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Ecology and Silviculture of Interior Spruce in British Columbia

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PREFACE

The major goal of this publication is to consolidate the information available concerning the ecology and silviculture of interior spruce in British Columbia. This publication builds on the earlier works of Dobbs (1972) and Stiell (1976) synthesizing information available to approximately early 1992. Compiling a review such as this is an ambitious undertaking that never ends. Much new information has since been published. We hope you will find the review valuable.

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Introduction

White spruce (*Picea glauca* [Moench] Voss) and Engelmann spruce (*P. engelmannii* Parry) hybridize freely wherever their ranges overlap, and in British Columbia the two species and their hybrids are known collectively as "interior spruce." This report summarizes the state of our knowledge on the ecology and silviculture of interior spruce. Its focus is British Columbia, but relevant literature on *P. glauca* and *P. engelmannii* has been drawn from across North America. The report is written primarily for silviculturists; however, researchers, land managers, students, and others with an interest in spruce biology or ecology should also find it useful.

Interior spruce is widely distributed in British Columbia east of the Coast Mountains (Figure 1). Approximately 23% of the public forest land in British Columbia consists of forest cover types dominated by interior spruce (B.C. Ministry of Forests 1984), while an additional large percentage of the land area includes spruce as a secondary or minor component. Interior spruce has historically been the backbone of the interior forest industry. In recent years, harvests of lodgepole pine have exceeded those of spruce (Table 1); however, spruce remains more valuable, and is the primary species planted. Between 1980 and 1985, 272 813 ha were planted to interior spruce, accounting for 54% of all planting in British Columbia (Kuhnke 1989). Across Canada, white or Engelmann spruce made up 37% of all planting (465 632 ha) during the same period.

Interior spruce is not an easy tree to regenerate successfully. It typically grows on wetter or more productive ecosystems where growth of competing vegetation is vigorous and effective site preparation is difficult to achieve. Initially, most interior spruce cutovers were left to regenerate naturally, but failed to do so, leaving a large backlog of not satisfactorily restocked (NSR) lands throughout the interior of British Columbia (B.C. Ministry of Forests 1990b). In the mid- to late 1970s, there was an almost complete shift to artificial regeneration, but it proved difficult to produce high-quality stock that was well adapted to outplanting conditions and did not suffer from an extended period of "planting check."

During the 1980s, the interior spruce planting program expanded dramatically (Figure 2) as successful regeneration became a legal requirement on all areas of current logging, while at the same time a major program to reforest the NSR backlog was initiated through the Canada-British Columbia Forest Resource Development Agreement (FRDA). Although thousands of hectares of NSR land have been reforested, thousands more hectares of productive spruce land remain unstocked (B.C. Ministry of Forests 1990b).

TABLE 1. Volume of spruce[a] logged in the interior of British Columbia on Crown, private, federal and Indian lands, 1980–1988.

	Year							
	1980–81	**1981–82**	**1982–83**	**1983–84**	**1984–85**	**1985–86**	**1986–87**	**1987–88**
Volume (million m^3)	12.594	12.074	15.256	18.542	17.883	17.833	16.716	17.403
Percent of total interior B.C. cut	34.4%	38.1%	39.1%	37.7%	37.4%	35.0%	32.1%	31.6%
Percent of total B.C. cut	23.4%	27.1%	25.0%	23.9%	24.0%	22.6%	20.9%	19.5%
Ranking relative to other tree species groups	1	1	1	1	1	2[b]	2	2

Source: B.C. Ministry of Forests, Annual Reports 1980–81 to 1987–88.

[a] includes a small but unknown volume of black spruce (*Picea mariana*).

[b] volume of lodgepole pine logged exceeds that of spruce.

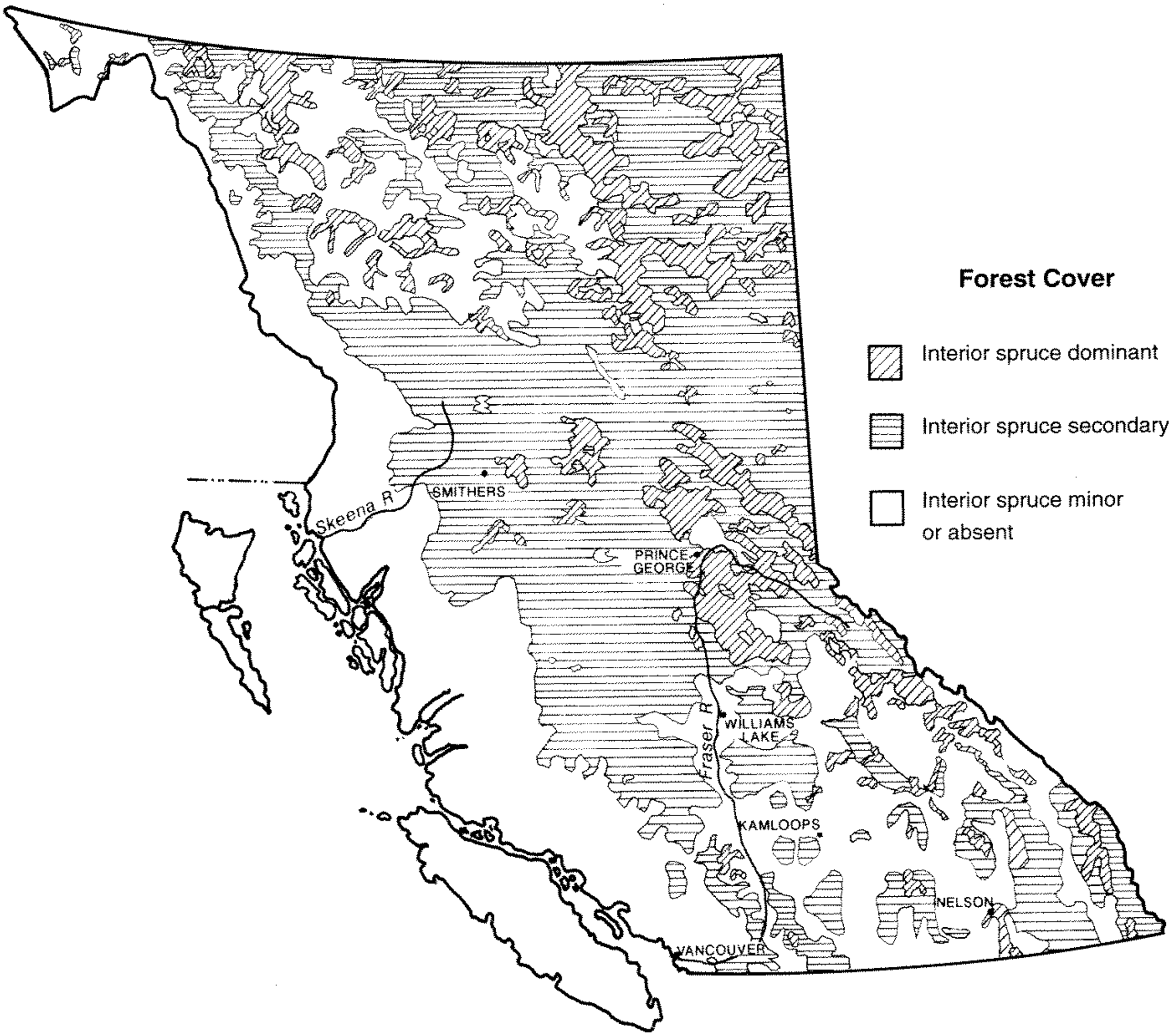

FIGURE 1. Distribution of British Columbia forest cover types with interior spruce as a dominant or secondary species (modified from B.C. Ministry of Forests, Forest and Range Resource Analysis 1984).

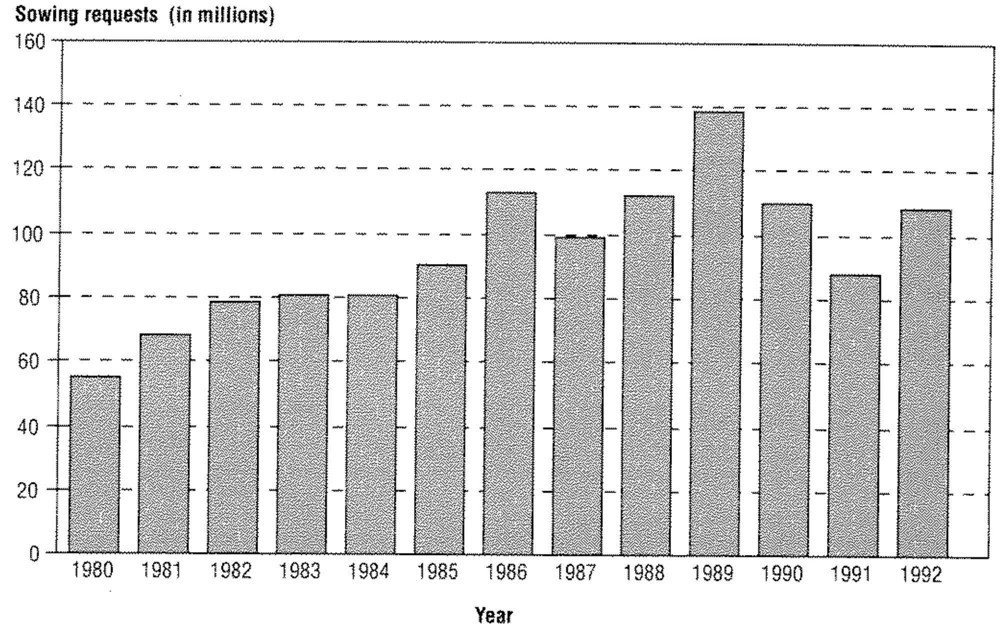

FIGURE 2. Growth of the interior spruce planting program in British Columbia since 1980. Numbers represent sowing requests for all types of spruce nursery stock, not the actual number of seedlings planted. (Source: B.C. Ministry of Forests, Silviculture Branch, 1992).

The tremendous growth of the interior spruce silviculture program since the late 1970s and 1980s was matched by a similar growth in technical and scientific knowledge of the species. Much of this knowledge came from the cumulative experience of silvicultural foresters involved in the day-to-day management of interior spruce forests. Another large part of this knowledge is due to a greatly expanded program of forest ecology and silvicultural research. In particular, the FRDA program of 1985–90 provided a major infusion of research funds to examine reforestation problems related to interior spruce, including such topics as site preparation, nursery practices, tree improvement, seedling ecophysiology, competing vegetation, and pest management. This recent knowledge is built upon a solid foundation of knowledge of the silvics and regeneration biology of spruce developed by early researchers in the Canadian and British Columbia forest services and in other parts of the world (Dobbs 1972; Stiell 1976).

Silviculturists, forest researchers and resource managers need to keep abreast of current information in order to meet the challenge of successfully managing interior spruce forests. Unfortunately, the demands of the job usually leave little time for gathering and reading the large number of reports published each year. This publication summarizes and interprets the knowledge gained in British Columbia, supplementing it, as needed, with information from other parts of Canada and the United States. We hope that it is easy and interesting to read and provides the reader with a way of quickly accessing publications on topics of special interest. An extensive reference list of publications relating to interior spruce is provided. The reference list includes publications not cited in the text and unpublished reports.

2 Biology

2.1 Distribution

2.1.1 White spruce

White spruce (*Picea glauca* [Moench] Voss) is one of the most widely distributed conifers in North America (Figure 3). Its native range is transcontinental and extends from Newfoundland and Labrador in the east to the coast of Alaska in the west. To the north it extends to the tundra treeline and almost reaches the Arctic Ocean at latitude 69°N in the Mackenzie District of the Northwest Territories. Its continuous distribution extends southwards into Montana, Minnesota, Wisconsin, Michigan and the New England states. Outlying populations exist in southern Montana, in the Black Hills of Wyoming and South Dakota, and in the Cypress Hills of Saskatchewan.

In British Columbia, white spruce occurs in most of the northeastern part of the province and is generally found east of the Coast Mountain range. Its most westerly limit is along the Skeena River where it comes within 100 km of the Pacific Ocean and its range overlaps that of Sitka spruce (*Picea sitchensis* [Bong.] Carr.). It extends south to the north Okanagan valley in the interior and down into the United States in the Rocky Mountains (Krajina *et al.* 1982).

The elevational range of white spruce extends from sea level in Alaska and eastern North America to approximately 1520 m in the southern Rocky Mountains (Nienstaedt and Zasada 1990). In British Columbia it is a low- to mid-elevation interior species occurring generally below 1000 m (Owens and Molder 1984).

2.1.2 Engelmann spruce

Engelmann spruce (*Picea engelmannii* Parry) has a more restricted and scattered distribution (Figure 4). Its range extends from north central British Columbia south and east into Alberta and down through the Rocky Mountains into New Mexico and Arizona. In the Cascade Mountains it extends south into California.

In British Columbia, Engelmann spruce occurs east of the Coast Mountains and extends to the Rocky Mountains. It ranges from the Skeena and Finlay river drainages in the north down to the southern border. Its distribution in the central interior is scattered and generally restricted to higher elevations (Krajina *et al.* 1982).

At the northern limit of its range, Engelmann spruce may grow as low as 610 m elevation. In the southern part of its range it is restricted to higher elevations and may be found at 3250 m in the central and southern Rocky Mountains.

2.1.3 Hybrids

Throughout much of British Columbia the ranges of the two species overlap (Figure 5) and extensive hybridization occurs at intermediate elevations (600–1500 m) (Dobbs *et al.* 1976). Identification of the species and their hybrid swarms is often difficult and they are collectively referred to as "interior spruce."

The exact range of the white–Engelmann spruce complex in British Columbia has not been clearly defined or mapped, although an estimated range is given in Daubenmire (1974, his Figure 1). Hybridization extends into Alberta and south into eastern Washington and northern Wyoming (Habeck and Weaver 1969; Daubenmire 1974). The extent of hybridization in northern and northeastern British Columbia is still not clear. Garman (1957), Roche (1969), and Daubenmire (1974) all report pure white spruce in the north and east of British Columbia.

In northwestern British Columbia, along the Nass and Skeena river valleys, the range of white spruce (or more precisely the white–Engelmann spruce complex) overlaps the range of Sitka spruce and hybridization occurs between them (Figure 5). The influence of Sitka spruce extends east along the Bulkley Valley to the Morice River (Douglas 1975, unpublished).

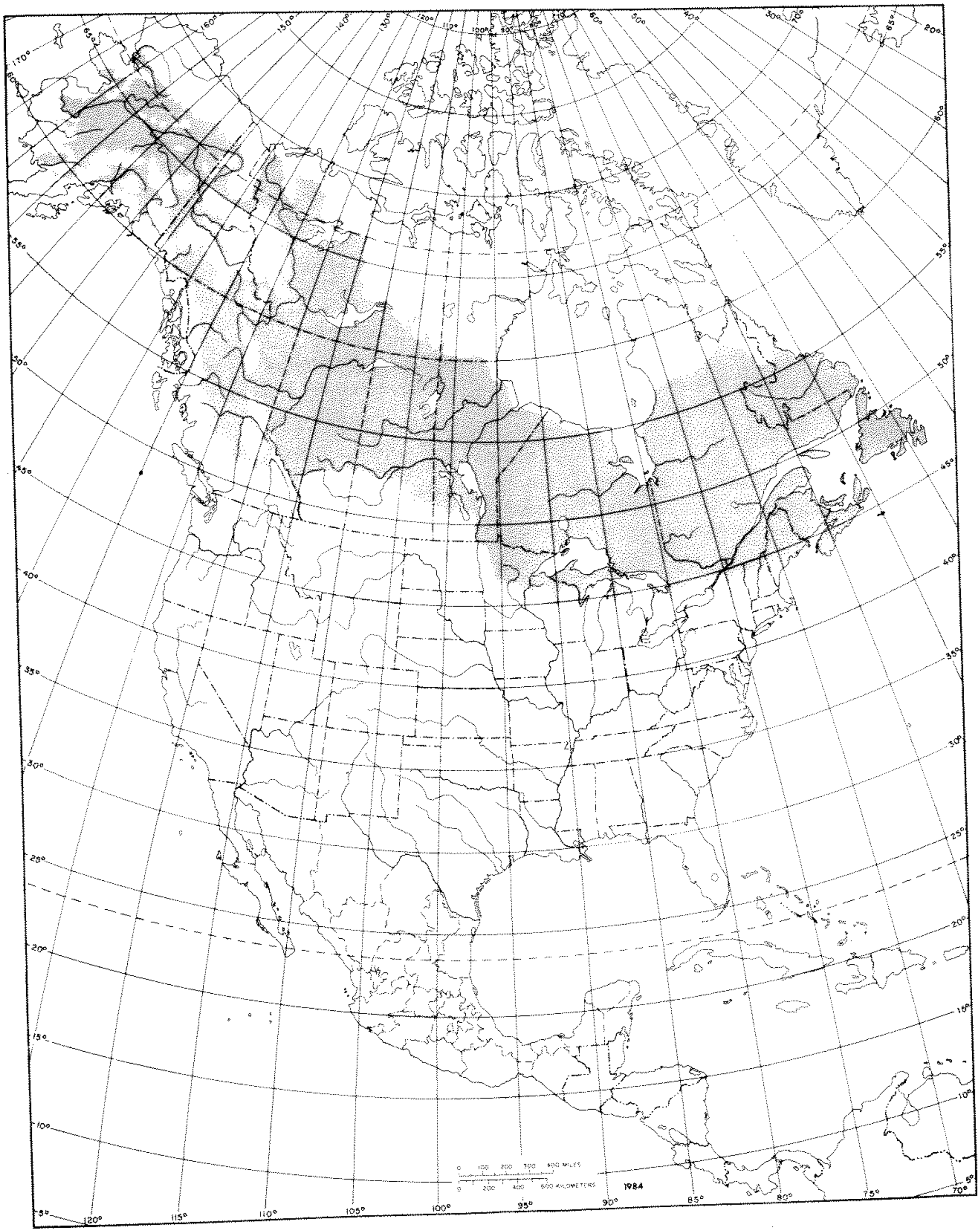

FIGURE 3. Geographic range of white spruce, *Picea glauca* (from Nienstaedt and Zasada 1990).

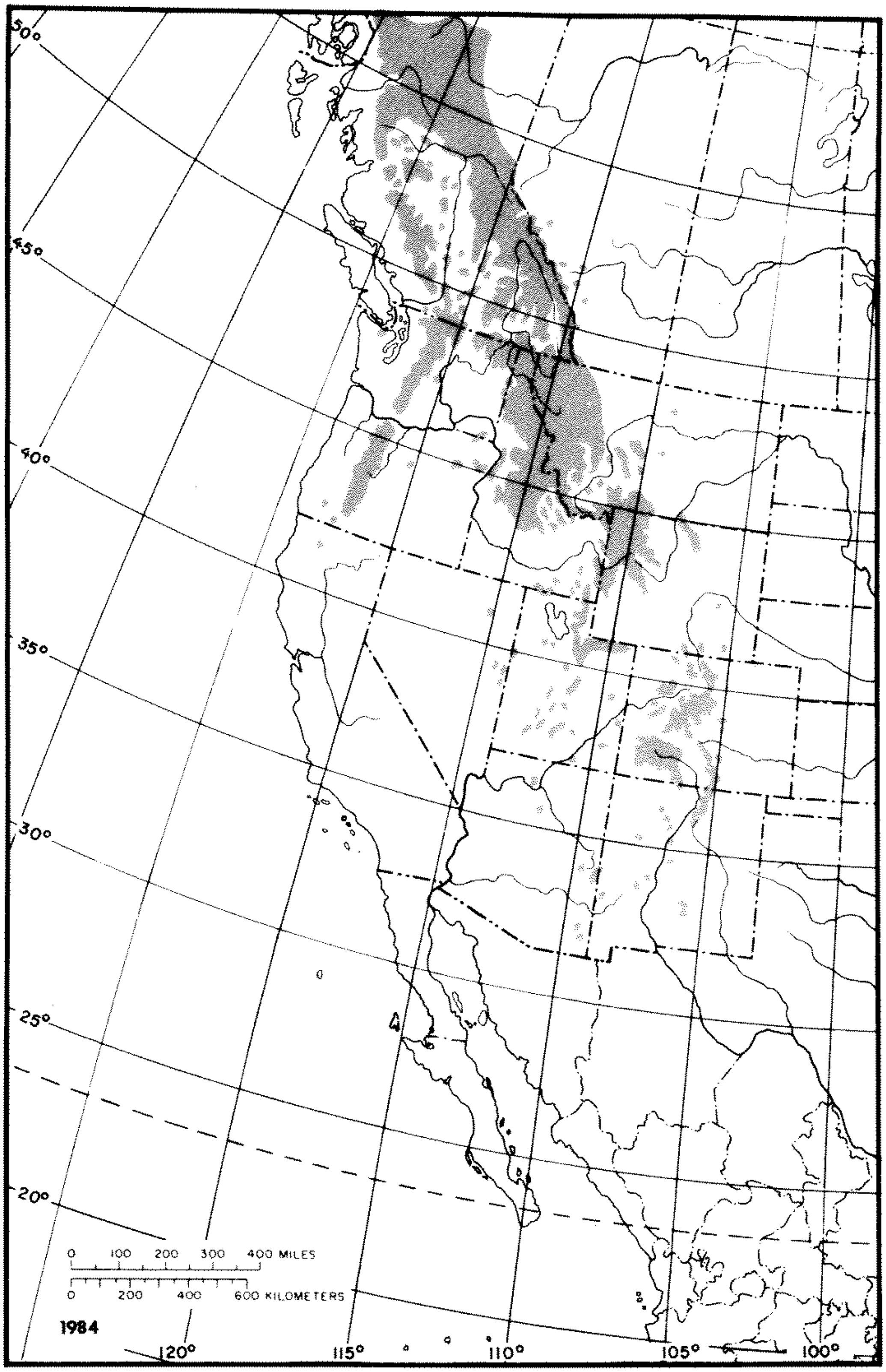

FIGURE 4. Geographic range of Engelmann spruce, *Picea engelmannii* (from Alexander and Shepperd 1990).

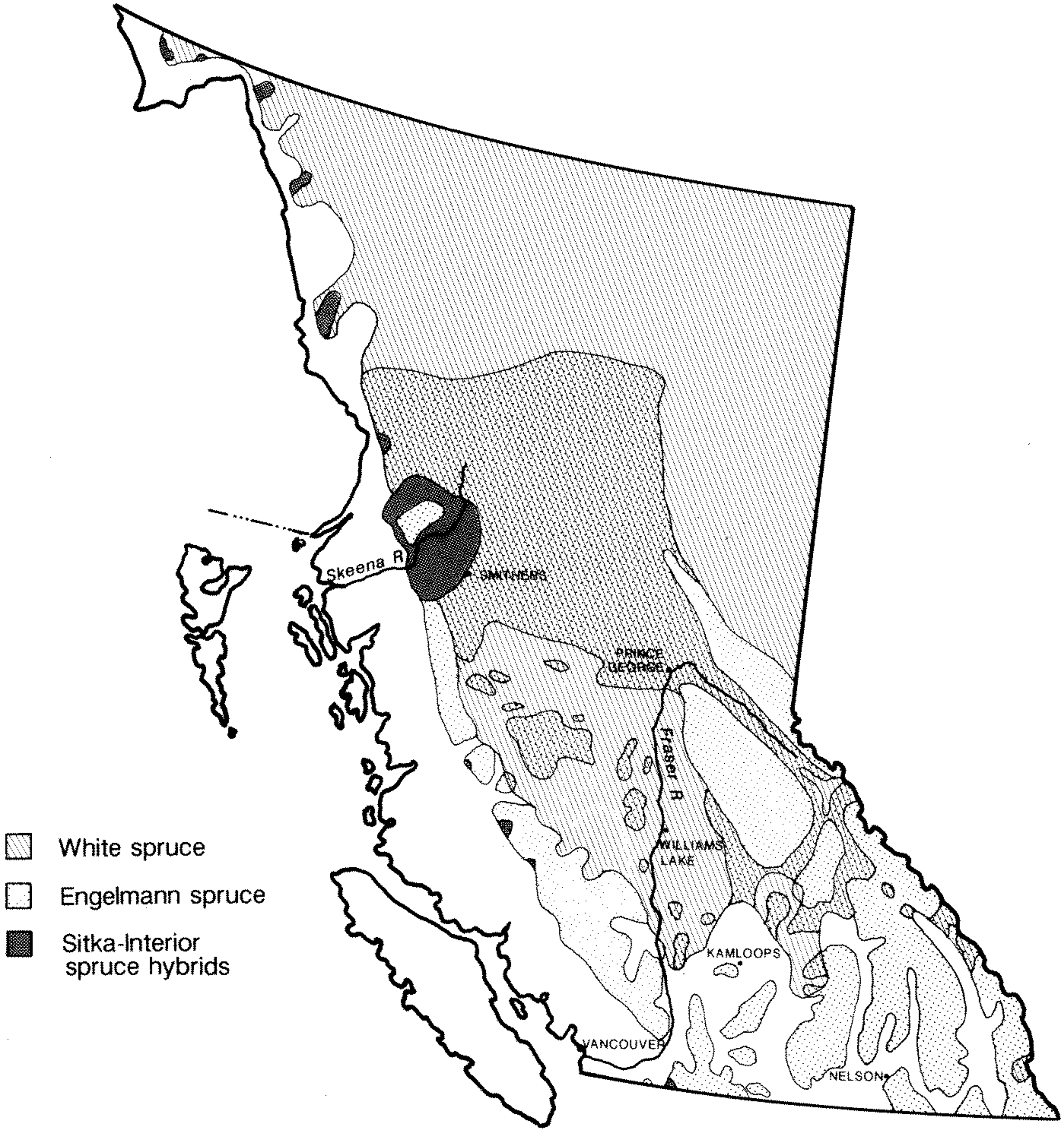

FIGURE 5. Ranges of white and Engelmann spruce and their hybrids in British Columbia. White × Engelmann hybrids occur primarily where the two species' ranges overlap (modified from Krajina *et al.* 1982).

Douglas (1975, unpublished) studied the extent of hybridization in the Hazelton/Smithers/Houston area by examining cone and twig morphology. More westerly hybrids were more strongly influenced by Sitka spruce and more easterly specimens were white × Engelmann hybrids. In between there existed a range of intermediate types. The hybridization zones in this same area were also delineated by Woods (1988) (Figure 6).

2.2 Taxonomy

The nomenclature of the species is summarized in Table 2. There are no recognized races of either white or Engelmann spruce.

2.2.1 Varieties

Four varieties of white spruce have been named: *Picea glauca* var. *glauca*, *P. glauca* var. *albertiana*, *P. glauca* var. *porsildii* and *P. glauca* var. *densata*.

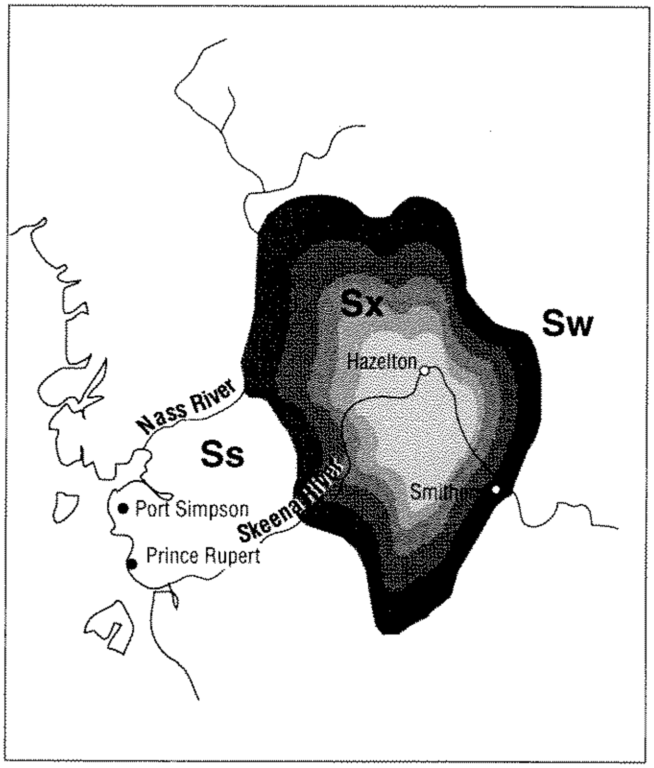

FIGURE 6. Estimated zone of Sitka (Ss)–interior spruce (Sx) hybridization in the Nass, Skeena and Bulkley river areas. Boundaries are approximate and may change as further information is available. Note: banding to darker areas represents increasing probability of hybridization (from Woods 1988).

P. glauca var. *albertiana* (S. Brown) Sarg. was described by Brown in 1907 as having "sterigmata which are strongly reflexed" (Daubenmire 1974). It has sometimes been considered an appropriate name for hybrids between *P. glauca* and *P. engelmannii*, although Daubenmire (1974) questions the validity of such a name application.

P. glauca var. *porsildii* Raup was the name applied to a variety with smooth, resin-blistered bark and a relatively broad crown. Daubenmire (1974) points out that crown shape is very subjective and that the smooth bark with resin blisters also occurs in *P. engelmannii*. These characters are not considered good enough to warrant separate recognition (Daubenmire 1974).

P. glauca var. *densata* Bailey was the name applied to the Black Hills population and the variety was distinguished by a more compact crown and bright to bluish green colour.

While some researchers still use the varietal names, it is generally conceded that it is unnecessary to recognize varieties (Daubenmire 1974; Nienstaedt and Zasada 1990). Taylor and MacBryde (1977) do not recognize any varieties or subspecies of white or Engelmann spruce in British Columbia.

2.2.2 Hybrids

Hybrids have been reported between *P. glauca* and *P. sitchensis*, *P. glauca* and *P. engelmannii*, *P. glauca* and *P. mariana* (black spruce), and between *P. glauca*, *P. mariana* and *P. engelmannii* in British Columbia (Wright 1955; Garman 1957; Taylor 1959; Daubenmire 1968, 1974; Roche 1969). In addition, Douglas (1975, unpublished) includes characters for *P. glauca* × *engelmannii* × *sitchensis* in his key to British Columbia spruces (published in Coupé *et al.* 1982). Hybrids between Sitka and Engelmann spruces may also occur in southwestern British Columbia (Klinka *et al.* 1982).

Hybridization between white and Engelmann spruce and between Sitka and white spruce is introgressive; that is, interbreeding between distinct species produces hybrids, which then hybridize with each other. Controlled "crossability" studies have successfully produced artificial hybrids between these species, indicating that they are very closely related (Ogilvie 1972; Fowler and Roche 1976; Fowler 1987; Kiss 1989).

TABLE 2. Nomenclature of interior spruces

Species	Synonyms	Common Names
Picea engelmannii Parry ex Englm.	*P. columbiana* Lemmon *P. glauca* ssp. *engelmannii* (Parry) T.M.C. Taylor	**Engelmann spruce** Columbia spruce mountain spruce white spruce silver spruce pino real
Picea glauca (Moench) Voss	*P. alba* Link *P. canadensis* B.S.P.	**White spruce** Canadian spruce Black Hills spruce skunk spruce cat spruce
var. *albertiana* (S. Brown)	*P. albertiana* S. Brown *P. alba* var. *albertiana* (S.Brown) Beissner *P. canadensis* var. *albertiana* (S.Brown) Rehd.	western white spruce Alberta white spruce
var. *porsildii* Raup		Porsild spruce
var. *densata* Bailey		Black Hills spruce
Picea sitchensis (Bong.) Carr.		**Sitka spruce** coast spruce tideland spruce Menzies spruce silver spruce
Picea mariana (Mill.) Brit., Sterns and Poggenb.		**Black spruce**
Hybrids		
P. glauca × *engelmannii*		interior spruce
P. × *lutzii* Little	*P. glauca* × *sitchensis*	Roche spruce
P. glauca × *mariana*		Rosendahl spruce

Sources: Daubenmire (1974); Safford (1974); Alexander and Shepperd (1990); Nienstaedt and Zasada (1990).

P. glauca × *P. engelmannii*

Hybrids in the white–Engelmann spruce complex are widespread in British Columbia (see Section 2.1, Distribution). This hybridization, associated with easy introgression especially in the Sub-Boreal Spruce zone, has resulted in this taxon being considered only as *Picea glauca* ssp. *engelmannii* (Parry *ex* Engelm.) (Taylor 1959), which is commonly referred to as "interior spruce."

Trees within the zone of hybridization exhibit a wide range of morphological variation. Based on studies of cone morphology, Roche (1969) concluded that this variation indicated that extensive introgressive hybridization has occurred. White and Engelmann spruce in their "pure" form represent extreme forms of a continuous gradation of variation between low elevations (white spruce habitat) and high elevations (Engelmann spruce habitat) (Roche 1969; Daubenmire 1974).

Ogilvie and von Rudloff (1968) concluded from studies analyzing leaf terpenes that there were no "pure" forms of either species near Bow River, Alberta and Douglas (1975, unpublished) came to the same conclusion about the Smithers, British Columbia area.

Taylor (1959) considered white and Engelmann spruce to be extremes of variation exhibited by a single, wide-ranging, highly variable species and classified them both as subspecies of *P. glauca*. This nomenclature was adopted by Garman (1970). However, most authorities believe them to be distinct species and Daubenmire (1974) suggests that, even though it may be desirable in theory to treat them as a single species, such a move would probably be opposed based on strongly entrenched usage.

P. glauca × *P. sitchensis* (= *P.* × *lutzii*)

Where the ranges of white and Sitka spruce overlap in the Skeena, Nass and Bulkley valleys of north central British Columbia, the hybrid *P.* × *lutzii* Little occurs. It is often referred to as the Roche spruce. The population in the Skeena Valley has been studied in detail and Roche (1969) concluded that it appears to represent a gradual transition from Sitka to white spruce resulting from introgressive hybridization. Woods (1988) contends that even in the centre of the hybridization zone, seed collected from a hybrid stand will contain a species gradient from pure Sitka to pure interior spruce.

P. glauca × *P. mariana*

Evidence of natural hybridization between black and white spruce where their ranges overlap has been reported by Little and Pauley (1958), Larsen (1965, 1989), Roche (1969), Dugle and Bols (1971) and Krajina *et al.* (1982). The hybrid origin of the so-called "Rosendahl" spruce in Minnesota (described by Little and Pauley in 1958) was confirmed in chromatographic studies by Riemenschneider and Mohn (1975). However, other studies have cast doubt on reputed hybridization between these two species (Gordon 1976; Parker and McLachlan 1978). Spruce trees with characteristics that superficially appear intermediate between those of white and black spruce are fairly common in wetland areas of central and northern British Columbia where the two species grow side by side. It is likely that most of these trees are not hybrids. Natural hybridization (if it truly does occur) is thought to be quite rare.

2.3 Identification

Because of the extent of spruce hybridization in British Columbia, exact identification of species and/or their hybrids is complex. There are two main approaches to identification of spruces:

1. approaches based on morphological characters
2. approaches based on chemosystematic studies.

2.3.1 Identification based on morphological characters

The most valuable morphological features for distinguishing between the spruces found in British Columbia are cone scale characters (Garman 1957; Daubenmire 1968, 1974; Roche 1969; Douglas 1975, unpublished).

Douglas (1975, unpublished) sampled intensively in the Smithers/Hazelton/Houston, British Columbia area. He concluded that the most useful cone scale characters are length, width, length/width ratios, the length of free scale (the distance from the imprint of the seed wing to the tip of the scale) and the percentage free scale (length of free scale expressed as a percentage of the total length of the scale). The latter two are especially important. His measurements agreed closely with those of Daubenmire (1974) who took samples from across the whole range of the species.

Based on cone scale characters, Douglas devised a taxonomic key for the identification of *Picea* species and their hybrids in British Columbia, which is published in Coupé *et al.* (1982). A summary of the key and other characters useful in distinguishing the "pure" species is given in Table 3.

In general, the mean free scale length and the percentage free scale of white spruce are smaller than those of Engelmann and Sitka spruce. Sitka spruce can be distinguished from Engelmann by the fact that Sitka scales are narrower and have a greater length/width ratio. Hybrids between these species show a range of intermediate characteristics. The most common types have a narrow scale width and high scale length/width ratio (characteristic of *P. glauca* × *sitchensis*) combined with the relatively short free scale and low free scale percentage (characteristic of *P. glauca* × *engelmannii*).

Scale samples should be taken from the middle of each of 10 cones from a single tree, then averaged. At least 5 trees from a population should be examined (Coupé *et al.* 1982).

For young trees without cones, other characteristics are needed to distinguish among species and their hybrids. Yeh and Arnott (1986) compared findings from chemosystematic studies with morphological characters of nursery-grown seedlings. They found that needle serration and the pattern of terminal budset with different daylengths were the most reliable characters for distinguishing between seedlots of white spruce, Sitka spruce and their hybrids in northwestern British Columbia. Hybrids with no or very few needle serrations were placed in a group with Sitka spruce whereas hybrids with a high degree of serration were allied to white spruce.

TABLE 3. Summary of characters most useful in distinguishing between *Picea glauca*, *P. engelmannii* and *P. sitchensis*

Character	***P. glauca***	***P. engelmannii***	***P. sitchensis***
Young twigs	smooth and shiny usually not hairy	hairy (occasionally smooth)	smooth, shiny
Needles (leaves)	4-angled	4-angled	somewhat flattened
Cones	2.5 – 3.5 cm long, up to 6 cm long	4 – 5 cm long	6 – 9 cm long
Scales:			
morphology	elliptical, rounded to blunt, margin smooth, stiffer than *P. engelmannii*, broader than long	blunt to sharp-pointed, finely irregular, wavy margin (ragged) longer than broad	rounded, finely irregularly toothed, somewhat stiff longer than broad, narrower than *P. engelmannii*.
mean free scale length	short (1.0 – 2.0 mm)	longer than *P. glauca*, slightly longer than *P. sitchensis* (up to 6.3 mm)	longer than *P. glauca*, narrower than *P. engelmannii* (4.0 – 5.0 mm)
free scale percentage	small (8 – 16 %)	greatest (30 – 40 %)	greater than *P. glauca* (24 – 34 %)

Hybrids show intermediate characteristics.

Sources: Douglas (1975, unpublished), van Barneveld *et al.* (1980) and Coupé *et al.* (1982).

Woods (1988) was able to categorize seedlots as Sitka spruce, interior spruce or hybrids by comparing growth performance of container-grown seedlings subjected to an extended daylength (interior spruce regime) with those receiving no supplemental light (Sitka spruce regime). Sitka spruce seedlings grown under the extended photoperiod tend to become excessively tall, while interior spruce seedlings grown without the extended photoperiod set bud early and did not reach the target size. Hybrid seedlots are intermediate, but tend to do better under the Sitka spruce regime.

