) grew white spruce for 8 years in ¼, ½, 3/4 and full sunlight. He found that seedlings grown in 3/4 sunlight had the best height growth and those grown in ¼ sunlight had the poorest. As in Logan's experiment, seedlings grown in ½ light and full light were about equal in height.

Ronco (127, 128, 129) reported that light injury (which he termed "solarization") was the major cause of mortality of potted and planted Engelmann spruce seedlings in western Colorado. Affected seedlings developed chlorosis, which was unrelated to nitrogen content. Seedlings grown at 10,500 feet elevation where the light intensity exceeded 16,000 foot-candles generally succumbed. However, even at lower elevations where light is less intense, chlorotic seedlings were observed. He observed that apparent photosynthesis was reduced in seedlings exposed to full light and suggested that this was due to damage to the photosynthetic mechanism by high light intensities (128).

The deleterious effects of shade primarily result from reduced photosynthesis and the plant's consequent low vigor and failure to accumulate sufficient reserve food materials to tide it over periods of stress (16). Insufficient light is undoubtedly a predisposing factor that renders a weakened seedling more subject to death from a number of causes. Shirley (136) noted that under canopies where light intensity is very low, ".... death may finally result from root-destroying fungi, insect feeding, surface soil drying, smothering by leaves, or innumerable other secondary factors, no one or several of which would have proved fatal had the plants been exposed to adequate light intensity." Shirley (136) also pointed out that seedlings under dense shade tended to die in late winter. He ascribed the mortality to a poorer capacity to withstand cold on the part of the weakened plants. However, Baker (16) suggested an alternative explanation, that the seedlings lacked food reserves to mobilize for spring growth.

Tolerance has been defined as the ability to survive under deep shade (16). Place (112) expanded this definition to the "....ability to survive in spite of deep shade and intense root competition, and retention of the capacity to respond to release...." Baker (16) rated white and Engelmann spruce as tolerant and their respective true fir associates, balsam and subalpine fir, as very tolerant. Tolerance is complicated by the fact that it varies with age (16) and site (16,112). Young trees tend to be more tolerant than older trees, and trees growing in fertile soil or a mild climate display more tolerance than those growing in a more austere environment.

Edaphic factors. White spruce occurs on numerous soil types including glacial, lacustrine, marine and alluvial deposits (148). Soils supporting white spruce may range in texture from clays to sand flats and coarse soils and, in some instances, the species occurs on organic soil (148). Gray wooded, brown forest and podzolized soils are typical of those supporting white spruce throughout its range (104).

Engelmann spruce also occurs on a variety of soil types. In the northern Rocky Mountains, it makes its best growth on moderately deep, well-drained silt and clay loam soils and on alluvial soils developed from a variety of parent materials (6).

White spruce will tolerate a considerable range in soil pH (104). Spurway (143) and Sutton (148) indicated its optimum range to be 5.0 to 6.0, with a maximum upper limit of 7.0. However, van den Driessche (157) indicated that spruces grow best on soils of pH 4 to 5. Thrifty white spruce stands in Manitoba have been observed growing on soil with a pH of 8.4 at a 17-inch depth (146). Symptoms of chlorosis have been observed on heavily limed nursery soil with a pH of about 8.3 (Stone, cited by Nienstaedt (104)). There is some evidence that damping-off fungi are encouraged in neutral and alkaline soils (22).

White spruce is apparently more exacting in its nutrient requirements than either red or black spruce (Stone, cited by Nienstaedt (104)). Heiberg and White (65) found that effects of potassium deficiency were more pronounced on white spruce than on any of several other conifers studied. Zasada and Gregory (170) stated that soil fertility may be limiting to white spruce growth in Alaska, but they discounted its importance to seedling establishment.

No information on the range of soil pH tolerated by Engelmann spruce or on the species' nutrient requirements was found.

Two considerations suggest that soil fertility may be quite important in regeneration:

(1) There is good reason to suppose that soil fertility is often reduced by our principal methods of site and seedbed preparation (i.e., blade scarification and prescribed burning), and

(2) Nutrient deficiencies, like light deficiencies, undoubtedly predispose the struggling seedling to mortality from a variety of secondary causes.

Total nitrogen on the site is generally decreased by burning (14,81), although there may be an increase in the residual material and the surface soil (81). The available supply of many nutrients (phosphorus, potassium, calcium, magnesium) is increased immediately following burning, but this increase is often temporary and the end effect may be a loss of fertility as these released nutrients may be readily leached away (14). Burning generally has the effect of increasing soil pH (14), which may increase problems of damping off.

There seems to be little information in the literature on effect of blade scarification on the fertility of the resultant seedbed. Certainly a major proportion of the nutrient capital is tied up in the duff and upper horizons which are scraped away. It may take years before the newly regenerated forest is in a position to exploit these nutrients through lateral expansion.

Competition. Virtually every study that has been concerned with the problems of securing white spruce regeneration has implicated vegetational competition as a major factor with which to content (e.g. 1,3,11, 24,31,39,40,42,46,47,50,58,59,62,69,72,76,87,94,96,101,104,107,108,109,112, 114,115,118,133,137,147,155,163,166,167,170). The picture that emerges from the literature on Engelmann spruce is less clear. Studies in the central interior of British Columbia indicate that vegetational competition may be a serious constraint on Engelmann spruce regeneration (33,141), but the few reports on the subject that emanate from the more southerly portion of the range do not emphasize the importance of this factor (e.g. 6,7,121,123). Indeed, Alexander (7) reported that ground vegetation may be beneficial to Engelmann spruce stocking.

Spruce seedlings may suffer competition from bryophytes, herbs, shrubs, overstory trees and their sprouts and, sometimes, from each other for the critical amenities of the site -- water, nutrients, light and space. The effects of competition may bear on germination, survival and growth. Given its broadest definition (the concept of competition has been the subject of considerable scholarly debate), the mechanisms of competition include root proliferation and exploitation of a soil mass, shoot development resulting in occupancy of space and interception of solar radiation and precipitation, and such deleterious effects on neighboring plants as exudation of toxic substances and prevention of germination or smothering of seedlings by litter. Vegetative reproduction and rapid initial growth gives many brush and hardwood species a considerable advantage over their coniferous competitors. The principal assets of conifers are their ultimate stature and longevity.