A morphological key for the identification of spruce seedlings in the United States is given in Jeffers (1974).

2.3.2 Identification based on chemosystematic studies

In recent years, biochemical methods, such as analysis of terpene compounds and isoenzymes, have been used increasingly as tools for distinguishing among species and their hybrids. Analysis of isoenzymes (isozymes) has proved useful in genetic studies for determining the extent to which trees within a stand are related, and is becoming an increasingly important tool for the identification of seedlots.

Morphological characters are controlled by many genes, each of which may have several different effects and which are often strongly influenced by environmental variation. Terpenes and isozymes, on the other hand, are under the control of relatively few genes and are not greatly influenced by environmental conditions. An annotated bibliography of work on the analysis and identification of isozymes, and their use as both a diagnostic tool and in establishing genetic variability, was compiled by El-Kassaby and White (1985).

Ogilvie and von Rudloff (1968) used analysis of leaf terpenes to study variation of spruce along an altitudinal gradient near Bow River, Alberta. They found that the terpenes of *P. glauca* and *P. engelmannii* were distinct and that there was a gradient of intermediate forms between low and high elevations. Monoterpenes of mature trees are more useful than those of seedlings (Schaefer and Hanover 1986).

The existence of introgressive hybridization between *P. glauca* and *P. sitchensis* in the Skeena area was confirmed by isozyme studies (Copes and Beckwith 1977; Yeh and Arnott 1986). Studies by Mitton and Andalora (1981) found no evidence to support the existence of hybrids between *P. engelmannii* and *P. pungens* in the United States Rocky Mountains.

Isozyme studies have been used to establish the identity of seedlots in Alberta and British Columbia (King and Dancik 1983; King *et al.* 1984; Yeh and Arnott 1986). The seedlot classification carried out by Yeh and Arnott (1986) did not completely agree with that of the British Columbia Ministry of Forests and the authors concluded that the criteria used by the agency to classify "hybrid" spruce seedlots were inaccurate. They suggested that spruce seedlots originating from the coast–interior zone of reported introgression be forwarded as standard reforestation practice to an electrophoretic laboratory for taxonomic classification.

Most researchers agree that mass screening and identification using terpenes and isozymes is simple and inexpensive. Initial species identification of stands is accomplished more easily with traditional taxonomic methods (i.e., morphological characters), but subsequent use of biochemical methods serves to clarify relationships where morphological identification leads to ambiguities (Copes and Beckwith 1977; Schaefer and Hanover 1986; Yeh and Arnott 1986).

2.4 Morphology

Spruces are distinguished from other conifers by the fact that their needles are more or less 4-angled and that they arise from small, woody, peg-like projections (called sterigmata or pulvini), which are retained on the twig when the needles fall (Figures 7 and 8).

2.5 Growth and Development

2.5.1 Height growth

Growth patterns Growth patterns and characteristics are highly variable and depend on a wide variety of factors, including climate, age, site location and conditions, inherent variation, previous photoperiod and seed quality (Sutton 1969b; Alexander and Shepperd 1984; Nienstaedt and Zasada 1990).

Young seedlings may exhibit different patterns of growth from mature trees. After germination seedlings produce and expand new needles continuously. This phenomenon is referred to as **indeterminate** or "free growth" (Pollard and Ying 1979a). Free growth will continue until some form of environmental limitation—often declining daylength—causes it to cease. At this point, development of the following year's buds will take place. Free growth is considered to be a juvenile characteristic. The number of seedlings exhibiting indeterminate growth rapidly declines after the second growing season and is unlikely to occur in white spruce seedlings much over 5 years old (Nienstaedt and Zasada 1990).

As seedlings get older, current annual growth becomes **determinate** or fixed. The amount of new foliage produced is pre-determined by the number of needle primordia laid down in the buds when they were formed during the previous growing season (Pollard 1974b; Pollard and Logan 1977). The implication of this fixed growth pattern is that the height growth potential of a spruce seedling is affected by the weather and environmental conditions during the period of bud development and by the conditions at the time of shoot elongation. Temperature and, to a lesser extent, light intensity and soil moisture all affect bud development. Daylength (photoperiod) is less important, although very short photoperiods may reduce primordia development (Pollard and Logan 1977, 1979).

The determinate pattern may be modified in two ways. There may be an initial growth period followed by a lull of 2–4 weeks, after which there may be one or several additional periods of elongation from the tip of the shoot before the next year's buds are developed

a) Tree: stunted to erect with a uniform, narrow, conical (spire-like) crown; branches tend to droop and, in open-grown trees, may extend almost to the ground; on average, mature trees are 25 m tall with a diameter of 0.6 m.

b) Bark: thin, scaly, light grayish brown.

c) Cones: oval to cylindrical, 2.5–3.5 (6) cm long; scales light brown, elliptical, rounded to blunt or indented at tip; short free scale, broader than long with broadest part being above the centre of the scale; scales stiffer than those of *P. engelmannii.*

d) Needles: straight, slender, usually less than 18 mm long, 4-angled, stiff with blunt to sharply pointed tips (prickly to touch); tending to project from all sides of the branch, but with lower ones curving upwards especially near the tips of the branchlets; aromatic when crushed; two resin ducts are obvious when cut in cross-section.

FIGURE 7. Morphological characteristics of white spruce (*Picea glauca*): (a) tree, (b) bark, (c) cones, (d) needles.

a) Tree: straight, spire-like with a broad, domed or pyramidal crown with parallel sides; branches tend to be nearly horizontal, although lower ones are often drooping; trunk tends to taper less than *P. glauca*; up to 50 m tall and with average diameter of 0.4–0.8 m.

b) Bark: very thin, broken into large purplish brown to russet red loosely attached scales.

c) Cones: 4–5 cm long, ovate to cylindrical, lacking stalks or with very short stalks; scales thin, somewhat papery, loose fitting, wedge shaped or blunt to sharp pointed, with finely irregular wavy margin; longer free scale, longer than broad with widest part below centre.

d) Needles: flexible, 4-angled, usually blue-green, occasionally with white bloom; up to 20 mm long; tips blunt or acute (softer than *P. glauca*); tend to be crowded on the upper side of the branchlets because those on the lower sides are curved upwards; with an unpleasant (cat- or skunk-like) odour when crushed; no resin ducts obvious in cross-section.

FIGURE 8. Morphological characteristics of Engelmann spruce (*Picea engelmannii*): (a) tree, (b) bark, (c) cones, (d) needles.

(Armson 1964, cited by Sutton 1969b). Alternatively, new buds laid down for the following year may expand prematurely. This is the phenomenon known as **lammas growth**. If normal seasonal growth is curtailed by lack of rain, a heavy rain later in the season is often followed by profuse lammas growth in young white spruce (Sutton 1969b). The incidence of lammas growth decreases with age as the expanding root system is able to obtain moisture from a larger volume of soil (Sutton 1969b).

Phenology The timing of shoot elongation and flushing of both white and Engelmann spruce in British Columbia varies with latitude and elevation. Trees in northern latitudes or on high-elevation sites may begin development later in the spring and stop sooner in the fall than trees in southern latitudes or at low elevations. However, development during the middle of the growth cycle occurs at more or less the same time in both species in most regions (Owens and Molder 1984). Table 4 shows the phenology of growth and the time of flushing of white and Engelmann spruce in British Columbia, with data from other areas provided for comparison.

Terminal and lateral shoot elongation occurs over a short time period and growth is usually complete by the end of July or early August (Owens *et al.* 1977; Harrison and Owens 1983). Cessation of height growth is related to declining daylength (Owens *et al.* 1977) and may occur in response to the timing of the first fall frosts (Pollard and Ying 1979a). Premature budset by northern latitude or high-elevation populations of interior spruce grown in coastal nurseries can be overcome by artificially extending the daylength (Arnott 1979).

Growth rates The rule that "those that start out big, get bigger faster" seems to apply well to interior spruce seedlings. Khalil (1981) showed that heavier seeds resulted in greater height growth at 4 years of age. Hellum (1967) demonstrated that the amount of leader growth is directly related to the size of the terminal bud. As seedlings grow taller they produce larger buds, which in turn produce longer leaders in the following year. Growth of taller seedlings also occurs over a longer period of time. There is ample evidence that planted seedlings grow more rapidly in the early years than smaller, naturally regenerated seedlings (see Section 5.1, Natural Regeneration) and that large nursery stock outgrows small nursery stock (see Section 5.3, Artificial Regeneration). However, the influence of seedling size on shoot growth potential decreases with increasing age (Pollard 1974a).

In the natural environment, early shoot growth of interior spruce is very slow. At the end of the first growing season, height growth of naturally regenerated seedlings is typically only 1–2.5 cm (Alexander and Shepperd 1984; Nienstaedt and Zasada 1990). Seedlings at this stage are unbranched. Growth continues to be slow for the first 5–6 years, but the number of branches increases during this period. Growth of planted seedlings, while somewhat faster, is also relatively slow for the first 5 years. In British Columbia, seedlings that are 15–20 cm tall one growing season after planting average about 50 cm in height after 5 years (Vyse 1981; Eis and Craigdallie 1983; Pollack *et al.* 1985).

Table 5 is a summary of reports of the time taken for planted interior spruce to reach breast height (1.3 m) in British Columbia. Pogue (1946) reported that advanced regeneration of white spruce in an area east of Prince George was only 0.3 m tall by 6 years and 2.7 m tall by 20 years of age. Nienstaedt and Zasada (1990) report that naturally regenerated white spruce trees may take between 10 and 20 years to reach breast height in the open and up to 40 years in a forest understory. Additional information on early growth rates of naturally regenerated and planted seedlings is presented in Section 5.1, Natural Regeneration and Section 5.4.1, Growth and yield information.

TABLE 4. Phenology and periodicity of growth

Species	Location and elevation	End of dormancy	Start of shoot elongation	Flushing	End of shoot elongation	Dormancy of vegetative buds	Source
white	Prince George 500 m	2nd wk. of April	beginning of May	late May – early June	early August	mid – end October	Owens *et al.* (1977)
white	Prince George 1000 m	end of May	mid–May		early August	mid – end October	Owens *et al.* (1977)
Engelmann	Prince George 1400 - 1670 m	mid-April	late May	late June	late July	mid-October	Harrison and Owens (1983)
For comparison:							
white	provenances from eastern Canada and U.S.			end of April to end of May			Blum (1988)
white	Alaska				June 28		Nienstaedt and Zasada (1990)

TABLE 5. Time to breast height (1.3 metres)

Location	Type of spruce	Natural or planted	Time (years)	Source
Pr. Rupert Region SBSmc subzone	interior	planted	10	Pollack *et al.* (1985)
ICHmc subzone	hybrid (Sitka x white)	planted	9	Pollack *et al.* (1985)
Cariboo Region	white	planted	approx. 8 – 9	Vyse (1981)
Prince George – Quesnel area	white	planted	9 – 10	Kiss and Yeh (1988)
East of Prince George	white	advanced regeneration	15 – 16	Pogue (1946)

Relatively little information is available on the growth rates of older trees. Height-over-age curves (Hegyi *et al.* 1981; Eis *et al.* 1982; Rauscher 1984) suggest that the most rapid height growth occurs when trees are in the neighbourhood of 40–100 years, but height growth continues to be strong for 200 or more years, especially on the more productive sites (see Figures 50–52; Section 5.4.1, Growth and yield information). This is in contrast to species such as lodgepole pine, which have more rapid early growth, but tend to increase relatively little in height after 100–120 years. At age 100, average heights of dominant spruce trees range from approximately 8 m on very low productivity ecosystems to approximately 43 m on highly productive ecosystems (Stanek 1966).

2.5.2 Radial growth

Phenology The timing and extent of radial growth varies with geographic location, with site conditions, and from year to year on the same site. In Alaska, the period of cambial activity was found to be only half as long as that in Massachusetts, but cell division was twice as rapid (Gregory and Wilson 1968, cited by Nienstaedt and Zasada 1990). Wood production was observed to begin in late April (Massachusetts) and early May (Alaska) with 80% of the tracheids produced in 95 and 45 days, respectively. An Ontario study by Fraser (1962a, cited by Sutton 1969b) showed considerable variation in the duration of diameter growth for the same tree in different years, and during the same year for trees on different sites. For example, in 1956 a tree growing on a fresh site began diameter growth on June 2 and ceased on August 1 (60 days); in 1958 the period of radial growth extended from May 14 to August 21 (101 days). A second tree, on a wet site, had only 49 days of cambial activity in 1956, and 95 in 1959. Day (1985) reports that in Ontario bareroot nurseries, diameter growth of first-year white spruce seedlings begins to slow in August and ceases by mid- to late September.

No published accounts of the phenology of radial growth exist for British Columbia, but recent unpublished data from moist forests east of Prince George indicate that diameter growth of healthy young seedlings continues at least into September (C. Delong, pers. comm., Sept. 1990). Unhealthy seedlings with heavy overtopping vegetation had no measurable diameter increment after July.

Radial growth is affected mainly by growing conditions during the current year and radial growth appears to be more sensitive than height growth to environmental changes. Cultural techniques such as brushing and weeding, spacing, thinning, watering and fertilization affect radial growth to a greater degree than they affect height growth. The amount of radial growth is increased, and growth may commence 2 weeks earlier in thinned and fertilized stands (Van Cleve and Zasada 1976). Fertilization may also extend the growing period (Sutton 1969b).

Growth rates Diameter increments culminated at about 60 years but radial growth continued at a slower rate until the trees were well over 200 years old in interior British Columbia (Eis *et al.* 1982). Diameter at breast height (dbh) varies with site conditions and stand density. Smith (1950) indicated that in older Engelmann spruce diameter increment may be as high as 10 cm per 10 years on rich sites, but is only 0.8 cm per 10 years on poor sites. A maximum dbh of over 80 cm was not uncommon on an open, alluvial site in British Columbia (Eis and Craigdallie 1983).

2.5.3 Maximum size and age

Like many conifers, white and Engelmann spruce grow to their maximum size on the best growing sites, but reach their greatest age on harsh sites where they are stressed and slow growing. The oldest trees are typically found at the treeline (both elevational and latitudinal).

On good sites, white spruce reach a maximum height of over 30 m and diameters of 60–90 cm (Hosie 1973; Nienstaedt and Zasada 1990). The largest known white spruce in British Columbia is located at Conroy Creek, a tributary of the Sikanni Chief River (between Fort Nelson and Fort St. John). It is 51.8 m tall and has a circumference of 2.23 m (B.C. Forestry Assn., Great Trees of B.C. Register).

The maximum size reached by Engelmann spruce trees is somewhat larger than that of white spruce. Large mature dominants may exceed 100 cm in diameter and 40 m in height (Fowells 1965). There is no record Engelmann spruce tree registered in British Columbia, but the largest known Engelmann spruce in North America is located just south of Chilliwack Lake in Washington state. In 1970 it was 73 m tall with a diameter of 2.4 m (Sharpe 1970, cited by Klinka *et al.* 1982).

On good sites, white spruce averages 100–250 years old and older trees (250–300 years old) may be found on sites protected from fires (e.g., islands) and in upland wet sites (Nienstaedt and Zasada 1990). Trees of nearly 1000 years old have been reported above the Arctic circle (Nienstaedt and Zasada 1990).

Engelmann spruce matures in about 300 years. In the United States, dominant trees are often 250–450 years old and 500–600-year-old trees are not uncommon (Alexander 1987). Luckman *et al.* (1984) report finding Engelmann spruce trees, which had escaped fire, with ring series of at least 680 years at 97 cm aboveground. The estimated age at the tree base was 720 years.

2.5.4 Growth form

In natural stands, under good growing conditions, white spruce has a straight, slightly tapering trunk, a conical crown, and branches that spread or droop slightly. In open stands the branches may extend to the ground, but lower branches are shed in dense stands (Hosie 1973).

Engelmann spruce on good sites is generally narrow and spire-like with a symmetrical, pyramid-shaped crown. In open stands branches may extend to the ground. Lower branches are often drooping. In dense stands branches may be shed up to halfway up the trunk, which develops without much taper (Hosie 1973; Alexander and Shepperd 1984; Alexander 1987).

At altitudinal and latitudinal treelines, the crown form may be considerably modified by harsh environmental conditions. As elevation or latitude increases, the trees become more and more stunted and deformed with typical prostrate (krummholz) forms occurring at tree limit (Marr 1977) (Figures 18 and 19, pages 36, 37). This growth form is a response to the short growing season, extremes of air and soil temperature, desiccation, and wind and snow damage.

Scott *et al.* (1987a) described the different crown forms of white spruce growing at or near treeline. The most stunted, shrub-like form occurs in open tundra where a basal rosette of branches remains permanently below the level of winter snow. In the forest-tundra transition, where conditions are less harsh, the plants are able to outgrow the damage. Most show varying degrees of damage (usually on the windward side) due to wind abrasion and desiccation. Trees occurring in the least harsh, forested conditions have a typical conical crown but may have some damage. This is more likely to result from fire, lightning or "other events that are not a direct result of wind desiccation or snow abrasion" (Scott *et al.* 1987a).

2.5.5 Root growth and development

Growth rates and size Root growth is extremely variable depending upon how favourable conditions are for growth. The factors affecting early root growth are reviewed by Sutton (1978b). Nienstaedt and Zasada (1990) report that under natural, outdoor conditions, white spruce may penetrate 2–10 cm by the end of the first growing season, depending on the site and seedbed type. Taproots develop laterals that may be 3–5 cm long. It takes 4–6 years for lateral roots to reach 1 m in length.

Sutton (1978b) reported that the main axis length of roots in 60-week-old white spruce, grown under the same conditions in homogenized soil in a greenhouse in Ontario, may vary from 2.9 cm to 17.2 cm. The total length of the roots on these seedlings varied between 2.9 cm and 28.6 cm. By 4–5 years of age the total root length varied from 405 cm to 2906 cm depending on the soil type. Burdett *et al.* (1984) found that, by the end of the second growing season, laterals of planted spruce in the central interior of British Columbia averaged over 1 m in length and vertical roots were followed to a depth of 50 cm. Maximum root penetration of 4–5-year-old outplants measured by Sutton (1978b) varied from 47 to 66 cm.

Von der Gönna (1989) reported that root growth of outplants varied with the site preparation treatment used in interior British Columbia. White spruce seedlings 95 weeks old, grown on mounded or ploughed treatments, produced significantly higher numbers of roots over 1 cm length than control or patch treatments. Differences appear to be related to the root zone temperatures. Good root growth appears to require soil temperatures of over 10°C through most of the growing season (Binder *et al.* 1989).

In mature trees, most roots are in the topmost layers of the soil. In the United States Rocky Mountains, Engelmann spruce roots are generally restricted to the top 30 to 45 cm (Alexander 1987), but may extend 2.5 m or more in deep porous soil (Alexander and Shepperd 1984). Taproots and sinkers of white spruce typically penetrate from 50 to 150 cm but may descend to a depth of 3 m depending on soil conditions (Eis 1978; Schultz 1978; Nienstaedt and Zasada 1990). Lateral spread in white spruce is reported to be as much as 18.5 m on sandy soils in Ontario (Nienstaedt and Zasada 1990), with individual lateral roots of white spruce extending 6 m or more (Markstrom and Alexander 1984). The rate of lateral root growth in white spruce has been reported to be 0.3 m per year (Stiell 1976; Sutton 1969a, cited by Nienstaedt and Zasada 1990).

In Alberta, more than 95% of the biomass of the white spruce root system was found to be in the lateral system (Strong and LaRoi 1983) and in Ontario, up to 85% of the total root system was found in the upper 0.3 m of soil (Stiell 1976). The fine root biomass in a 39-year-old white spruce plantation was estimated to be approximately 3 kg/tree (Safford and Bell 1972). At a site north of Prince George, British Columbia, most of the fine root biomass beneath a mature spruce and subalpine fir stand was located in the top 8.3 cm of soil (Kimmins and Hawkes 1978).

Reduction in light intensity (due to crown competition) or the amount of tree foliage (due to insects or pruning) has a greater effect on root growth than on shoot growth (Rauscher 1984). Root systems are not as severely affected by moisture stress as are shoot systems.

Phenology Root growth in white spruce begins in the spring at the same time as shoot growth (Rauscher 1984) and, with adequate moisture, continues into the fall when temperatures become too cold for growth to continue. Growth of the roots is least in June, the period of maximum shoot growth, suggesting that, within the tree, shoots and roots compete for nutrients necessary for growth (Rauscher 1984). The phenology of root growth is further described by Day and Stupendick (1974) and Day *et al.* (1976).

Rooting habit The origin and development of white spruce root forms in Alberta and the Northwest Territories has been studied by Wagg (1964b, 1967), and by Eis (1978) in British Columbia, but no similar work is available for Engelmann spruce. Both species are generally considered to have shallow root systems. However, the extent of root penetration depends a great deal on soil properties (Wagg 1967; Sutton 1969a; Eis 1978; Strong and LaRoi 1983) and site modifications during the life of the tree (Wagg 1967). Wagg (1967) described four basic root forms (Figure 9):

1. an elongated taproot on well-drained soils of nearly uniform texture;
2. a restricted taproot on soils with compact horizons or textural changes between horizons;
3. a monolayered root with or without a vestigial taproot on soils with excess moisture near the surface; and
4. a multilayered root on sites with accumulating moss layers or periodic alluvial or lacustrine deposits.

Rooting depth and extension are also under genetic control and are influenced by competition from other plants.

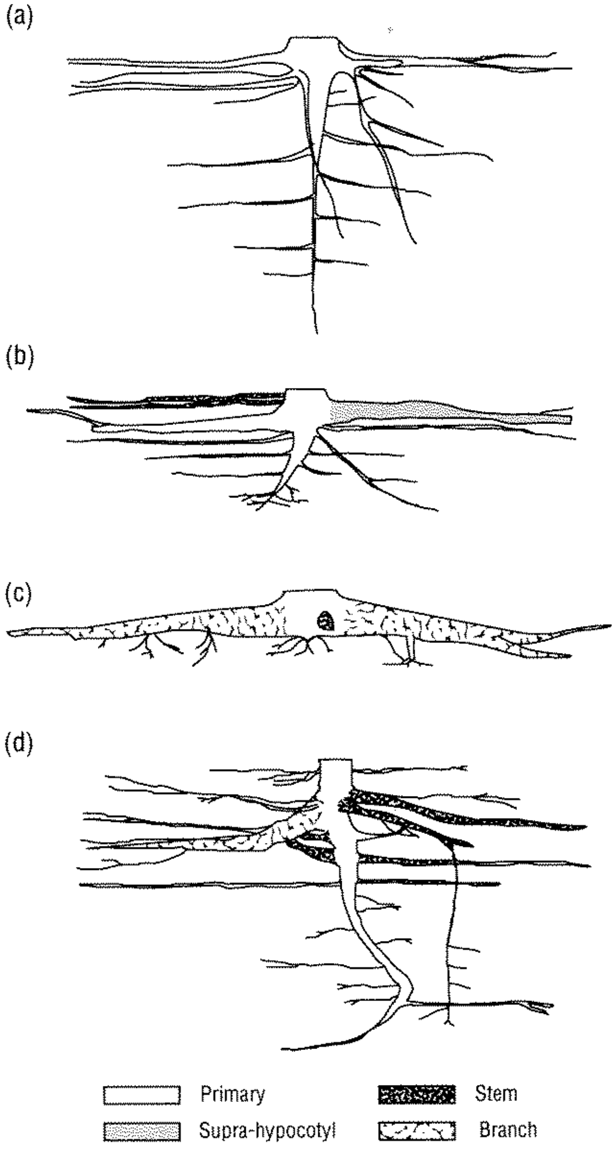

FIGURE 9. Typical root forms of white spruce: (a) elongated taproot; (b) restricted taproot; (c) monolayered root; and (d) multilayered root (from Wagg 1967).

Young trees have a central taproot and several horizontal laterals. The taproot may continue to grow and become well developed in uniform textured, well-drained soils (Eis 1978; Schultz 1978). However, growth of the tap-root is often restricted and does not persist beyond the juvenile stage, especially where obstructions (rocks or compact horizons) are encountered (Eis 1978; Alexander and Shepperd 1984).

At an early age, lateral and oblique roots take over the function of anchoring (Eis 1978; Strong and LaRoi 1983). White spruces from two different soil types in Canada had 4–6 horizontally spreading primary laterals (Strong and LaRoi 1983), which make up the main part of the root system and are located primarily in soil organic layers. At the ends of these laterals a system of fine roots spreads horizontally to form a broad band of moisture and nutrient absorption, usually extending beyond the tree crown (Strong and LaRoi 1983).

Vertically descending root branches develop from the underside of the laterals—called "heart roots" by Wagg (1967) or sinker roots by Eis (1978). These enlarge and elongate with increasing age of the tree. Finer roots also develop from the main laterals and probably function in both anchoring and absorption.

Root systems of dominant trees are better developed, more branched, more symmetrical and are larger in proportion to the aboveground parts of the trees than those of suppressed trees (Eis 1978). Root systems of suppressed trees typically develop in only one or two directions, and are thought to grow into spaces unoccupied by dominant tree root systems (Eis 1978).

Asymmetrical root systems also occur in dominant trees growing on stony soils or on slopes. On slopes, the downhill side of the root system tends to be more dominant. The symmetry of the crown has no bearing on root symmetry (Eis 1978).

Root systems of interior spruce are almost always mycorrhizal. For information on mycorrhizae, refer to Section 3.2, Environmental Factors.

2.6 Sexual Reproduction

The reproductive cycles of white and Engelmann spruce have been reviewed in detail by several authors (Dobbs 1972; Fowler and Roche 1976; Alexander and Shepperd 1984; Owens and Molder 1984; Owens 1986; Nienstaedt and Zasada 1990). The following summary is based primarily on the review of Owens and Molder (1984) who compared the reproductive cycle of white spruce at low elevations with that of Engelmann spruce at high elevations within the same general geographic area of British Columbia.

The reproductive cycles of white and Engelmann spruce are essentially the same. Both species have a 2-year reproductive cycle in which male (pollen) and female (seed) cones are differentiated in one year and continue their development to maturity in the following year (Figure 10).

The main differences between the two species are in the phenology, or timing, of reproductive events. At intermediate elevations, where the two species occur together, the phenology is similar, but events in white spruce at low elevations occur at quite different times from those of Engelmann spruce at high elevations. Events may vary as much as a month between individuals at the extremes of their elevational distribution and even more at extremes of their geographical distribution.

2.6.1 Reproductive bud development

Seed- and pollen-cone determination (differentiation) begins at the time shoot elongation ceases—about mid-July in white spruce at low elevations and mid- to late July in Engelmann at high elevations. In British Columbia this lasts over a period of about 2 weeks through a wide range of sites for white spruce.

Whether or not a bud differentiates into a vegetative or reproductive bud—and into which type of reproductive bud—depends upon its relative position on the shoot, or within the tree, and on whether conditions favour sexual reproduction.

Buds may be produced at the tips of the shoots (terminal) or in the axils of the leaves along the stem (axillary). When conditions do not favour sexual reproduction, the terminal buds remain vegetative. If conditions are favourable, however, many terminal buds on vigorous shoots in the upper parts of the crown will develop into seed-cone buds. Terminal buds on less vigorous shoots in the crown or those on shoots closer to the trunk in lower regions of the crown, may develop into pollen-cone buds.

Axillary buds may also develop into seed- or pollen-cone buds when conditions favour reproduction. Otherwise they may develop into vegetative buds, especially if the terminal buds are damaged, or they abort or become latent (Figure 11).

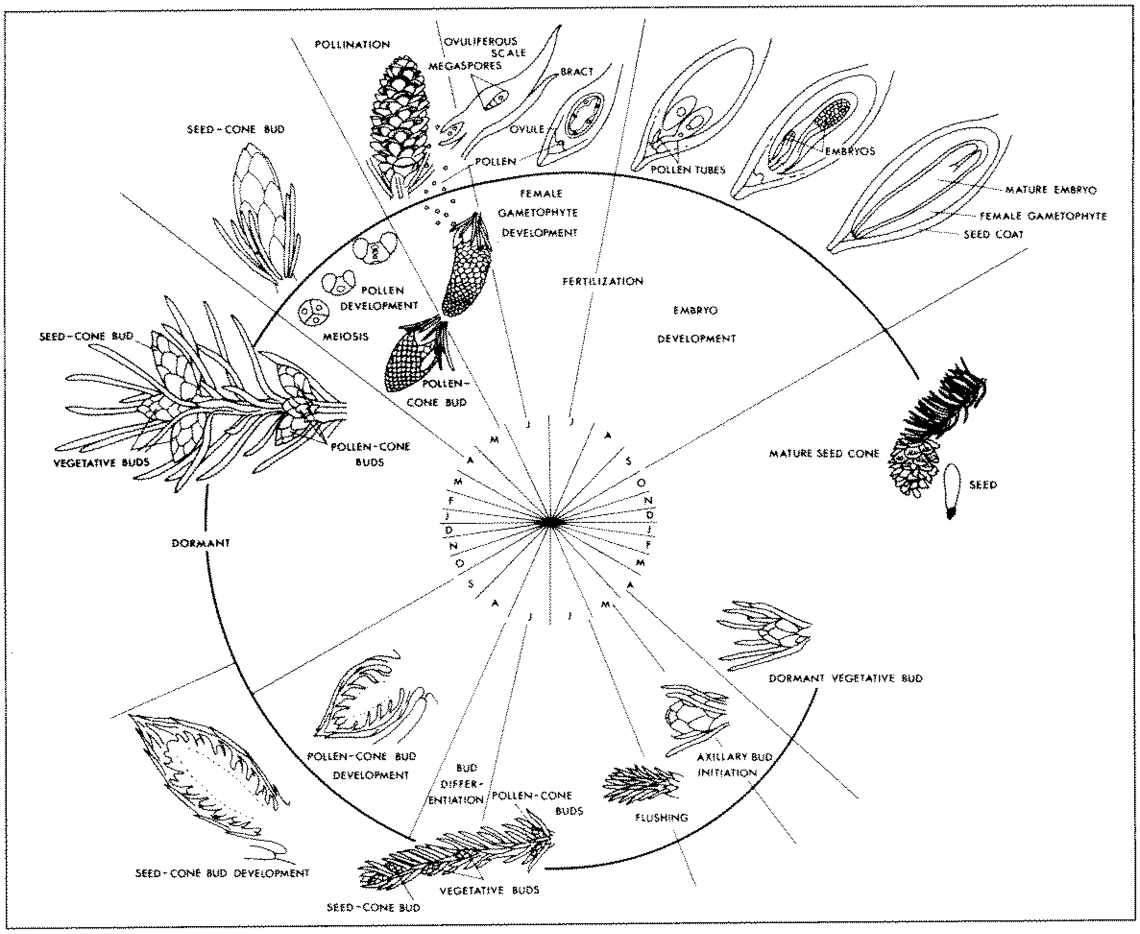

FIGURE 10. The reproductive cycle of interior spruce (from Owens and Molder 1984).

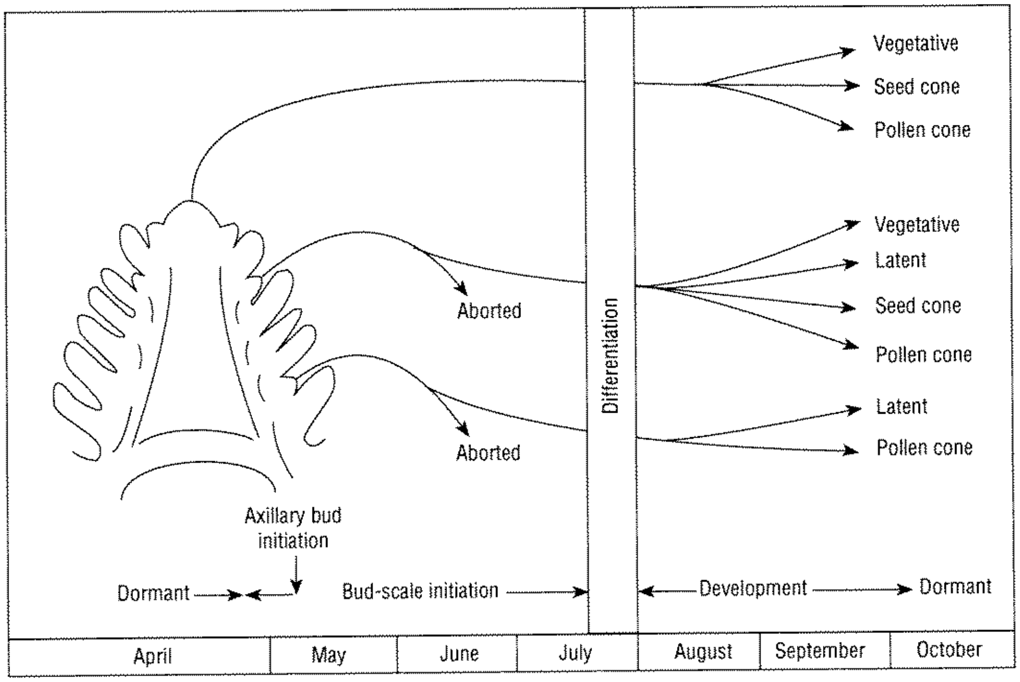

FIGURE 11. Potential pathways of terminal and axillary bud development (from Owens and Molder 1984).

Conditions favouring reproductive bud development are high temperatures, abundant sunshine, low rainfall and soil moisture, and high soil fertility at, or preceding, the time of bud determination (Marquard and Hanover 1984c; Owens and Blake 1985).

Seed-cones are generally concentrated in the upper parts of the crown, whereas pollen-cones are found in the lower regions.

Reproductive buds continue to mature for 2–5 months with male buds becoming dormant first (around October 1st for white spruce in Prince George) and female cones entering dormancy about 2 weeks later (Owens and Molder 1979).

2.6.2 Pollen-cone development

Pollen-cone development (Figure 12) resumes in the second year when dormancy is broken. This is generally around mid-April, but may be earlier in white spruce at low elevations. The cones enlarge very slowly and their tips gradually emerge from the bud scales. After about 1 month, meiosis occurs and is accompanied by a clearly visible swelling of the cones.

The rate of pollen-cone development varies with temperature, elevation and geographic location. At low elevations in British Columbia, white spruce pollen grains take approximately 3–4 weeks following meiosis to mature, with maximum shedding occurring at the end of May—2 months after dormancy ends.

At higher elevations, dormancy of Engelmann spruce may end at the same time, but because of extended snow cover and cool temperatures, maximum shedding may not occur until early July—3 months after dormancy.

In general, pollen shedding occurs earlier in southern latitudes than in northern latitudes, with the latest shedding at elevational and latitudinal tree limits. Maximum dispersal of white spruce pollen may occur as late as mid-July north of latitude 53°N (Zasada and Gregory 1969). Dispersal follows a diurnal pattern that is regulated by temperature, humidity, and wind (Zasada *et al.* 1978).

At the time of shedding, pollen cones may be horizontal or drooping on the branch. They change from red to yellow and become dry. After pollen shedding, the dried, empty cones may be retained on the branch for several weeks before dropping off.

2.6.3 Seed-cone development

Seed-cone development (Figure 13) resumes in the second year about mid-April in natural stands in British Columbia. This is about 6–8 weeks before pollination in white spruce and 10 weeks before pollination in Engelmann spruce. Cell division occurs before any visible signs of growth. Cones start to elongate and emerge from mid-May (white spruce) to late June (Engelmann spruce). After 1–2 weeks they are fully emerged, vary in colour from green to deep red, are erect on the branches, and the scales are open to receive pollen.

FIGURE 12. Pollen-cone development: before opening, male buds are broadest in the midsection (top); red-tipped pollen cones emerging from bud (middle); mature cones shedding pollen (bottom).

FIGURE 13. Seed-cone development: dormant female buds are broadest near the base (top); receptive seed cones have bright red or purple bracts and stand erect with scales open to allow pollen to enter (centre); after pollination, the enlarging cone turns downward and the scales expand, covering up the bracts (bottom).

2.6.4 Pollination

The period of maximum receptivity of seed cones coincides with maximum pollen shedding. The most receptive period for seed cones is thought to last approximately 4–6 days per cone, but is longer in any one tree because the rate of development varies throughout the tree. Maximum pollen shedding occurs over a 1-week period.

Spruces produce copious amounts of pollen and are wind pollinated. The amount of pollen available for cross-pollination varies with the wind and stand conditions at the time of pollination as well as the climatic conditions during pollen formation (Zasada and Gregory 1969).

Studies using controlled pollination techniques have confirmed that there is no barrier to self-pollination (King *et al.* 1970, 1984; Nienstaedt and Teich 1972). However, selfing causes an increase in the frequency of empty seeds due to embryo failure, which in one study averaged over 90% in white spruce (Fowler and Park 1983). Selfing also results in slightly lower germination, reduced survival, seedlings that are genetically inferior to those of unrelated matings and seedlings that exhibit a slower growth rate in subsequent years (Ying 1978a; Fowler and Park 1983). There is little information on the extent of selfing in natural stands. Coles and Fowler (1976) found that trees growing close together in natural stands were related but trees growing more than 100 m apart were not. It is generally felt that natural selfing is common and probably contributes to seed failure.

Pollination mechanism The pollination mechanism involves the secretion of a pollination droplet from a nectary-like tissue in the ovule. The arms at the tip of the ovule also secrete a sticky substance to which pollen grains adhere for several days before droplets are formed. Pollen is collected and drawn down towards the ovule when pollination droplets flood the area between arms. The mechanism and some factors controlling it are described in Owens and Molder (1984); Owens and Blake (1985); Owens (1986) and Owens *et al.* (1987).

Pollination droplets are secreted over a period of several days and are not produced all at one time. Within any one cone they are produced at the base first and hence it is this area that is receptive first. The droplets develop progressively towards the tip of the cone. Cones are receptive over a 10-day period and the first pollen grains to reach the cone are the most likely to achieve fertilization (Ho 1984, 1985).

Owens *et al.* (1987) found that high humidity decreased the rate of evaporation of pollination droplets in Engelmann spruce and could conceivably increase the number of ovules fertilized, provided the humidity was not so high that it prevented pollen shedding.

Laboratory tests simulating the effects of pesticides (Sutherland *et al.* 1984) and acid rain (Sidhu 1983) suggest that changes in pH, or very low pH values, respectively, may have adverse effects on pollen germination and pollen tube growth. Atmospheric sulphur dioxide at 1.4 ppm reduced pollen germination and pollen tube growth in moist spruce pollen (Karnosky and Stairs 1974, cited by Owens and Blake 1985).

2.6.5 Fertilization and embryo development

Fertilization takes place approximately 3 weeks to 1 month after pollination—late June to early July for white spruce and late July to early August for Engelmann spruce (depending on location and weather conditions). Embryo development takes place after the cones have attained maximum size (determined by water content and fresh weight) and is described in detail in Owens and Molder (1984). Final cone size depends partly on heredity, but is also influenced by weather conditions during the previous year and during cone expansion (Zasada *et al.* 1978).

Seeds of white spruce are mature in late August. In Prince George, seeds of Engelmann spruce matured between August 1 and September 15 (Fowler and Roche 1976).

The success of the seed crop is very dependent on the weather conditions at the time of peak pollination and female receptivity. Pollination, fertilization and subsequent seed production are easily disrupted by adverse weather conditions such as frost and rain (Nienstaedt and Zasada 1990). Cool or wet weather may prolong the receptive period of pollination while warm, dry weather may shorten it. Studies carried out by Ross (1988a) showed that higher pre- and post-pollination temperatures accelerated pollen shedding in Engelmann spruce but this was accompanied by an increased proportion of undeveloped and rotted cones and a decreased pollen yield per cone.

2.6.6 Cone and seed production

Cones and seeds have been produced in white spruce by 4-year-old trees (Sutton 1969b). Ten- to 15-year old trees have been reported to produce seed "in quantity," but in most trees of this age production is low and depends on the site or weather conditions. For most natural stands, reliable seed production commences at age 30 or older and reaches the optimum when trees are 60 years or older (Fowells 1965). Seed production is delayed and more infrequent at northern latitudes (Fowells 1965). Zasada and Gregory (1969) report that in Alaska good crops may be obtained from trees as old as 170 years.

Engelmann spruce begins seed production at an earlier age (16–25 years) and produces the most abundant crops on healthy, vigorous dominant trees of 38 cm or more in diameter and 150–250 years of age (Fowells 1965; Alexander and Shepperd 1984). Good cone crop production in interior spruce in British Columbia commences at age 40, although it is variable (Eis and Craigdallie 1981).

Both species are considered to be relatively good cone producers at low elevations but at higher elevations the crop size may decrease. Cones at higher elevations are often smaller and may produce fewer seeds than at lower elevations in the same species.

Both species may produce good to excellent crops every 2–6 years (Fowells 1965), but the interval between good crops (periodicity) is highly variable and may be as much as 10–12 years (see Figure 49, Section 5.3.1, Seed procurement). The average frequency of good crops for interior spruce in British Columbia is estimated at 7 years for low-elevation, dry sites and at 12 years for high-elevation sites (British Columbia Ministry of Forests 1990a). Reports on periodicity of good crops are reviewed in Dobbs (1972); Safford (1974); Alexander and Shepperd (1984); and Nienstaedt and Zasada (1990).

Cone and seed production will depend on geographical location as well as weather conditions during different developmental stages. Rain, wind, and stand density influence the amount of pollen available for pollination and hence subsequent seed crop. The time of flowering may be critical, especially in northern latitudes where weather conditions can be severe at the peak of flowering and meiosis (mid-May) (Zasada and Gregory 1969).

Factors affecting seed and cone development are reviewed by Puritch and Vyse (1972), Owens and Blake (1985), and Owens (1986). Factors may be external (environmental) or internal (physiological state of the tree) and are so interrelated that it is difficult to ascribe a bumper crop to any one factor. Environmental factors affecting bud determination are described above (see Section 2.6.1, Reproductive bud development).

The physiological condition of the tree plays a role in the size of the crop. Trees that produce a bumper crop one year, rarely do the next. Cone maturation requires a high nutrient input and because it occurs at the same time that the succeeding year's buds are being laid down, it is in direct competition with bud development for nutrients (Owens and Blake 1985).

Natural phenomena leading to stress may also result in increased sexual reproduction, and bumper crops may ensue—so-called "stress crops." Some factors leading to stress are injury due to frost, girdling by animals, fire, insects and disease, root damage and defoliation (Owens and Blake 1985).

It is difficult to give an accurate estimate of seeds produced per cone. Although Fowells (1965) reported between 59 and 109 filled seeds per cone (average 80) for white spruce, Owens and Molder (1984) suggest that 30 full seeds per cone may be more common. Available information for Engelmann spruce is more limited, but 40 full seeds per cone is considered an average for southern British Columbia (Owens and Molder 1984). Eis and Craigdallie (1981) state that interior spruce has 8 to 20 seeds per cone.

The proportion of sound seed per cone varies from tree to tree and with location. In general, seed quality is better in years of heavy production and declines with increasing elevation. The most common causes of empty seed are lack of pollination, ovule abortion and insect damage.

Seeds of both species are small, light and have relatively large wings. The seeds of white spruce are smaller, with an average of 513 000 seeds per kg. The average number of cleaned seeds of Engelmann spruce is approximately 485 000 per kg (Owens and Molder 1984; British Columbia Ministry of Forests 1990a).

(Refer to Section 5.1, Natural Regeneration and Section 5.3.1, Seed procurement for more information on seed production and dispersal.)

2.6.7 Cone induction

To ensure a supply of high-quality interior spruce seed for planting, breeding programs aimed at increasing cone and seed production have been initiated. However, the process is hampered by the long "juvenile phase" before reproduction starts and the subsequent irregular flowering in conventional orchards. To overcome these problems, considerable research has been carried out to find reliable cone induction treatments.

Over the years, various cultural treatments have been employed to enhance cone and seed production in conifers. Early studies in this field are reviewed by Puritch and Vyse (1972). More recent studies (reviewed by Owens and Blake 1985) report some success in spruce with girdling, root pruning and application of fertilizers (Holst 1959, 1971; Remrod 1972) and by growing seedlings under continuous light to reduce the age of flowering (Young and Hanover 1976).

Other cultural treatments such as banding, strangulation, branch pruning, bending, sheltering, use of cover crops, moisture stress (drought) and increased temperatures have all been shown to enhance cone crop production in various conifer species by producing "stress crops" (Puritch and Vyse 1972; Owens and Blake 1985).

Growth regulators (hormones) are also used to stimulate cone production. Early work in this field is reviewed by Puritch and Vyse (1972). The results of more recent studies are reviewed and summarized by Owens and Blake (1985, Appendix 8). In general, gibberellins (GAs) have been the most successful, but results are still inconclusive.

Gibberellins, and in particular Gibberellin A_3 (GA_3) were first used in the late 1950s on members of the Taxodiaceae and Cupressaceae and 19 species in 10 genera have responded positively to their application (Owens and Blake 1985). More recently, mixtures of GA_4 and GA_7 ($GA_{4/7}$) have been used to induce cones of 17 species of the Pinaceae including the genus *Picea*. The best results have been obtained when $GA_{4/7}$ has been applied in conjunction with other cultural treatments such as root pruning, non-destructive girdling, high temperature, or water stress (Marquard and Hanover 1985; Ross 1985, 1988a; Pharis *et al.* 1986; Owens and Simpson 1988). However, these GAs are expensive, not readily available, and treatments are difficult to apply.

The timing of GA application is extremely important and must be correlated with the stages of bud development. Several studies report that treatment is most effective when applied to spruces in the early stage of shoot elongation (May to mid-July) before bud-type differentiation (Marquard and Hanover 1984b; Cecich 1985; Ross 1985, 1988a; Ho 1988). Pharis *et al.* (1986) report that application by injection and spraying was effective when applied later during the period of slow elongation of the shoot.

Most researchers think that the quality of seed produced by cone induction compares favourably with that produced without artificial induction. However, excessive flowering can cause seed and cone abortion and may possibly reduce seed quality because of increased competition for nutrients and water between shoots and reproductive systems, especially when trees are young.

2.7 Vegetative (Asexual) Reproduction

2.7.1 Layering and cloning

Vegetative reproduction by layering occurs in both Engelmann and white spruce (Alexander and Shepperd 1984; Nienstaedt and Zasada 1990). In Engelmann spruce it is widespread at the alpine timberline where plants are deformed by wind and snow abrasion. Dwarfed and prostrate clumps (krummholz) are produced by stem-tip layering (Marr 1977; Shea and Grant 1986). Similarly, layering occurs in white spruce at subarctic treeline sites in northern Canada and Alaska producing candelabra-form clonal growth (Stone and McKittrick 1976; Nienstaedt and Zasada 1990) (see Figures 18 and 19, Section 3.1.2, Alpine Tundra Zone).

Layering is also reported to occur in Engelmann spruce when a few trees have survived fire or other catastrophes (Alexander and Shepperd 1984) and in white spruce in coastal areas where windblown sand covers lower branches (Payette and Boudreau 1972, cited by Stone and McKittrick 1976). Some layering may occur in open stands of white spruce when lower branches are retained and come into contact with the ground (Stone and McKittrick 1976), especially if the upper central stem was damaged or killed. Multi-trunk clusters of clonal Engelmann spruce have been reported on very wet sites (Shea and Grant 1986).

Layering is generally considered to be insignificant in establishing and maintaining closed forest stands of either species (Stone and McKittrick 1976), but it appears to be an important method of maintaining a stand on extreme sites where environmental conditions are unfavourable for sexual reproduction and seedling establishment.

Artificial air-layering of white spruce has been successfully carried out on 6-year-old trees and is best done in early May (Fowells 1965).

2.7.2 Cuttings

Interior spruce can be successfully propagated from cuttings (Nienstaedt and Teich 1972; Nienstaedt and Zasada 1990; Russell and Ferguson 1990). Rooting ability varies with the age of the donor plant and from tree to tree, but, in general, is considered too poor for practical use by the time trees are 10–15 years old. In addition, rooted lateral branches must undergo a period of adjustment as they change from a creeping form to an upright form. Rooting ability can be increased in older trees if the scions are first grafted to vigorous rootstock (Holst *et al.* 1969).

Tognoni *et al.* (1977) found that cuttings rooted poorly during the winter months and better in the spring. This pattern follows closely the abundance of a water-soluble rooting substance isolated from seedlings in an earlier study (Kawase 1971).

A grower's manual describing the techniques needed to produce interior spruce "stecklings" (plantable rooted cuttings) was recently published for British Columbia (Russell and Ferguson 1990). The stecklings are intended to speed up the availability of genetically improved stock for reforestation, and to reduce genetic variability among seedlings used in research trials. Figure 14 illustrates the production technique. First, cutting donors are grown from genetically improved seed collected from a seed orchard (clonebank). The donor seedlings are grown for 9 months under high light intensity and wide

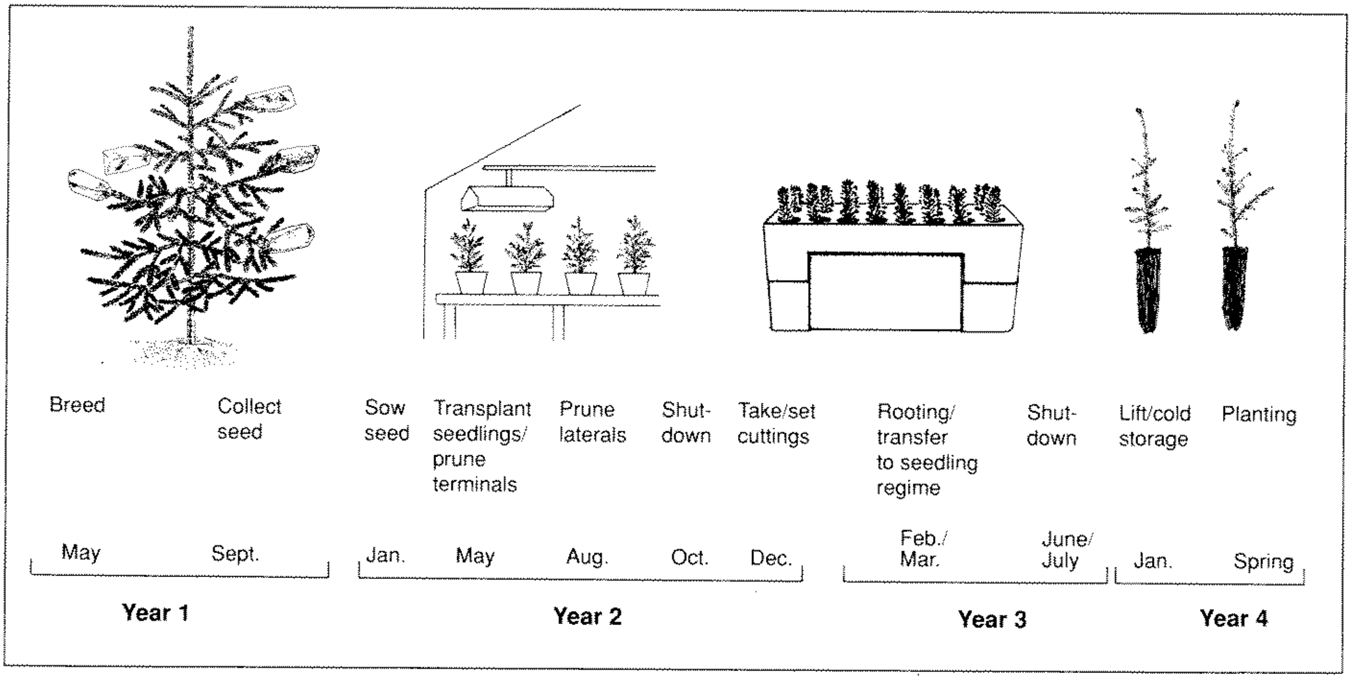

FIGURE 14. Production of interior spruce "stecklings" using rooted cuttings taken from genetically superior donor plants (from Russell and Ferguson 1990).

spacing, and pruned regularly to produce a bushy form. After hardening-off for 1–3 months, the donor plants are destroyed to produce approximately 50 3–6 cm cuttings. The cuttings are dipped in a rooting powder (talc and indole-butyric acid) and inserted into styroblock containers used for standard nursery seedling production. The containers are placed in a special rooting environment (15–20°C bottom heat, high relative humidity and temperatures above 12°C). After 6–8 weeks the cuttings have rooted and can be treated like standard nursery seedlings.

First-year results of outplanting trials suggest that stecklings are slightly shorter and stockier than seedlings from the same family, but it is expected that over the long term they will have very similar survival, growth and form (Russell and Ferguson 1990). However, some earlier studies have suggested that the growth rate of cuttings may be slower than that expected from seedlings "thus cancelling out gains which may be expected from the use of cuttings from superior genotypes" (Campbell and Durzan 1976b).

2.7.3 Grafting

Methods for grafting white spruce are reviewed in Nienstaedt and Teich (1972). Grafting is most successful if done in February or March in the greenhouse using forced rootstock in pots and dormant scions (Nienstaedt and Zasada 1990). Fall grafting is also possible. Late winter–early spring grafting in the field should be done before the buds are obviously swelling (Nienstaedt and Zasada 1990). Grafting is widely used in tree improvement programs to establish clonebanks and breeding orchards.

Kiss (1971) found that fall grafting of both species in the greenhouse was far superior to field or greenhouse grafting in the spring. Of 175 parent trees selected near Prince George, and of 132 trees selected in the East Kootenays, most were successfully established in a clonebank by grafting.

2.7.4 Tissue culture and biotechnology

The propagation of forest trees *in vitro*—using various tissue culture techniques—is emerging as an alternative to asexual propagation through rooted cuttings. The ultimate goal of research in this area is to produce large numbers of plants identical to parent plants that have superior genotypes developed through conventional breeding programs.

Research on the various techniques for *in vitro* propagation and *in vitro* genetic manipulation (e.g., insertion of genes conferring resistance to disease) is collectively referred to as "conifer biotechnology" and has been reviewed by Dunstan (1988).

Research on interior spruce has primarily focussed on the use of organogenesis—that is, the induction of organs from excised plant tissue (explants)—for *in vitro* propagation. Studies have investigated the cultural requirements of explants, the phases of their development, and the stages of development of different tissues in them (Chalupa and Durzan 1973; Patel *et al.* 1986; Rumary *et al.* 1986). Campbell and Durzan (1975, 1976a) reported the induction of many needles and buds from embryo tissues. Thorpe and Patel (1986) compared the performance of different types of white spruce explants.

Most of the explants are taken from very young tissues such as the epicotyl, hypocotyl and cotyledons of embryos. However, since an assessment of genetic superiority can be made from trees of 12–15 years of age, it would be desirable if explants could be taken directly from mature vegetative buds of these older trees rather than having to wait until they reach reproductive age to obtain embryo tissue. Work by Mohammed *et al.* (1986) investigates this possibility.

2.8 Genetics and Tree Improvement

In recent years there has been a considerable increase in the number of genetic studies carried out on spruces—in particular on white spruce. This interest is prompted by the desire to produce genetically improved trees in breeding programs. Studies involve:

- examining the variability of the species;
- determining whether or not the variation observed is under genetic control and hence whether or not it will be maintained throughout the life of the tree (heritability studies);
- the extent to which trees are related, either within or between populations; and
- the extent to which genetic variation is modified by environmental conditions.

If characters are found to be under genetic control and they are positively correlated with superior growth, they may then be used in the selection of parent trees for breeding programs aimed at producing faster-growing trees.

2.8.1 Genetic variation

Variation exists at two levels: the population level and the individual level. Variation among populations at different locations (provenances) results in species developing into races that have characteristics related to survival and adaptation to local environmental conditions (inter-provenance variation). This level of variation is used to select seed sources and delineate zones within which seed can be safely transferred. Variation also exists within populations or stands as a result of differences in the genetic makeup of individual trees (intra-provenance variation). Individual tree variation is used in tree breeding programs to develop genetically superior planting stock. Studies on genetic variation in Engelmann spruce have been reviewed by Fowler and Roche (1976) and in white spruce by Nienstaedt and Teich (1972) and Nienstaedt and Zasada (1990).

Variation among populations White spruce is a highly variable species throughout its range and its variability is well documented. Information on Engelmann spruce, while not so readily available, suggests that it is also a highly variable species. Natural variation in growth and morphological characters is generally the result of interaction between inherent (genetic) variation and habitat-related (environmental) factors (Mergen *et al.* 1974).

Variation is influenced by the degree of hybridization between the species where their ranges overlap. In both the "pure" species and their hybrids, genetic variation tends to be "clinal"; that is, it follows a pattern of continuous gradual changes that corresponds to changes in latitude or altitude.

Provenance studies, in which seedlings from different geographic locations are grown together, show the extent to which growth characteristics vary with the seed source and help to identify patterns of geographic variation. Starting in 1965, interior spruce provenance tests were established at various locations in the interior of British Columbia (Figure 15), and they are now beginning to yield useful information (Jaquish 1982; Konishi 1985, 1986). There is now fairly strong evidence that interior spruces are quite adaptable to being transferred outside their area of origin and that properly selected non-local seed sources may be just as hardy and may outperform the local provenances.

Superior provenances have been identified in the "wet-belt transition zone" extending from east of Williams Lake southwards to Shuswap Lake (Figure 15). These fast-growing provenances appear to perform well in a variety of environments and show promise for wider planting throughout the interior of British Columbia south of 55°N latitude (Jaquish 1982; Lester *et al.* 1990). The "Birch Island" provenance, from a low-elevation site (425 m) near Clearwater, is one example of a provenance from this region that has demonstrated superior growth potential over a wide geographic range (Konishi 1985; Nienstaedt and Zasada 1990). Seed transfer guidelines and seed planning zones have recently been revised based on information from the provenance tests (Figure 16; Table 6) (Konishi 1985, 1986; Lester *et al.* 1990).

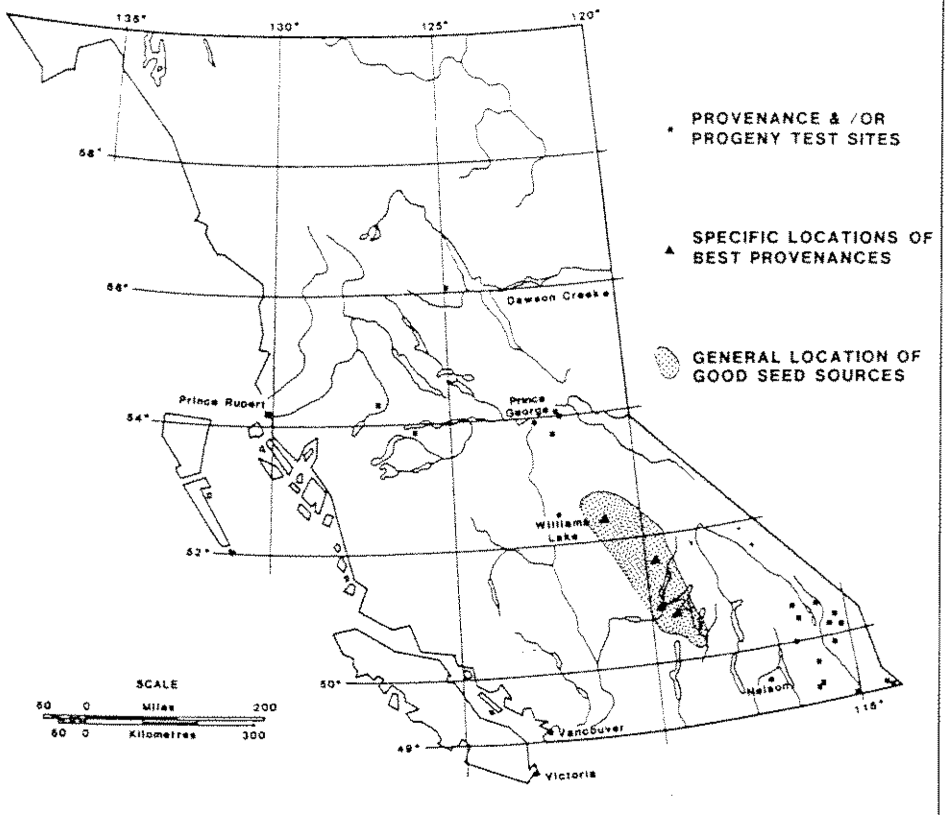

FIGURE 15. Interior spruce provenance and progeny test sites and location of good seed sources (from Konishi 1986).

TABLE 6. Seed transfer guidelines for interior spruce (from Lester *et al.* 1990)

1. As a general rule, seed collected in a zone should be used in that zone with the following elevational constraints:

Latitudinal range	Maximum transfer (m) Upward	Maximum transfer (m) Downward
49 – 53° (Nelson Forest Region only)	400	200
49 – 56°	300	200
56 – 58°	200	100
58 – 60°	100	50

2. Transfer between zones is allowed within the following constraints:
Latitude: no more than 2° northward; no more than 1° southward.
Longitude: no more than 3° eastward; no more than 2° westward.
Elevation: as in (1) above.

Seed transfer from the coast or coast–interior transition into the interior is prohibited. Seed transfer across major biogeoclimatic subzone boundaries is prohibited in the absence of substantial test results indicating minimal risk and significant potential for productivity gains.

Variation in growth performance with the elevation of the seed source is clearly evident (Lester *et al.* 1990). High-elevation spruce provenances are the first to break dormancy in the spring, the first to become dormant in the fall, and overall the slowest growing (Fowler and Roche 1976; Lester *et al.* 1990). Low- to mid-elevation provenances tend to be the fastest growing. These findings are supported by a provenance study in the Colorado Rockies, where the British Columbia seed sources outperformed all other (higher-elevation) provenances (Shepperd *et al.* (1981). Nienstaedt *et al.* (1971) also report that low-elevation populations from British Columbia grew taller than the experimental average when tested in both Wisconsin and British Columbia. In Norway, low-elevation provenances of interior spruce from southern British Columbia were healthier and more resistant to spring frosts, but slower growing, than white spruce provenances from eastern Canada (Dietrichson 1971, cited by Fowler and Roche 1976). The vigour of the British Columbia material was attributed to white × Engelmann hybridization.

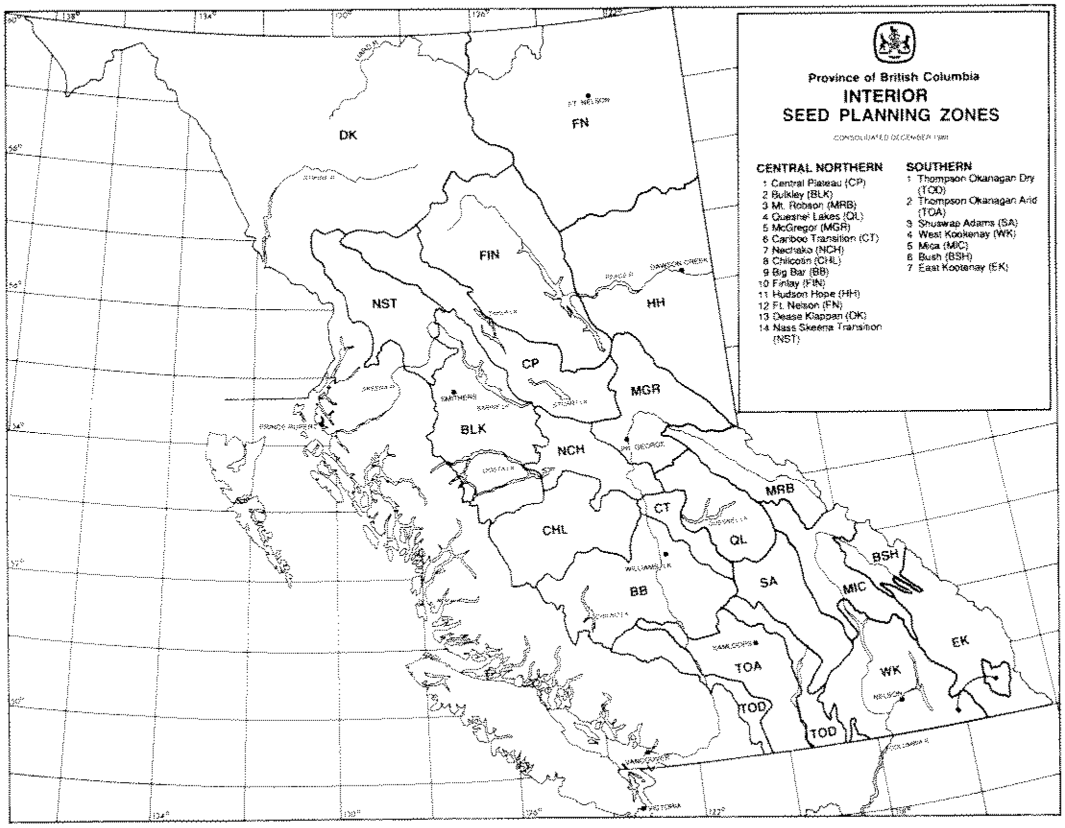

FIGURE 16. Seed planning zones for the interior of British Columbia, 1988 (from Lester *et al.* 1990). (See Table 6 for further information.)

In the central and southern interior of British Columbia, spruce has shown no clear pattern of genetic variation associated with either latitude or longitude (Lester *et al.* 1990); however, eastern Canadian sources of white spruce perform as well or better than local sources (G. Kiss, pers. comm., June 1992). Latitudinal variation is reported elsewhere. Southern provenances of white spruce from Ontario were the fastest growing and flushed the latest when tested at the southern edge of their range (Nienstaedt and Teich 1972). Alaskan trees planted outside their native range are smaller and flush earlier, making them more susceptible to frost. Seed sources are more hardy from northern than from southern Alberta sources (Dunsworth and Dancik 1983).

The number of needles initiated in the bud varies considerably between white spruce provenances (Pollard 1973b, 1974b). This variation appears to be under genetic control (Pollard 1974b) but may be modified by environmental conditions, especially temperature (Pollard and Logan 1977). Development of a large complement of needles appears to be related to the ability to prolong the period of needle initiation. The trend towards the initiation of fewer needles in northern latitude seed sources may be a response to a shorter frost-free season (Pollard and Ying 1979a).

Adaptation to different soil types has been reported in Nienstaedt and Teich (1972), Khalil (1985a) and Perala (1987), and variation in germination temperature requirements has been observed (Nienstaedt and Teich 1972). In British Columbia, efforts to identify adaptation to various soil types have proven to be unsuccessful (G. Kiss, pers. comm., June 1992).

Work by Beaulieu and Corriveau (1985) shows that wood density varies among white spruce provenances, confirming earlier reports in Nienstaedt and Teich (1972) that indicated that wood of white spruce from British Columbia had the greatest density. No relationship between wood specific gravity of white spruce provenances and their respective growth performance was found. Beaulieu and Corriveau (1985) recommend that a first selection be made at the provenance level to maximize volume production and a second selection be made on the basis of wood specific gravity values within selected provenances.

Trees that produce abundant seed at an early age are valuable as a seed source, but vegetative growth may be reduced if this trait is passed on to progeny (Tiech 1975). In Tiech's study, the apparent reduction in height growth of cone-producing white spruce provenances averaged 14%, presumably because the heavy cone crops diverted carbohydrate and nitrogen supplies that would otherwise have been used in height growth.

Variation among individual trees The degree of genetic variation existing among families or individual trees within spruce stands is reported to be very large (Khalil 1985a). This has been confirmed by isoenzyme studies by Copes and Beckwith (1977), Tsay and Taylor (1978), King *et al.* (1984), Cheliak *et al.* (1985), Yeh and Arnott (1986), Alden and Loopstra (1987) and others. A bibliography of the use of isoenzymes in genetic studies has been prepared by El-Kassaby and White (1985).

Variation in height growth within families and between populations has been demonstrated (Nienstaedt and Teich 1972; Ying and Morgenstern 1979; Kiss and Yeh 1988). Several studies have shown that superior growth shown by juvenile trees is maintained throughout the life of the tree, making it feasible for breeding programs to select superior trees at an early age (Nienstaedt and Teich 1972; Ying and Morgenstern 1979; Khalil 1985b; Kiss 1985; Nienstaedt and Riemenschneider 1985; Kiss and Yeh 1988). In one study, seedlings of superior height were selected in the nursery and outplanted together with seedlings of average height. After 18 years, the selected seedlings continued to have a significant height growth advantage over control seedlings (Nienstaedt 1981a). Results of this study do not, however, imply that superior families should be selected solely on the basis of nursery performance.

Pollard and Ying (1979a, 1979b) demonstrated that considerable variation exists among families of seedling white spruce in the time at which flushing and cessation of growth occur in response to photoperiod. Variation in flushing and budset may be adaptive strategies to cope with spring and fall frosts, respectively. Early spring frost damage is avoided or can be greatly reduced in trees with late flushing. The authors hypothesized that selecting parent trees that flush early to increase growth rates would therefore be likely to reduce the adaptability of the seedling population.

However, Nienstaedt (1985) found that spring growth initiation was not significantly correlated with either total height growth or frost damage. Although in the year of frost, the fastest-growing trees were the most severely damaged and had the greatest number of terminals the following year, damage was not permanent. The adverse effects on form had largely disappeared 7 years after damage, and the fastest-growing, most severely damaged trees had maintained their growth advantage for up to 15 years from seed. Nienstaedt (1985) concluded that a large, costly progeny test would be required to produce rapidly growing, late-flushing trees that would be less susceptible to frost damage.

The feasibility of selecting for late flushing in order to increase resistance to spruce budworm is discussed by Blum (1988).

Roche (1969), Nienstaedt and Teich (1972) and Khalil (1974) all report that the wide variation in white spruce cone characteristics and number of seeds per cone is under genetic control, but is not positively correlated with growth superiority. Hence these characters may not be useful in selection of fast-growing trees.

It may be possible to select individuals with superior height growth characteristics by seed weight. Khalil (1986) found that germinative capacity and juvenile characteristics were positively correlated with white spruce seed weight. He suggests that seed weight can be used as a criterion for selection of "plus" trees and superior provenances. However, Hellum (1976) reported that the influence of seed weight on seedling size disappears almost completely in 5 years. As well, sorting by seed weight might reduce genetic variability in subsequent populations because seed weight is highly specific to each tree. Seed weight may not be positively related to germinability, tree form, drought hardiness, or other desirable tree characteristics. Sorting by weight might therefore lead to the removal of the best-adapted trees.

Variation in stem diameter, and in needle, bud, branch and cone characteristics has also been reported (Roche 1969; Roche *et al.* 1969; Nienstaedt and Teich 1972; Fowler and Roche 1976; Dunsworth and Dancik 1983; Khalil 1985a; Merrill and Mohn 1985).

2.8.2 Breeding programs

Because interior spruce is so highly variable genetically, it is an excellent candidate for tree improvement. The British Columbia Ministry of Forests initiated a genetic improvement program for interior spruce in 1968 (Kiss and Yeh 1988). An overview of the program is provided by the B.C. Ministry of Forests, Research Branch (1985), Konishi *et al.* (1986) and Lester *et al.* (1990). Breeding programs for genetic improvement of white spruce are also well established in eastern Canada and the United States. Problems encountered in establishing these programs are reviewed and discussed in Nienstaedt and Kang (1987).

Desired qualities for spruce trees include rapid growth rate, stem straightness, compact crown form with small branches, high wood density, tolerance to cold and resistance to disease. The appearance of the tree (its phenotype) is the result of the interaction of the genetic makeup of the tree (its genotype) and the environment in which it is growing. The ultimate goal, therefore, is to produce a superior genotype. Trees produced must also be well adapted to the environment into which they are to be planted.

The genetic improvement program in British Columbia includes four components (Kiss 1971):

1. selection of phenotypically superior parent trees ("plus" trees);
2. vegetative propagation of parent trees in breeding arboreta and seed orchards;[1]
3. open-pollinated progeny testing[2] of select trees; and
4. production of improved seed for reforestation.

The overall goal of the program is to provide enough genetically improved orchard seed to satisfy approximately one-half of the anticipated demand for planting stock by the year 2000 (Lester *et al.* 1990).

Three breeding zones, termed "selection units," were delineated for "plus" tree selection: the Prince George selection unit, the Smithers selection unit, and the East Kootenay selection unit. Each selection unit represents "an area within which climatic and ecological conditions are tolerably homogeneous" (B.C. Ministry of Forests, Research Branch 1985). Parent trees were selected in each selection unit, and seeds and scions (branch tips used for grafting) were collected for propagation in breeding arboreta and seed orchards. As of 1989, a total of 3209 interior spruce parent trees had been selected, more than for any other tree species in British Columbia (Lester *et al.* 1990).

In the mid-1970s, breeding arboreta were established at Kalamalka (in Vernon), clonebanks at Red Rock (near Prince George), and the first clonal seed orchard was established at Skimikin in 1979 (Birzins 1986). By 1985 there were 30 ha of clonal interior spruce orchards established, with another 57 ha to be developed, representing a total of 34 800 ramets[3] (Birzins 1983, 1986). Most of the orchards are located in the Okanagan Valley where the hot, dry climate stimulates high rates of cone production (Kiss 1978; Birzins 1986) and there is a low risk of contamination from local spruce pollen.

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[1] A breeding arboretum is a plantation or group of trees (usually grafted) used for genetic experimentation and as parental stock for future seed orchards. A seed orchard is a collection of superior phenotypes or genotypes established and maintained for the purpose of seed production.

[2] Progeny tests are outplanting trials that test the growth performance of the offspring of phenotypically superior parent trees. In an open-pollinated test, pollination is not controlled, so only one parent (the cone-producing parent) is known for certain.

[3] A ramet is an independent, free-living organism, always reproduced by vegetative means. In the case of the seed orchard program, a total of 34 800 cone-producing trees will be established either by grafting or from seed. Because most of these trees are produced by cloning, the number of genetically distinct individuals (genotypes) represented will be far less than 34 800.

In the seed orchard, natural or "open" pollination takes place among the randomly located trees. Seed from these orchards is used to establish open-pollinated progeny trials that are outplanted at various locations within the original selection units (Figure 15). The first progeny tests of seedlings grown from "plus" trees in the Prince George selection unit were planted in 1972 and 1973. Similar tests were later established for the East Kootenay and Smithers selection units (B.C. Ministry of Forests, Research Branch 1985). By 1989, 1850 of the 3209 originally selected parents were represented in progeny tests (Lester *et al.* 1990).

The progeny tests indicated that it is possible to identify good clones of interior spruce while progenies are at an early age (B.C. Ministry of Forests, Research Branch 1985). As a result, 1.5 generation (improved) seed orchards were established based on 6-year results of the open-pollinated progeny trials. The top 50% of the clones identified in the progeny trials were used to create a new generation of seed orchards. Within 10–15 years, these orchards will again be culled by 50%, leaving only the top 25% of the original population of parent trees selected in the wild. It is estimated that the improved seed from these 1.5 generation orchards will average 10–15% greater height growth than plantations grown from unimproved seed (Kiss 1982). Improved seed orchards are established or under development for seven of the interior seed planning zones shown in Figure 16 (BLK, CP, FIN, MGR, HH, MRB, QL). None of the seed orchards is yet producing commercial quantities of seed.

2.8.3 Inbreeding

A major problem facing tree breeders in general, and seed orchard breeders in particular, is the degree of self-pollination that occurs in both the natural stands from which trees are initially selected and within seed orchards. Considerable self-pollination occurs in natural stands from which "plus" trees are selected. Ying and Morgenstern (1979) and Fowler and Park (1983) demonstrated that trees growing close together in natural stands are closely related. Similar problems exist in field seed orchards where trees are grown out in the open and there is no control over pollination. Trees may be self-pollinated or receive pollen from a close neighbour that is closely related (often a clone). Self-pollination or inbreeding leads to a reduction in genetic diversity (genetic depression) and tends to dilute or negate the genetic gains made. Decreased seed viability, germination capacity and subsequent growth are some of the consequences of self-pollination (Ying 1978a; Fowler and Park 1983). It also reduces the ability of the trees to withstand environmental stress (Schoen *et al.* 1986).

Consequently, there is considerable research aimed at reducing the negative effects of inbreeding. Khalil (1978) found that "plus" trees of white spruce were superior because they were the result of outbreeding (i.e., crosses between unrelated trees). Cheliak *et al.* (1985) recommended that selection of parent trees should be made from widely separated sources to ensure "assembling a rich pool of variation" and Khalil (1978) suggests that selected trees should be bred further using controlled pollination techniques.

The tendency for breeding programs to use crosses between different provenances has been criticized by those who argue that trees in natural stands benefit from years of evolutionary selection and are well adapted to local environmental stress. Inter-provenance hybridization may reduce the level of local adaptation. However, Ying (1978b) showed that hybridization between seed sources from different provenances resulted in offspring that grew faster and he suggested that this was because it countered the already existing effects of natural inbreeding.