Eis (52) studied the establishment of white spruce regeneration in the North Central Interior of British Columbia. He noted that, because of shallow root penetration, drought was the principal cause of mortality during the first growing season on all sites studied. However, subsequent mortality on moist habitats was mainly due to competition from ground vegetation and frost heaving. Based on observations of white spruce, Engelmann spruce and Douglas-fir plantations in the Prince George Forest District, Schmidt (23) concluded that "....the most serious factor....is competition by vigorous brush growth and damage from snow press." This was true even on scarified sites where brush quickly reinvaded. Good form and vigorous growth was attained only where brush competition was negligible. Prochnau (114), working at Aleza Lake in the North Central Interior of British Columbia, also noted that heavy mortality of spot-seeded white spruce on moist sites (Equisetum-Sphagnum, (73)) after the first growing season was due mainly to a dense invasion of grasses and horsetail.

The effects of competition are difficult to quantify. An examination of 2- to 3-year-old white spruce seedlings growing on ploughed seedbeds in Riding Mountain National Park showed that 52% of dead seedlings had died either from the direct effect of vegetational competition or from smothering by aspen leaves (76). Ackerman (1) recorded increases in germination and survival of white spruce seedlings where vegetation was removed from a good site. On a drier site, germination was higher following vegetation removal but the treatment did not benefit seedling survival. Lees (87) presented data combined from dry, moist and wet sites that showed small but significant reductions in mean leader length of young (4 years old or less) natural white spruce seedlings with increasing vegetational competition. Smith and Clark (141) reported more than twice the height growth on Engelmann spruce and alpine fir seedlings growing free of competition on mineral soil and burned seedbeds compared to those growing in a moss layer. Sutton (149) found that, after 7 growing seasons since planting, white spruce in weed-controlled plots were 36% taller than trees not freed from competition. He noted, however, that there was an interaction between weed control and soil type. Weed control was particularly beneficial on sand areas of low fertility.

Trenching experiments suggest that root competition provided by the residual stand is not an important factor in the germination and initial survival of white spruce. Griffith (62) reported that trenching to remove competition by tree roots had no appreciable effect on spruce seedlings, although the luxuriance and density of the herbaceous flora was considerably increased. Contrarily, Stettler (151) suggested that one of the main values of residual stems might be in hindering the formation of excessive brush.

Smothering by leaves. Numerous workers have reported seedling losses from smothering by leaves and other litter (34,61,76,80,104,112,166, 170). Koroleff (80) listed several ways in which conifer regeneration suffers from fallen leaves. These include failure of germination on or between leaves, failure of germinants to emerge from beneath leaves, and mechanical damage and smothering of small seedlings by fallen leaves.

Rowe (133) reported that mechanical smothering by annual leaf accumulation from herbs, shrubs and hardwood trees from September to May "....may be the most important cause of mortality in the first few years." He noted that of 1100 dead or dying 2-year-old white spruce seedlings on ploughed plots, 50% had definitely been crushed by leaves. Because furrows act as catch basins for leaves (112,133), the problem may be averted by planting on ridges. Jarvis et al. (76) reported that of 1152 dead white spruce seedlings tallied, 52% had died either from direct competition by the ground vegetation or from smothering by aspen leaves. Waldron (166) indicated that crushing by aspen leaves was responsible for 45% of the mortality on disked seedbeds and for 36% on undisturbed seedbeds.

Gregory (61) conducted an experiment to evaluate the effect of leaf smothering upon the establishment of white spruce beneath a paper birch stand in Alaska. He compared seedspots protected with hardware cloth screens with unprotected seedspots. Protection from leaf litter significantly improved survival for the first four growing seasons following germination. After the fourth growing season, most surviving seedlings were large enough to avoid being smothered or crushed by fallen leaves.

Mortality due to falling leaves is not confined to mixedwood stands. In the British Columbia Interior, Clark (34) found that shade cast by ground vegetation was only slightly better for Engelmann spruce survival than no shade, because of the offsetting losses by leaf smothering.

Prochnau (114) also noted losses due to smothering and crushing by litter, and Arlidge (11) observed that spruce seedlings that survive the intense competition of thimbleberry were smothered by its heavy leaf fall. One of the advantages of the rotten wood seedbed in undisturbed forests, other than favorable moisture relations, is that fallen leaves are less likely to accumulate on elevated stumps or fallen logs (104).

Animal damage. Various animals may cause damage and mortality of young seedlings. Mice consume cotyledonous seedlings as well as ungerminated seed (121,161). A particularly serious problem in the mixedwood forests of central Canada has been crushing of seedlings by elk (*Cervus canadensis*) (153,166). Tucker *et al*. (153) noted in Riding Mountain, Manitoba, that 22% of white spruce transplants on disked strips and 8% of those on hand-scalped areas and undisturbed ground had been killed by elk trampling. Waldron (166) also noted that elk trampling was much more severe on disked seedbeds, which provided travel routes for elk, than on undisturbed seedbeds. Roe *et al*. (121) stressed the importance of cattle in damaging Engelmann spruce seedlings, particularly those in furrows. Deer (*Odocoileus* spp.) and moose (*Alces* spp.) may also cause trampling damage although they rarely feed on white spruce (104). Swift (150), however, lists white spruce as a starvation diet for deer.

Other animals have caused problems. Perhaps most noteworthy is the varying or snowshoe hare (*Lepus americanus*). Hares nip off buds and stems, thus deforming the trees and retarding their growth. During its population peaks, this animal has caused serious damage to conifer seedlings and transplants (5,76,104,133,148,163,170). Examples of white spruce up to 3 feet tall being killed by repeated browsing have been noted (133). Rowe (133) pointed out that damage from the snowshoe hare is confined to aspen-covered or brushy areas. Nienstaedt (104) and Aldous and Aldous ~~(44)~~ (5) suggested that planting be confined to open areas when hare populations are high. Ronco (126) reported that established Engelmann spruce plantations could be completely devastated by mountain pocket gophers (*Thomomys talpoides*) up to 3 or 4 years after planting. Another rodent, the red squirrel (*Sciurus hudsonicus*), clips spruce leaders and the ends of lateral branches to cache buds for winter provision during years of cone crop failure (130).