Ross *et al.* (1986) present the case in favour of using indoor potted orchards for the production of genetically improved white spruce. Within greenhouses, self-pollination can be reduced and supplemental pollination can be carried out under carefully controlled conditions. Other advantages of the indoor potted orchards over field orchards are that optimum environmental conditions can be maintained, intensive cone enhancement techniques can be employed (see Section 2.6.7, Cone induction), and protection and harvesting of cones is simplified (B.C. Ministry of Forests, Research Branch 1985). The British Columbia Ministry of Forests has been researching development and evaluation of indoor potted seed orchards for interior spruce since 1980.

3 Ecology

3.1 Ecological Classification

Characterization of the ecological conditions in which interior spruce grows in British Columbia has progressed rapidly during the past decade. Spruce ecosystems have been classified and described primarily within the framework of the biogeoclimatic ecosystem classification (BEC), a system developed by Krajina (1965, 1969) and his students, and adapted by the British Columbia Ministry of Forests (Pojar *et al.* 1987) from 1978 to the present. BEC is a multi-level hierarchical classification of ecosystems that synthesizes climate, vegetation and soil data. The system is now widely accepted and in use by most agencies and organizations involved in forest management in British Columbia and will be used throughout this review as a basis for describing ecological conditions within British Columbia. Readers unfamiliar with BEC should refer to the comprehensive review of ecosystems in British Columbia by Meidinger and Pojar (1991) or refer to Pojar *et al.* (1987) or Pojar (1983).

3.1.1 Occurrence within biogeoclimatic zones

British Columbia is divided into 14 biogeoclimatic zones (Figure 17). White or Engelmann spruce and their hybrids occur in all but two of those zones—the treeless Bunchgrass zone (BG) and the Coastal Douglas-fir zone (CDF). White spruce and hybrids with mostly white spruce characteristics dominate the Boreal White and Black Spruce (BWBS), Sub-Boreal Spruce (SBS) and Spruce–Willow–Birch (SWB) zones of the central and northern interior. Engelmann spruce and its hybrids are widespread in the cool Montane Spruce (MS) and Engelmann Spruce–Subalpine Fir (ESSF) zones of the southern interior. Other zones in which interior spruce is common, but not dominant, include the Interior Cedar–Hemlock (ICH), Interior Douglas-fir (IDF), and Sub-Boreal Pine–Spruce (SBPS) zones. Interior spruce also occurs sporadically in the Ponderosa Pine (PP), Mountain Hemlock (MH) and Coastal Western Hemlock (CWH) zone and in krummholz form at the lower elevations of interior portions of the Alpine Tundra (AT) zone. Table 7 summarizes the occurrence of native spruce species and their hybrids in the biogeoclimatic zones and subzones of British Columbia.

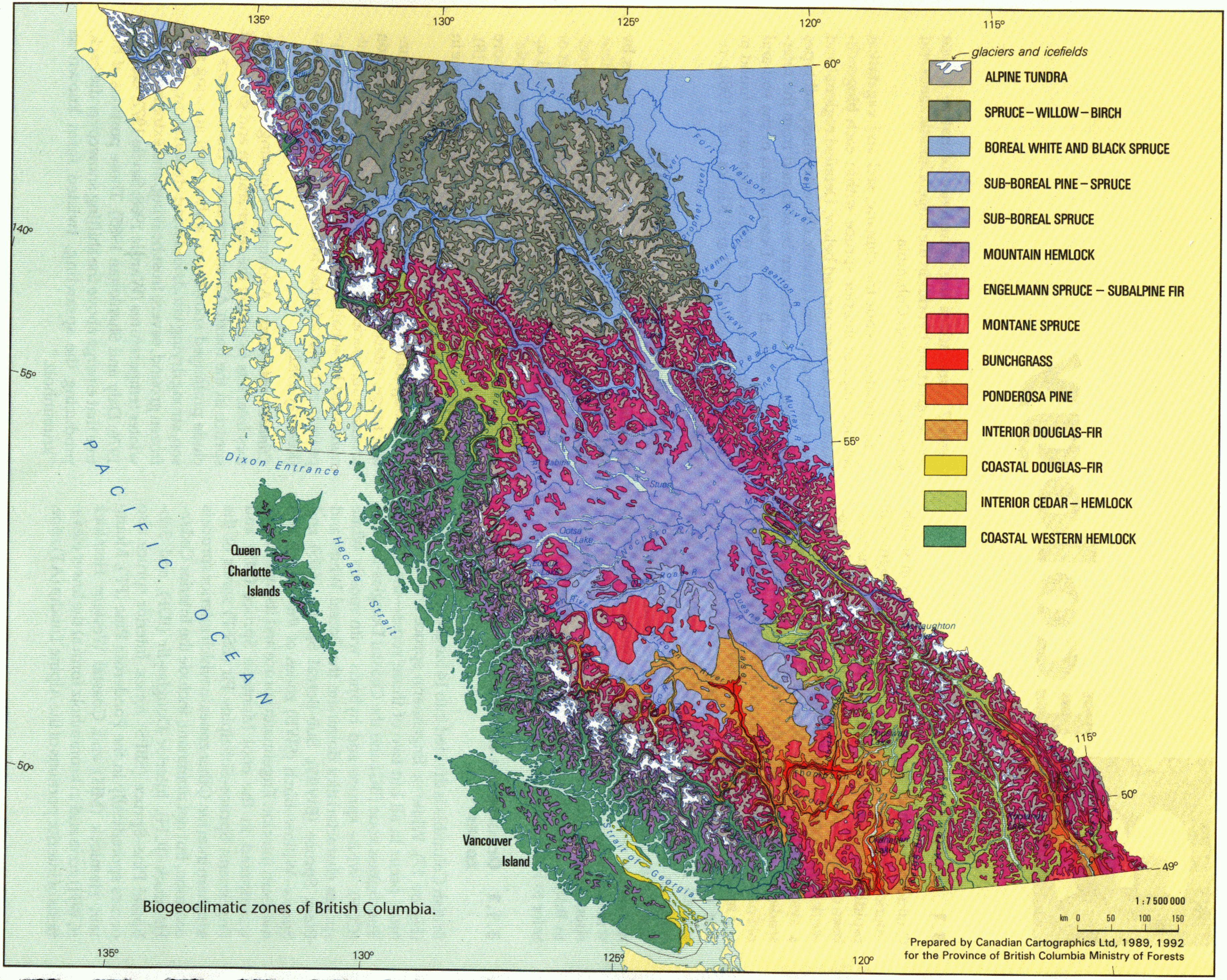
Information about the climatic, soil and vegetation relationships of interior spruce within each biogeoclimatic zone is summarized below. Detailed regional and local information on climatic characteristics, soil types and plant communities can be obtained from the references cited for each zone. Descriptions of the soil and humus forms mentioned in this section can be found in Agriculture Canada (1987) and Klinka *et al.* (1981), respectively.

3.1.2 Alpine Tundra Zone (AT)

Occurrence of interior spruce The alpine tundra is, by definition, a treeless zone, occurring above the timberline. However, as Wardle (1968) points out, "timberline seldom sets an abrupt limit to the upward distribution of this species, for wind-deformed spruce occurs well up into the alpine tundra as compact islands of "krummholz" that become smaller in area, low in stature and more widely scattered with increasing altitude" (Figure 18). This section summarizes the ecology of interior spruce in the krummholz zone.

Throughout British Columbia east of the Coast Mountain range, interior spruce is one of the most common krummholz species. In most areas, however, it is outnumbered by subalpine fir (*Abies lasiocarpa*), which appears to be better adapted to the harsh alpine conditions (Kearney 1982).

Climatic relations A complex of limiting climatic factors interacts to inhibit the regeneration and growth of spruce in the harsh AT environment. These factors include prolonged snowcover, a short cool growing season, strong drying winds and wind-driven snow, deeply frozen ground, severe frost heaving, and extremely cold winter temperatures (Wardle 1968; Savile 1972; Bennett 1976; Daly and Shankman 1985). Those portions of the tree that emerge above the shifting snowcover die back, producing the sprawling, twisted form known as "krummholz."



Biogeoclimatic zones of British Columbia.

Prepared by Canadian Cartographics Ltd, 1989, 1992
for the Province of British Columbia Ministry of Forests

TABLE 7. Distribution of native *Picea* species and their hybrids in the biogeoclimatic zones and subzones of British Columbia

Zone	Subzone/Variant	Sw	Sx	Se	Ss	Sxs	Sb
AT	Alpine Tundra						
	(trees present in krummholz form only)	C					
	northern interior						
	central interior	A	C	C			
	southern interior			C			
	coastal			R	U		
SWB	Spruce – Willow – Birch						
	all subzones	A	R				U
BWBS	Boreal Black and White Spruce						
	BWBSdk1 (Stikine)	A				U	C
	all other subzones/variants	A	R				C
SBPS	Sub-Boreal Pine – Spruce						
	all subzones	A	U				C
SBS	Sub-Boreal Spruce						
	westernmost: SBSmc2 (Babine) and SBSdk	C	A	R		R	C
	all other subzones	C	A	R			C
MH	Mountain hemlock						
	eastern variants: MHm2 and MHmp2 (Maritime leeward)			U	U	R	
	all other subzones/variants				U		
ESSF	Engelmann Spruce – Subalpine Fir						
	coastal transition: ESSFmk, mkp, mw, mwp, wv, wvp		C	C		U	
	southern subzones		U	A			
	northern subzones	U	C	U			
MS	Montane Spruce						
	all subzones	U	A	A			
BG	Bunchgrass						
	all subzones						
PP	Ponderosa Pine						
	all subzones	R	R				
IDF	Interior Douglas-fir						
	northern	U	C				
	southern	U	C	U			
CDF	Coastal Douglas-fir						
	all subzones				U		
ICH	Interior Cedar – Hemlock						
	coastal transition: ICHmc, vc		R		R	C	U
	northern						U
	southern						
CWH	Coastal Western Hemlock						
	CWHws (Skeena–Nass)				C	C	
	southern				C		
	northern				A		

A = Abundant; C = Common; U = Uncommon; R = Rare

← **FIGURE 17.** Biogeoclimatic zones of British Columbia.

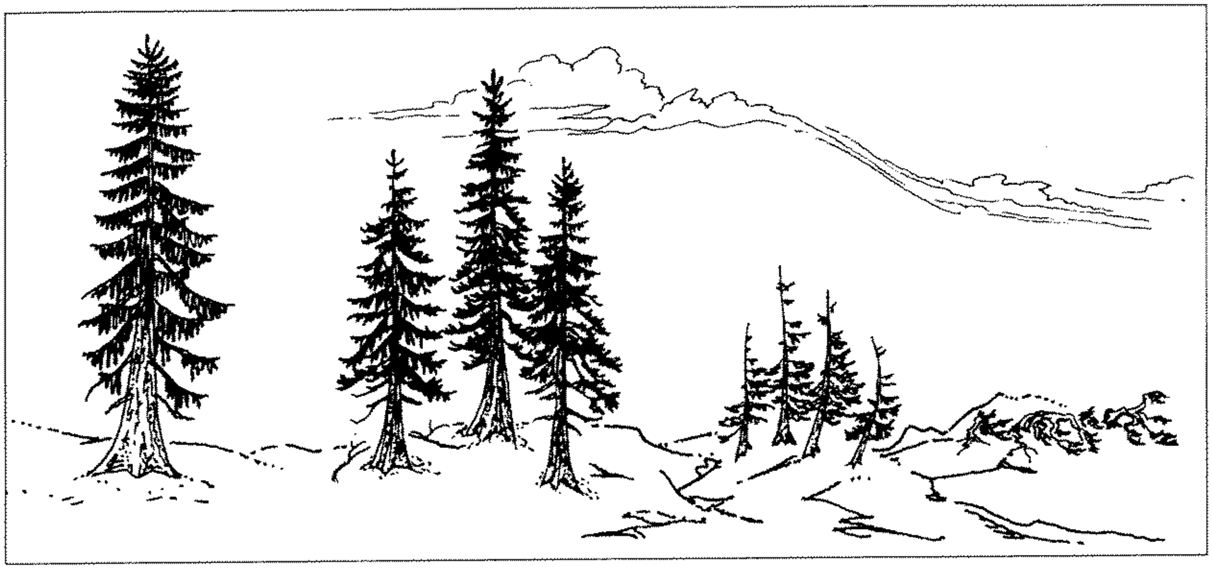


FIGURE 18. Growth forms of Engelmann spruce at the alpine timberline (from Wardle 1968).

Winds are thought to be the chief cause of krummholz formation (Arno and Hammerly 1984). The injury is due primarily to abrasion by wind-driven snow crystals (Savile 1972). An additional factor is the phenomenon known as frost-drought or physiological drought: the low temperature and short growing season of the high-elevation environment prevents trees from maturing the new growth of tissues, so that the trees are susceptible to desiccation during winter when water can not move upwards through frozen soils, roots and stems (Savile 1972; Ogilvie 1976; Tranquillini 1979). Wardle (1981, 1985) also believes that direct freezing of tissues may be an important cause of winter desiccation in Engelmann spruce krummholz.

Foliage buried within the snowpack is protected from the damage described above, but if burial is too prolonged, black felt "snow-mold" fungi (principally *Herpotrichia* spp.) can cause extensive damage (Wardle 1968; Arno and Hammerly 1984).

Site and soil conditions In the Okanagan area, Eady (1971) observed that clumps of Engelmann spruce and subalpine fir occupied submesic alpine sites, while both wetter and drier topographic positions supported herbaceous or heath/dwarf shrub vegetation. Other studies, summarized by Hamilton (1983), also suggest that spruce–subalpine fir krummholz occurs on more or less mesic sites, and is absent from the wet and dry extremes. Wardle (1968) noted that spruce krummholz is usually more abundant and ascends higher on convex surfaces (ridges, spurs, knolls) than in concave valleys and hollows, except where convex surfaces are exposed to extreme winds. Apparently the most favourable topographic positions for spruce at the timberline are those that provide enough snow to protect the tree from wind and excessively cold temperatures, yet not so much that the length of the snow-free season is critically limited (Ogilvie 1976; Arno and Hammerly 1984; Selby and Pitt 1984; Daly and Shankman 1985).

Alpine soils occurring beneath coniferous vegetation are typically Humo-Ferric Podzols, sometimes Dystric Brunisols, and often have high concentrations of silt or volcanic ash in surface horizons (Valentine 1976).

Associated vegetation Subalpine fir is the most common associate of spruce in krummholz vegetation. Other associated coniferous species include alpine larch (*Larix lyalli*), whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*) and western white pine (*Pinus monticola*) in southern British Columbia, and mountain hemlock (*Tsuga mertensiana*) on the eastern slopes of the Coast Range and in the Revelstoke area. Lodgepole pine (*Pinus contorta* var. *contorta*) is a minor associate in most of the British Columbia interior, except in dry alpine areas of the southwest Cariboo/Chilcotin district where it is abundant (Pojar 1985). Ericaceous species (*Vaccinium scoparium*, *V. membranaceum*, *V. caespitosum*, *Cassiope mertensiana*, *Phyllodoce empetriformis*) are common in the snow accumulation zone around the base of krummholz colonies.

Succession and stand development Several studies have examined factors affecting the development of spruce at the timberline. Some of these studies (Savile 1963; Bryson *et al.* 1965; Payette 1974, 1976; Elliot 1979; Payette and Filion 1985; Scott *et al.* 1987a,b) describe the dynamics of white spruce at the Arctic treeline in northern Canada, while others examine Engelmann spruce at the alpine timberline in Alberta and the western United States (Wardle 1968; Baig 1972, cited by Kearney 1982; Dunwiddie 1977; Kearney 1982; Ives and Hansen-Bristow 1983; Shankman 1984; Daly and Shankman 1985). There are parallels among these studies that may shed light on the timberline ecology of interior spruce in British Columbia.

Fluctuations in the position of the timberline take place very slowly and are thought to be primarily caused by changes in regional climate, especially summer temperatures. During periods of climatic warming, trees advance into the tundra zone, while cooling trends are accompanied by a retreat in the elevation of the timberline. Wildfires, stimulated by a decrease in precipitation, may also cause a significant retreat in the treeline (Elliot 1979). Seedlings are most likely to become established at the timberline when good seed years coincide with warmer than average summer temperatures (Kearney 1982). Elliot (1979) speculates that a series of warm summers is necessary, first to allow viable pollen and seed to develop, then to enable young seedlings to become established.

The current position of the treeline is not necessarily in equilibrium with the climate. Several researchers have hypothesized that the treeline in many areas represents a relict of warmer climates in the past (Bryson *et al.* 1965; Larsen 1965; Elliot 1979; Hansen-Bristow and Ives 1984; Daly and Shankman 1985). Once established in the forest-tundra transition, spruce is able to persist for up to thousands of years by reproducing vegetatively (i.e., layering) in climatic conditions where sexual reproduction is unsuccessful. The more favourable microclimatic conditions created by surrounding trees may also enable spruce to survive (Savile 1972; Shankman 1984) (Figure 19).

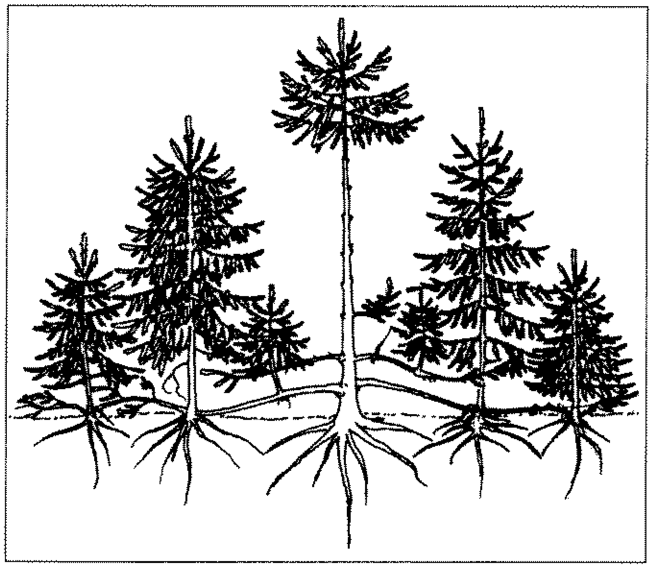


FIGURE 19. Clonal spruce grove resulting from layering of basal branches. Grouped trunks afford mutual protection from snow abrasion by reducing wind velocity through eddying (modified from *Arctic Adaptation in Plants*. Canadian Department of Agriculture Monograph #6, by permission of the Minister of Supply and Services Canada, 1994).

Kearney (1982) observed that young seedlings of Engelmann spruce were much less common than subalpine fir seedlings at the timberline. Whether the competitive disadvantage of spruce was caused by lower seed availability or poorer seedling survival was not determined.

AT references Wardle 1968; Eady 1971; Ogilvie 1976; Valentine 1976; Annas and Coupé 1979; Selby 1980; Kearney 1982; Hamilton 1983; Arno and Hammerly 1984; Selby and Pitt 1984; Pojar 1985.

3.1.3 Spruce–Willow–Birch Zone (SWB)

Occurrence of interior spruce White spruce is the most abundant conifer in the SWB, except at the upper (parkland) elevations, where subalpine fir dominates. Engelmann spruce and hybrid white × Engelmann spruce are absent. Lack of Engelmann spruce is a primary feature distinguishing the SWB from the more southerly ESSF zone.

Climatic relations The climate of the SWB is both boreal and subalpine, and, as such, is quite unproductive for tree growth. Many of the high, wide valleys are subject to massive cold air ponding and do not support tree growth. There has been little or no study of spruce growth in the SWB, but climatic limiting factors are presumably linked to the very brief, cool summers, short frost-free period, cold soils, and severe winter conditions.

Site and soil conditions White spruce is most common on submesic to subhygric upland sites where the soils are typically Humo-Ferric Podzols and Dystric Brunisols with Hemimor and Mormoder humus forms on well-drained to moderately well-drained morainal parent materials. Dry, low nutrient ecosystems developed on coarse textured outwash deposits usually only have a minor component of slow-growing white spruce. On wet sites with Gleysolic or Organic soils, white spruce is either absent or scattered and stunted. These low-lying, frost-prone sites, may simply be too cold for white spruce.

Associated vegetation Subalpine fir is the most common associate of white spruce in the SWB. Black spruce (*Picea mariana*), lodgepole pine and trembling aspen (*Populus tremuloides*) are relatively minor associates. Many spruce stands are quite open with a well-developed shrub layer dominated by a variety of willows (*Salix glauca, S. planifolia, S. scouleriana, S. bebbiana)* and scrub birch (*Betula glandulosa*). Other common shrubs include *Potentilla fruticosa, Shepherdia canadensis, Empetrum nigrum, Vaccinium vitis-idaea, V. caespitosum* and *Ledum groenlandicum*. Common herbs are *Linnaea borealis, Festuca altaica, Epilobium angustifolium, Lupinus arcticus* and *Mertensia paniculata*. In addition to the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*, the forest floor contains a diversity of lichens.

Succession and stand development Fire is the most important disturbance factor in the SWB, and charcoal can be found in the soil profile of most stands. Nevertheless, wildfires are less frequent and widespread than in the adjacent BWBS, owing to cooler temperatures and more frequent topographic barriers and fuel discontinuities. Consequently, older stands dominated by white spruce and subalpine fir are more common than in the BWBS. Although spruce can become established immediately following a fire, regeneration occurs slowly at these high elevations, especially where the burned area is extensive and there are few seed sources. Regeneration periods commonly exceed 70 years (Parminter 1983c). Where lodgepole pine and trembling aspen are present, they tend to regenerate more quickly, forming an overstory to white spruce and subalpine fir.

Spruce can be totally eliminated from areas that have been repeatedly burned at short intervals (e.g., steep, south-facing slopes), replaced by fire-adapted trembling aspen or balsam poplar clones or grassland-scrub vegetation. On sites that are too wet or too cold for coniferous trees, a scrub willow–birch community persists.

SWB references Krajina 1975; Birks 1977; Pojar *et al.* 1982; Meidinger and Lewis 1983; Parminter 1983a,b,c, 1984, unpublished; Pojar 1983, 1985; Meidinger *et al.* 1986.

3.1.4 Boreal White and Black Spruce Zone (BWBS)

Occurrence of interior spruce White spruce is the most abundant tree species in the BWBS except in the Fort Nelson area where the poorly drained lowlands are dominated by black spruce. Engelmann spruce is absent, although some white × Engelmann hybrids may be present at the southern margins of the zone where it borders on the SBS.

Climatic relations The BWBS has a long, extremely cold winter and short growing season with long days. Snowpacks are relatively low; the soil freezes deeply and discontinuous permafrost is found in the extreme northeastern part of the zone. Primary climatic limiting factors to spruce growth are thought to be cold (often poorly drained) soils and the short cool growing season (Annas 1983; Butt 1988a). Winter damage caused by low snowpacks and sudden intermittent freeze-thaw cycles is common on newly planted white spruce seedlings, but rarely affects naturally regenerated trees or older plantations (Herring 1989).

Site and soil conditions White spruce can be found in all forested ecosystems of the BWBS and dominates on well-drained to imperfectly drained upland soils. It is uncommon and grows poorly on extremely dry or wet soils. Best growth in the zone occurs on rich, well-drained alluvial soils of the Peace River valley, where white spruce may reach heights of over 50 m (Annas 1983). Within the Cordilleran BWBSdk subzone, soils are mainly Grey Luvisols or Dystric Brunisols on glacial parent materials and Humo-Ferric Podzols in mountainous areas with heavier precipitation. On the Great Plains (BWBSmc or wk) there are extensive areas of flat or rolling terrain with fine textured, stone-free, often saline soils developed from lacustrine or marine parent material. These can be excellent growing sites for white spruce, but tree growth is often inhibited by poor soil aeration or low soil temperatures. The Organic Cryosols (peat soils with permafrost) that cover extensive areas in the northeast are poor growing sites for white spruce.

Associated vegetation Mixed stands of white spruce and trembling aspen (often with a minor component of balsam poplar [*Populus balsamifera*], birch [*Betula papyrifera, B. neoalaskana*] or lodgepole pine) are the most abundant forest cover on warm mesic sites in the BWBS. In areas of colder soils (e.g., on north-facing slopes), pure white spruce or mixtures of white and black spruce dominate. Lodgepole pine is the typical associate of white spruce on coarse textured parent materials, while balsam poplar–spruce mixtures occur frequently on floodplains. Subalpine fir appears often in western subzones, but is uncommon or absent east of the Rockies. Wetland black spruce stands often have a minor component of slow-growing white spruce.

Typical vegetation in boreal white spruce stands includes the common shrubs *Rosa acicularis, Viburnum edule, Shepherdia canadensis, Salix bebbiana*, and *Alnus viridis*, with *Ribes triste* and *Lonicera involucrata* on wet sites, and *Ledum groenlandicum* and *Vaccinium vitis-idaea* on cold sites. Characteristic herbs are *Linnaea borealis, Rubus pubescens, Mertensia paniculata, Petasites palmatus,* *Pyrola asarifolia, Cornus canadensis* and *Calamagrostis canadensis*, with *Equisetum* spp. on wet sites. The thick moss carpet has *Hylocomium splendens, Pleurozium schreberi* and *Ptilium crista-castrensis* and the lichen *Peltigera aphthosa*.

Succession and stand development In the boreal forest generally, white spruce is a late successional or climax species on warmer and drier ecosystems, but functions as a mid-successional species on colder and wetter sites where black spruce would eventually predominate in the absence of disturbance. In interior Alaska and northern Canada where permafrost is widespread, succession tends towards a black spruce climax over most of the landscape, with white spruce climax types restricted to favourable warm sites lacking permafrost (south-facing slopes, dry sunny ridges, river floodplains). In the BWBS of British Columbia, located at the southern margins of the boreal forest, the situation is reversed. Warmer, more productive ecosystems capable of supporting white spruce at climax cover a large proportion of the landscape, while black spruce communities tend to be restricted to unfavourable topographic situations such as north-facing slopes, frost hollows and depressions, as well as to more extensive wetland areas such as the Fort Nelson Lowland. The colder the climate, the more important these black spruce ecosystems become.

The ecosystem processes driving succession, and the important role that fire plays in reversing successional patterns, have been the focus of most of the ecological research taking place in the boreal forest of interior Alaska (Van Cleve and Dyrness 1983; Van Cleve *et al.* 1983), eastern North America (Rowe and Scotter 1973; Heinselmann 1978, 1981; Wein and McLean 1983) and northern British Columbia (Parminter 1983a,b, 1984, all unpublished). This research has shown that the mosaic of vegetation types in the landscape and the state and function of ecosystems is primarily controlled by soil temperature (Van Cleve and Dyrness 1983).

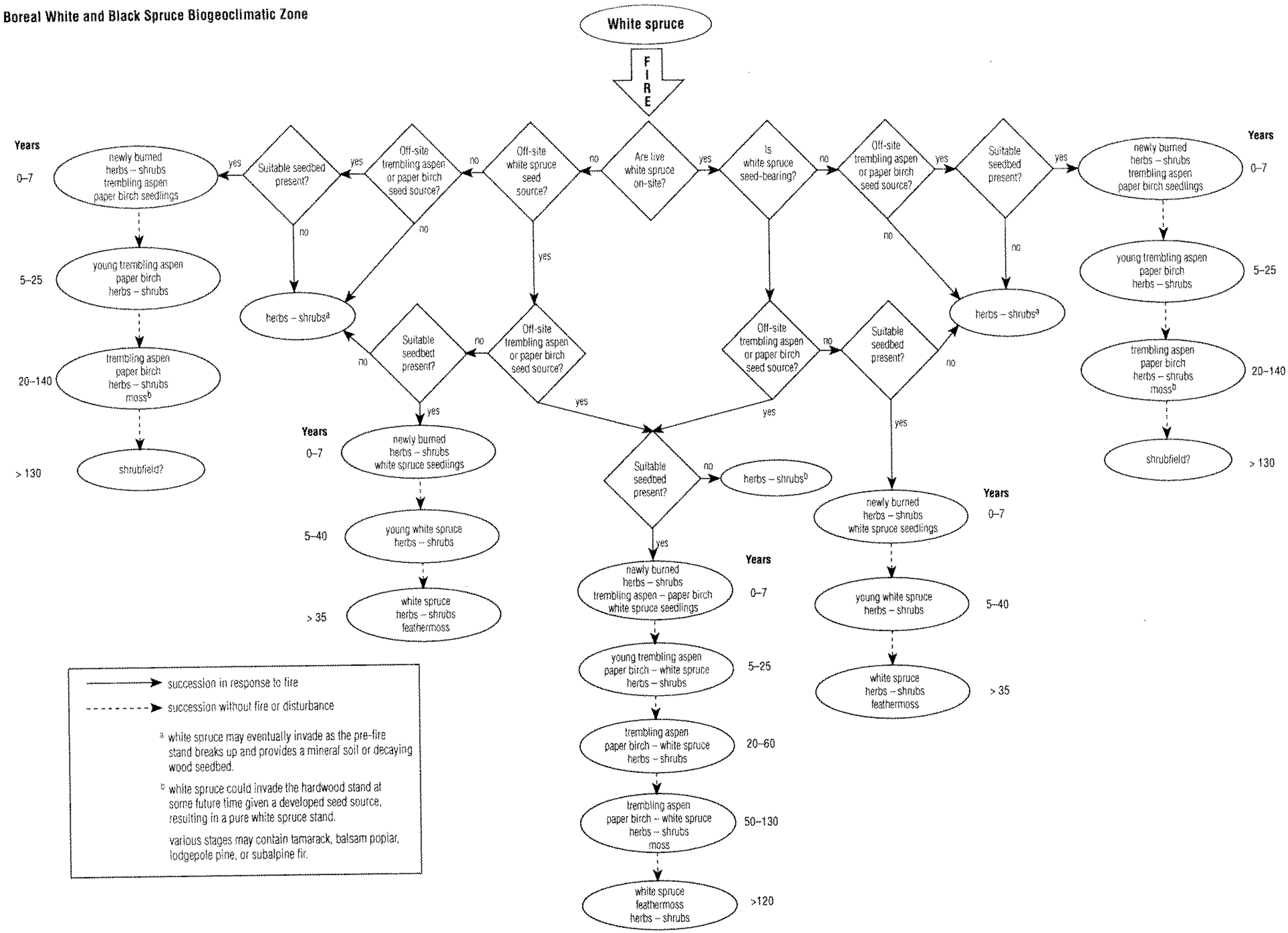
In the absence of fire, a thick mat of organic matter and mosses gradually builds up on the forest floor, insulating the forest floor and in some cases allowing the buildup of a permafrost layer. As the mineral soil becomes colder, nutrient cycling slows down and nutrients become increasingly tied up in the acidic forest floor. Nutrients such as nitrogen and phosphorus become less and less available for plant use, forest productivity declines, and eventually the ecosystem is capable of supporting only an unproductive black spruce community that is extremely tolerant of cold temperatures and low nutrient availability.

Fire is essential for rejuvenating these cold, unproductive forest sites. It consumes the forest floor layers, releasing stored nutrients and allowing heat to penetrate into the mineral soil. The extent and severity of the fire controls the pattern of post-fire succession (Yarie 1983a,b; Rowe 1983). The period of increased productivity due to site warming depends on the degree to which the forest floor is consumed. Species composition of post-fire communities is determined by survival of seed sources and resprouting vegetative structures and the distribution of suitable seedbeds, all of which are tied directly to the total amount of forest floor destroyed and the distribution of burned and unburned patches of vegetation. Figure 20 shows how the availability of white spruce seed sources and suitable seedbeds affects post-fire successional patterns in the BWBS.

Because of recurrent, patchy fires, the vegetation of the BWBS is a mosaic of stand ages and successional stages. The dominant natural fire regime is one of high-intensity crown fires or severe surface fires with rotations probably averaging 50 to 100 years (Heinselmann 1985) and few stands surviving for more than 200 years (Parminter 1983c). White spruce commonly colonizes burned sites, but because it must rely on an off-site seed source it is at a disadvantage relative to lodgepole pine and black spruce (which have serotinous cones), and deciduous trees and shrubs (which regenerate vegetatively). Thus white spruce often comes in gradually beneath an understory of trembling aspen, lodgepole pine, or deciduous shrubs. Repeated burning at short intervals, practiced widely in the BWBS for range enhancement, originally by native Indians and more recently by guide outfitters, ranchers and wildlife management officials (Feller and Thomson 1988), tends to eliminate white spruce in favour of trembling aspen or shrub and herb communities.

Floodplain ecosystems, the most productive growing sites for white spruce, are less commonly affected by fire than other ecosystems. On these sites, periodic flooding is the primary disturbance factor. Succession proceeds from a herb/willow/alder complex to a balsam poplar/white spruce community, and finally to a white spruce climax.

Strong and LaRoi (1983) believe that the morphology of tree root systems may play an important role in determining the direction and rate of succession in boreal forests. Their root excavation studies in Alberta suggest two possible mechanisms: 1) nutrient and water deprivation, and 2) niche partitioning. An example of the former mechanism occurs when white spruce roots grow through the litter and humus layers above the roots of (jack) pine, which established earlier in the mineral soil.



[a] white spruce may eventually invade as the pre-fire stand breaks up and provides a mineral soil or decaying wood seedbed.

[b] white spruce could invade the hardwood stand at some future time given a developed seed source, resulting in a pure white spruce stand.

various stages may contain tamarack, balsam poplar, lodgepole pine, or subalpine fir.

FIGURE 20. Possible successional pathways after fire in a white spruce stand in the BWBS biogeoclimatic zone (from Parminter 1983b, unpublished).

The white spruce is thus in a better position to compete for rainwater and recycled nutrients, and eventually succeeds the pine. Co-existence of white spruce and (balsam) fir in the climax forest is an example of long-term niche partitioning. Fir roots tend to extend deeper into medium and coarse textured soils than those of spruce, allowing the species to grow together with minimal belowground competition. Kimmins and Hawkes (1978) suggest that on some sites, (subalpine) fir may even act as a nutrient pump for the spruce, bringing up mineral nutrients from deeper in the soil profile and redepositing them on the forest floor through litterfall.

BWBS references La Roi 1967; Anderson 1970; Annas 1977; Harcombe 1978; Pojar *et al.* 1982; Meidinger and Lewis 1983; Parminter 1983a,b,c, 1984, unpublished; Jang *et al.* 1987; Delong 1988a; Delong *et al.* 1989, 1990; McKinnon *et al.* 1990.

3.1.5 Sub-Boreal Pine–Spruce Zone (SBPS)

Occurrence of interior spruce White spruce is the second most important tree species in the SBPS, but is greatly outnumbered by lodgepole pine. It occurs most often in the understory of lodgepole pine stands, but scattered stands dominated by white spruce can be found on moist sites. Pure Engelmann spruce is absent from the SBPS, and where hybrid spruce is present, it appears to have mainly white spruce characteristics.

Climatic relations The SBPS is a low-productivity zone for tree growth. It has a rainshadow climate with low rainfall and snowpacks (335–580 mm precipitation), radiative frosts occur throughout the summer, and there are fewer growing degree-days above 5°C than in either the SBS or BWBS zones. Limiting factors to the growth of spruce include strong moisture deficits (dry soils, low humidity) that limit spruce to wetter ecosystems, a short growing season with below-optimum air and soil temperatures, and frequent frosts.

Site and soil conditions Throughout the SBPS, the abundance and productivity of white spruce appears to be directly related to moisture and nutrient availability. In the wetter northern and eastern subzones of the SBPS, white spruce can be found on all but the most xeric Pine-Lichen ecosystems. In these subzones it is common as a minor overstory component in more or less mesic pine stands and occurs frequently in the understory, but growth is poor. However, in the very dry southwestern part of the zone, spruce is uncommon even in the understory of pine stands. The best growth of spruce occurs on rich, subhygric to hygric ecosystems, with Regosolic, Brunisolic or Gleysolic soils on lacustrine or fluvial parent materials. Spruce is also common, but grows poorly, on cold, nutrient-poor sites with high water tables or compact subsurface horizons and thick organic surface horizons.

Associated vegetation Lodgepole pine is the most common tree associated with white spruce in the SBPS. Spruce also appears with trembling aspen in seral stands, and mixed stands of black and white spruce are found on cold low-lying sites. Floodplain stands of black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) and white spruce are uncommon in the zone.

Typical understory vegetation of moist spruce ecosystems includes the shrubs *Lonicera involucrata, Rosa acicularis, Shepherdia canadensis, Juniperus communis, Salix glauca, Betula glandulosa, Ribes lacustre, R. hudsonianum,* and *Viburnum edule*, and the herbs *Cornus canadensis, Linnaea borealis, Epilobium angustifolium, Petasites palmatus, Fragaria virginiana, Equisetum arvense, Calamagrostis canadensis* and *Mitella nuda.* In addition to the usual feathermosses (*Pleurozium schreberi, Hylocomium splendens* and *Ptilium crista-castrensis*) the moss layer characteristically includes *Aulacomium palustre* and *Peltigera, Cladina* and *Cladonia* lichens.

Succession and stand development In the SBPS, both lodgepole pine and white spruce function as "climatic climax" species, reproducing under their own canopy on zonal (mesic) ecosystems (Pojar 1985; Annas and Coupé 1979). However, a combination of widespread fire and the cold, dry climate give lodgepole pine a major competitive advantage over white spruce. Even in the absence of fire, succession to spruce dominance is thought to be very slow. The paucity of spruce in the overstory of young stands, and its presence in the understory of older stands suggests that some amelioration of the microenvironment may be required before spruce will regenerate naturally. On moist or wet sites, spruce is found in all successional stages, but again it becomes increasingly important as stands age. Regeneration in the understory of mature forests is often confined to decaying logs and other raised microsites.

SBPS references Annas and Coupé 1979; Pojar *et al.* 1984; Lewis *et al.* 1986; B.C. Ministry of Forests 1987, unpublished.

3.1.6 Sub-Boreal Spruce Zone (SBS)

Occurrence of interior spruce Interior spruce (mostly hybrid white × Engelmann, some pure white) is a dominant tree species in all subzones.

Climatic relations The SBS climate is continental with cold, snowy winters, and short, relatively cool, moist to somewhat dry, summers. Precipitation ranges from 336 to 931 mm annually, mean annual temperatures are

0.3–4.4°C. Soils are frozen during the winter months, but there is no permafrost. Primary climatic limiting factors to spruce growth are thought to be low soil and air temperatures, the short frost-free season, low humidity and—in drier subzones—lack of available soil moisture (Draper *et al.* 1985; Binder *et al.* 1989; Stathers 1989; Sutherland and Vyse 1989; Macadam 1991).

Site and soil conditions Interior spruce occurs across the full range of topographic and site conditions supporting forest vegetation in the SBS, although in drier subzones (SBSdh, dw, dk) it grows poorly on dry (submesic to very xeric) sites with excessively gravelly, sandy or shallow soils. Major soil types supporting interior spruce include Gray Luvisols, Dystric Brunisols and Humo-Ferric Podzols, but interior spruce also occurs commonly on poorly drained Gleysols and Organic wetland soils. Best growth is found on alluvial or floodplain soils.

Associated vegetation Lodgepole pine is the most common associate of interior spruce in the SBS. Subalpine fir is abundant in cooler, moister subzones (SBSmw, mm, mk, mc, wk, vk), while trembling aspen and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) are often found with spruce in warmer, drier and more southerly subzones (SBSdh, dw, dk, mw, mk). Black cottonwood is the main associate of interior spruce on active floodplain sites, and mixtures of white and black spruce are common in wetlands.

Typical understory vegetation in mesic spruce stands includes a moderately well-developed shrub layer dominated by *Vaccinium membranaceum, Rubus parviflorus, Viburnum edule, Rosa acicularis, Alnus viridis*, a variety of herbs (*Cornus canadensis, Clintonia uniflora, Rubus pubescens, Rubus pedatus, Arnica cordifolia, Smilacina racemosa, Orthilia secunda, Aralia nudicaulis*) and a well-developed carpet of feathermosses (*Pleurozium schreberi, Ptilium crista-castrensis, Hylocomium splendens, Rhytidiadelphus triquetrus*). Wetter spruce sites have *Lonicera involucrata, Oplopanax horridus, Ribes lacustre, Cornus sericea, Gymnocarpium dryopteris, Tiarella trifoliata, Equisetum arvense* and *Mnium* mosses. Characteristic species of spruce bog, fen or swamp ecosystems are *Salix* spp., *Betula glandulosa, Ledum groenlandicum, Carex* spp. and *Sphagnum* moss.

Succession and stand development Interior spruce is considered a climatic climax tree species in the SBS. In dry subzones it is the most shade-tolerant tree species present and in the absence of disturbance it will eventually replace associated shade-intolerant tree species. In moister, cooler subzones, spruce gradually loses dominance to subalpine fir as stands age. However, because of the ubiquitous fire history within the SBS, stands reaching an advanced successional state are extremely rare, and most mature stands contain species that cannot regenerate efficiently beneath their own canopy (Pojar *et al.* 1984).

Vegetative succession following clearcut logging, slash-burning, and mechanical site preparation in the SBS near Prince George is described by Eis (1981) and Hamilton and Yearsley (1988). These authors found major differences in species composition and rate of vegetation development with ecosystem (site series). Mesic and drier ecosystems were invaded by *Epilobium angustifolium* and developed much more slowly than moister richer Devil's club and Alluvium/Horsetail ecosystems, which were dominated by shrubs present in the understory before logging. The heavy shrub growth on these wetter sites inhibits spruce regeneration and leads to open stands with low tree stocking.

SBS references Garman 1957; Illingworth and Arlidge 1960; Revel 1972; Wali and Krajina 1973; Kimmins and Hawkes 1978; Annas and Coupé 1979; Eis 1981; Meidinger and Pojar 1983; Pojar *et al.* 1984; Lewis *et al.* 1986; B.C. Ministry of Forests 1987, unpublished; Delong *et al.* 1986, 1987a,b; Hamilton and Yearsley 1988; Meidinger *et al.* 1988.

3.1.7 Mountain Hemlock Zone (MH)

Engelmann spruce can be found sporadically in inland portions of the MH (MHmm2 variant) particularly towards the eastern limits of the zone where it borders on the ESSF (Klinka *et al.* 1984). In northern British Columbia, Sitka × white × Engelmann or Sitka × white hybrids, known as "Roche" spruce, are present in eastern portions of the zone.

3.1.8 Engelmann Spruce–Subalpine Fir Zone (ESSF)

Occurrence of interior spruce Interior spruce is one of the two dominant tree species within the ESSF. Over most of southern British Columbia, spruce dominates the canopy of mature stands, while subalpine fir is most abundant in the understory; however, at the upper elevations of the zone, particularly in the north and in wet, heavy snowfall areas, subalpine fir dominates and spruce is present only as a secondary or minor component.

In southern British Columbia, the spruce is pure Engelmann, but, moving north, white spruce characteristics become increasingly evident, first only at the lowest elevations of the zone, then gradually throughout the zone. At the northern limits of the ESSF, where it merges with the SWB, Engelmann spruce characteristics are rare.

Climatic relations Because the ESSF is so widely distributed, there is considerable climatic variation. Throughout, it has a cold, continental climate with a short cool growing season and a long snowy winter. Recorded mean annual temperatures range from -2 to +2°C. Precipitation ranges from about 400–500 mm in some rainshadow areas to as much 2200 mm. Most of this precipitation falls as snow, covering the ground for 5–8 months of the year. Climatic limiting factors to the growth of spruce in the ESSF are primarily the short growing season, cold soils and low nighttime air temperatures, and, in some areas, snow, wind or frost damage. Particularly at upper elevations, a combination of climatic stresses contribute to poor spruce establishment and growth.

Site and soil conditions Spruce occurs over the full range of forested site conditions within the ESSF, but, as in other zones, it is uncommon and grows poorly on submesic and drier sites in dry climate subzones and on the most xeric sites in the wetter subzones. Best growth of spruce occurs in lower slope seepage habitats (widespread in wetter subzones) or in rich alluvial ecosystems (generally of minor extent) (Klinka *et al.* 1982). In the mountainous topography of the ESSF, colluvial and morainal soils dominate, and shallow soils over bedrock are common. Most soils in wet subzones are Podzolic; in dry subzones Brunisolic. Humus forms are typically acidic, slowly decomposing Hemimors. Melting snowpacks are an important source of soil moisture during the growing season, especially in areas with low summer precipitation.

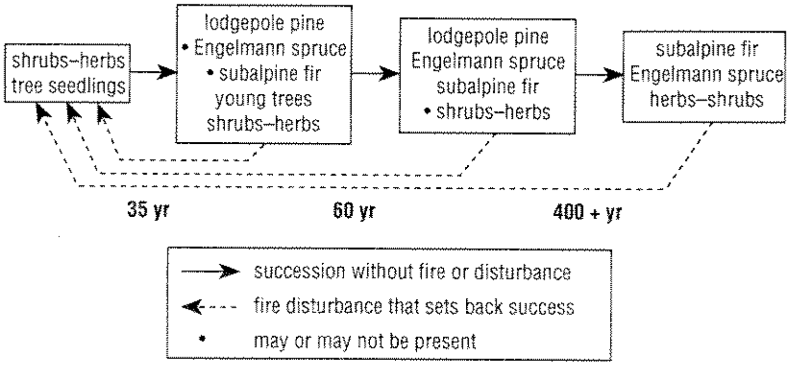
Associated vegetation Subalpine fir is ubiquitous in the ESSF and is the most common associate of spruce throughout. Lodgepole pine is the most common seral species. Deciduous species such as trembling aspen, paper birch and black cottonwood are present, but uncommon. Whitebark pine, limber pine and alpine larch (the latter two in southeastern British Columbia only) can be found in association with spruce, but tend to occur on the driest ecosystems, usually at high elevations, where spruce is not abundant. At low elevations in the zone, spruce may mix with Douglas-fir, western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*) and western white pine. Mountain hemlock and amabilis fir (*Abies amabilis*) are also found with spruce in the ESSF, principally adjacent to the MH zone.

The dominant plant community in the ESSF has an understory of ericaceous shrubs, mainly *Rhododendron albiflorum*, *Vaccinium membranaceum*, and *Menziesia ferruginea*, with *Vaccinium ovalifolium* in high-precipitation areas and *Vaccinium scoparium* in dry areas. *Ribes lacustre*, *Oplopanax horridus*, and *Lonicera involucrata* are common shrubs on moist to wet sites. Herbs characteristic of the ESSF forest include *Valeriana sitchensis*, *Gymnocarpium dryopteris*, *Rubus pedatus*, *Streptopus roseus*, *Veratrum viride*, *Athyrium filix-femina*, *Cornus canadensis*, *Lycopodium annotinum*, *Tiarella* spp. and *Arnica cordifolia*. Dominant bryophytes are *Pleurozium schreberi*, *Dicranum* spp., *Barbilophozia* spp., *Rhytidiopsis robusta*, and *Brachythecium* spp. Lichens are abundant on the forest floor and include *Peltigera* spp., *Nephroma arcticum*, and *Cladonia* spp.

The most productive ecosystems for interior spruce in the ESSF belong to the *Valeriana sitchensis–Ribes lacustre* association (Klinka *et al.* 1982).

At the upper parkland elevations of the ESSF, closed forest and tree islands of spruce and subalpine fir are interspersed with moist herb meadows and drier ericaceous heath. The meadows typically include the following herbs: *Valeriana sitchensis*, *Veratrum viride*, *Senecio triangularis*, *Lupinus arcticus*, *Thalictrum occidentale*, *Epilobium angustifolium*, *Pedicularis bracteosum*, *Castelleja miniata*, *Erigeron peregrinus*, *Carex* spp. and *Luzula* spp. Subalpine heath includes *Empetrum nigrum*, *Cassiope mertensiana*, *C. tetragona*, *Phyllodoce empetriformis*, *P. glandulifera*, and *Vaccinium caespitosum*.

Succession and stand development A typical succession in the ESSF follows the sequence shown in the diagram below (from Parminter 1983b, unpublished).



Fire affects all parts of the ESSF, but topographic and fuel discontinuities, as well as the short, cool and moist growing season, cause fires to be smaller and less frequent than at lower elevations. Estimates of the average fire interval in the ESSF range from 150 years (Arno 1980) to 300–400 years (Romme 1982). Because recovery from fire is slow, a diversity of forest cover types will be maintained even with relatively infrequent fire (Habeck and Mutch 1973). Fire occurs only rarely in wet ESSF subzones lying above the ICH zone; in these subzones, the landscape is dominated by all-aged stands of subalpine fir with scattered spruce and sometimes mountain hemlock. Subzones in low-precipitation areas above the MS, IDF and SBS zones have been greatly affected by fire; these subzones have extensive areas dominated by lodgepole pine, mid-successional stands dominated by spruce, and infrequent pockets of relatively pure, all-aged subalpine fir.

There is some disagreement over the successional role of spruce in the ESSF. Subalpine fir seedlings and saplings far outnumber spruce seedlings in understory layers of mixed stands throughout the ESSF, and the dominance of subalpine fir increases as stands age. Pre-eminence of spruce over subalpine fir clearly seems linked to a history of fire. Day (1972) and others (e.g., Wirsing and Alexander 1975) have argued that the presence of spruce is fire-dependent: in the absence of fire, spruce is unable to regenerate and will eventually be replaced by pure all-aged stands of low-vigour subalpine fir.

Other researchers contend that the relative abundance of subalpine fir in understory layers simply reflects the dissimilar regenerative strategies of the two species (Knapp and Smith 1982; Veblen 1986b). Subalpine fir is highly successful at regenerating in the undisturbed forest understory. Large numbers of seedlings and saplings are present below the canopy, but because the species is short-lived and susceptible to decay, few ever reach the overstory. In contrast, spruce produces only a few seedlings on specialized microhabitats; for example, small windthrow openings. However, spruce is long-lived and has greater resistance to decay, and a higher percentage of seedlings survive to an advanced age. Thus, a component of spruce will be maintained in the stand indefinitely, even in the absence of fire.

Krajina (1969, 1975) offers an alternative viewpoint, specific to those areas where Engelmann and white spruce hybridize. In his view, Engelmann spruce is very well adapted to the high-elevation, heavy snow environment of the ESSF, while white spruce is better adapted to low-elevation environments. In those areas of the ESSF where pure Engelmann spruce occurs, spruce has equal or greater presence than subalpine fir; but where white spruce genes prevail, subalpine fir has a competitive advantage.

The successional role of spruce in the ESSF has practical significance for managers concerned about using prescribed fire and wildfire to maintain ecological diversity and ecosystem health within parks, wilderness areas and ecological reserves (Day 1972; Lotan *et al.* 1985). Given the wide geographic range and climatic variability of the ESSF within Canada and the corresponding spruce-fir type within the adjacent United States, it seems most likely that the competitive relationship between spruce and subalpine fir is not absolute, but varies from place to place with local climatic and physiographic conditions, with the fire history of the area, and with variations in the genetic makeup of both species.

Tisdale *et al.* (1966) studied primary succession on glacial moraines ranging in age from 50 to 180 years in the ESSF near Mount Robson. Engelmann spruce was the only tree to regenerate on the newly deglaciated soils.

ESSF references Arlidge 1955; Krajina 1975; Annas and Coupé 1979; Selby 1980; Klinka *et al.* 1982; Utzig *et al.* 1986; Aplet *et al.* 1988; Lloyd *et al.* 1990; Yole *et al.* 1989.

3.1.9 Montane Spruce Zone (MS)

Occurrence of interior spruce Spruce is the second most abundant species in the zone, after lodgepole pine. Engelmann × white hybrids predominate, but pure Engelmann can be found at higher elevations and white spruce occurs in some northern parts of the zone.

Climatic relations The MS climate is intermediate between that of the IDF and ESSF. It is cool continental with relatively long, cold winters and moderately short, warm summers. Mean annual temperatures are 1–4°C. Mean annual precipitation ranges from 380 to 900 mm, with snowpacks covering frozen soils for approximately 6 months each year. Primary climatic limiting factors to spruce growth are thought to be moisture and heat stress, and the short frost-free growing season (Stathers 1989; Black and Mitchell 1991a).

Site and soil conditions Interior spruce occurs across the full range of topographic and site conditions supporting forest vegetation in the MS, but it has very poor vigour on xeric ecosystems within the driest MSxk subzone. Both the abundance and productivity of spruce are highest on moist, rich sites. Dystric Brunisols with thin Hemimor humus forms developed on loamy to clayey morainal parent materials are the most common soils in the MS. Humo-Ferric Podzols and Gray Luvisols are also common.

Associated vegetation A distinctive feature of the MS is the prevalence of young and maturing stands of lodgepole pine that have formed following wildfire. Spruce, together with some subalpine fir, dominates later successional stands, especially on moister sites. Douglas-fir, trembling aspen, and western larch (*Larix occidentalis*—in the Rocky Mountain Trench only), are common seral tree species.

Characteristic understory plant species in spruce stands are *Lonicera utahensis, Paxistima myrsinites, Vaccinium membranaceum, V. scoparium, Alnus incana, Calamagrostis rubescens, Arnica cordifolia, Linnaea borealis,* and *Pleurozium schreberi*. *Ledum glandulosum*, *Ribes lacustre* and *Equisetum arvense* typically occur in wetter ecosystems; *Juniperus communis* and *Arctostaphylos uva-ursi* are found on dry sites.

Succession and stand development Spruce is the dominant climax tree species in the MS. It regenerates in its own shade except on very moist, productive ecosystems, where it appears to regenerate only on disturbed microsites or rotting logs. On the driest ecosystems, spruce apparently requires at least partial shade for regeneration. Wildfires within the MS are typically stand-destroying and have created extensive areas of even-aged lodgepole pine on mesic and drier sites. Reduced frost and surface drying beneath the lodgepole pine canopy apparently enables spruce and subalpine fir seedlings to become established, but succession towards a spruce-fir climax on such sites is very slow.

Cattle grazing and seeding of domestic grasses are widespread within the MS and have a major impact on coniferous regeneration and stand development (Clark and McLean 1978; McLean and Clark 1980).

MS references McLean 1970; Mitchell *et al.* 1981a,b; Mitchell 1983; Utzig *et al.* 1986; Lloyd *et al.* 1990; Webber 1990.

3.1.10 Bunchgrass Zone (BG)

No spruce present.

3.1.11 Ponderosa Pine Zone (PP)

White spruce or white × Engelmann hybrids are found only rarely within the PP zone in cool, moist, sheltered situations such as on steep north-facing canyon headwalls (W. Erickson, pers. comm., October 1989).

3.1.12 Interior Douglas-fir Zone (IDF)

Occurrence of interior spruce Hybrid Engelmann × white spruce is a secondary tree species in the IDF, occurring mainly in wetter subzones and at higher elevations transitional to the MS, SBS or ESSF.

Climatic relations The IDF lies in the rainshadows east of the Coast, Cascade and Columbia Mountains and has a dry climate, with fairly long, warm growing seasons and cool winters. Snowpacks are low or intermittent. Mean annual temperatures are 1.8–9.5°C with precipitation typically in the 300–750 mm range. The main limiting factors to the growth of spruce in this zone are the shortage of moisture and high evapotranspirative stresses during the warm, dry growing season. Growing season frosts (Stathers 1989; Sutherland and Vyse 1989) can also cause regeneration problems, particularly because spruce tends to occur in the most frost-prone sites within the IDF.

Site and soil conditions Spruce is found on moist to wet sites, typically on sheltered north-facing aspects or in moist draws and gullies where evapotranspirative stresses are minimized. Soils are generally Orthic and Gleyed subgroups of Brunisols and Gray Luvisols formed from base-rich bedrock, with relatively high nutrient status.

Associated vegetation The most common associate of spruce is Douglas-fir, which dominates the zone. Lodgepole pine is abundant in the IDF but tends to be present only in small amounts on the wetter spruce sites. Western redcedar, western larch, and grand fir (*Abies grandis*) occur together with spruce, particularly in the southeastern part of the zone. Trembling aspen, paper birch and black cottonwood are common seral species.

Mixed shrub or horsetail-dominated plant communities are typical of moist, rich ecosystems in which spruce can be found. Common shrub associates include *Ribes lacustre*, *Lonicera involucrata*, *Cornus sericea*, *Rosa acicularis*, *Symphoricarpos albus* and *Acer glabrum*. The well-developed herb layer contains *Linnaea borealis*, *Cornus canadensis*, *Aralia nudicaulis*, *Actaea rubra* and *Osmorhiza chilensis*, together with *Equisetum* and *Carex* spp. on wetter sites. Bog forests with *Sphagnum* spp., *Ledum groenlandicum*, and *Gaultheria hispidula* are infrequent but usually have a tree canopy of pure spruce.

Succession and stand development Spruce, along with western redcedar and grand fir, is among the most shade-tolerant tree species in the IDF, and generally regenerates beneath its own canopy, becoming more abundant as stands age. It apparently requires some shade for successful establishment on subhygric and drier sites.

Frequent ground fires were historically the most important form of disturbance to IDF forests. Such fires discouraged establishment of fire-sensitive species such as spruce, creating open stands of fire-resistant Douglas-fir intermixed with grassland. Spruce tends to be most abundant in moist, protected habitats and at higher elevations where ground fires are least likely to occur. However, current fire suppression practices have had a major impact on the natural fire regime (Parminter 1978). Studies in other western North American ecosystems with a natural regime of frequent ground fires show that continued fire suppression has created a shift in species composition towards more shade-tolerant, fire-sensitive tree species such as spruce (Kilgore 1981; van Wagtendonk 1985).

IDF references Tisdale and McLean 1957; McLean and Holland 1958; Beil 1969, 1974; McLean 1970; Parminter 1978; Annas and Coupé 1979; Mitchell *et al.* 1981a,b; Utzig *et al.* 1986; Steen and Roberts 1988; Lloyd *et al.* 1990.

3.1.13 Coastal Douglas-fir Zone (CDF)

No interior spruce present.

3.1.14 Interior Cedar–Hemlock Zone (ICH)

Occurrence of interior spruce Interior spruce is a common secondary component of ICH forests. It is most abundant in the northern or eastern parts of the ICH, close to the SBS (Krajina 1969) or at high elevations bordering the ESSF, and least abundant in drier ICH subzones (ICHxw, dm, dw, dk) bordering the IDF. White and Engelmann spruce and their hybrids are all present. Engelmann spruce dominates in southeastern British Columbia, particularly at high elevations, while white spruce dominates in the north. In the coast-interior transition of northwestern British Columbia (ICHvc and mc subzones), interior spruce forms hybrids with Sitka spruce.

Climatic relations The humid climate of the ICH includes some of the most productive growing sites for interior spruce in British Columbia and Canada (Krajina 1969; Ketcheson *et al.* 1983). In dry, warm subzones of the ICH, spruce regeneration and growth may be inhibited by the high evapotranspirative stresses that accompany the warm summer weather. In wetter ICH subzones, where the climate is highly favourable to tree growth, spruce may be inhibited more by competition from other conifers, deciduous trees, shrubs and herbs than by climatic factors. As a consequence, spruce is often most abundant in areas of cold air ponding where it has a competitive advantage over other species. Heavy snow loads, cool air temperatures, cold wet soils and frost damage are thought to restrict regeneration performance of spruce in the ICHmc and vc subzones of northwestern British Columbia (Beaudry and McCulloch 1989).

Site and soil conditions Throughout the southern portion of the ICH, spruce is most abundant in cool, moist shaded areas, such as north-facing slopes, and in low-lying areas subject to temporary flooding and cold air ponding. In northern subzones, it occurs over a much wider range of sites and soils, but again it dominates only on the cooler, moister sites. As in other zones, best growth of spruce occurs on moist rich "Devil's-club" ecosystems and on active floodplains. Orthic Humo-Ferric Podzols with well-developed Hemimor humus forms are the zonal soils of the ICH, but spruce grows best and most abundantly on azonal soils: Regosols, Gleysols and gleyed subgroups of Podzols and Brunisols. Forested wetlands with Organic soils are less common in the ICH than in other interior zones, but, where they occur, they often contain a component of poorly growing interior spruce.

Associated vegetation The ICH has a greater diversity of tree species than any other interior zone. Western hemlock and western redcedar are the climax dominants of the zone and interior spruce often occurs as a secondary stand component with these species. To the north, subalpine fir is a major associate. Black cottonwood, lodgepole pine, trembling aspen and paper birch are found with spruce in seral communities throughout most of the zone. In the central and southern ICH, spruce may also occur in association with Douglas-fir, western larch, western white pine and grand fir.

A typical spruce or redcedar-spruce stand on a seepage ecosystem has a diverse shrub layer dominated by *Oplopanax horridus*, *Ribes lacustre*, *Cornus sericea*, *Acer glabrum*, *Rubus parviflorus*, *Viburnum edule*, and *Lonicera involucrata*. Characteristic herbs include *Gymnocarpium dryopteris*, *Athyrium filix-femina*, *Tiarella unifoliata*, *Viola glabella*, *Circaea alpina*, *Streptopus* spp., *Osmorhiza chilensis*, *Dryopteris assimilis* and *Actaea rubra*. Swampier sites may include *Lysichiton americanum*, *Equisetum* spp. and *Carex* spp. The moss layer contains *Mnium* spp., *Rhytidiadelphus triquetrus* and *Hylocomium splendens*.

Seral ecosystems on mesic sites in the northern ICH have a mixed overstory of spruce, subalpine fir, lodgepole pine, paper birch and trembling aspen. The following shrubs are typical: *Rubus parviflorus*, *Viburnum edule*, *Rosa acicularis*, *Paxistima myrsinites*, *Amelanchier alnifolia*, *Shepherdia canadensis*, *Alnus viridis* and *Vaccinium membranaceum*. Major herbs include *Cornus canadensis*, *Clintonia uniflora*, *Aralia nudicaulis*, *Lathyrus nevadensis*, *Rubus pubescens*, *Smilacina* spp., *Orthilia secunda*, *Osmorhiza chilensis*, and *Petasites palmatus*. The moss carpet is dominated by *Rhytidiadelphus triquetrus*, *Ptilium crista-castrensis*, *Pleurozium schreberi* and *Hylocomium splendens*.

Succession and stand development Successional patterns in the ICH are more complex than in other interior zones because of the diversity of tree species of differing shade tolerances and life histories. Interior spruce is only of medium tolerance, and generally requires small openings or mineral soil to reproduce. Thus on most zonal sites in the ICH it acts as an early to mid-successional species, giving way to western hemlock and/or western redcedar at climax. Individual spruce dominants often persist in old-growth hemlock-redcedar stands, but spruce does not regenerate successfully in the understory.

On sites affected by cold air ponding or high water tables, where hemlock or redcedar grow poorly, spruce is more likely to continue regenerating beneath the tree canopy. However, in the northern ICH, spruce may eventually be replaced by subalpine fir as the climax dominant on cold sites.

In much of the ICH, except in the driest, southern subzones and on warm, dry ecosystems in moister, cooler subzones, spruce is able to establish as a pioneer following disturbance. It is a common species on naturally regenerated openings, and is the leading species planted after clearcut logging. Establishment can be slow on moist, rich ecosystems where deciduous trees and shrubs tend to dominate the early stages of succession. Under these circumstances, spruce, together with western hemlock, redcedar and subalpine fir, may gradually replace an overstory of black cottonwood, trembling aspen and paper birch.

Pure stands of lodgepole pine or trembling aspen, established following repeated fire, are not as widespread in the ICH as in drier interior zones, but they are locally common in wide low-elevation valleys or plateaus and on south-facing ridges. In areas such as these, spruce is rare or absent because seed sources have been eliminated by frequent fire.

ICH references Bell 1965; Smith 1965; Hamet-Ahti 1965; Annas and Coupé 1979; Pojar *et al.* 1982; Ketcheson *et al.* 1983; Haeussler *et al.* 1985; Houseknecht *et al.* 1986; Utzig *et al.* 1986; B.C. Ministry of Forests 1987, unpublished; Fischer and Bradley 1987.

3.1.15 Coastal Western Hemlock Zone (CWH)

White spruce is absent from the CWH, but Engelmann spruce can be found in eastern portions of the CWHms subzone, which occupies the coast-interior transition of southwestern British Columbia (Klinka *et al.* 1982). There is some evidence that occasional hybrids between Sitka and Engelmann spruce may occur in this area, but most of the individuals present show little evidence of introgression (Klinka *et al.* 1982). This is in strong contrast to the Sitka × white × Engelmann hybrid swarm found at the eastern margins of the CWHws subzone in the Skeena and Nass river drainages (Haeussler *et al.* 1984).

The study by Klinka *et al.* (1982) determined that some of the largest Engelmann spruce trees and the most productive ecosystems for Engelmann spruce in British Columbia are found in the CWHms subzone. The climate in this subzone is mild for interior spruce, with a strong oceanic influence, abundant precipitation, and a long growing season. Soils on the most productive ecosystems are developed from alluvial parent materials and are deep loamy textured Dystric Brunisols or Humo-Ferric Podzols with Mull or Moder humus forms, subhygric moisture regimes and eutrophic soil nutrient regimes. Floristically, the ecosystems were classified as belonging to the *Athyrium filix-femina–Oplopanax horridus–Thuja plicata–Abies amabilis* association. Site indices for Engelmann spruce on the ecosystems studied were exceptionally high, ranging from 35 to 47 m at 100 years.

3.2 Environmental Factors

Tree growth is the combined expression of a tree's genetic potential and its environmental influences. The genetic variability and potential growth rates of interior spruce are discussed earlier in this report. Plant survival and growth depends on the availability of the primary resources—light, water, nutrients, and the gasses necessary for photosynthesis and respiration. Plant performance may also be affected by conditions in the environment such as soil and air temperature, rooting depth, soil porosity and density, or wildlife browsing. This section will discuss the light, water, temperature, nutrient, and soil relations of white and Engelmann spruce and show how an understanding of spruce ecophysiology can improve forest management, especially regeneration silviculture practices.

Summarizing how trees respond to specific environmental factors is made difficult by the fact that not all growth parameters (e.g., height, diameter, root length, biomass) respond in the same manner to changes in light, water, nutrient, or temperature levels. For example, spruce seedlings growing at low light levels often show similar height growth to trees growing in full sunlight, but their diameter growth may be greatly reduced. To measure height only, and conclude that light competition is not a problem, could be incorrect.

Another difficulty in reviewing literature on the physiological ecology of spruce is the extensive use of terminology that may not be familiar to the reader. However, to ensure that the topic is reviewed correctly, and that statements will not be misinterpreted, the original terminology used in the papers cited must be retained.

3.2.1 Light relations

The important characteristics of light are its intensity, quality, and duration (or photoperiod). Light is one of the major driving forces in photosynthesis.

White and Engelmann spruce behave similarly in their response to light. Photosynthesis increases with increasing light intensity up to a point (the saturation point) after which further increases in light intensity do not increase net photosynthesis. In general, the saturation point is reached at ¼ to ½ of full sunlight on a clear day. In field experiments near Prince George and Williams Lake, maximum summer photosynthesis rates for white and interior spruce seedlings were reached at photosynthetic photon flux densities (PPFD)[4] of 600 μmol/m^2•s and 400 μmol/m^2•s, respectively, or between 30 and 20% of full sunlight[5] (Lister and Binder 1985; Binder *et al.* 1987; Bassman 1989). Further increases in PPFD (light intensity) did not increase photosynthesis. In the eastern United States, Clark (1961) found similar results for white spruce. There are no data available on light saturation of pure Engelmann spruce in British Columbia. In Colorado, high-elevation open-grown Engelmann spruce seedlings saturated at 4000 to 5000 foot-candles (800–1000 μmol/m^2•s) (Ronco 1970b). In Wyoming, understory Engelmann spruce saturated at 1060 μmol/m^2•s (Knapp and Smith 1982).

Young white spruce are able to achieve optimum height growth if they receive on average about 50% or more of full sunlight. Logan (1969) reported no difference in height growth of white spruce between 45 and 100% of full light. Gustafson (1943) grew white spruce for 8 years in ¼, ½, and ¾ full sunlight. Seedlings in ½ and ¾ sunlight were about equal in height growth; seedlings at ¼ sunlight were considerably shorter. In another study, height growth of white spruce at 60% full sunlight was twice that of seedlings under 20% sunlight (Eis 1967b).

Although young white spruce seedlings can achieve optimal height growth at around 50% of full sunlight, growth is greatest at full light intensity for trees older than 10 years (Logan 1969; Eis 1970). Eis (1970) found that reducing light by 50% decreased height growth by 25% and shoot weight by 50% in 10-year-old trees. White spruce growing under trembling aspen are smaller in both height and diameter compared to free growing spruce (Johnson 1986; Yang 1989).

Diameter growth is more sensitive to light levels than height growth. In a greenhouse study, Brix (1972) found no difference in white spruce height growth, but a great improvement in diameter growth, when light levels were increased from 450 to 1000 foot-candles (86 to 192 μmol/m^2•s). Light intensities above 60% of full sunlight resulted in better white spruce diameter growth (Eis 1967b). Several field studies have shown that the diameter or basal area of newly planted white spruce increases after brush control but height does not (Brand and Janas 1988; Coates *et al.* 1991). Binder *et al.* (1987) observed that white spruce seedlings in heavy shade grew taller than lightly shaded or unshaded seedlings, but lost considerable lower needle volume and had significantly lower dry weight when harvested.

The light compensation point of a plant is that light intensity at which net photosynthesis equals zero; that is, the plant's loss of energy through respiration is exactly balanced by photosynthetic gains. Plants subjected to light levels below the compensation point for extended periods cannot survive. For white spruce the compensation point appears to be between 2–6% of full sunlight (40–100 μmol/m^2•s). When air temperatures are below 10°C, the compensation point is at the lower end of the range; however, in the early morning, positive rates of net photosynthesis can take place at light intensities as low as 25 μmol/m^2•s (Binder *et al.* 1987). Place (1955) observed that naturally established white spruce seedlings died within 2–3 years if light levels were as low as 12% of full sunlight. In another experiment, no white spruce survived at 15% full sunlight (Eis 1970).

There are no data on the light compensation point of Engelmann spruce in British Columbia. In Wyoming, the compensation point of understory Engelmann spruce was between 60 and 80 μmol/m^2•s (Knapp and Smith 1982). In a controlled environment, the Engelmann spruce compensation point was near 80 μmol/m^2•s at 20°C soil temperature (Delucia 1986). In this experiment, reducing soil temperature to near 0° increased the compensation point; that is, more light was required to achieve positive photosynthesis.

Both white and Engelmann spruce require light for germination (Dobbs 1972). In the field, partial shade is best for germination and initial survival of spruce (Zasada and Gregory 1969; Dobbs 1972). Shading reduces the chance of early mortality from either drought stress or high surface temperatures (Day 1963).

Too much light may reduce spruce survival and growth under certain conditions. In Colorado, solarization (chlorophyll destruction) has been observed in Engelmann spruce exposed to high light intensities at elevations above 3000 m (Ronco 1970a, 1975). In a clearcut near Prince George, Binder *et al.* (1987) noted that the top surfaces of white spruce needles were more brownish yellow on open-grown seedlings than on shaded seedlings. They were unable to detect any differences in

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[4] Photosynthetic photon flux density is a measure of the intensity of light in the 400 to 700 nm wavelength bands. The unit of measure in current use is μmol/m^2•s: 1.0 μmol/m^2•s = 1.0 μE/m^2•s = 10 lux = approx. 5.2 foot-candles.

[5] In the Prince George area, the intensity of clear sunlight between noon and 1400 hours is approximately 2000 μmol/m^2•s; a bright cloudy day would be in the range of 1000 to 1500 μmol/m^2•s; a dark rainy day about 600 μmol/m^2•s (W. Binder, pers. comm., August, 1990).

photosynthetic rate between chlorotic and healthy green trees in the field. However, at a nursery plantation near Prince George, the photosynthetic rate of yellow trees was 3–5 times less than that of green trees (W. Binder, pers. comm., August 1990). Solarization is thought to be at least partly responsible for the chlorosis in these two Prince George examples, but nutrient limitations may also be involved. It is unlikely that solarization is an operationally significant problem in British Columbia because the intense solar radiation experienced at high elevations in Colorado is rarely found here.

The photoperiod, or daylength, influences many aspects of spruce growth and phenology. It can affect height and diameter growth, shoot/root ratios, timing of budset and flushing, dormancy induction, and cold-hardiness (Arnott 1974, 1979, 1982, 1985; Arnott and Mitchell 1982; Colombo *et al.* 1982; Arnott and Simmons 1985; Hawkins and Draper 1988; Hawkins and Hooge 1988). Most research on the effect of photoperiod on interior spruce has been done for nursery management purposes; for example, to induce cold-hardiness or to obtain seedlings with optimal caliper and shoot/root ratio. Under field conditions, the effects of varying photoperiod are most readily observed in provenance studies (see Section 2.8, Genetics and Tree Improvement).

There is considerable research to suggest that light quality (the proportion of red, far-red, blue, and other wavelengths received by the plant) influences plant morphology and physiology (Morikawa and Asakawa 1976; Morgan and Smith 1981; Hoddinott and Hall 1982; Corre 1983; Kwesiga *et al.* 1986); however, no information specific to either white or Engelmann spruce has been published.

3.2.2 Water relations

Xylem pressure potential (XPP) is a measure of the water status of a plant. The more difficult it is for a plant to extract water from the soil, the more negative the XPP reading. Once the XPP of a plant drops below a threshold level the stomates (leaf pores) close, causing leaf conductance (the amount of CO_2 going into the plant) to drop to zero, and photosynthesis to cease. Stomatal closure in spruce is affected by a variety of environmental factors other than soil moisture levels. These include soil and air temperature, relative humidity, the vapour pressure deficit (VPD: the difference between the moisture content of the air and the leaf), and light intensity (Kaufmann 1976, 1979, 1982a,b; Goldstein *et al.* 1985; Binder *et al.* 1987).

The XPP at which spruce stomates close also varies somewhat by season, with more negative potentials required later in the growing season (Binder *et al.* 1987; Grossnickle and Blake 1987). This suggests that osmotic adjustment takes place during the growing season, enabling spruce to continue photosynthesis at greater water stress later in the summer.

White spruce have been reported to close their stomata at XPP values of -1.6 MPa[6] (Lopushinsky 1969; Binder *et al.* 1987) and -1.7 to -1.8 MPa (Goldstein 1981, cited by Goldstein *et al.* 1985). Grossnickle and Blake (1987) report white spruce turgor loss (a similar measurement to reporting when stomates close) at -1.27 MPa in the spring and -1.92 MPa in the fall. Binder *et al.* (1987) report photosynthesis continuing (stomates open to some degree) at -2.0 to -2.1 MPa in the fall, when earlier in the summer photosynthesis rarely occurred below -1.7 MPa.

In field studies in Alaska, white spruce leaf conductance decreased to about 50% of maximum when XPP dropped below -0.8 or -0.9 MPa and to 33% of maximum at a pressure potential of -1.7 MPa (Goldstein *et al.* 1985). In a laboratory study, rates of photosynthesis in white spruce did not begin to decline until a pressure potential of -1.24 MPa was reached; photosynthesis rates were 50% of maximum at -1.73 MPa and zero at -2.86 MPa (Brix 1979a). In another study, white spruce leaf conductance decreased by 75% as XPP went from -0.5 to -1.2 MPa, but changed little from -1.2 to -1.9 MPa (Grossnickle and Blake 1987). These studies suggest that there are considerable photosynthetic gains to be made by maintaining XPP above -1.0 to -1.2 MPa.

XPP should be measured at two times of the day: predawn and midday. Predawn measurements provide an indication of seedling stress. If soils are well watered, then healthy seedlings will recharge their moisture supplies during the night. If soil water is low, then seedlings will be unable to replenish their moisture and will remain stressed. Predawn white spruce XPP in soils at field capacity are around -0.4 to -0.5 MPa (Brix 1979a, Binder *et al.* 1987). At good spruce growing sites in British Columbia, predawn XPP remains at around -0.5 MPa throughout the growing season, suggesting an ample supply of water (Binder *et al.* 1987; Black 1987; Coates *et al.* 1991). However, early in the growing season, water stress has been observed in some predawn measurements even when soil water was abundant (Coates *et al.* 1991). Early growing season water stress often occurs as a result of cold soil temperatures that restrict water uptake (Kaufmann 1975; Running and Reid 1980).

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[6] MPa = megapascal; -1.0 MPa is equivalent to -10 bars

Predawn XPP readings are traditionally taken between 0200 and 0400 hours. However, Binder *et al.* (1987) found that predawn XPP readings for white spruce seedlings could be taken between 2000 and 2400 hours, by which time the seedlings had already recharged their water supply.

Midday XPP readings are affected by many different factors and thus provide less useful information than predawn readings. However, they may provide indirect evidence of when stomatal closure is occurring. The greater the moisture stress, the earlier in the day a spruce seedling will close its stomata to conserve moisture, and the less opportunity there will be for photosynthesis and growth to occur. In an Ontario field study, midday XPP readings were most negative by 1000 hours (Grossnickle and Blake 1987) and in British Columbia, Binder *et al.* (1987) found that during the hottest part of the summer, the XPP at which stomata close (-1.7 MPa) was reached as early as one-half hour after sunrise.