Nienstaedt (104) indicated that birds may be important factors in spruce regeneration; he pointed out that spruce buds are one of the principal foods of the spruce grouse (*Canachites canadensis*). Place (112) reported that juncos (*Junco* spp.) killed many white spruce seedlings while the seedcoats still adhered to the cotyledons. Losses were especially heavy on exposed litter seedbeds where the seedlings were especially conspicuous against this background.

Effect of environment on germination, survival and initial growth. Moisture, temperature, light, competition and various other environmental factors that have been reviewed exert their individual effects to form the innumerable environmental complexes in which a seed or seedling may occur. Some environments, of course, are superior to others but few, if any, are optimal for all three facets of seedling establishment - germination, survival and initial growth.

For example, in the British Columbia Interior, Eis (52) listed the following as the most favorable conditions:

For germination - mineral soil seedbeds in the shade on moist to wet sites.

For survival - mineral soil seedbeds in partial shade on dry sites.
For growth - mineral soil seedbeds in full sunlight on moist sites.
Waldron (166) found germination to be higher on burned seedbeds than on mineral soil seedbeds beneath a partial canopy, but in openings, germination was higher on mineral soil than on burned seedbeds. Arlidge ~~(69)~~ (11) reported that seedbeds with a rough surface had more seedlings than smooth seedbeds. Even the slight roughening made by tractor tracks improved the seedling catch. He and Prochnau (114) generally found mineral soil seedbeds the best for survival, but mixed (mineral soil and humus) seedbeds were better for height growth. Waldron (166) obtained contrary results in Manitoba. He reported that early height growth of white spruce seedlings was greater on mineral soil and burned seedbeds than on seedbeds containing a high organic content (i.e., mixed mineral soil and humus). He also found that survival and height growth were better on scalped than on disked seedbeds as brush reinvaded the latter more rapidly. Rowe (133) pointed out that decayed wood and mineral soil were the two most favorable seedbeds for germination and early survival but that the latter promoted a much greater rate of growth.

Place (112) found that initial establishment of white spruce was better under an overwood but survival and growth were better in the open. Similarly, Roe and DeJarnette (122) observed that natural establishment of Engelmann spruce seedlings was best in a partial cutting but clear-cut areas provided a better environment for subsequent growth. Waldron (166) also reported that white spruce seedlings grew better in the open than in shade but, in shade, they grew better on burned than on mineral soil seedbeds. On disked seedbeds, regeneration was more abundant under heavy crown cover than under light crown cover (166). Phelps (107) noted that stands of moderate density were more favorable to the establishment and survival of seedlings than those where the density was either light or heavy. Day (45) indicated that both spruce and alpine fir regeneration increased considerably in abundance with increasing residual stand density up to 50%. He also pointed out that shade reduced the growth rate of both spruce and fir seedlings. ~~Less~~ Lees (85), on the other hand, reported that regeneration establishment was not significantly affected by stand density. Day (45) stated that "....microenvironments most suited to germination and survival may not be best for later development. If shade is a necessity for early seedling development, it should be removed as soon as satisfactory stocking is achieved."

REGENERATION SILVICULTURE IN THE BRITISH COLUMBIA INTERIOR

Introductory

Occurrence of spruce. Commercial stands of white or Engelmann spruce occur throughout the Boreal Forest Region and in the Interior Subalpine Section (SA.2), Montane Transition Section (M.4), and the Northern Columbia Section (CL.2) of the Subalpine, Montane, and Columbia Forest Regions, respectively. The climate is continental in character with long, moderately cold winters and short growing seasons.

The principal associate of both spruces is alpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Lodgepole pine (*Pinus contorta* Doug. var. *latifolia* Engelm.) occurs as a seral species following fires in pure stands or in mixtures.

Site types. Five principal site types in spruce-alpine fir stands, based on observations in the M.4 and SA.2 sections near Prince George, were described by Arlidge (73). In descending order of site quality these are: Oplopanax site type (O), Disporum site type (D), Aralia-Dryopteris site type (A-D), Cornus-Moss site type (C-M) and Equisetum-Sphagnum site type (E-S).

Management. Forest management is the responsibility of the British Columbia Forest Service. White or Engelmann spruce occur in the Nelson, Kamloops, Cariboo, Prince George and Prince Rupert Forest Districts.

Development of harvesting methods. In 1914, the Prince George Forest District executed its first timber sale, providing that all trees over 10 inches d.b.h. and over 50% sound were to be cut (3). For several decades thereafter, diameter limit cuttings (generally to a 12 d.b.h.) were carried out in the mature uneven-aged white spruce-alpine fir stands of the B.C. Interior. It was intended that the residual stand and advance growth would make up the second cut, and the third cut would depend on regeneration following the initial cutting. Griffith (62) drew attention to the difficulties inherent in this approach when he showed that although spruce dominated the overstory of original stands (generally comprising over 60% of the basal area), it ran a poor second (about 18%) to alpine fir in the understory. Moreover, the anticipated spruce regeneration did not materialize, due to the intact layers of moss and herbaceous and shrub growth on the forest floor.

Initially, trees were bucked into logs and skidded by horse. Following the Second World War, heavy logging machinery was introduced and the residual stands were further deteriorated by heavy logging damage (3). Because of logging damage and windfall, the spruce poles forming the residual stand were of little value as a subsequent crop (145).

In 1949, Pogue (113) reported that cutover areas were poorly stocked and recommended that the 12-inch diameter limit be replaced by a single tree selection system which would provide for a more uniform residual stand. This system was generally unsuccessful, due to continued logging damage (60) and windfall problems (92). The regeneration that did occur was generally alpine fir (92).