White spruce can survive to an XPP of -11 MPa (Brix 1979a). In the field, healthy white spruce should have an XPP less negative than -1.0 and -1.7 MPa at predawn and midday, respectively (Binder *et al.* 1987).

The water relations of Engelmann spruce have been extensively studied in both laboratory and field studies in Colorado. Stomatal closure occurs at an XPP of around -1.5 MPa (Lopushinsky 1969; Kaufmann 1976). At a high-elevation Colorado site that received ample precipitation throughout the growing season, predawn XPP ranged between -0.28 and -0.37 MPa (Grossnickle and Reid 1985). Kaufmann (1976, 1979, 1982a,b) has concluded that water stress is less important than some other factors, such as the time of year, in determining leaf conductance rates of Engelmann spruce in the field. Conductance rates are not affected by XPP readings less negative than -1.5 MPa (Kaufmann 1976) and water stresses to -2.2 MPa had no effect when PPFD was above 1500 $\mu mol/m^2 \bullet s$ (Kaufmann 1982a). Xylem pressure potentials between -1.5 and -1.9 MPa had no effect on Engelmann spruce conductance in August, whereas the same potentials caused significant stomatal closure in September. In contrast, Grossnickle and Reid (1985) reported that at a high-elevation field site in Colorado, Engelmann spruce leaf conductance steadily decreased as XPP went from -0.5 to -1.5 MPa.

In British Columbia, water relations of Engelmann spruce have received little study, but are probably most similar to those reported for white spruce.

Assessing the comparative drought tolerance of different tree species is difficult because each species has evolved a unique physiological response to moisture stress. Interior spruce has traditionally been thought to be more susceptible to water stress than its common associate lodgepole pine. While pine may show superior growth on dry sites, it is not necessarily a more drought-tolerant species. Recent studies, both in controlled environments and in the field, suggest that white spruce may be more tolerant of drought and tissue desiccation than lodgepole pine, jack pine, or black spruce (Cowling and Kedrowski 1980; Buxton *et al.* 1985; Roberts and Dumbroft 1986). In general, the pines are able to remain active (i.e., stomates open and their roots still finding new moisture) when environmental conditions become dry. Spruces, on the other hand, have evolved a more conservative strategy with regard to drought. They tend to close stomates very quickly in response to moisture stress and persist in an inactive state until conditions improve. Under extreme drought, pine may die before interior spruce. These conclusions are probably of most relevance to young seedlings without well-developed root systems.

In terms of seed germination and initial seedling establishment, spruce is more sensitive to drought than either subalpine fir or lodgepole pine because it has a smaller seed and is slower to develop a radicle or taproot that penetrates through surface soil layers to the moisture below (Day 1964; Eis 1965a; Arnott 1974; Knapp and Smith 1982). Thus, the moisture condition of the seedbed is the most important factor controlling germination and early survival of interior spruce (Dobbs 1972). Fresh, moderately moist, and moist sites are generally better for spruce germination than very moist to wet sites unless it is an unusually dry summer (Waldron 1966). Day (1963) observed that the longer new spruce germinants were able to grow before the onset of drought, the more resistant they were to drought stress. Tear *et al.* (1982) found that 1-month-old white spruce seedlings were more sensitive to drying soils than 3-month-old seedlings.

Poorly drained conditions In the northern interior spruce forests of British Columbia, excess water rather than too little water is often a limitation to tree survival and growth. Seasonal water deficits are common only on rapidly drained sites and in southern regions of the province.

Short periods of flooding decrease or inhibit root and shoot growth and can lead to mortality if flooding continues (Ahlgren and Hansen 1957; Lees 1964b; Levan and Riha 1986; Grossnickle 1987). White spruce seedlings taken out of cold storage and immediately planted into flooded soils grew no new roots and had 15% more negative XPP than trees in well-drained soils (Grossnickle 1987).

White spruce does not grow roots into flooded soil (Levan and Riha 1986). In their laboratory study, roots of 2- to 4-year-old trees penetrated only 2 cm below a water table in 30 days. Root tips flooded for more than 1 day were killed, whereas root tips flooded for less than a day recovered. Transpiration was depressed after the first day of flooding, and after 5 to 7 days of flooding it decreased by 50–60%. Transpiration levels recovered quickly to preflooding levels once soils were drained.

Lees (1964b) found that 1- and 2-year-old white spruce seedlings tolerated complete water immersion for a day or two, but that after 14 days of immersion all trees had died. Two-year-old trees were more tolerant of immersion than one-year-old trees for the first 7 days. Age did not affect survival if the immersion period was longer than 7 days. Lees found that the effect of repeated immersion was cumulative. Following three cycles of 3 ½ days of immersion followed by 8 recovery days, survival was 14 and 20% for 1- and 2-year-old seedlings, respectively. After four cycles, survival was 2% for both ages.

In a field study (Ahlgren and Hansen 1957), 30–60 cm tall white spruce had up to 10% mortality when flooded for 28 days; mortality increased steadily with flooding periods longer than 28 days. Complete mortality occurred on areas flooded for longer than 48 days. Larger trees were more resistant to flooding.

Zinkan *et al.* (1974) reported that oxygen levels below 25–44% saturation (2.0–3.3 ppm) limited growth of white spruce. Low oxygen levels resulted in decreased growth and increased needle discoloration—yellowing, browning, and purple tipping. Their data suggest that white spruce is less tolerant of flooding than either black spruce or jack pine. Ahlgren and Hansen (1957) also found white spruce to be less tolerant of flooding than black spruce.

Poor soil aeration can also occur in areas with compacted or heavy textured soils that do not necessarily suffer excess soil moisture problems. There is no information on the physiological effect these conditions have on interior spruce, but some studies have shown reduced shoot and root growth in soils with high bulk densities (Corns 1988; see Section 3.2.5, Soil physical properties).

Stomatal relations and atmospheric humidity There is a strong interaction between stomatal closure, xylem pressure potential, VPD, relative humidity, and light intensity in both white and Engelmann spruce (Kaufmann 1976, 1979, 1982a,b; Goldstein *et al.* 1985; Binder *et al.* 1987). The difference in atmospheric moisture between the inside of the leaf and the outside atmosphere is the most important factor controlling stomatal activity in Engelmann spruce (Kaufmann 1976, 1982b) and white spruce (Goldstein *et al.* 1985). In both species, leaf conductance decreases sharply as the vapour pressure deficit between leaf and air increases above 0.5 kPa, and in white spruce, stomata are closed at vapour pressure deficits above 1.0 kPa. Under field conditions, Binder *et al.* (1987) observed that white spruce shut down photosynthesis completely when VPD reached 1.5 kPa. This is one of the most sensitive stomatal response reported for any conifer species (see Hinckley *et al.* 1978).

The XPP and VPD combine to control leaf conductance when VPD is less than 1.0 kPa, in that for any given XPP, a higher VPD results in lower leaf conductance (Kaufmann 1982a,b; Goldstein *et al.* 1985). These responses are confounded by low soil temperatures. At soil temperatures below 8°C, Engelmann spruce conductance is sharply decreased, regardless of soil moisture levels (Delucia 1986) or atmospheric humidity.

3.2.3 Temperature relations

The thermal environment of a spruce tree can be described in terms of the maximum or minimum temperature attained, its duration, and the extent of temperature fluctuation. Both soil and air temperatures are important to spruce performance.

Soil temperature For many temperate conifer species there appears to be a threshold soil temperature occurring between 2 and 10° C, below which root resistance to water uptake increases sharply. Low soil temperatures can decrease water flow in the roots, increase water stress, decrease root growth, decrease leaf conductance, and ultimately decrease net photosynthesis in both white and Engelmann spruce (Kaufmann 1975; Tyron and Chapin 1983; Goldstein *et al.* 1985; Grossnickle and Blake 1985; Smith 1985a; Delucia 1986; Binder *et al.* 1987; Carter *et al.* 1988; Grossnickle 1988a,b).

Delucia (1986) showed that soil temperatures below 8°C resulted in a sharp decrease in stomatal conductance and photosynthesis of Engelmann spruce (Figure 21). Maximum rates of conductance in Engelmann spruce did not occur until soil temperature increased above 7–8°C (Carter *et al.* 1988). Water flow resistance increased sharply in white spruce when soil temperature was below 7°C (Grossnickle 1988a). These studies suggest that a critical threshold soil temperature of 7–8°C exists for interior spruce, below which physiological functioning is inhibited. As long as nighttime air temperatures are above freezing, low soil temperature is the primary limitation to photosynthesis at high elevations (Delucia and Smith 1987). Low soil temperature can limit photosynthesis throughout the growing season.

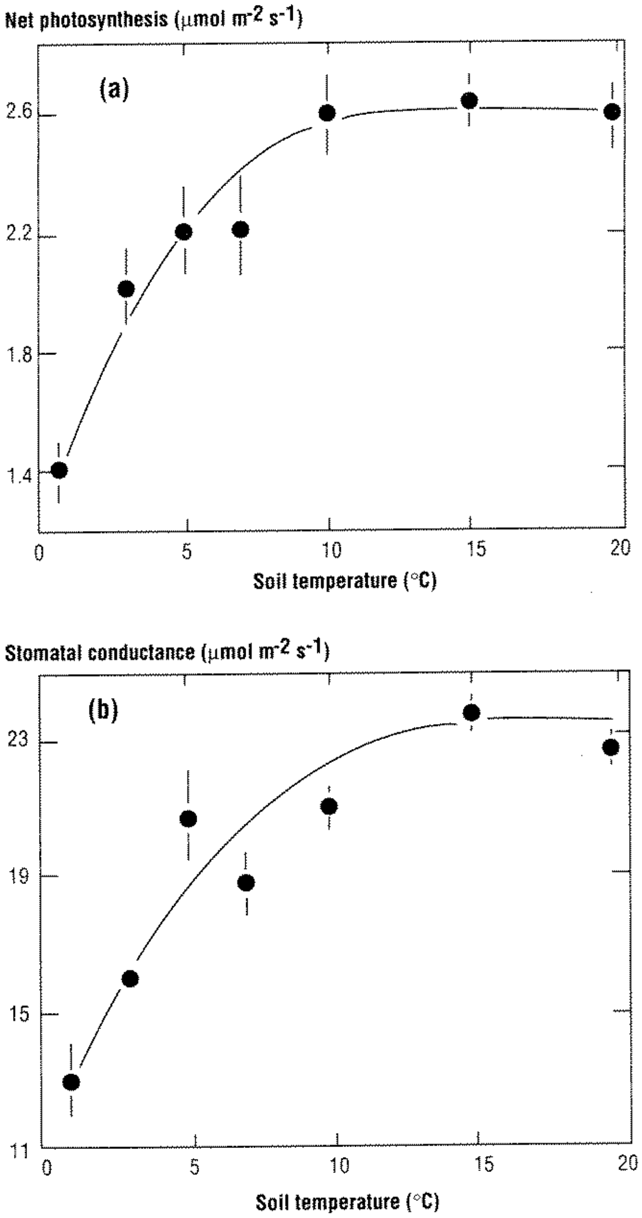

FIGURE 21. The effect of different root temperatures at a constant shoot temperature on (a) net photosynthesis and (b) stomatal conductance in Engelmann spruce seedlings (from Delucia 1986).

White spruce roots can begin to grow at soil temperatures as low as 1°C (Day 1985), but the optimum soil temperature for root growth of spruce is between 19 and 21°C (Chalupa and Fraser 1968; Heninger and White 1974; Ritchie and Dunlap 1980; Binder *et al.* 1987). It is unrealistic, however, to assume that such high temperatures have to be reached in order to obtain good growth. Soil temperatures between 10 and 20°C had no effect on net photosynthesis of Engelmann spruce (Delucia 1986; Figure 21a). Root growth capacity was the same when white spruce was grown in growth chambers at soil temperatures of 10, 16, and 22°C (Grossnickle and Blake 1985).

The research results summarized above strongly suggest that for management purposes the first priority of interior spruce site preparation should be to increase soil temperature above 7–8°C. Further increases in soil temperature are benefical to seedling growth, but the gains are not as apparent as those associated with reaching the critical 7–8°C temperature threshold.

In a greenhouse study, increasing soil temperature from 10 to 20°C improved root growth in white spruce (Grossnickle 1987). A field study near Prince George found that the number of new roots produced on trees following different site preparation treatments was well correlated with the cumulative soil degree-days above 5°C (Binder *et al.* 1987). An Ontario field experiment involving vegetation control, fertilization, and soil temperature manipulation, found that soil temperature was the single most important factor influencing white spruce performance (Brand and Janas 1988). At the lowest soil temperature, vegetation control and/or applying fertilizer provided little net benefit to tree growth unless soil temperature was increased. The authors concluded that seedlings in untreated areas were under soil temperature induced moisture stress and were unable to respond to other treatments effectively. Minimum soil temperatures in this experiment were considerably above the threshold of 7–8°C reported elsewhere.

White spruce seedlings are most susceptible to the water stress induced by cold soils when they are first planted (Grossnickle 1988a). After removal from cold storage, the seedlings may take 18–20 days to adjust to environmental conditions and begin root growth (Grossnickle and Blake 1985).

Air temperature Extensive nursery trials on the influence of different day/night temperature combinations have been carried out for both white and Engelmann spruce (Shepperd 1981; Arnott 1982; Tinus 1984). These studies are not reviewed here. Comparatively few studies have examined the effect of air temperatures on spruce in the natural environment.

High temperature damage to 2- to 4-week-old Engelmann spruce seedlings depended on the temperature reached and the duration of exposure (Seidel 1986). No mortality occurred below 44°C. Above 44°C, mortality depended upon the length of exposure; trees suffered no damage up to 60°C if exposure time was very short. Interior spruce germinants are susceptible to stem girdling caused by excess heat at the soil surface (Smith 1955; Day 1963). Surface temperatures of 45–50°C can cause stem girdling; temperatures above 50°C can cause severe mortality even when the soil is moist. At his southern Alberta field site, Day (1963) concluded that acute midsummer heating of upper soil layers in clearcuts is one of the major causes of mortality for newly germinated seedlings.

Needles of white spruce in Alaska began photosynthesis once air temperature reached 0°C (Cowling and Kedrowski 1980). At a field site near Prince George, net photosynthesis occurred when air temperatures were between 5 and 28°C (Binder *et al.* 1987). In Colorado, Kaufmann (1982a) believes that once air temperature is greater than 4°C it becomes a secondary factor in controlling stomatal conductance of Engelmann spruce.

Cold nighttime temperatures can affect subsequent photosynthetic activity. When nighttime air temperature dropped to between -4 and -5°C, Engelmann spruce photosynthesis was substantially decreased the next day (Delucia and Smith 1987; Figure 22). Inhibition of photosynthesis by cold night temperatures was most severe later in the growing season. In early June, -5°C for 1 night caused a 25–35% reduction in photosynthesis the next day; in midsummer the same temperature for 1 night caused an 80–90% reduction in photosynthesis the next day (Delucia and Smith 1987). After 3–5 nights of subzero temperatures, photosynthesis can be impaired for the remainder of the growing season (Tranquillini 1979).

In a growth chamber study, Engelmann spruce seedlings subjected to -2.5°C for 10 hours suffered a slight but reversible decrease in photosynthesis the next day (Delucia 1987). At -4 to -5°C, irreversible decreases in photosynthesis occurred. The combination of day/night temperature just prior to freezing nights influenced the severity of photosynthesis reduction. Trees experiencing warm day/night temperatures (24° C day/19°C night) were more severely affected by frost than trees from cooler day/night regimes (14°C day/9°C night). One implication of these results is that trees growing at low elevations may be more severely affected by summer frost than higher-elevation seedlings.

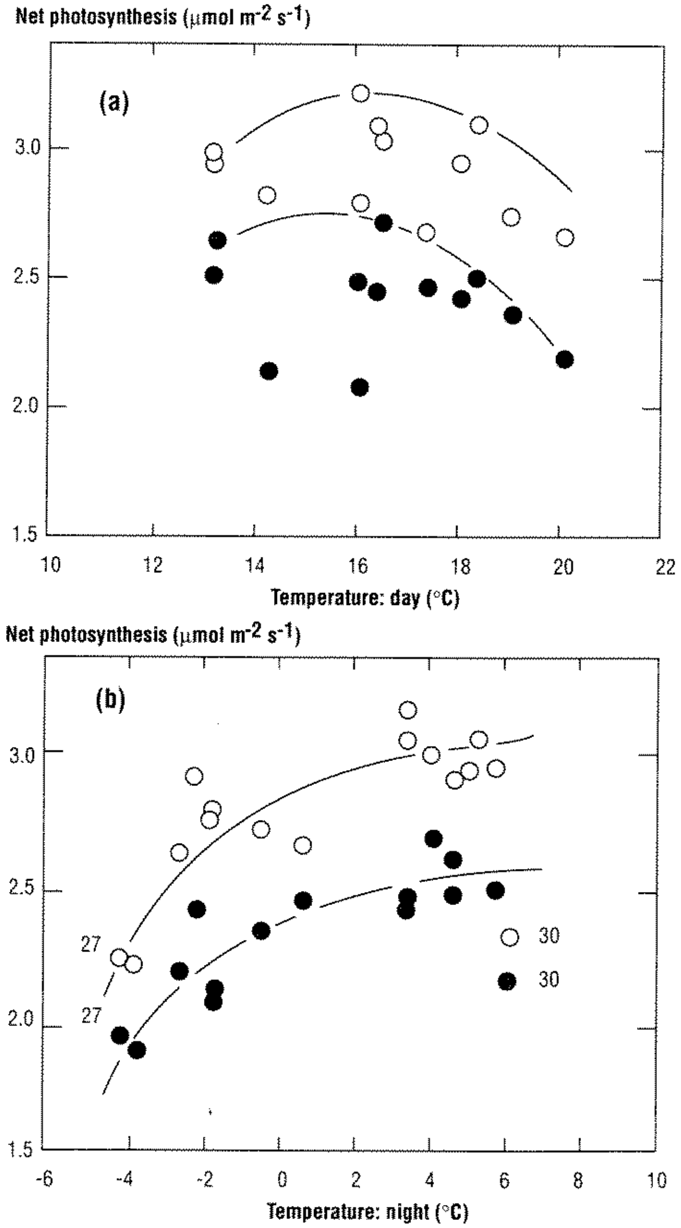

FIGURE 22. The photosynthetic response of Engelmann spruce trees to (a) air temperature at the time of measurement, and (b) minimum air temperature the previous night. Open circles represent trees in warm soil; filled circles are trees in cold soils. A hard freeze occurred on June 27 and 28. Photosynthetic rates on the days immediately following the freeze, and 2 days after the freeze are indicated by 27 and 30, respectively (from Delucia and Smith 1987).

Growing season frost damage White and Engelmann spruce are both susceptible to tissue damage from growing season frosts. Frosts can deform white spruce seedlings and delay their normal development by killing newly flushed needles and succulent shoots (Rowe 1955; Fraser 1965, cited by Stiell 1976). A series of frosts in late May and early June contributed to the 20% mortality rate of 1-year-old white spruce seedlings (Jarvis *et al.* 1966). Ronco (1967), in a review of Engelmann spruce artificial regeneration practices in Colorado, states that new growth of planted seedlings is extremely sensitive to frost. Stathers (1989) and Steen *et al.* (1990) review the physical principles governing the causes and occurrence of summer frost, the effect of frost on planted conifer seedlings, and management techniques for frost-prone sites. Extensive frost damage to young interior spruce plantations has been observed at locations throughout the southern and central interior of British Columbia (Beaudry and McCulloch 1989; McMinn 1989, unpublished; Stathers 1989; Sutherland and Vyse 1989; Black and Mitchell 1991a,b; Coates *et al.* 1991).

Frost damage is not restricted to newly planted seedlings. Older plantations or naturally regenerated stands in frost-prone locations may be repeatedly injured by frost, causing growth reductions and stem deformation. Bud mortality due to frost damage was considered the causal factor of terminal leader failure in 19- to 43-year-old white spruce plantations in Ontario (Harding 1986). About 46% of the trees surveyed had suffered terminal leader failure at some time. Dominant trees 33–43 years old had a 3-year failure rate ranging from 16 to 51%; each incident caused an 18% reduction in height growth. Harding (1986) estimated a 2 m height reduction for 50-year-old trees.

Vegetation can have either beneficial or detrimental effects on the occurrence of frost, depending on its height, structure, and density (Stathers 1989; Steen *et al.* 1990). Frost damage appears to be most prevalent in open-grown trees. In Ontario, frost damage in open-grown 6-and 12-year-old white spruce trees was 67 and 30%, respectively (Clements *et al.* 1972). In natural stands, white spruce overtopped by other trees had an incidence of frost damage of less than 5%. In British Columbia, the presence of overtopping herbaceous and shrub canopies has not necessarily protected newly planted spruce from frost damage (Black 1987; Coates *et al.* 1991).

Newly planted interior spruce seedlings are more susceptible to growing season frost damage than lodgepole pine, but are less sensitive than interior Douglas-fir.

Winter damage Becwar *et al.* (1981) report that the winter hardiness limit for Engelmann spruce is near -40°C, and pronounced stem injury occurs at temperatures below -45°C. Sakai (1983) tested coniferous trees from throughout the world to determine the winter hardiness limit of bud, leaf and stem tissues. His results for Engelmann spruce from Colorado are similar to those of Becwar *et al.* (1981), but white spruce material from Alaska was able to tolerate temperatures as low as -70°C. In general, Sakai's (1983) results suggest, as one might expect, that coniferous trees have adapted to withstand the minimum winter temperature to which they might historically have been exposed. Bud primordia are often killed at temperatures 5–10°C warmer than those that kill leaf and stem tissue.

At a clearcut site near Fort St. John, portions of planted white spruce seedlings emerging above the snow layer were exposed to temperatures of -55°C and had no visible damage the next growing season (D. Crampton, pers. comm., September 1990). Air temperatures that fluctuated from 3–4°C (day) to -30°C (night) also caused no apparent damage to these seedlings.

Winter hardiness problems may arise when newly planted seedlings that are poorly acclimated to the outplanting environment are exposed to extreme or unusual temperatures. In the Peace River area, for example, extensive winter damage has occured in young white spruce plantations (Herring 1989). Symptoms include foliage and apical bud mortality, and, in extreme cases, shoot death. The subsequent growth performance of winter-injured seedlings is greatly reduced. The damage is almost entirely restricted to spring-planted seedlings during their first overwinter period in the field. These observations suggest that nursery cultural practices are at fault—first-year seedlings develop inadequate cold-hardiness because they continue active growth too late into the growing season. The damage typically occurs where there is a shallow snowpack and seedlings are exposed to rapid and extreme temperature fluctuations (i.e., "Chinook" conditions). Herring (1987, unpublished) reviewed the possible causes of winter injury to white spruce, drawing on literature from North America and Europe. Direct freezing of seedling tissues appears to be the most likely cause of damage, but frost-drought (desiccation) may also be involved.

Severe winter damage has also been observed on Engelmann spruce seedlings planted in fall on high-elevation sites in ESSF and MS zones of the Lillooet Forest District (Krumlik 1987). In this case, damage was attributed to early snowmelt and the desiccating effects of dry winds while soils were still frozen (i.e., frost-drought).

Extensive winter bud damage was observed on planted and naturally regenerated interior spruce growing between Williams Lake and Fort St. James, after a sudden

February cold snap that followed 4 months of unusually warm weather (van der Kamp and Worrall 1990). On trees less than 30 years old, most of the buds above the snowline were killed, even on trees growing beneath taller vegetation. Some small axillary buds escaped damage and developed into abnormally vigorous shoots the following spring. On trees older than 30 years, damage was much less severe. The authors hypothesize that mild December–January temperatures caused trees to break dormancy and lose cold-hardiness earlier than normal, rendering them sensitive to the sudden cold snap.

3.2.4 Nutrient relations

This section discusses the mineral nutrient requirements of spruce. Growth response of spruce to fertilizer application is discussed in Section 5.4.5, Fertilization. The effect of spruce trees on the nutrient properties and dynamics of forest ecosystems is discussed in Section 3.2.6, Soil chemistry, and Section 3.2.8, Soil biology.

Nitrogen is frequently deficient in British Columbia forest soils. Ballard and Carter (1986) suggest that for white spruce in British Columbia, foliar nitrogen concentrations of greater than 1.55% (dry mass basis) indicate an adequate supply of nitrogen. Moderate deficiency occurs between 1.3 and 1.55%, severe deficiency between 1.05 and 1.3%, and very severe deficiency at levels below 1.05% nitrogen. Table 8 shows the levels of foliar nitrogen found in white and Engelmann spruce under field conditions. Ballard and Carter (1986) present similar data for the other major macronutrients, and provide a list of the visual symptoms of nutrient deficiencies in conifers. The Munsell colour manual can be used to assess nutrient stress in white spruce. A healthy colour for needles is 7.5GY 5/4 to 4/2 while stressed needles are 2.5GY 5/6 or 6/6 (Sutton 1975).

TABLE 8. Nitrogen concentrations observed in field-grown interior spruce

Type of sample	N concentration (%)	Source
seedling shoot	1.6–1.8	Zasada and Grigal 1978
new tissue	0.8–1.3	Walker and Chapin 1986
current needles, 3-yr-old seedling, clearcut	1.39–1.51	Gordon and Van Cleve 1987
current twigs, 3-yr-old seedling, clearcut	0.94–0.95	Gordon and Van Cleve 1987
current needles, 3- to 5-yr-old seedlings, under forest canopy	1.16	Gordon and Van Cleve 1987
current twigs, 3- to 5-yr-old seedlings, under forest canopy	0.96	Gordon and Van Cleve 1987
current foliage, 30-yr-old trees	1.1–1.4	Salonius 1978
current foliage	1.03–1.27	Kabzems and Lousier 1989, unpublished

Ballard (1984, unpublished) in a survey of the Prince George and Cariboo forest regions of British Columbia, found that N, Mg, Fe, and Cu were often seriously deficient in young planted white spruce, and that S could become growth-limiting if the N deficiency was relieved. Deficiencies in B, Mn, P, K, Ca, or Zn were rare. White spruce growth in a sand culture was unaffected by P level (Chapin *et al.* 1983). Wilde (1966) suggested minimum soil fertility requirements for white spruce of 0.12% total N; 45 kg/ha available P; 3.0 me/100 g exchangeable Ca; 145 kg/ha available K; and 0.7 me/100 g exchangeable Mg.

Ballard (1984, unpublished) found that both the frequency and severity of N, Fe, and Cu deficiencies appeared to be greater where burning and/or mechanical site preparation had been carried out. Interestingly, these deficiencies did not translate into decreased tree growth. In a follow-up study, Ballard and Hawkes (1989) found that tree growth was either unaffected or improved on burned sites. At two sites near Prince George, white spruce leader length averaged 36% less in unburned areas even though concentrations of foliar N, active Fe, and Cu were 27, 66, and 44% higher, respectively, than in burned areas. Total height and leader length were negatively correlated with duff depth and positively correlated with the extent of bare mineral soil. These findings suggest that the negative impacts of poorer nutrition are outweighed by beneficial effects on other growth-limiting factors such as soil temperature or vegetative competition (Ballard and Hawkes 1989).

Another interesting observation in the Ballard and Hawkes study is that where the nitrogen-fixing shrub Sitka alder (*Alnus viridis* ssp. *sinuata*) was present on windrowed areas where large amounts of N had been lost, white spruce foliar N increased by 27% and leader growth was 50% greater compared to seedlings in windrowed areas without Sitka alder.

The nutritional status of white spruce can be used to assess site nutrient regime (Gordon and Van Cleve 1987). Foliar N levels give a good indication of availability of soil nitrogen in the upper mineral soil horizon. Gordon and Van Cleve (1987), sampled 3- to 5-year-old seedlings in a clearcut and an adjacent old-growth stand and found that seedlings in the clearcut had greater concentrations of N in current foliage than those in the uncut area.

Optimal growth of white spruce is possible on soils with pH between 5.0 and 7.0 (Sutton 1969b). However, thrifty spruce have been reported on soils with pH as high as 8.4 (Dobbs 1972).

3.2.5 Soil physical properties

Soil degradation refers to the loss of productivity caused by soil disturbance resulting from forestry practices employed during tree harvest, site preparation or stand tending (Utzig and Walmsley 1988). In spite of the widespread scope of the problem within the B.C. interior and the potentially major impacts on forest productivity, there has been relatively little field or laboratory research to examine the effect of soil degradation on interior spruce growth (Utzig and Walmsley 1988, their Tables 6.1 and 6.2).

Smith and Wass (1976, 1979, 1980) examined the growth of interior spruce regeneration on and adjacent to contour skidroads on steeply sloping cutblocks in the ESSF and ICH zones of southeastern B.C. On average, skidroad surfaces on these clearcuts account for more than 32% of the total land area (Smith and Wass 1976; Schwab and Watt 1981). Reductions in spruce productivity, pro-rated over the whole clearcut, were estimated as high as 12% at an age of about 12 years (Smith and Wass 1979).

The impact of skidroads on the growth of young spruce varies with soil texture, soil acidity, and climate (Smith and Wass 1979, 1980). Growth reductions were greatest on calcareous soils where skidroad construction exposed alkaline subsurface horizons with a probable low availability of nutrients such as P, Fe, Zn, B and Mn. Growth on skidroads was also poor in areas of wet climate with coarse textured or shallow acidic soils subject to rapid leaching of nutrients. Spruce seedlings on some skidroads had yellow foliage, suggesting nutrient deficiencies.

On some sites (particularly cool, north-facing clearcuts with moderately coarse textured soils), spruce growth appeared to be enhanced by soil disturbance on skidroads. Three possible causes for improved growth were suggested: 1) soil warming associated with removal of organic layers; 2) improved solar insolation caused by reduction in slope steepness; and 3) reduced vegetative competition (Smith and Wass 1979, 1980).

Tree growth also varied with the position on the skidroad (Figure 23). Best growth was observed on the berm and sidecast materials on the downslope side of the skidroad, where soils are relatively uncompacted and there is some mixing of topsoil and subsoil. In general, the outside (downslope) portion of skidroads should be favoured over the inside (upslope) portion during planting, brushing, or spacing operations (Smith and Wass 1979).

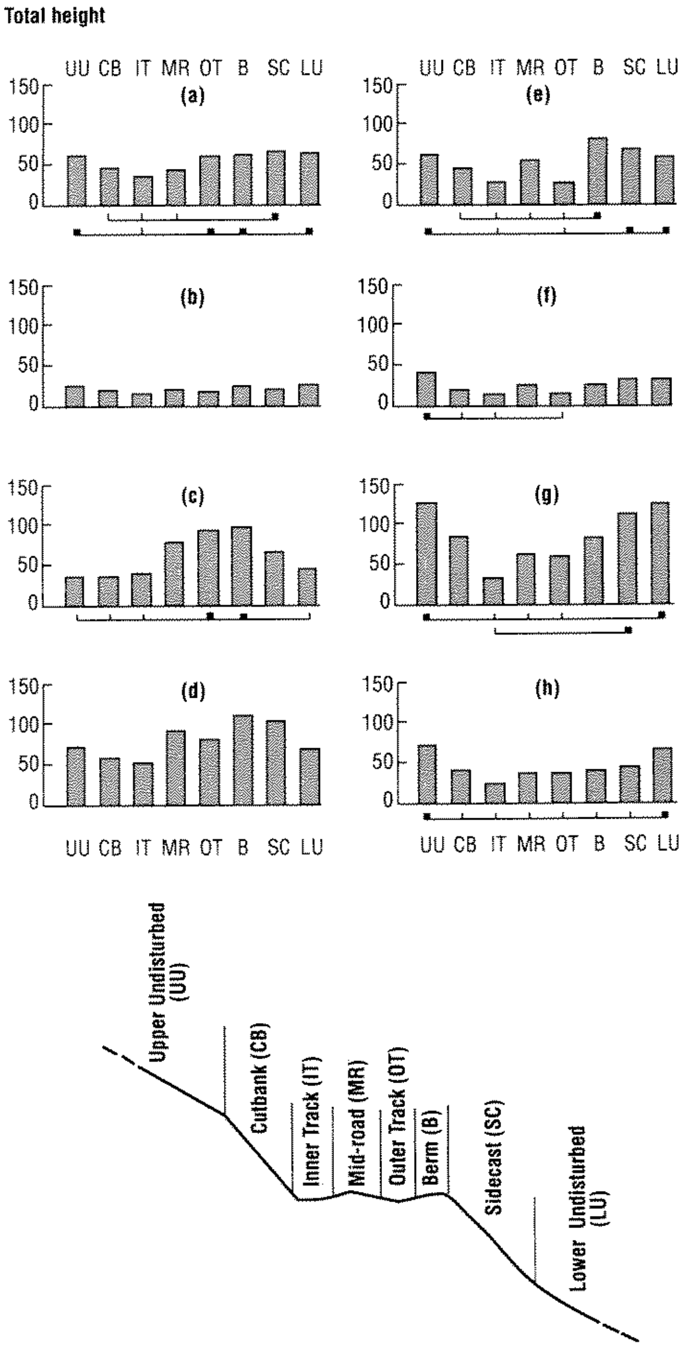

FIGURE 23. Effect of soil disturbance on average total heights of Engelmann spruce at eight ESSF study sites (a–h) in southeastern B.C. Heights with solid squares below the bars are significantly greater (5% level) than those with short vertical marks joined by the same horizontal line. The cross-sectional diagram indicates soil disturbance classes on and adjacent to the skidroad: UU = upper undisturbed; CB = cutbank; IT = inner track; MR = mid-road; OT = outer track; B = berm; SC = sidecast; LU = lower undisturbed (from Smith and Wass 1979).

Brush blade scarification appreciably reduced the growth capacity of an ESSF site northwest of Clearwater, British Columbia, over the first two decades following treatment (Herring and McMinn 1980). Twenty-one years after release, the mean height of spruce advance growth was eight times that of naturally regenerated seedlings on adjacent bladed strips. Only a small portion of the difference was attributed to the "head start" of the advance growth. The major cause for the discrepancy was believed to be the reduction in soil fertility following removal of surface organic horizons containing the bulk of soil nitrogen and other mineral elements. Soil compaction, poor soil structure, and competing vegetation were not considered to be major factors contributing to the poor seedling performance on the scarified soils in this study.

Soil compaction affects tree growth by impairing root growth and function (Graecen and Sands 1980). Effects on root growth occur because of a complex interaction between soil strength, water and nutrient availability and soil aeration. Compaction decreases the amount of large pore space within the soil and increases soil strength, making it more difficult for roots to penetrate small pores. This reduces the rate of root elongation, and decreases the amount of root surface available for water and nutrient uptake. A study by Noble (1972) suggests that soil compaction and crusting may affect the survival of germinating Engelmann spruce seedlings by inhibiting the root penetration into the soil and exposing the seedlings to drought.

Corns (1988) studied the effects of soil compaction on white spruce and lodgepole pine seedling growth in Alberta. Field surveys indicated that soil density levels are significantly increased as a result of standard summer logging by power saw and rubber-tired skidder followed by some means of mechanical site preparation, but the degree of compaction varies with soil texture and type. In a laboratory study, spruce and pine were grown in four soil types artificially compacted to three densities representing conditions found on roads immediately after logging, on clearcuts 5–10 years after logging, and under undisturbed conditions. In general, white spruce appeared less affected by changes in soil bulk density than lodgepole pine. In a coarse textured fluvial soil, spruce root growth was not significantly affected by compaction; however, on both a loamy eolian soil and glaciolacustrine clay, compaction to densities observed in the field caused significant reductions in a variety of spruce growth parameters including rooting depth, total seedling weight, and shoot height. Corns (1988) concluded that on typical clearcut areas, effects of soil compaction on tree growth may not become evident until 10–12 years after establishment, when the young tree roots are exploiting soil at 20–30 cm depth. Growth reductions would be expected to appear sooner in areas where soil was displaced and traffic was heavy.

3.2.6 Soil chemistry

Numerous studies have investigated how the presence of spruce affects the the chemical properties of the soil. Early research (reported by Alban 1982) suggested that conifers (particularly spruce) reduce soil pH and Ca content and have a generally deleterious effect on soil compared to hardwoods. More recent studies have also shown marked differences in soil and forest floor chemistry in stands dominated by different tree species (Perala and Alban 1982; Van Cleve and Harrison 1985; Brand *et al.* 1986; Fyles and McGill 1987a), but suggest that the nutrient dynamics of an ecosystem are far too complex to be generalized in terms of what is "good" or "bad" for the soil. The newer studies indicate that:

- it is essential to examine relationships among all ecosystem components (subsoil, surface soil, forest floor, aboveground biomass) in order to understand the impact of a tree species on a site;
- the impact of spruce on soil properties may be quite different in boreal ecosystems where most tree roots and nutrient cycling occur within forest floor layers than in more temperate ecosystems where nutrient uptake takes place mainly in the upper layers of mineral soil; and
- many soil differences attributed to present vegetation existed prior to the current vegetation and may actually be independent of vegetation (Stone 1975, cited by Alban 1982; Alban 1982; Fyles and McGill 1987b).

In the boreal forests of interior Alaska, forest floor chemistry has a major impact on nutrient cycling and tree growth. Van Cleve and Harrison (1985) found that, in general, forest floor nutrient content decreases and lignin content increases in the following order: birch; aspen; white spruce; black spruce. Phosphorus concentrations in the forest floor were highest beneath birch and aspen stands, intermediate in balsam poplar and upland white spruce, and lowest in black spruce and floodplain white spruce. Phosphorus deficiencies were found in seedlings grown in floodplain white spruce forest floor layers, presumably because P, which is concentrated in organic matter, was diluted by siltation.

Van Cleve *et al.* (1986), using a bioassay approach with paper birch seedlings growing in a standardized mixture of quartz sand or forest floor organic matter, found that the white spruce forest floor supplied only 20% of the amount of N taken up by seedlings growing in other forest floor types. White spruce forest floors yielded 15 times less extractable N than a birch forest floor.