Alternate strip clear-cutting was introduced in 1954 (3). The cut and leave strips were 4 to 10 chains wide and usually less than 30 chains long (3). The initial hope that advanced regeneration would provide an acceptable new crop was not fulfilled, due to heavy logging damage. Moreover, natural regeneration did not materialize because winter logging left the forest floor virtually undisturbed. Thus, in 1956, scarification of logged areas was introduced (3). This technique was moderately successful when a good seed crop followed seedbed preparation within a year or two. However, good sites become unreceptive within 2 or 3 years after scarification due to reinvasion of brush (11), while good seed crops are generally separated by several years (114). This has limited the effective use of scarification.

Alternate strip clear-cutting also produced the problem of regenerating the leave strips when they were eventually cut. This problem was approached by scarifying the leave strips (pre-scarification) usually at the time the adjacent cut strips were being scarified. The same difficulties of seed crop periodicity and brush reinvasion were encountered in pre-scarification as well as several additional problems. Standing trees make it more difficult to obtain good coverage, and damage to root systems was thought to increase windthrow (118). There was also the problem of eventually harvesting the leave strips without excessively damaging the regeneration that had been obtained. Alternate strip clear-cutting is still a principal cutting method, although there is a current trend toward large clear-cuts of several hundred acres.

Seedbed and Site Preparation

"Dense brush....occupies all high and medium sites shortly after logging, and precludes satisfactory regeneration without site preparation" (118). Planting on high sites without prior site preparation has invariably met with failure (3, 118). Seedbed and site preparation is generally accomplished by scarification, prescribed burning or, haphazardly, by summer logging.

<u>Scarification</u>. In the British Columbia Interior, scarification

generally refers to seedbed preparation, while treatment of a site for planting is referred to as mechanical site preparation (M.S.P.).

It has been well established that mineral soil seedbeds are a virtual necessity for successful spruce regeneration, and scarification is an important means of achieving such seedbeds. In Manitoba, Phelps (108) found over 5 times as many first-year seedlings on plots scarified with an Athens plough as on undisturbed plots. In the British Columbia Interior, Glew (60) found that white spruce stocking on unscarified strips was 27.7%, while stocking on scarified strips was 52.4%. Crossley (42) stated that "....the more completely the mineral soil is bared and compacted, the better the results in initial germination." Waldron (166) found that germination was considerably higher on scalped than on disked seedbeds.

Scarification was introduced to the British Columbia Interior in 1956 (60). Decie and Fraser (47) tested various methods of scarification and endorsed bulldozer blades with and without ripper teeth. They found that various drag scarifiers produced good seedbeds but they rejected these for reasons common to all: weak hitch, loss of manoeuverability, restricted use of winch, and operator having to divide his attention forward and rearward. Clark et al. (33) also found the brush blade to be the most economical and practical mechanical method in the Engelmann spruce/alpine fir type. However, they suggested that hand scarification should not be overlooked in future trials. Blade scarification has been used almost exclusively on spruce sites. Some success is being achieved on lodgepole pine cutovers with a drag scarifier composed of tractor pads and spiked anchor chains.

Arlidge (11) studied the effectiveness and durability of blade scarified seedbeds and found that their receptiveness to spruce regeneration began decreasing immediately and that within three years they were virtually unreceptive due to reinvasion by brush. Larger seedbeds remained receptive for a longer time and generally provided better spruce survival than smaller seedbeds. Interestingly, seedbed receptiveness to alpine fir and birch seedlings did not decrease so rapidly. Quaite (115) found that blade scarified seedbeds in Alberta remained receptive to spruce "....for several years", and Lees (85) found that they remained receptive for five years.

Arlidge (11) made several other pertinent observations regarding blade scarified seedbeds. For example, regeneration success varied directly with plot size and, for this reason, success was greater on plots scarified by large tractors than on those scarified by smaller tractors. He noted also that rough surfaces, even those provided by tractor tracks, improved seedling establishment. He indicated that "harrowing" to produce a rough seedbed is an important aspect of seedbed preparation. He also reported that success was greater on A-D site types than on 0 site types.

Apparently, not only is success on 0 site types less, but cost is considerably greater. Gilmour and Konishi (59) indicated that scarification cost is directly related to precipitation and, consistent with this observation, Glew (60) reported that it cost about three times as much to scarify an 0 site as to scarify a C-M site. In terms of cost, glacial till soils offer the best overall opportunity for blade scarification (59).

The introduction of blade scarification in the British Columbia Interior followed shortly after alternate strip cutting was instigated

(3). For silvicultural and economic reasons, cut strips (post-scarification) and leave strips (pre-scarification) were often scarified in the same operation. The rationale for pre-scarification depends on being able to subsequently remove the leave strips without seriously damaging the regeneration. Winter logging on a snowpack is usually depended on to avoid damage to the regeneration. Arlidge (11) found no difference between pre-scarified and post-scarified areas in terms of regeneration success. One advantage of post-scarification is that it reduces fire hazard (60).

Blade scarification is not without its problems. Loss of fertility through the scalping away of top soil may occur. According to Gilmour and Konishi (59), pre-scarified stands are more subject to windthrow because of root damage caused by scarification. Soil compaction may be a problem (170) and scarified soils may tend to "bake", thus providing an austere environment for germinants (59). Gilmour and Konishi (59) pointed out that scarification of 0 sites is possible on leave strips because the water table is held down by forest transpiration; however, 0 sites on cut strips are often impossible to scarify because of high water tables. They also suggested that well-drained soils should be treated during the wetter periods, and vice versa. Quaite (115) observed that scarification may not be successful on the very wet sites. Hughes (72) and Lees (86) noted that spruce establishment and growth may be hindered by water standing in depressions left by scarification.

Due to standing trees, slash, and the need to deposit the scalped soil, mineral soil exposed by scarification may be confined to about 30% of the area (11). Distribution of mineral soil patches may be just as important as the percentage of mineral soil exposed. Decie and Fraser

(47) introduced the concept of "effective work" and "total work" in reference to scarification. "Effective work" is the percentage of milacres on an acre having at least one square foot of exposed mineral soil, while "total work" is the areal percentage of an entire tract having exposed mineral soil. (This distinction is analogous to that between stocking and tree density.) They found a direct relationship between "effective work" and "total work". The point of diminishing returns in "effective work" is reached at about 25-30% "total work".

Since scarification is often intended to provide a seedbed for natural regeneration and since seedbed receptivity decreases year by year, it is important to time the treatment to precede good seed years as closely as possible. Glew (60) particularly stressed that pre-scarification should be timed to coincide with good seed years. Scarification for natural regeneration should be avoided in years following a "bumper" seed crop since heavy crops are normally followed by light or nil seed crops (59).

Revel (118) suggested that on poor sites where organic layers are thin and brush competition is minimal, summer logging may expose sufficient mineral soil to obviate the need for scarification. However, most logging in the British Columbia Interior is conducted during the winter on 1 to 7 feet of snow (60).

Finally, the possibility of successful winter blade scarification has been demonstrated in Saskatchewan by Gilmour (58). He pointed out that depth of winter scarification depends on depth of frost which, in turn, depends on the kind and amount of humus and litter and on the depth of snow. In a well-drained sandy loam with a 3-to 4-inch L-F layer and a thin H layer, up to 50% exposure of mineral soil has been achieved by winter scarification. Compaction damage and excessive scalping are presumably less likely to occur with winter scarification than with summer scarification. Perhaps most significant was the opportunity provided to treat areas that were virtually inaccessible during the summer.

Prescribed burning. Prescribed burning has been successfully used for seedbed and site preparation in many parts of North America, but the results obtained on spruce sites have often been discouraging. Crossley (42) observed lower stocking of spruce on burned areas in the Subalpine Region of Alberta; Muri (97) made similar observations in B.C. Jarvis and Tucker (77), in Manitoba, concluded that fire alone did not provide a satisfactory seedbed treatment. Ackerman (1) noted that removal of organic material by burning had an adverse effect on germination and survival. Place (112) and Rowe (133), on the other hand, observed that "severe" fires in late summer on well-drained soils with thin organic mantles can provide favorable seedbeds for white spruce establishment, although Place (112) also pointed out that charred surfaces may be too hot for germination in dry years. Revel (118) stated that early experience in the North Central Interior confirms Place's and Rowe's observations.

In Manitoba, Waldron (166) reported that following a hot, dry summer, survival of germinants was 56, 40 and 27% for mineral soil, undisturbed, and burned seedbeds, respectively. In a laboratory experiment, Muri (97) reported that ashes had no significant effect on Engelmann spruce germination, but survival on ash-covered seedbeds was about half that of unburned surfaces due to a greater incidence of damping-off. Jarvis et al. (76) presented experimental data indicating that, under shade, burned seedbeds in Manitoba were more favorable for germination and establishment of seedlings than mineral soil seedbeds. However, in the open, burned seedbeds appeared less favorable. Seedling growth was somewhat better on burned seedbeds than on scarified seedbeds.

Rowe (131) observed a one to one-and-a-half month delay in white spruce germination on a burned seedbed as compared to an unburned mineral seedbed. Such a germination delay may predispose the germinants to heavier mortality.

In the interior portion of the Prince Rupert Forest District, Armit (24) noted that burned mineral soil provided a seedbed inferior to mixed soil and humus and disturbed humus. Later, reporting on the same general region, he stated that "....spring and fall seeding of pine and spruce have been unsuccessful on burned seedbeds" (26) and "....all three species (white spruce, lodgepole pine and Douglas-fir) were more successful on mineral soil seedbeds than on burned seedbeds...." (27). Clark (27), in the central interior, noted that seeding of Endrin-treated Engelmann spruce on the "Mag" fire was a complete failure. Smith and Clark (141) observed that Engelmann spruce survived equally well on burned, mineral and rotted wood seedbeds, although survival was generally low even with screen protection against rodents.

Artificial Regeneration

Planting. White spruce has been planted with moderate to good success in many parts of its range since the early part of the century (76, 148). Planting, though initially expensive, is presently the surest means of artificially regenerating white spruce and may therefore be the most economical in the long run. Zasada and Gregory (170) list several advantages to planting: "....selected genotypes can be used, spacing can be regulated, collected seed is used more efficiently than in artificial seeding operations, the critical periods of germination and initial survival under uncontrolled conditions are bypassed, and the older seedling is better able to compete with fast-growing, herbaceous, and woody vegetation."

As a rule, planting will be confined to the more highly productive sites—those that provide the most severe competition from brush and herbaceous vegetation. Scarification or intense burns may be a necessary pre-treatment, and the period following treatment during which competition is retarded will be short. This places a premium on the production of large, thrifty seedlings which, when outplanted, will begin rapid growth and root development. Unfortunately, white spruce is well known to exhibit a characteristic known as "planting check" (50,94,95,96) whereby the growth of the out-planted seedling is nil or exceedingly slow, often for a period of several years.

Mullin (95) suggested that "....by definition, a tree be considered in check until it has achieved a rate of terminal growth equivalent to that it would have attained in the next season in the nursery." Check was found to reduce leader length by about 50% in the first year after outplanting and the effect has been known to exist for 10 years or more in many instances (95). Eis (50) compared the mortality and growth of out-planted white spruce seedlings to that of undisturbed wildlings. He found that out-planted seedlings suffered twice the mortality, and that height growth reduction due to planting check amounted to 47% in the first year and 15% in the second year.

Various phenomena have been implicated in planting check. Mullin (94) has pointed to frost and root necrosis, although basic causes of the latter remain unassessed. He has also underscored the importance of competition from other plant species (94,96): "All considerations indicate the importance of proper site selection and preparation in planting (white spruce). In view of the economic loss during the period of check, consideration should be given to drainage, size of stock, and reduction of competition." Revel (118), approaching the problem from a somewhat different direction, recommended the "....development of successful fertilizer or hormone root dips which would stimulate the normally slow initial growth of white spruce seedlings...."