A series of studies in central Minnesota compared soil chemical properties and tree nutrition and growth in 40-year-old stands of white spruce, red pine, jack pine and trembling aspen planted on uniform sites (Alban *et al.* 1978; Alban 1982; Perala and Alban 1982). In this environment, rates of organic matter decomposition and nutrient turnover are much higher than those observed in boreal forests, and forest floor layers under young and maturing stands remain more or less at a steady state, rather than accumulating over time. Of the four tree species, spruce had the highest levels of organic matter in the soil and forest floor and the lowest rates of decomposition and nutrient turnover. Total spruce litterfall was less than that of pines but more than that of aspen. Spruce and aspen remove more nutrients from the mineral soil, accumulating more in aboveground biomass and returning more in litterfall than pine. Thus aspen and spruce forest floors have higher pH and higher levels of Ca than pine forest floors, but pH, Ca and CEC (cation-exchange capacity) levels in the mineral soil are lower. Nutrient weights in the trees were greatest in aspen, followed generally by spruce, red pine and jack pine. If the stands were harvested, more nutrients would be removed from the aspen and spruce sites than the pine sites. Because foliage and branches contain much higher concentrations of nutrients than boles and bark, about three times as many nutrients would be removed if the entire aboveground tree were taken than if only the boles were removed. Nutrients in aboveground spruce biomass, expressed as a percentage of the nutrients in the top 36 cm of soil were 15, 84, 77, 26 and 12%, respectively, for N, P, K, Ca and Mg.

At Petawawa research station near Ottawa, abandoned farmland was planted to plots of white spruce, red pine and Scots pine in the 1920s. Soils sampled on permanent plots in 1938 and again in 1984, showed a general decline in pH of the mineral soil over the 46-year period (Brand *et al.* 1986). In 1938, there was no significant difference in pH by tree species, but by 1984 the white spruce plots had become significantly more acidic than red pine plots. Average pH decrease under white spruce plantations was 1.28 (from 6.0 to 4.7) compared to 0.67 for red pine (from 6.0 to 5.3). The authors attributed the pH change to uptake and immobilization of exchangeable cations from the soil pool into stand biomass and the forest floor, and to acidic decomposition products from tree litter. The relatively greater acidification under spruce was attributed to the greater demand by this species for basic cations such as Ca and Mg (see above). Soil pH was expected to level off as both the stand biomass and forest floor thickness approach a steady state. It is not known whether the acidification of these soils has led to diminished forest productivity, increased susceptibility to pathogens, or reduced soil-buffering capacity.

A group of studies in Alberta compared litterfall rates, and litterfall and soil chemistry of spruce and jack pine stands. Litterfall rates on relatively unproductive sites in northern Alberta are similar to those observed in Alaska but lower than those observed further south (Fyles *et al.* 1986). Spruce litterfall is highest in fall when most needle drop occurs, and in late spring when male cones are shed. Departures from the normal pattern could reflect ecosystem stresses such as disease or insect outbreaks, drought or air pollution.

Fyles and McGill (1987a) found that white spruce litter decomposed more rapidly than jack pine, balsam fir, *Pleurozium* or *Hylocomium* foliage, and at a similar rate to green alder foliage, even though it had the highest C:N and lignin:N ratios of these species. Fyles and McGill (1987b) examined nitrogen mineralization rates at various depths in the soil profile. The nitrogen characteristics of LFH horizons primarily reflected the age and species composition of the present vegetation, the A horizons reflected both present and previous vegetation, while B horizons were independent of vegetation and stand age, implying long-term processes.

3.2.7 Site quality evaluation

Rather than looking at how interior spruce affects soil properties, some researchers have looked instead at how soil properties affect interior spruce. Specifically, these researchers have sought ways of predicting tree growth by measuring selected soil properties. This method has not been used in British Columbia, where instead a non-quantitative ecosystem classification approach has been adopted as a means of rating sites for spruce growth.

Rawinski *et al.* (1980) examined the relationship of white spruce seedling height to soil organic matter content, clay percentage, silt percentage and pH on a single soil type in northern Wisconsin. There was no relationship between seedling height and organic matter content, but growth was better on coarser soil textures and at lower soil pH (range 5.3–6.1). In Ontario, soil type was not a useful predictor of white spruce seedling survival or height growth (Payandeh and Wood 1988).

Harding *et al.* (1985) used discriminant analysis to identify growth response groups for white spruce plantations in northern Minnesota. Slope (plots with slopes greater than 10% had poor spruce growth), soil phosphorus, and nutrient synecological coordinates (similar to the "trophotope" or "nutrient regime" used in biogeoclimatic ecosystem classification) were all major discriminators. Other significant discriminators included the depth to free carbonates, depth to clay film, depth to B horizon, and percent sand.

In west central Alberta, Corns and Pluth (1984) were able to explain 53% of the variation in white spruce mean annual volume increment (MAI) and 58% of the variation in site index at age 70 using an array of site and soil variables. Some of the more significant variables included the hydraulic conductivity of the soil, the colour (hue) of the B horizon, elevation, and slope angle. Spruce growth decreased with increasing elevation and (unlike the results of Harding *et al.* [1985]) was generally greater on steeper, better-drained sites. The hue of the B horizon primarily reflects internal soil drainage. Increased hydraulic conductivity (which also affects internal soil drainage) had a highly significiant positive effect on MAI, but a significant negative effect on site index.

3.2.8 Soil biology

Relatively little is known about the soil organisms associated with interior spruce trees and spruce-dominated ecosystems. This section summarizes information about decomposer organisms. Information on mycorrhizae is summarized separately below.

Research on upland white spruce ecosystems in interior Alaska near Fairbanks provides some information on the effects of timber harvesting and thinning on the activities of soil organisms. Gordon *et al.* (1987) studied the effect of timber harvesting on soil respiration, while Piene and Van Cleve (1978) examined the effect of thinning white spruce on the rate of forest floor decomposition. In both studies, the highest rates of respiration and decomposer activity were associated with the treatments that caused the greatest increase in soil temperature, suggesting that low soil temperatures limit the amount of microbial activity in these ecosystems, and that disturbances such as clearcutting and heavy thinning stimulate the rate of organic matter breakdown and nutrient release by allowing sunlight to reach the forest floor. Moisture availability is also important for high rates of microbial activity, but appears to be less of a limiting factor in these northern ecosystems than low soil temperatures.

The quality of forest floor organic matter may be even more important than temperature and moisture in controlling the rate of decomposition and mineralization. Litters with low pH, low base saturation, low N and P concentration, high carbon:nitrogen ratios (C/N) and a high content of decay-resistant substances (e.g., lignins and tannins) provide an unfavourable environment for microbial activity. Flanagan and Van Cleve (1983) compared the quality of white spruce litter with that of black spruce, aspen, birch and balsam poplar. White spruce consistently ranked behind the deciduous species, but ahead of black spruce, in terms of pH, base saturation, and N and P concentration. However, lignin levels in white spruce forest floors were similar to, or slightly lower than, those of birch and aspen. The respiration rate, the rate of organic matter decay, and the rate of forest floor turnover all followed the ranking: black spruce < white spruce < deciduous species. Fertilizing the spruce forest floor litter with N, P and K did not increase the decomposition rate; however, microbial activity was greatly enhanced by adding an energy-rich carbon source (glucose), suggesting that the microbes are energy-limited rather than nutrient-limited.

Harmer and Alexander (1986) observed similar results when they added starch to Engelmann, white and hybrid spruce litter taken from a species trial in Scotland. Nitrogen mineralization rates were low in all three spruce species, and starch enhanced the rate of mineralization.

Few studies have directly examined the soil invertebrate and microbial populations beneath spruce stands. Microbial biomass measurements by Flanagan and Van Cleve (1983) in Alaska indicated that fungi dominate the microflora in spruce forest floors, with bacteria making up less than 5%. Six to eight grams of active fungal mycelia were found in 13 kg of organic matter. Kienzler *et al.* (1986) compared soil organism populations beneath 39-year-old pure white spruce and pure aspen stands growing on the same soil type in Minnesota. Aspen soils had about 10 times as many bacteria and 30–50% more fungi than white spruce. Although it is generally acknowledged that bacteria are favoured over fungi at higher pH levels, the microorganism counts in this study were not closely related to soil pH (5.4 for spruce; 5.6 for aspen). White spruce and aspen had similar populations of soil invertebrates (worms, insects, spiders, and mites). Soil organisms were 10–1000 times more abundant in the surface 10 cm of soil than in the next 15 cm.

3.2.9 Mycorrhizae

Mycorrhizae are structures formed when young roots are invaded by fungal hyphae (Figure 24). The fungi form a symbiotic association with the living cells of plant roots, and play an important role in tree physiology (Kramer and Kozlowski 1979). Spruces, like other members of the Pinaceae family, have ectomycorrhizal roots, in which the fungal mycelium grows between the cortical cells of the root without actually entering individual root cells. The fungal mycelia extend outwards from the host, greatly increasing the absorptive surface area of the root system. Spruce roots infected with mycorrhizae lack root hairs (Figure 25); the fungal hyphae effectively take over the function of the root hairs, while providing a variety of additional benefits to the tree.

Mycorrhizal associations benefit the tree primarily by increasing nutrient uptake. Improved phosphorus nutrition appears to be most important, but there is also evidence that absorption of nitrogen and other minerals may be improved (Langlois and Fortin 1982; Danielson 1985). Recent research suggests that mycorrhizal species that function well at low soil temperatures may enhance the ability of spruce to take up nutrients in cold soils (Husted and Lavender 1989).

Other possible benefits of mycorrhizae include exclusion of toxic chemical elements such as heavy metals (Langlois and Fortin 1982; Danielson 1985), increased

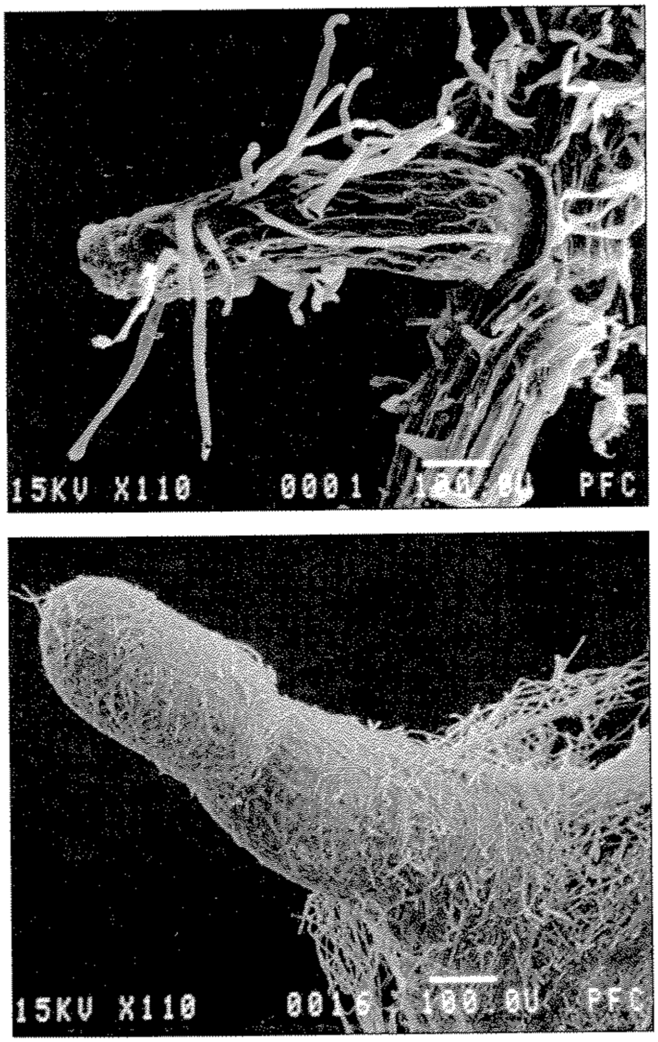

FIGURE 24. Nonmycorrhizal (top) and mycorrhizae infected (bottom) short roots on white spruce (from Trofymow and van den Driessche, 1991).*

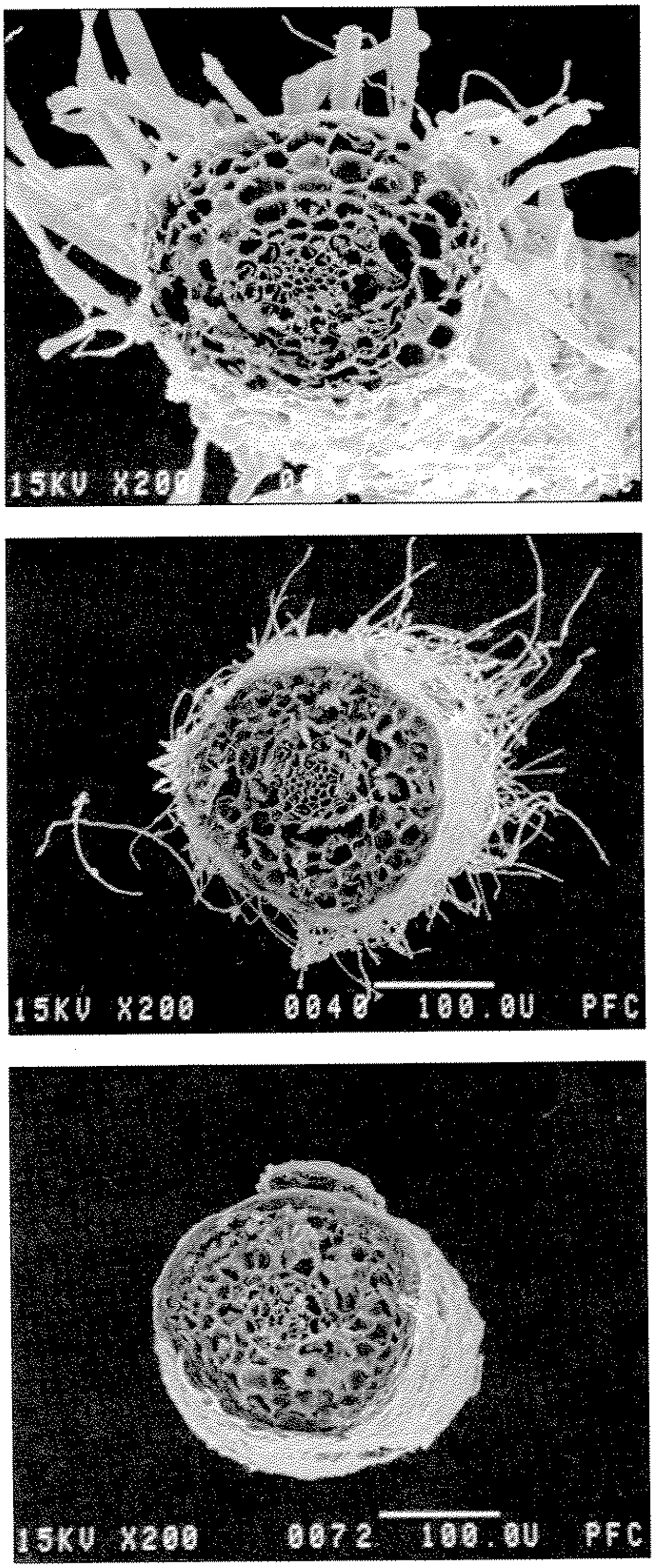

FIGURE 25. Nonmycorrhizal (top) and mycorrhizal with *Thelephora* spp (centre) or E-strain (bottom) fungi white spruce roots. Note the lack of root hairs on the mycorrhizal roots (from Trofymow and van den Driessche, 1991).*

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resistance to pathogens (Kramer and Kozlowski 1979), and slower root turnover (Harley and Smith 1983). It has also been suggested that mycorrhizae may increase the ability of tree seedlings to withstand drought, but there is no direct experimental evidence to support this hypothesis (Danielson 1985).

Natural forest soils normally possess a wide variety of locally adapted fungi capable of forming mycorrhizal associations with spruce. Suitable inoculum may, however, be lacking in highly disturbed or artificial materials such as mine tailings, or the sterile rooting media used in container tree nurseries. There is also evidence that certain strains or species of fungi may be more effective than others in enhancing the ability of tree seedlings to survive and grow in stressful environments. In particular, there are concerns that the "weedy" strains of ectomycorrhizal fungi commonly found in nursery environments may be poorly suited to the outplanting environment.

Research on the mycorrhizal relations of interior spruce is concentrated in the following areas:

- identifying and quantifying populations of ectomycorrhizae in natural forests, seedling nurseries, and in mine spoils;
- determining the influence of ectomycorrhizal fungi on the performance of seedlings in the field;
- determining the post-planting fate of fungi spontaneously occurring in nurseries and those intentionally introduced;
- selecting candidate species of fungi for inoculation; and
- studying the impact of forest pesticides on mycorrhizal activity.

Work related to reclamation of mine wastes has been carried out with white spruce in Alberta (Danielson *et al.* 1979, 1984; Danielson 1988) and with Engelmann spruce in Colorado (Grossnickle and Reid 1982, 1983).

In natural forest ecosystems there is an orderly succession of mycorrhizal fungi in which one group of species replaces another as tree seedlings mature. Fungi forming mycorrhizae with spruce in open, recently disturbed sites differ from those found in mature forests. Naturally regenerating spruce seedlings on disturbed sites in southern Alberta were overwhelmingly dominated by E-strain, *Amphinema* and *Tomentella*. Agarics (typical forest mushrooms), which dominate in mature forests, appear to be of minor importance in early successional spruce stands (Danielson 1988).

A similar succession also occurs in highly disturbed and nursery environments. For example, on minespoils in Alberta, nonmycorrhizal spruce seedlings were quickly colonized by E-strain fungi, which dominated for the first 2–3 years after planting. After 7 years, E-strain fungi were largely replaced by *Amphinema*, which in turn was replaced principally by *Hebeloma* and *Tomentella*.

A survey of forest nurseries in Alberta and British Columbia found that the degree of infestation varied, with some nurseries producing nonmycorrhizal white spruce seedlings. The most common fungi in the infested nurseries were E-strain, *Thelephora terrestris* and *Mycelium radicis atrovirens*. *Amphinema byssoides* succeeded E-strain and *Thelephora* on spruce seedlings in the nursery (Danielson 1988).

Hunt (1988b, 1989) found five species of mycorrhizal fungi colonizing spruce seedlings in a Kamloops forest nursery. Which colonizer was dominant depended on whether or not controlled-release NPK fertilizers (Osmocote®, Nutricote®) were used. Seedlings receiving Osmocote® or Nutricote® were predominantly colonized by *T. terrestris*, while those without the supplement were dominated by E-strain fungi. Osmocote® also reduced mycorrhizal diversity. Overall, the seedlings dominantly colonized by E-strain performed better in the nursery than those dominated by *T. terrestris*.

Soil temperature is an important factor affecting the type and degree of mycorrhizal activity. Research on species other than spruce has also shown that cool temperatures may eliminate the benefits normally derived from mycorrhizal infection. Heninger and White (1974) grew white spruce seedlings at five soil temperatures (15, 19, 23, 27, and 31°C) in a controlled-environment chamber. Seedlings showed some mycorrhizal development at all temperatures except for the 15°C treatment where mycorrhizae were completely absent. Best mycorrhizal development and the best seedling growth occurred at 19°C. The species of mycorrhizal fungi were not identified, but a natural forest soil was used to grow the seedlings.

Husted (1991) investigated the potential of artificially inoculating interior spruce seedlings in the nursery to improve reforestation success on cool sites in the northern interior of British Columbia. It was felt that artificial inoculation could enhance root growth and water and nutrient uptake during the first outplanting season before significant natural colonization takes place. Another consideration was that mycorrhizae that spontaneously colonize seedlings in the warm, fertile soils of container nurseries might be poorly adapted to the cold soils of northern interior planting sites. A variety of ectomycorrhizal strains were tested for their ability to colonize seedlings at low temperatures, their persistence in the field and their ability to promote seedling growth.

Husted's (1991) laboratory study indicates that artificially inoculating seedlings with either natural forest soil containing mycorrhizal propagules, or with specifically selected ectomycorrhizal strains, has good potential to improve field performance in cool (6–12°C) wet soils during the first growing season. Some of the fungal species tested (particularly *Laccaria bicolor*) increased seedling growth over uninoculated controls, some had no effect (*A. byssoides*, and *T. terrestris*—both common nursery species), and others (E-strain and *Hebeloma crustuliniforme*) reduced growth. Whether the fungal inoculum originated in a northern spruce forest or in a nursery environment did not seem to have a consistent impact on spruce performance. Seedlings inoculated with natural forest soils performed well and may have benefitted from the diversity of mycorrhizal species present.

The use of herbicides or other pesticides may temporarily damage or eliminate mycorrhizal fungi in the soil. In a greenhouse study by Chakravarty and Sidhu (1987), application of granular hexazinone (Pronone®5G) at rates of 1, 2, and 4 kg ai/ha (kilograms of active ingredient per hectare) caused a reduction in mycorrhizal development on spruce seedlings. At the 1 kg ai/ha rate, there was an initial reduction in mycorrhizal development, but a recovery to control conditions occurred after 4 months. At application rates of 2 and 4 kg ai/ha, damage was more severe. Although the degree of mycorrhizal infection had improved after 6 months, it was still significantly lower than the control and 1 kg ai/ha treatment. The phytotoxic effects of the herbicide are expected to be less severe under field conditions.

3.3 Vegetation Interactions

This section describes how competing vegetation interferes with the growth of interior spruce, and identifies when and how vegetation management can be used to enhance the performance of spruce plantations and stands. Forest vegetation management has received considerable study in recent years. For a general discussion of the principles behind vegetation management see Walstad and Kuch (1987) or Newton and Comeau (1990).

Techniques or tools used in vegetation management (e.g., prescribed fire, herbicides, mechanical or manual methods, animal grazing, grass seeding) can affect aspects of forest management other than spruce performance, for example, wildlife habitat management, or the maintenance of site productivity and water quality. In some cases the targets of vegetation management prescriptions may themselves have the potential to become crop species as economic conditions and species utilization change. This discussion does not attempt to evaluate these potential side effects of vegetation management practices, but rather restricts itself to the effects of vegetation management on interior spruce performance.

Non-crop vegetation affects the growth of interior spruce in many ways. It may compete directly for site resources (light, water, nutrients), it may modify the physical environment (e.g., shading may reduce soil temperature), or it may cause physical injury to the tree (vegetation press or wind-whipping). Vegetation management treatments are directed at remedying resource limitations or improving the physical environment for the tree. Before vegetation management techniques are prescribed, the underlying causes of poor spruce performance must be identified. Only then can it be determined whether or not vegetation management will remedy the situation.

3.3.1 Major vegetation complexes

Across British Columbia there is a great diversity of early successional plant communities that occur in association with stands of interior spruce. The most widespread of these plant communities, and the ones with the greatest potential to interfere with successful growth of interior spruce, have been classified into a limited number of complexes of competing vegetation (Newton and Comeau 1990). These major vegetation complexes are described in Table 9, along with information on how they interfere with interior spruce growth and how they might be successfully managed. Vegetation management research on these complexes is just beginning, and, as a result, many of the studies referenced in Table 9 are preliminary and/or unpublished.

3.3.2 Spruce response to vegetation management

Most research on white or Engelmann spruce response to vegetation management practices falls into one of two general categories: 1) the impact of competing vegetation during the period of establishment and early growth, and 2) the impact of overtopping deciduous trees on older, established spruce.

Establishment period Vegetation control has improved survival and growth of white and Engelmann spruce seedlings in British Columbia (Eis 1981; Eis and Craigdallie 1983; McMinn 1985a; Draper *et al.* 1988; MacKinnon and McMinn 1988; Herring 1989; Presslee 1989; Black and Mitchell 1991a,b; Coates *et al.* 1991) and elsewhere (e.g., Vincent 1954; Waldron 1959; von Althen 1972; Sutton 1972, 1975, 1978a, 1986). Other studies have reported little gain or negative impacts on spruce performance following early vegetation control (Sutton 1975,

TABLE 9. Major complexes of competing vegetation affecting interior spruce performance (adapted from Newton and Comeau 1990)

Complex	Major species	Biogeoclimatic zones	Site conditions	Type of interference	Potentially successful vegetation management treatments	References
Fireweed	*Epilobium angustifolium*	Throughout B.C.; Mainly in SBS, ESSF, ICH, BWBS, MS, SBPS	Dominates early succession on a wide range of sites. Especially abundant after burning.	Vegetation (snow) press; Low light levels; Moisture and nutrient competition; Generally only a serious problem when very dense.	Plant sturdy, large caliper stock; Avoid burning; Glyphosate; Mounding; Sheep grazing; Mulching.	Herring 1984c; Herring and Fahlman 1984, 1985b; Comeau 1988; Delong 1988b; Simard and Nicholson 1990.
Reedgrass	*Calamagrostis canadensis*	Abundant and dominant in BWBS, east of Rocky Mtns. Also found in SBS, ICH, and ESSF of northern and central B.C.	Early succession on moist to wet sites.Often takes over after other species have been set back after MSP or herbicides.	Vegetation (snow) press; Provides habitat for snowshoe hare and other small mammals; Prevents soil warming; Nutrient and moisture competition.	Intensive cultivation (plows, discs, mounds); Glyphosate or hexazinone (mixed results); Plastic mulch; Avoid clearcutting (mixedwood management).	Whitehead 1983, unpub.; Fahlman and Herring 1985a,b; Peterson 1988; Herring 1989; Peterson *et al.* 1989.
Fern	*Athyrium filix-femina* *Dryopteris assimilis*	Wetter ICH, ESSF, SBS and BWBS	Fresh to wet sites. Present before logging and expands following light to moderate disturbance.	Vegetation (snow) press; Low light levels; Prevents soil warming. Generally only a serious problem in very vigorous, developed stands.	Mounding or plowing; Glyphosate; Mod.-high impact broadcast burn; Plant sturdy, large caliper stock; Mulching.	Herring and Fahlman 1984, 1985b; Draper *et al.* 1985, 1988; Binder *et al.* 1989; Spittlehouse *et al.* 1990.
Bracken	*Pteridium aquilinum*	Warmer, wetter ICH, ESSF, SBS	Dry to wet, usually warmer sites. May take over after other species eliminated by severe or repeated disturbance.	Vegetation (snow) press; Provides small mammal habitat; Moisture, nutrient and light competition; Allelopathy.	Glyphosate or asulam; Deep plowing or other intensive cultivation.	Whitehead *et al.* 1982, unpub.; Herring 1984b.
Subalpine herb	*Valeriana sitchensis* *Senecio triangularis* *Veratrum viride* *Luzula* spp. *Epilobium angustifolium*	ESSF	Fresh to wet, snowy sites. Present before logging, especially in forest openings.	Prevents soil warming; Light and nutrient competition; Vegetation (snow) press; May increase frost damage.	Broadcast burn; Mounding or other MSP treatment that creates raised microsite; Sheep grazing; Mulching; 2,4-D or glyphosate (mixed results).	Caza and Kimmins 1988, 1990a,b; Coates 1988a,b; Coates *et al.* 1991.
Ericaceous shrub	*Rhododendron albiflorum* *Menziesia ferruginea* *Vaccinium* spp.	ESSF (upper elev. ICH) in southern and central B.C.	Well established on ± mesic, snowy sites receiving little disturbance during logging.	Low light levels; Prevents soil warming; May increase frost damage; Reduced nutrient availability?	Summer logging; Broadcast burn; Mechanical site prep.; Manual cutting with screefing; Avoid clearcutting.	Scagel 1987, unpub.; Caza and Kimmins 1988, 1990a,b; Coates 1988a,b; Butt 1990, unpub.; Coates *et al.* 1991.
Mixed shrub	*Rubus parviflorus* *R. idaeus* *Lonicera involucrata* *Acer glabrum* *Alnus viridis* *Sambucus racemosa* *Salix* spp. *Cornus sericea* *Epilobium angustifolium* *Ribes* spp.	ICH, SBS, MS, ESSF, most abundant in wetter subzones	Fresh to wet sites. Typically established in forest understory and expands after logging.	Low light levels; Litterfall and vegetation press; Prevents soil warming; Provides small mammal habitat; May increase frost damage.	High impact broadcast burn with prompt planting of vigorous stock; Glyphosate; Disc trenching, mounding or plowing; Repeated manual cutting and/ or power screefing.	Whitehead *et al.* 1982, unpub.; Comeau 1988; Delong 1988b; Hamilton and Yearsley 1988; LePage and Pollack 1988; Presslee 1989; Taylor *et al.* 1992; LePage *et al.* 1991.

TABLE 9. Major complexes of competing vegetation affecting interior spruce performance (adapted from Newton and Comeau 1990) (continued)

Complex	Major species	Biogeoclimatic zones	Site conditions	Type of interference	Potentially successful vegetation management treatments	References
Wet alder	*Alnus viridis* *A. incana* *Rubus parviflorus* *Lonicera involucrata* *Calamagrostis canadensis* *Athyrium filix-femina* *Dryopteris assimilis*	ICH, MS, SBS, BWBS, ESSF	Wet sites, often along watercourses or in depressions. Often well established on sites with few or no trees before logging. May invade areas of soil disturbance.	Low light levels; Litterfall and whipping damage; Provides mammal habitat; Prevents soil warming.	Mechanical site prep. followed by manual cutting or glyphosate; Avoid soil disturbance if not already severe; Repeated manual cutting.	Wray and Hanlon 1987, unpub.
Willow	*Salix* spp.	BWBS, SBS, ICH, MS, ESSF, SBPS, IDF	Mesic to wet sites. Most common on sites with a history of past fire. Invades areas of soil disturbance.	Light, moisture and nutrient competition; Litterfall and whipping damage; Provides small mammal habitat; Generally only a serious problem if dense thickets exist.	If well established: intensive cultivation followed by manual cutting, glyphosate or hexazinone; Otherwise: Glyphosate or hexazinone; Prompt planting of vigorous stock followed by manual cutting; Avoid soil disturbance.	Wray and Hanlon 1987, unpub.; Bancroft 1990; Pollack *et al.* 1990.
Cottonwood	*Populus balsamifera* *Lonicera involucrata* *Cornus sericea* *Sambucus racemosa* *Rubus parviflorus* *Alnus viridis* *A. incana* *Calamagrostis canadensis* *Cinna latifolia*	ICH, SBS, MS, IDF, BWBS	Floodplains. Usually well established prior to logging.	Low light levels; Litterfall and whipping damage; Provides small mammal habitat; Prevents soil warming.	Intensive cultivation or high-impact broadcast burn followed by grass seeding or manual cutting; Avoid clearcutting (mixed ssp.manage.); Glyphosate; Repeated manual cutting.	Hanlon 1987, unpub.
Mixed hardwood	*Populus tremuloides* *P. balsamifera* *Betula papyrifera* *Salix* spp. *Alnus incana* *A. viridis*	ICH, SBS, MS, IDF, BWBS	Dry to moist sites, usually with a history of past fire.	Light, moisture and nutrient competition; Whipping damage and litterfall; Provides small mammal habitat.	Preharvest: girdling or hack-and-squirt; Post-harvest: (if clumpy or not excessively dense) manual girdling or spot applications of glyphosate or hexazinone; intensive sheep or cattle grazing; (if dense) intensive cultivation followed by chemical applications, girdling or grazing.	Sutton 1978a; Presslee 1989; Simard and Nicholson 1990.
Aspen	*Populus tremuloides*	BWBS, SBS, ICH, MS	Dry to moist sites, usually with a history of repeated fire.	As above		Peterson 1988; Baker 1989; Bancroft 1989; Herring 1989; Peterson *et al.* 1989.
Boreal poplar	*Populus tremuloides* *P. balsamifera*	BWBS, SBS	Fresh to moist sites, usually with a history of repeated fire.	As above	Aerial application of glyphosate; Avoid clearcutting (mixedwood management)	Herring 1984a,b; Fahlman and McArthur 1985; Herring and Fahlman 1985a; Brace and Bella 1988; Day and Bell 1988; Drew 1988.

1984b; Blackmore and Corns 1979; Brand and Janas 1988; Wood and Dominy 1988). Although most studies report improved spruce performance following vegetation control, the nature and degree of response is extremely variable.

Part of the reason for conflicting results following vegetation control is that two factors are often unclear: 1) how vegetation control improves the seedling environment, and 2) how much vegetation must be controlled. In low-elevation forests of the United States Pacific Northwest, where summer drought limits forest productivity, competition for soil moisture has been identified as the major reason for poor conifer performance (Stewart *et al.* 1984; Walstad and Kuch 1987), and vegetation control has dramatically increased conifer seedling survival and growth. The picture is not so clear for spruce in British Columbia.

At high-elevation ESSF sites in the southern interior, soil moisture content remained high throughout the growing season both in undisturbed vegetation and on vegetation control plots (Caza and Kimmins 1990a; Black and Mitchell 1991a; Coates *et al.* 1991). All three studies conclude that improved Engelmann spruce performance on vegetation control plots was not caused by alleviating moisture stress. In contrast, at a lower-elevation site in the MSxk, a dry subzone, Black and Mitchell (1991a) observed significant water deficits in the latter part of the growing season on plots with undisturbed vegetation. They conclude that water conservation from vegetation control was the primary reason for improved spruce growth.

On a freshly logged Ontario site, no water deficits were observed during the first growing season on either herbicide-controlled or undisturbed vegetation plots (Brand and Janas 1988). However, as the vegetation continued to develop over the second and third growing seasons, water deficits began to appear in the undisturbed vegetation plots (D. Brand, pers. comm., July 1990). Another Ontario study showed that vegetation control on a moisture-limiting site increased white spruce survival from 22 to 94%, but survival was not affected where moisture was not limiting (Sutton 1975).

It is clear, however, that dense non-crop vegetation overtopping young spruce seedlings can cause high mortality. For example, in undisturbed vegetation on a very brushy site in the SBS zone near Prince George, white spruce survival was 95, 48, and 6% after one , three, and five growing seasons in the undisturbed vegetation (Eis and Craigdallie 1983). This study and others demonstrate that when spruce seedlings are completely overtopped by shrubs and herbs, survival is poor; however, complete vegetation control is not required to achieve excellent spruce survival. Binder *et al.* (1987) believe that early spruce performance is best at light levels approximately 30–35% below full sunlight conditions. Coates *et al.* (1991), in an experiment that created different levels of shrub and herb competition, observed excellent Engelmann spruce survival, provided the vegetation did not completely overtop the seedlings. The experimental evidence suggests that when high levels of spruce mortality occur on areas with only moderate levels of vegetation, factors other than the vegetation are probably responsible.

Vegetation control treatments often fail to produce a significant reduction in the cover of competing vegetation. Herbicide treatments are not always effective (e.g., Fahlman and Herring 1985a), plant regrowth following treatment may be extremely rapid (e.g., after a manual cutting [LePage *et al.* 1991]) or a species shift may occur that creates competition problems that are equal to or worse than pre-treatment conditions (Herring and Fahlman 1985a; Thompson 1988). Even when treatments are successful in reducing vegetation cover, they may not result in improved performance if factors such as cold soils (Brand and Janas 1988; Draper *et al.* 1988; Wurtz and Zasada 1988), winter damage (Herring 1984a), or frost damage (Sutton 1984b) are more important than vegetation in limiting the establishment and early growth of spruce.

In reviewing a series of experiments carried out in the northern interior of British Columbia, MacKinnon and McMinn (1988) noted that:

- blade scarification provided good vegetation control but spruce growth was poor;
- continual vegetation clipping provided good vegetation control and good spruce growth;
- hand mixing of the soil provided poor vegetation control, but good spruce growth;
- control plots had poor vegetation control and poor spruce growth;
- mounding site preparation provided a good level of vegetation control and good spruce growth; and
- on several sites complete vegetation control was only achieved at the cost of significant frost damage.

These results indicate that vegetation control alone is not enough to ensure good spruce performance, and that good spruce performance can occur even where vegetation control is relatively poor. As the last item suggests, there may be an optimum amount of vegetation cover that provides protection while interfering little with growth. The studies of Draper *et al.* (1988) near Prince George, and Brand and Janas (1988) in Ontario, reach similar conclusions. In both of these studies, competing vegetation contributed to poor spruce performance but it was not the primary limiting factor. The problem of low soil temperatures had to be addressed before vegetation management treatments could be effective.

On most spruce sites, competing vegetation is only one of many factors affecting seedling establishment success and early growth. Other constraints, such as cold or wet soils, frost damage, or pest problems, are often of equal or greater importance. It is essential that limitations to spruce establishment and growth be identified on individual sites; only then can the value of a vegetation control treatment be determined.

Deciduous overstory While shrubs and herbs pose problems for spruce establishment and early growth, competition from hardwood trees provides the most serious long-term threat (Stiell 1976). The interactions between trembling aspen and white spruce have received extensive study in the mixedwood forests of Canada since the 1950s and 1960s. Most of the early research concerning the release of white spruce from an aspen overstory is summarized by Jarvis *et al.* (1966). Johnson (1986) provided a comprehensive review of information on the release of white spruce from aspen overstories. Yang (1989) presented 30- to 50-year results of the effects of (aspen) release cuttings on white spruce diameter, height, basal area, and volume increments. The findings from these three reports are summarized below, and should be applicable to the mixedwood forests of the BWBS zone in northeastern British Columbia. No comparable research has been published describing the competitive interactions of spruce-hardwood mixtures in central and southern British Columbia forests.

Young white spruce must be at least 3 m tall and probably closer to 4 m tall to avoid being overtopped by aspen suckers following a single release cutting. The most vigorous response to release occurs when spruce are younger than 40 years, but trees up to 75 years old will respond to release; older trees do not release well. Free growing white spruce require 40 to 65 years to equal the height of free growing aspen while suppressed spruce need 50 to 75 years. Suppressed spruce emerging above an aspen canopy may be in poor condition as a result of prolonged whipping damage. The wind-whipped branches of aspen can cause extensive scarring or repeated breakage of spruce leaders and foliage.

Complete release of spruce from aspen increases diameter, height, basal area, total volume, and merchantable volume. On good sites, pure stands of spruce will reach the culmination of mean annual increment 30–40 years earlier than spruce in mixed stands. Yield tables for Saskatchewan suggest that at age 90, the total volume of spruce will be 35% less in mixed stands than in pure stands. Where release treatments are carried out, the density of spruce residuals dictates stand yield development. Between 690 and 840 stems per hectare (sph) of spruce residuals released at 20–40 years of age will provide adequate yield development. Stands containing less than 250 sph of spruce are not well enough stocked to justify release cutting; stands with over 2500 sph of spruce will require thinning. If spruce stocking is adequate, the gross total yield of a mixed stand and a released stand will be similar. However, in the released stand the yield is concentrated on the spruce trees.

Yang (1989) found that diameter response of spruce trees following release varied considerably depending on stand age, density, and pre-release diameter, but that diameter growth always increased following release. Spruce diameter increment, averaged over a large number of stands, was 31% greater after 30 years of release, but increases of up to 177% were recorded. Height growth did not improve for at least 5 years after release. Released trees averaged 42% greater height increment over 30 years than suppressed trees. The greatest height response occurred on trees less than 6 m tall at the time of release. In terms of periodic annual increment of merchantable volume, released spruce stands averaged 4.25 m^3/ha per year compared to 1.94 m^3/ha per year for untreated stands, an improvement of 114% (Yang 1989).