The initial stature of planting stock appears to have an important bearing on field survival and early growth. Armit (12) followed the development of 4 classes of white spruce stock after outplanting in the Prince Rupert Forest District. The classes were 2+0, 2+1 R (reclaimed undersize 2+0 stock transplanted for one year), 2+1 L (standard transplants) and 3+0. Survival after 5 years was satisfactory for all stock classes, although the survival percent for the 2+1 R class was significantly lower than that of the other classes. Height growth was also significantly different, with 2+1 L stock growing considerably better than the other classes and 2+0 stock exhibiting markedly inferior height growth. Gillespie (28) also reported on a planting trial in the Prince Rupert Forest District. He noted that the 5-year survival and growth of outplanted 2+1 white spruce stock was considerably better than that of 3+0 stock.

Various other factors related to planting of bare-root stock have been studied but, in many cases, deserve further attention. For example, the use of herbicides calls for further study. Sutton (147) showed that the non-selective fenuron herbicide, Dybar,"....can safely be applied at the time of planting to vegetation competing with planted white spruce, even when the herbicide is applied as close as one foot from the planted tree."

Method of planting as a variable affecting economic efficiency and survival was studied by Armit (13). He compared the mattock and planting bar with and without screefing and found that non-screefed mattock planting resulted in the greatest production per man-day at significantly lower cost per established seedlings. The main mortality factors were smothering and vegetational competition for light.

Time of planting has biological and economic importance. Clark (25) found spring planting of Engelmann spruce superior to fall planting. However, Thompson (28) found fall planting to lead to best survival of Engelmann spruce and spring planting resulted in best growth. Armit (25) reported that "....spring and fall planting can produce equally successful survival, growth, and seedling costs on sites with light to moderate vegetal cover and fresh to moist conditions." On wetter sites with lush vegetation, only spring planting was recommended. Revel (28) studied the feasibility of planting white spruce throughout the growing season in the North Central Interior. Freshly lifted and cold-stored stock was planted at two-week intervals throughout the 1968 growing season. Survival after 3 years was high for all plantings but the growth of stock planted after July 15 was reduced. Growth reduction was more severe with cold-stored stock.

The performance of mudpacked Engelmann spruce stock is being studied in the Kamloops and Nelson Forest Districts (28). Mudpacks are prepared by rolling the roots of 2+0 seedlings in a moistened mixture of clay and peat moss. This results in a cylindrical capsule which may be dibble-planted. Clark and Thompson (28) compared the performance of mudpacks and bare-root stock and reported that while overall survival was low, bare-root stock showed better survival than mudpacks.

Research on the performance of container-grown white spruce seedlings has been underway throughout Canada for several years (30). Results have been variable and quite specific to technique, geographical region and out-planting site. Emphasis in the British Columbia Interior has been on seedlings grown and planted in 4½-inch plastic bullets and, more recently, on plug seedlings — seedlings grown in containers and withdrawn at the time of planting. For an interim period, plug seedlings were those grown in bullets and removed for planting (bullet plugs) but this method has given way to styro-plug seedlings which are grown in cavities in a polystyrene block. (See Vyse et al. (160) for a description of the styroblock reforestation system and definition of terms).

Survival and growth of bullet and plug spruce seedlings has compared favorably with that of bare-root stock in the British Columbia Interior. Clark and Thompson (28), in an interim report on first-year survival of Engelmann spruce outplants, observed that "....container stock (bullets and plugs) survived as well as, if not better than, bare-root stock...." Van Eerden (158), reporting on container planting trials in the Prince George Forest District, observed that "....plugs (including white spruce) are outperforming all other types of stock in survival." In a more recent report (159), he noted that styro-plugs "....are superior in survival to bullets and have somewhat faster growth rates."

Van Eerden (158) recently summarized progress with container planting techniques in the Prince George Forest District. He reported the following conclusions:

1. Survival of container-grown seedlings is high, provided seedlings are of high quality and sufficient size.

2. Seedling vigor and size are the most important factors affecting survival.

3. Growth of container seedlings follows the same pattern as bare root stock, and has been satisfactory on high sites only.

4. Container seedlings perform to the site, i.e., conditions adversely affecting seedling survival will be manifested sooner on the high sites than on the low sites.

5. Growing prescriptions for the production of container seedlings are being formulated.

6. While container growing offers certain advantages in terms of quality control and stock production, it is an intensive care system.

7. Although container growing of Interior species has largely been done in coastal climates, there is a need to explore the feasibility of Interior growing, particularly the aspect of longer day lengths of Northern localities. Crop scheduling under Interior climatic conditions should also be investigated.

8. Planting rates of two to three times those of conventional systems have been achieved with container planting.

9. On the basis of present knowledge, the styro-plug offers the best combination of biological and economic advantages, at least for many sites in the Sub-Alpine Forest Region.

Direct seeding. The potential benefits and occasional successes in direct seeding of white spruce have engendered considerable research on the subject over the past several years. Direct seeding, if perfected, would provide a highly flexible, economical and rapid means of regenerating cutover or burned areas. These potential benefits derive from the facts that seed can be stored for long periods and aircraft or motorized toboggans can be utilized to deliver it to virtually any site, including those that cannot easily be reached in the summer.

Unfortunately, the results of direct seeding trials have been varied and heavily marked by failure (148). Smithers (142) reviewed the outcome of 34 trials on white spruce in eastern Canada and found a quarter of them to be moderately successful and nearly half of them to be failures. He listed as major causes of mortality, drought, competition, drowning of seedlings in depressions, and frost heaving. To this list of principal mortality factors, McLeod (102) added destruction of seed and seedlings by birds and rodents, high insolation at the soil surface, and soil erosion.

A major exception to the generally poor results of white spruce direct seeding trials was reported by Haig (64) on experimental seeding in 1920 in western Manitoba. An area, which was heavily disked, seeded, then harrowed, supported a dense (3,400 to 5,000 trees per acre) and apparently thrifty stand in 1957.

Several factors operate against direct seeding success. Mineral soil seedbeds are a prerequisite (26,34,35,114,170 and others) not always easy to provide. Blade scarification provides a mineral soil exposure of about 30% on most spruce cutovers (11). This means that 70% of seed broadcast by air would be wasted on unreceptive ground. Clark (35) stated that areas selected for broadcast seeding should have at least 65% exposed mineral soil. Where mineral soil exposure is limited and patchy, spot seeding may be indicated, but this surrenders many of the advantages we hope to achieve by direct seeding.

Seed losses to rodents are often very severe, even when seed is treated with repellents (116,118 and many others). Clark (35) mentioned that a new chemical for deer mouse control, Diphacinone, shows some promise as a repellent in pre-baiting type treatment, but further testing is required. Many other sources of seed loss that may militate against success, even with heavy natural seedfall, have previously been discussed.

Several direct seeding trials employing white or Engelmann spruce seed have been carried out in the British Columbia Interior, with results varying from very poor to good (35). Results have varied with site, seedbed, method and rate of application, and weather during the critical germination and post-germination period. Revel's (118) problem analysis on silviculture of the spruce-alpine fir type provides a good account of the status of direct seeding as a silvicultural tool for the regeneration of spruce in the Interior:

> "In the past ten years, sixteen, full-scale, direct seeding studies have been undertaken by Regional Research Officers in the interior of British Columbia.... Most of these studies have explored the potential of broadcast - or spot-seeding of spruce. A review of these projects indicates that:-
>
> - high populations of seed-destroying rodents exist under virtually all field conditions.
> - current protection of seed against rodent depredation (1 gram Endrin 50W per 100 grams of seed) is only partially effective, and significant volumes of treated seed are being destroyed.
> - site and seedbed conditions favorable to the germination and establishment of spruce are reasonably defined, and are frequently found on large forest fires which have occurred during hot dry summers.
> - spring seeding has been more reliable than autumn seeding, due probably to the reduced period of seed exposure to rodents.
> - weather patterns during the spring and early summer subsequent to sowing are generally the critical limiting factor to the success of seeding. These patterns cannot be predicted or controlled.
> - success can be achieved by broadcasting 4 ozs of spruce seed per acre, or by sowing 10 to 15 viable seeds on

each of 800 spots per acre, provided that rodent depredation is negligible, favourable seedbeds are well-distributed, and adequate precipitation occurs during the first growing season.

"The widespread application of direct seeding appears to depend on:-

- development of methods which require a minimum of time and labour (emphasize broadcast seeding, preferably by motorized toboggan or helicopter).
- maximum application of 6 ozs of seed per acre (cost and/or availability of seed).
- more adequate protection of seed from rodents (substantially increased concentration of Endrin, application of a more desirable food supply with the tree seed).
- application of seed (if possible) into the snow pack during midwinter, which would cause no conflict in labour requirements between seeding and planting."

SUMMARY

The botanical ranges of white and Engelmann spruce overlap in the British Columbia Interior where hybridization takes place between the two species. Literature pretaining to the regeneration ecology of both species is reviewed, as well as literature relating to the regeneration silviculture of spruce in the British Columbia Interior.

White spruce begins to flower and produce substantial seed at about 30 years of age; abundant crops occur on trees about 60 years old. Good cone crops occur every 2 to 6 years and light crops generally occur in the intervening years. At the more northerly latitudes, seed production is more delayed and infrequent. Engelmann spruce apparently begins commercial seed production at an earlier age (16-25 years) and produces most abundant crops at 150-200 years. Good crops occur every 2 or 3 years.

Seed production as high as 5,000,000 per acre has been recorded in white spruce. As many as 11,900 cones and 271,000 viable seed have been produced by a single white spruce tree. Engelmann spruce stands

produce 570,000 to 760,000 seeds per acre in an average good year. Engelmann spruce seed are nearly twice as large as white spruce seed.

The proportion of sound seed is generally higher in years of heavy production than in years of light production. Early- and late-falling seed tend to be less sound than seed falling during the peak dispersal period. Engelmann spruce seed has, on the average, higher germinative energy and higher germinative capacity than white spruce seed.

Seed dispersal distances of 5 chains from a forest edge have been recorded for white spruce and over 9 chains for Engelmann spruce. Most seeds are undoubtedly deposited within 2 to 4 chains of their source.

The vast majority of white and Engelmann spruce seeds are naturally dispersed in the fall and early winter. During the winter period, mice are the most important sources of seed losses. The use of repellents has met with some success in direct seeding programs.

Although several insect pests bring about heavy seed losses in the cone, no important insect enemies are known to attack seed on the ground. No significant losses of overwintering seed may be attributable to fungi, although heavy damping-off losses may occur upon germination.

High surface temperatures, often the cause of seedling mortality, may also be lethal to ungerminated seed.

Field germination on mineral soil generally takes place in June or July, although it may occur later on burned seedbeds. Late-germinating seedlings are more subject to over-wintering losses. Seeds may remain dormant until the second growing season following dispersal.

The initial growth of the germinant, particularly its rate of root penetration, is an important determinant of its survival chances. A crucial requirement is that the advancing root reach soil with a stable moisture supply before the surface layers dry out. Although shoot growth ends in early August, root growth may continue until late fall.

The rate of initial growth and the stature of the first-year seedling depends, in part, on seed size.

Most seedbeds in the undisturbed forest are organic and most, because of their tendency to dry out readily, are unsuitable for spruce establishment. Spruce regeneration in the undisturbed forest is generally found on decaying wood or on rare patches of exposed mineral soil which have more favorable moisture regimes. Mineral soil is often requisite for the natural or artificial regeneration of cutover or burned-over areas.

During dry summers, wetter sites are more favorable and, conversely, during wet summers, the dryer sites may be better. However, on wet sites, flooding may be a source of mortality in wet years.

Winter drying, which occurs when warm weather brings about foliar water loss at a time when water absorption by roots is prevented by frozen ground, may be an important cause of mortality of young seedlings.

Tree seedlings in the succulent stage following germination may be susceptible to stem girdling caused by excessive heat at the soil surface. Engelmann spruce, and probably white spruce, have a particularly low tolerance for high temperatures. Soil surface temperatures exceeding 140 F are likely to be lethal. Dark surfaces and organic layers are especially prone to excessive surface temperatures. Soil moisture is an important moderator of surface temperature. Even small amounts of shade can prevent lethal surface temperatures.

Unseasonal frosts may kill unhardened foliage. Soil heaving may be an important source of mortality of seedlings up to 4 years old. Heaving is most serious in heavy, poorly drained soils deficient in organic matter, when freezing weather occurs in the absence of snow.

The effects of light, heat, moisture and plant competition are generally confounded and difficult to separate. Light improves the germination of spruce seed. Apparently, field germination and survival is most benefitted by partial shade. There is evidence that white spruce growth is best at about 75% of full sunlight. Insufficient light is a predisposing factor that renders a weakened seedling more subject to death from a variety of secondary causes. A chlorotic condition (termed "solarization") has been reported due to excessive light.

White spruce will tolerate a considerable range in soil pH. Thrifty trees have been observed growing in soil from pH 4 to 8. The optimum pH is apparently from 5 to 6. Soil fertility is undoubtedly important in regeneration because (1) our principal methods of site and seedbed preparation (i.e., blade scarification and prescribed burning) probably reduce soil fertility, and (2) like light deficiencies, nutrient deficiencies predispose the seedling to mortality from a variety of secondary causes.

Competition from vegetation seems to be one of the most universal problems in securing white spruce regeneration; this constraint has been less emphasized in respect to Engelmann spruce regeneration. Reduction of competition from herbs and brush ranks with the need to expose mineral soil as reasons for site preparation. Scarified seedbeds "brush-in" rapidly on fertile sites and are generally non-receptive within 3 years.

Smothering or crushing of seedlings by fallen leaves can be quite serious, especially in mixedwood forests. The problem is apparently also serious in the Subalpine Region of British Columbia. The problem of fallen leaves may be enhanced where scarification creates furrows that may act as catch-basins.

Various animals cause damage and mortality of young seedlings. Mice and certain birds consume cotyledonous seedlings as well as seed. Large animals, such as elk and cattle, may cause damage by trampling, especially in furrowed areas. Browsing by the snowshoe hare during its population peaks, has often been very damaging to white spruce in brushy areas. Similarly, Engelmann spruce plantations may be devastated by the pocket gopher and, in some instances, birds may be important factors limiting spruce regeneration.

Optimal environmental requirements for germination, survival and initial growth often do not coincide. Germination and survival are favored on mineral soil seedbeds. A moderate amount of shade from a residual stand seems generally favorable. Unfortunately, micro-environments most suited to germination and survival may not be best for later development.

Mineral soil seedbeds have been shown to be a virtual necessity for spruce regeneration in the British Columbia Interior; mechanical scarification is an important means of achieving such seedbeds. The more completely mineral soil is exposed, the better the results in terms of regeneration establishment. This fact, together with the heavy slash accumulations common on spruce cutovers, has generally favored blade scarification over drag scarification. No clear advantage of ripper-toothed blades over straight blades has been demonstrated.

On a high site, blade-scarified seedbeds often lose their receptivity within 3 years due to brushing-in. This places considerable importance on timing scarification to coincide with good seed years if dependence is placed on natural regeneration. Regeneration success has been shown to increase with surface roughness and size of the scarified patch.

Scarification effectiveness and cost vary with site type. Effectiveness is generally least and cost is greatest on moist, brushy site types. Glacial till soils offer the best overall opportunity for this method of site preparation.

Problems associated with blade scarification are soil compaction, surface "baking" and, possibly, fertility loss due to scalping away of topsoil. Pre-scarified stands may be more subject to windthrow as a result of root damage. Furrows and depressions may hold standing water or trap leaves, thus preventing germination or killing germinants.

Due to trees, slash, and the need to deposit scalped soil, blade scarification generally provides about 30% coverage of a cutover. Distribution of mineral soil patches is just as important as the amount of mineral soil exposed. On dry sites with thin organic layers and minimal brush competition, summer logging alone may expose sufficient mineral soil. However, most logging in the British Columbia Interior is conducted in the winter on snow. Successful development of winter scarification would provide the opportunity to treat extensive areas that are virtually inaccessible during the summer.

Research results do not consistently support prescribed burning as a means of preparing spruce cutovers for regeneration. Germination and survival seem reduced on exposed burned areas, while growth may be somewhat enhanced. Germination delays, with consequent increased winter mortality, may also occur on burned sites. The paucity of information on prescribed burning effects on spruce sites, as well as inconsistent research results, argue for further research on this subject.

Planting is presently the surest means of regenerating spruce cutovers. Advantages are the more efficient use of collected seed and the avoidance of the critical period of germination and early development under uncontrolled field conditions. A disadvantage of planted white spruce stock is its usual slow initial growth. This renders the outplanted seedling subject to suppression and possible death due to vegetational competition. These problems may be avoided by proper site selection and preparation and by the use of large, thrifty seedlings.

Time of planting has biological and economic importance. Spring planting has more often produced good results than fall planting, although the latter may be satisfactory on drier sites with moderate to low vegetational competition. Planting throughout the growing season with freshly lifted stock appears promising, but cold-stored stock does not perform well when planted after mid-July in the British Columbia Interior.

Planting production with mudpack stock and container-grown stock is considerably higher than with bare-root stock. It appears, however, that mudpacks are not performing as well as bare-root stock. Production and planting of container-grown stock, is giving very favorable results.

If perfected, direct seeding would provide an economical and highly-flexible means of artifical regeneration. Results of field trials have been variable and often discouraging. Major controllable factors are good quality seed and adequately prepared mineral soil seedbeds. Major hindrances to direct seeding success are seed-destroying rodents and climatic patterns unfavorable to germination and establishment of seedlings.

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