There are few data available describing the response of spruce to partial removal of an aspen overstory, but, in general, spruce trees appear to respond positively to partial release. There is also little information available on the age at which spruce growth begins to decline under an aspen canopy or on the effect of growing spruce and aspen at controlled densities from an early age. A problem analysis examining paper birch and conifer interactions has recently been prepared for the southern interior of British Columbia (Simard 1990). This review draws on information from Scandinavia (Hagglund and Peterson 1985), where the birch and spruce are of different species, but similar ecologically to those in British Columbia. Their report concludes that spruce and birch can be successfully grown in mixtures when density is carefully managed.

In conclusion, there is a wealth of information on interactions between spruce and aspen, especially on the growth rates of spruce following aspen overstory removal. There is little information on growing spruce and aspen in mixtures, and little information on the interactions between other deciduous species and spruce.

4 Pest Management

The practice of pest management in interior spruce forests is changing as management emphasis shifts from old-growth forests of natural origin to managed young stands. Pests that were once considered of minimal importance, such as the black army cutworm, may become serious problems. Some important problems may still be "undiscovered," as was Tomentosus root rot until only recently. These new patterns of pest occurrence reflect new patterns in silvicultural practice and forest utilization. The rise in black army cutworm incidence appears to have coincided with widespread use of prescribed fire as a site preparation tool. Tomentosus root disease was recognized because of an increasing awareness of the symptoms of pest damage.

More surprises may be close at hand. Increased investment in stand management means that growth loss and/or deformity in young trees will become less acceptable, placing more emphasis on the protection of individual stems. The spruce budmoth (*Zeiraphera canadensis*) has emerged as a serious problem in the Canadian Maritimes, apparently in association with extensive monocultures of planted white spruce. Spruce budmoths are common though not yet serious pests in British Columbia; the implications of the Maritime experience are obvious. Large-scale pollution problems such as acid rain, or forecast changes in global climate patterns will affect our forests, and consequently our pest problems (Borden 1988).

The following sections summarize important pest problems of interior spruce in British Columbia, including current management strategies and readily available references. Mention of specific pesticides implies neither endorsement nor current registration; readers are advised to consult appropriate sources for current information.

4.1 Major Insect Pests

4.1.1 Spruce beetle (*Dendroctonus rufipennis*)

The spruce beetle occurs throughout the range of spruce in British Columbia and is the most serious pest of mature and overmature interior spruce. All species of spruce are susceptible, but attacks on Sitka and black spruce are rare. Major outbreaks originate from stand disturbances such as windthrow, which can create ideal conditions for population increases. Large volumes of timber can be killed during epidemics. For example, an outbreak in 1961–1965 in the Prince George and Prince Rupert Regions covered 243 000 ha, and killed an estimated 14.1 million m^3 of spruce (Cottrell 1978).

Schmid and Frye (1977a,b) provide a comprehensive review of spruce beetle life history, behaviour, host relations, mortality agents, and the impact of infestations in the western United States; Cottrell (1978) provides a brief review of the beetle in the interior of British Columbia. The spruce beetle generally has a 2-year lifecycle, although varying percentages of broods will develop on a 1- or 3-year cycle. The length of the development cycle is temperature dependent; the 1-year cycle is more common during warm summers, at sunny exposed locations, or in open slash. The 3-year cycle is rare and confined to unusually cool locations. Emergence of adults has three phases: 1) spring emergence for attack; 2) re-emergence of parent adults after making an initial attack; and 3) emergence for hibernation. In the spring, adults emerge and attack new host material when temperatures in the shade reach about 13–16°C (snow may still be on the ground) (Cottrell 1978; Safranyik and Linton 1988). This generally occurs from mid-May to early July, with peak flight occurring in early June. Adult beetles can reemerge after making an initial attack in the spring resulting in a second peak flight and attack between late July and early August. In the common 2-year lifecycle, larvae overwinter under the bark, and develop into adults during the following summer. In standing trees newly developed adults often, but do not always, emerge in late summer or early autumn to overwinter in chambers in the thick bark at the root collar region, below the duff line, to a depth of about 25 cm (Knight 1961). Adults that develop in downed materials generally do not emerge prior to overwintering.

Red boring dust (frass) accumulates at the base of attacked standing trees, or in small piles around entrance holes on downed materials (Figure 26a). Pitch tubes infrequently form around entrance holes on standing trees, but are quite variable in occurrence, and are not reliable indicators of an infested tree. Spruce beetle egg galleries extend upwards in standing trees, or parallel to the bole in downed trees. The egg galleries are usually packed with frass (Figure 26b). Larvae feed out from the egg gallery as a group, and then feed individually. *Ips* spp. bark beetles often infest the upper surfaces of downed materials exposed to direct sunlight. Adult *Ips* are readily distinguished from spruce beetles by their concave posterior, which has spines along each side (Furniss and Carolin 1977). *Ips* galleries are free of frass, and often form a 3-branched "Y" etched on the surface of the sapwood (Furniss and Carolin 1977). Spruce beetle larvae can be distinguished from *Ips* larvae by the two sclerotized plates on their posterior (Figure 26c). Sclerotized posterior plates are absent on *Ips* larvae; however, the plates are present on some other bark beetle species. Spruce beetles can often be found on the underside of *Ips*-infested logs.

The foliage of successfully infested trees normally fades to yellow or yellowish green and falls during the summer following attack, but it is difficult to classify spruce by foliage colour (Figure 26d).

Spruce beetles are nearly always present in low numbers in mature spruce stands, inhabiting scattered blowdown and injured or otherwise weakened trees. Fresh logging slash and stumps are readily infested by spruce beetles and can produce significant numbers of brood if a 1-year lifecycle predominates (Dyer and Taylor 1971). All documented outbreaks have been associated with extensive windthrow or large accumulations of man-made slash (Safranyik 1980), where populations build up and then move into adjacent standing trees. Localized problems develop in association with debris from right-of-way clearing, abandoned log decks, excessive logging slash, blowdown around stand edges, and stands affected by root disease.

A system for rating Engelmann spruce stand susceptibility to spruce beetle attack was developed by Schmid and Frye (1977b), and subsequently tested for spruce beetle populations in the Prince George Forest Region by Safranyik (1985) (Table 10).

TABLE 10. Risk categories for potential spruce beetle outbreaks (from Schmid and Frye 1977b)

Risk category	Site	Average diameter of live spruce > 25 cm dbh (cm)	Basal area (m^2/ha)	% spruce in canopy
High	well-drained creek bottoms	> 40	>34	> 65
Medium	good sites	30–40	23–34	50–65
Low	medium sites	< 30	< 23	< 50

Hard (1985) and Safranyik (1985) suggest that spruce trees may be more susceptible to attack if radial growth is slower than average over the previous 5 years, which suggests that stand treatments to reduce competition and increase the vigour of residual stems may enhance resistance to beetle attacks (Hard 1985; Hard and Holsten 1985).

Logging is the most effective way to remove beetle brood from standing trees in an infested area. However, logging will only be partially effective in removing spruce beetle brood if an infested stand is logged after newly developed adults begin to emerge for overwintering at the base of their brood tree. Populations in residual materials can be minimized by cutting low stumps, limbing cull logs, and removing all log decks promptly (Schmid 1977).

Live uninfested spruce trees can be felled to attract, absorb, and trap spruce beetles by taking advantage of the beetles' natural preference for downed materials. Once these "trap trees" are infested they can be removed, or disposed of in some other manner such as burning or spraying with an insecticide. Normally, the 2-year cycle of the beetle allows substantial time to treat trees, but trees must be monitored to ensure that beetle broods have not entered a 1-year development cycle. If the trees are injected with an arsenical silvicide such as monosodium methanearsenate (MSMA) prior to falling, "lethal trap trees" are created. These absorb and kill large numbers of adult beetles without allowing brood development (Buffam and Yasinski 1971; Frye and Wygant 1971; Hodgkinson 1985; Holsten *et al.* 1985), and eliminates the need for follow-up treatments.

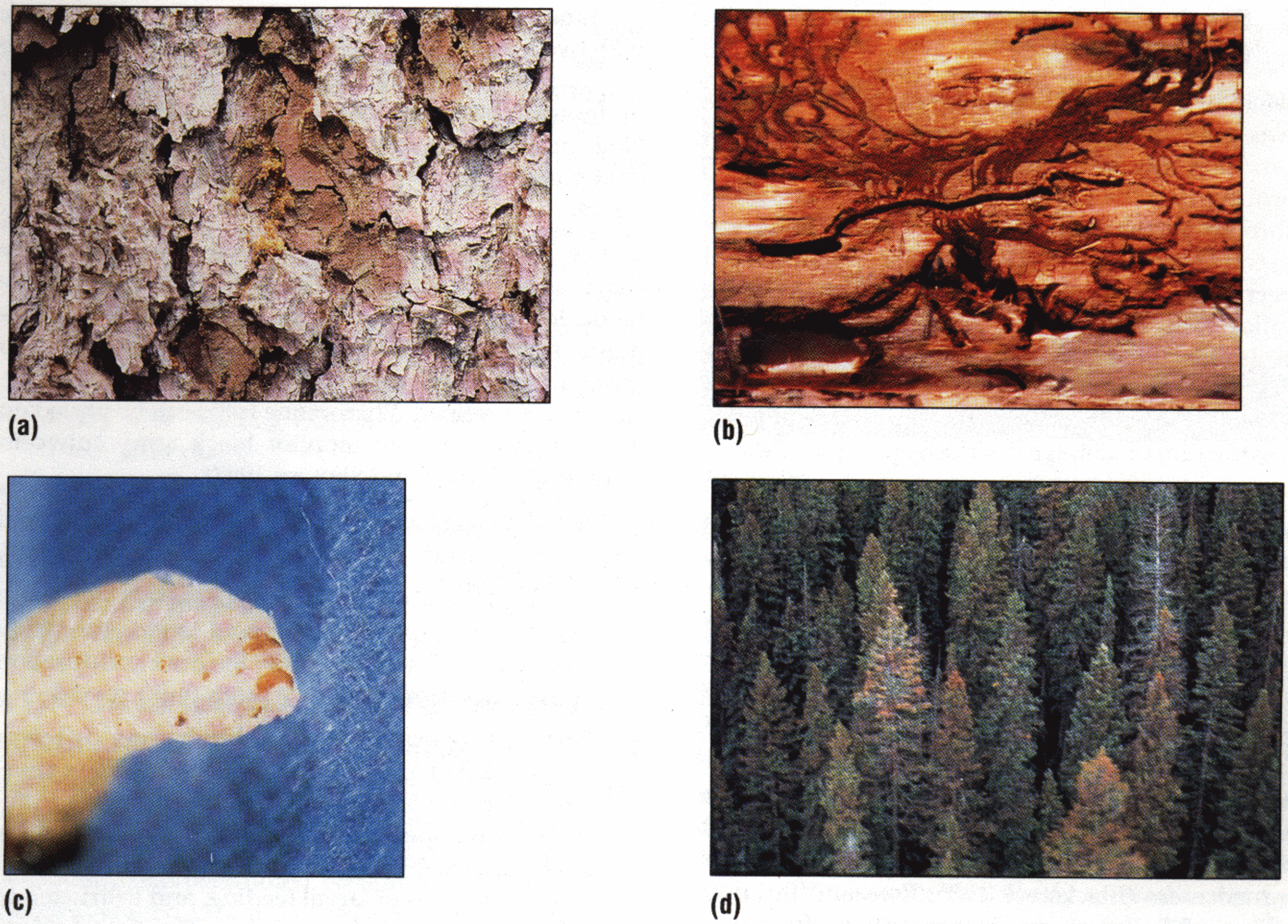

FIGURE 26. Identifying characteristics of spruce beetle (*Dendroctonus rufipennis*) attack: (a) external appearance of attacked standing tree showing boring dust; (b) spruce beetle egg galleries, packed with frass; (c) spruce beetle larva with sclerotized posterior plates; and (d) aerial view of beetle-infested trees.

Insecticides such as Carbaryl® have been applied as external sprays to protect individual trees (Dyer 1975; Werner *et al.* 1986). They could be used in situations where high-value trees are at risk.

Pheromones An attractive pheromone (frontalin, used in combination with alpha-pinene) is available for the spruce beetle (Dyer and Chapman 1971). Pheromone-baited standing trees treated with an external insecticide spray have been used as lethal trap trees to attract and kill beetles (Dyer *et al.* 1975). These attractants are not as effective as trap trees for concentrating spruce beetle attack. There is currently an effort to discover more effective attractants for the spruce beetle. The pheromone MCOL is being tested in British Columbia and early results suggest the pheromone may be as effective as trap trees for concentrating spruce beetle attack. The success of pheromone baiting of standing trees could be reduced if windfall suitable for attack is available in the stand.

Methylcyclohexanone (MCH), an antiaggregation pheromone for the Douglas-fir beetle, has been shown to reduce spruce beetle attack on downed trees, although results have been inconsistent (McGregor *et al.* 1984; Holsten *et al.* 1987; Lindgren *et al.* 1989). Potential exists for further development of MCH to control population build-up in windthrow or cutblock edge blowdown (McGregor *et al.* 1984). MCH can be used to protect single trees in high-value situations. Verbenone is currently being tested.

General References Schmid and Frye 1977a; Werner *et al.* 1977; Cottrell 1978; Hard and Holsten 1985; Hodgkinson 1985; Safranyik and Linton 1988; Safranyik 1989.

4.1.2 Black army cutworm (*Actebia fennica*)

The black army cutworm is a defoliating moth larvae that was once considered solely an agricultural pest (Ross and Ilnytzky 1977). In recent years, however, the cutworm has become a major concern in conifer plantations throughout the interior of British Columbia. Larvae feed on conifers when preferred plant species such as red elderberry, Indian hellebore, or false Solomon's-seal, are not available (Blackstock 1985; Hodgkinson 1986). Damage levels are variable, ranging from localized seedling deformity and loss of height growth to complete loss of plantations (Hodgkinson 1986). Interior spruce appears to be less tolerant of damage than lodgepole pine (Maher 1988).

The black army cutworm has a 1-year lifecycle (Wood and Neilson 1956). Young larvae become active as snow recedes and vegetation begins to grow (Blackstock 1985), often in early May, although this is influenced by the weather (Ross and Ilnytzky 1977). Larvae begin to pupate in June, and adults emerge and begin to fly in early July (Ross and Ilnytzky 1977). Adult females lay their eggs in the soil.

Historical records show a clear relationship between black army cutworm damage and the use of prescribed fire, although it is not known if adult moths actively seek out burned areas (Blackstock 1985; Ross and Ilnytzky 1977) (Figure 27). Female moths appear to prefer south-facing upper slopes for egg laying, and these areas are often where cutworm activity is first noted (Blackstock 1985). Feeding larvae migrate downslope as vegetation is depleted (Blackstock 1985).

Mature larvae are 30–40 mm in length, and are black with two longitudinal white lines along the back (Figure 28). Larvae are nocturnal feeders, spending the day underneath litter or burrowed into the duff (Wood and Neilson 1956). In cold habitats when feeding is reduced or eliminated at night, feeding may occur in the morning hours.

The Forest Insect and Disease Survey of Forestry Canada has been forecasting black army cutworm population levels with some success. Duff sampling techniques for pupal and larval counts, and pheromone trap monitoring systems exist for the cutworm, and are currently being refined. Pheromone traps can be placed on newly burned sites to monitor black army cutworm moth flight (Unger and Stewart 1987).

The following recommendations are summarized from Unger and Stewart (1987), Koot and Vallentgoed (1988), and Maher (1988):

- Pheromone traps should be used to monitor newly burned blocks, and to identify the peak and duration of the black army cutworm moth flight period.
- Early spring examination for black army cutworm larvae feeding on emerging plants should be a regular component of the spring planting program, especially where moth trapping indicates potential for seedling damage. Planting crews should be trained to identify signs of larval feeding, and instructed to report observations immediately. Careful examination for larvae in duff samples can provide a better indication of cutworm population levels and locations. Particular attention should be given to areas where herbaceous vegetation is light, as such areas run a higher risk of damage to seedlings.

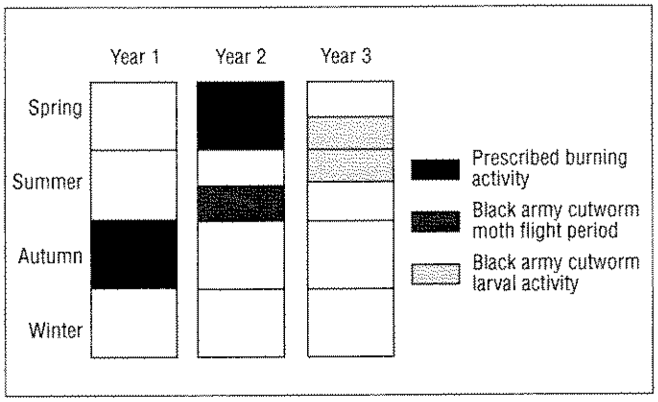

FIGURE 27. Seasonal relationship between burning and black army cutworm activity on a given site.

FIGURE 28. Mature black army cutworm larvae on a burned clearcut. Note the two longitudinal white lines on the back.

- Locations with a low potential for cutworm damage, especially areas with abundant herbaceous vegetation, should be given a high priority for planting. If infestation potential is high, planting should be delayed until early to mid-June when most cutworms are in late-instar and pre-pupal stages.
- If alternate planting options are limited, plant on schedule, and favour lodgepole pine as the species of choice. Be prepared to spot-treat with an approved insecticide and/or accept some second-year defoliation and possible mortality. Mortality levels for all species are higher when defoliation occurs concurrently with planting than when defoliation occurs 1 year after planting.
- Accurate maps should be drawn of affected areas and survival plots established to determine mortality and damage.

General References Ross and Ilnytzky 1977; Hodgkinson 1986; Maher 1988.

4.1.3 Sitka spruce weevil (*Pissodes strobi*)

The spruce weevil is an extremely serious pest of spruce regeneration in coastal British Columbia. The weevil is present in interior spruce plantations at some level throughout interior regions of the province, and significant damage has been noted. New attacks on Engelmann spruce averaged 11% at six sites in the Nelson Region in 1988 (Wood and Van Sickle 1989a). The full impact of the weevil in the interior may not yet be realized. Cozens (1983), for example, pointed out that generally low levels of damage reported in the Prince George Forest Region could be due to the fact that very few plantation-grown trees had reached susceptible size.

The weevil has one generation per year. Adult females oviposit at the top of spruce leaders from mid-May to mid-July, with peak activity occurring in late June (Stevenson 1967). New adults emerge from late August through September, and usually overwinter in the duff.

Trees from 1 to 25 m in height are attacked (Wood and McMullen 1983). Developing larvae feed downwards towards the base of the leader, usually converging in a single feeding area, encircling the stem, and causing leader death. Thus, both the current and previous year's leader growth is killed. On white spruce in the interior, larvae may feed down through 2 years' growth, effectively setting height growth back by 3 years (Wood and McMullen 1983) (Figure 29) . The leader droops, and foliage begins to turn yellow (Kline and Mitchell 1979). Stem deformities such as crooks and forks are other consequences of attack. Trees suffering repeated attacks are stunted and may be overtopped by competing vegetation (Alfaro 1982, 1989).

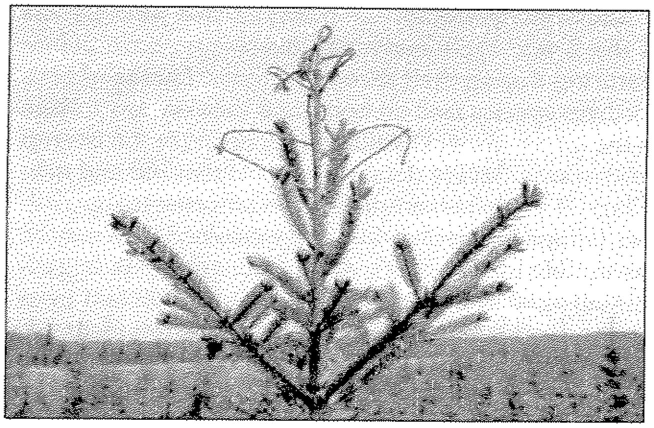

FIGURE 29. Spruce leader weevil attack on interior spruce.

It has proven extremely difficult to control weevil infestations. The problem is so serious in the Vancouver Region that planting of Sitka spruce has been restricted to areas where weevil hazard is considered minimal (Heppner and Wood 1984). A variety of insecticides has been tried, with limited success (Cozens 1983). Breeding of resistant Sitka spruce has shown some potential, but development is still (generally) in the testing stage (Wood 1987a); no similar work is being carried out on interior spruce. Provision of cool shady microclimates by manipulating stand densities or growing a "nurse crop" of alder has been shown to control weevil damage to some extent, but such practices are still in the research stage (Cozens 1983). Cozens (1983) identified clipping and burning of infested leaders as one available operational control method. Clipping is labour-intensive, and therefore expensive. It may not be cost-effective in many situations (Heppner 1989). Severely attacked stands may have to be rehabilitated (Jeklin and Wood 1983).

General References Cozens 1983; Wood and McMullen 1983.

4.1.4 Spruce budworms (*Choristoneura* spp.)

Three species of spruce budworm inhabit forests with white and Engelmann spruce. The western spruce budworm (*Choristoneura occidentalis*) occurs in southern British Columbia, primarily on Douglas-fir, amabilis fir, and grand fir (Unger 1983). The (eastern) spruce budworm (*C. fumiferana*) occurs in the boreal forests of northern British Columbia, and the 2-year-cycle spruce budworm (*C. biennis*) occurs in the subalpine and boreal forests of interior British Columbia. The latter two species feed primarily on subalpine fir, Engelmann spruce, and white spruce (Unger 1983).

Budworm larvae appear in May to early June. Larvae of the 2-year-cycle budworm overwinter once before maturing during their second summer. Larvae of both northern species feed on buds, and then on new foliage as the larvae grow. Defoliation occurs from the treetop downwards. Severe defoliation consumes old and new foliage. Repeated severe defoliation can cause tree growth loss, deformity, and top-kill, and weakened trees may be susceptible to bark beetle attacks (Unger 1983). In general, all-aged multi-level stands of shade-tolerant trees are the most susceptible to spruce budworm (Schmidt 1985). High densities of budworm larvae can seriously damage advance understory regeneration, causing deformity, growth loss, and mortality (Van Sickle 1987).

Widespread outbreaks and severe defoliation do occur, but direct control measures do not appear to be justifiable in interior spruce stands (unlike the case for outbreaks of *C. occidentalis* in Douglas-fir stands). Even-aged silviculture practices are likely to be the best option for dealing with these budworms (reviewed in Fellin 1985). Establishing a species mix that includes seral tree species, and maintaining stand densities that minimize tree stress, are important in reducing stand susceptibility to spruce budworm.

General References Unger 1983; Brookes *et al.* 1985, 1987.

4.2 Root Diseases

In general, damage from root diseases occurs through increment reduction, butt cull, live windthrow, or standing mortality. These diseases should be considered "site" problems, since residual inoculum in roots of cut stumps will remain on site for long periods of time (decades), reducing site productivity for conifer growth. The two most important root diseases of interior spruce are *Armillaria ostoyae* and *Inonotus (= Polyporus) tomentosus*. Interior spruces are not listed as hosts for laminated root rot (*Phellinus weirii*) by Wood (1986). However, Wallis (1976) records spruce as a host; spruce was highly susceptible in inoculation trials.

It is always necessary to know accurately the amount and distribution of disease within a stand, using the best available survey methodology, before attempting any management strategy.

Opportunities to reduce losses include: 1) avoiding stand tending treatments in diseased stands where investment may not be recovered; 2) reducing losses from tree mortality in established stands; and 3) rehabilitating infested sites (Morrison 1981).

4.2.1 Armillaria root diseases (*Armillaria* spp.)

Armillaria root rot occurs on all commercially important conifers in British Columbia (Morrison 1976). The disease has been variously described as an aggressive killer of healthy trees, a secondary pathogen of stressed trees, and/or a saprophytic decay of dead trees (Wargo and Shaw 1985). Development of disease centres and mortality in conifer stands appears to be primarily associated with *Armillaria ostoyae*, which occurs province-wide south of 53°N latitude (Morrison *et al.* 1985) (Figure 30). Damage is consequently more severe in the southern interior (Morrison *et al.* 1991) where trees of all ages are killed. Single trees or groups of trees up to several hectares in size may be affected. The incidence of mortality of conifers is relatively low in the northern interior (Morrison *et al.* 1985).

The fungus invades living tissue during its parasitic phase and uses dead material (e.g., stumps) as a food base during its saprophytic phase. The disease can survive for several decades in large roots and stumps (Morrison 1981). Armillaria spreads by rhizomorphs (red-brown to black strands—"shoe-strings"), or by root contact. Root contact is the primary mode of spread in the interior (Morrison 1976).

Symptoms of Armillaria infection are declining leader growth, chlorosis and thinning of the crown, and often a distress crop of small cones (Morrison 1976). Resin is exuded at infection points on the roots, and necrotic lesions are found beneath the bark. Basal resinosis, with white fans of mycelia beneath the bark, occurs when the disease reaches the root collar. Clusters of fruiting bodies


Morrison, Canadian Forest Service

FIGURE 30. Armillaria root disease centre in a 100-year-old Douglas-fir stand near Invermere, B.C. Note the ring of dead trees with mortality in the centre of younger trees.

are produced near the base of infected trees following rains in September–October (Morrison 1976). Fruiting bodies have honey-coloured caps with dark scales, whitish gills, and a yellow-brown stem with a ring below the cap (Morrison 1976). Butt rot seldom extends more than 2 m aboveground. Incipient decay has a water-soaked appearance, and advanced decay is spongy, yellowish to white, with black zone lines (Morrison 1976).

In general, silvicultural and other site disturbances such as harvesting, partial cutting, excessive grazing, fire suppression, and chemical or mechanical spacing tend to increase the incidence of Armillaria (summarized in McDonald *et al.* 1987b). The fungus colonizes roots and stumps of cut trees from quiescent lesions that were present on roots prior to harvesting, thus creating an inoculum source and a route for the fungus to spread to healthy trees (Wargo and Shaw 1985). These quiescent lesions may also become active if host tree vigour declines (Morrison *et al.* 1985).

Resistance to Armillaria increases with age for most conifer species. Increasing order of species susceptibility at 40 years in interior British Columbia is: larch, western redcedar, Engelmann spruce, and Douglas-fir (Morrison 1981; Morrison *et al.* 1988). McDonald *et al.* (1987a) suggest that pathogenicity of Armillaria decreases as site index increases.

The following management recommendations are summarized from Shaw and Roth (1978), Morrison (1981), and Wargo and Shaw (1985). It is essential to carefully evaluate the extent and impact of the disease within infested stands before any management operations can be planned. Spacing should be avoided within disease pockets unless resistant species can be favoured. Heavily infested stands should not be spaced. In commercially thinned stands where the entry intervals are less than 10 years, dead and obviously infected trees should be salvaged. If entry intervals are greater than 10 years, dead and symptomatic trees and any trees within 10 m of infected trees should be salvaged. Commercial thinning is not recommended in extensively infested stands. The regeneration phase of stand management provides the best opportunity for disease reduction or control. Stump removal, or planting of alternate species, are the two available options.

Uprooting stumps from infected sites is another viable control method. Results of a stump removal trial near Salmon Arm show that 20-year survival of planted Engelmann spruce was significantly improved by site treatment to remove Armillaria inoculum from the soil using a root rake mounted on a bulldozer (Morrison *et al.* 1988). Twenty-year mortality of Engelmann spruce was 11% in the untreated plot compared with 2% in the treated plot (Morrison *et al.* 1988). Results also suggested that tree growth was improved by the treatment. It is recommended that all diseased stumps and all stumps within 20 m of diseased stumps be removed. In severely infected areas all stumps should be removed.

Less susceptible species can be favoured for regenerating infested sites; however, some mortality should be expected since none of the species is completely resistant. Alternate species should be planted in a mixture, rather than single-species plantations. Host susceptibility in southern interior forests is as follows.

- least: Ponderosa pine, western larch
- moderate: spruces, western redcedar, lodgepole pine, western white pine, hardwoods
- high: true firs, Douglas-fir, western hemlock.

Managers should rely on natural regeneration on infested sites where inoculum removal or alternate species are not feasible options.

General Reference Morrison *et al.* 1991.

4.2.2 Tomentosus root rot (*Inonotus [=Polyporus] tomentosus*)

The incidence and impact of *I. tomentosus*, which occurs on both white and Engelmann spruce, and other conifers, are not well known at present. However, it is becoming increasingly apparent that the disease can be a serious impediment to the regeneration and management of interior spruce in British Columbia. *I. tomentosus* is very common in mature and overmature spruce and spruce–lodgepole pine stands in the Prince George, Prince Rupert, and Nelson forest regions. It is less common in pure pine stands. Infection centres are usually not obvious in natural or planted spruce or spruce–lodgepole pine stands less than 10 years of age (Unger and Humphries 1985; Garbutt and Turnquist 1986; Wood 1986; Unger and Stewart 1987; L. Unger, pers. comm., October 1989).

Damage can occur through increment reduction, butt cull, windthrow, or mortality of standing trees. The disease is also considered to predispose trees to attack by spruce beetles (Unger and Humphries 1984). Disease transmission from infected spruce to the next rotation occurs primarily by root contact with colonized stumps (Whitney 1962); however, there is good evidence to suggest that spores are also an important means of spread (Lewis and Hansen 1991a). Research suggests that residual inoculum in roots of cut stumps will remain on site for at least 30 years (Lewis and Hansen 1991b).

Symptoms are a function of how long the tree has been infected and the amount of root damage, not the age of the tree. Symptoms in young trees (crown thinning or reduced growth) can be obvious early if infection occurred soon after establishment (Schulting 1987). Most infected spruce with well-developed root systems will survive for a long period without obvious external symptoms or mortality. Field identification in mature stands relies heavily on examining windthrown trees for the presence of pitted rot and dark staining in the roots (Merler 1984).

Decay development in spruce roots begins as a light red stain at, or near, the centre of the roots, which becomes darker towards the point of infection (Figure 31a). Rotting wood becomes rusty brown with white pits (Figure 31b). Advanced rot has larger, yellowish pits, with or without (if old) white mycelium. Fruiting bodies occur in abundance following late summer–early autumn precipitation (Figure 31c).

The options available for the control of the disease include pushover logging or destumping and the planting of more resistant species. Trials are under way to assess the effectiveness of root removal as a control method. There is evidence that subalpine fir and Douglas-fir are moderately resistant to the disease, but they also can become infected (K. Lewis, pers. comm., November 1991). Although lodgepole pine is quite susceptible, its vertical rooting habit decreases the chance of spread by root contacts and is therefore a better choice than spruce for root-disease sites, particularly if established as a mixture with other resistant species. Hardwoods such as aspen or birch are immune and are good species choices where they are accepted for regeneration. Understanding of *I. tomentosus* is improving rapidly, and foresters are advised to consult with local forest pathologists to obtain current information.

4.2.3 Rhizina root disease (*Rhizina undulata* Fr.)

Rhizina undulata, which occurs in all regions of British Columbia (Wood 1986; Wood and Van Sickle 1989a,b), is a root disease that attacks newly planted seedlings. Newly planted spruce are susceptible. The fungus is generally present as a saprophyte in coniferous forests, but conditions created by recent wildfires or prescribed burns can stimulate its development (Baranyay 1972). Seedling mortality is most severe in the year following a fire, varying from 1 to 80%, and declines to negligible levels by the third year (Baranyay 1972).

FIGURE 31. Signs and symptoms of Tomentosus root rot in interior spruce: dark staining of the wood near the base of the tree (top); advanced decay in large root (centre); leathery fruiting bodies on the forest floor (bottom).

The primary symptom of Rhizina root rot is foliage discoloration resembling (and sometimes mistaken for) symptoms of drought, other root diseases, poor planting quality, or poor stock quality (D.A. Norris, pers. comm., October 1989). Severely infected seedlings have extensive white mycelia attached to the roots (Baranyay 1972). Fruiting bodies occur in early summer, often at, or near, an infected seedling, and persist until killed by frost (Baranyay 1972). Mature fruiting bodies are irregular ("brain-like") dark brown to black, and 5–12 cm across (Baranyay 1972).

Baranyay (1972) recommends delaying planting for at least 2 years in plantations where damage is severe enough to require replanting, or where fruiting bodies are detected prior to planting. Unfortunately, there seems to be little correlation between the occurrence of fruiting bodies and seedling loss (Thies *et al.* 1977; Wood and Van Sickle 1989a). Silviculturists are advised to consult with local forest pathologists for current recommendations pertaining to interior spruces.

4.3 Insects and Diseases of Minor or Periodic Importance

4.3.1 Cone and seed pests

The spruce seedworm (*Cydia strobilella*) and the spiral spruce-cone borer (*Hylemya anthracina*) are the two most important insect pests of spruce seed crops in interior and northern British Columbia (Ruth *et al.* 1982). Larvae of the seedworm feed only on seeds, from late June to September, and tunnel into the cone axis to overwinter. Larvae of the spiral spruce-cone borer feed indiscriminately on cone tissues, completing feeding in July. Inland spruce cone rust (*Chrysomyxa pirolata*) is the most important disease of spruce cones (Hunt 1978). It occurs throughout North America. Infected cones turn yellow, then brown, and open prematurely, while healthy cones are still closed and green (Hunt 1978). Preventative measures against damaging agents are generally carried out only in limited areas such as seed orchards or seed production areas. Cone and seed pests in natural stands do not usually affect natural regeneration (Hedlin *et al.* 1980).

4.3.2 Gall aphids (*Pineus* and *Adelges* spp.)

Gall aphids are the most common insect pest of young spruce plantations, but are of economic importance only in nurseries, on ornamental trees, and in Christmas tree plantations (Wood 1977). Damage on spruce is in the form of cone-like galls on the tips of new growth (Duncan 1986). Occasionally, aphid damage in combination with frost damage can contribute to stunting and deformity of young spruce in plantations, and damage can be locally severe (Garbutt and Turnquist 1988).

4.3.3 Heart, butt, and trunk rots

Agents of rot include the bleeding fungus (*Haematostereum sanguinolentum*), ring scale fungus (*Phellinus [=Fomes] pini*), and red belt fungus (*Fomitopsis [=Fomes] pinicola*). Decays in interior spruces are generally a natural condition of mature and overmature stands (Hiratsuka 1987). Losses can be minimized by avoiding damage to main stems, proper pruning practices, and harvesting stands before losses become severe (Hiratsuka 1987).

4.3.4 Foliage diseases

Interior spruce stands are commonly subject to several foliage diseases that occur at low levels. These diseases seldom cause serious damage unless infections persist. Repeated severe defoliation can reduce growth rates.

4.3.5 Northern spruce engraver (*Ips perterbatus*)

This bark beetle may increase to epidemic levels by breeding in slash and stumps, or in tops of decadent trees, or trees killed by the spruce beetle. It is normally a secondary pest.

4.3.6 Spruce broom rust (*Chrysomyxa arctostaphyli*)

The spruce broom rust, or yellow witches' broom, forms a conspicuous perennial yellow broom on interior spruce. The obligatory alternate host is kinnikinnick (*Arctostaphylos uva-ursi*). The broom may cause growth loss, or allow entry of stem rots, but seldom causes economic losses or mortality (Hepting 1971; Baranyay and Ziller 1972).

4.3.7 Spruce budmoths (*Zeiraphera* spp.)

The impact of spruce budmoths in British Columbia is minimal at present. Observations on white spruce in the Prince George Region indicated that all age classes are attacked (Garbutt and Turnquist 1988), but that damage was negligible and only a small amount of foliage was lost. Similar circumstances were experienced in the Canadian Maritimes until recently, but a spruce budmoth, *Z. canadensis*, is now considered an economically important and persistent pest of monoculture white spruce plantations (Pendrel 1985). Larvae emerge in early summer, mine under the cap of a new bud, and begin feeding on new needles (Turgeon 1985). Severe damage can cause multiple leaders, reduced growth, and deformed trees (Turgeon 1985).

General References Unger 1972; Hedlin 1974; Etheridge 1978; Etheridge and Hunt 1978; Hunt 1978; Ruth *et al.* 1982; Sutherland *et al.* 1987.

4.4 Abiotic Damage

4.4.1 Acid rain

Possible effects of acid deposition or other air pollution on forest trees include decreased frost and drought resistance, induced nutrient deficiencies, reduced growth rates, poor regeneration quality, and mortality (Bell 1986). Forestry Canada established the Acid Rain National Early Warning System (ARNEWS) across Canada in 1984 to gather baseline data and monitor long-term changes in forest soils, tree growth, and other conditions. There are 15 ARNEWS plots province-wide in British Columbia (Canandian Forest Service 1987). To date no scientific proof of any damage caused by acid rain to interior spruce trees in western forests has been established (Wood and Van Sickle 1989b).

4.4.2 Climatic injuries

Various climatic conditions, or combinations of conditions such as unseasonal frosts, sunscald, and drought, can damage spruces. Spruce bud mortality is common in interior regions of the province. The cause appears to be widely fluctuating spring temperatures. Early warm spells cause terminal buds to partially open, allowing moisture to penetrate the bud. Subsequent freezing temperatures lead to partial or complete bud mortality (Unger and Stewart 1988). For additional information on frost and winter damage see Temperature relations in Section 3.2, Environmental Factors.

Wind damage Mature white and Engelmann spruce have shallow rooting systems that make these species relatively susceptible to windthrow. Extensive blowdown in natural stands after strong windstorms will create conditions that are ideal for the build-up of spruce beetle populations. Even if trees are not knocked down, their root systems, particularly the fine feeder roots, may be damaged. This creates stressed trees ("standing blowdown") that may be susceptible to beetle attack. Harvesting patterns can significantly influence windthrow in residual stands and/or cutblock edges (reviewed in Alexander 1987).

Snow damage Dense herbaceous vegetation can smother seedlings if snowpress develops (McMinn 1982b). Snow molds, *Herpotrichia* spp., can develop on branches that are covered by snow for long periods. The molds leave conspicuous felt-like mats of mycelium on infected branches or small seedlings (Hiratsuka 1987).

Sunscald Achieving good regeneration of spruce in clearcuts means striking a balance between improved microclimatic conditions, and avoiding conditions detrimental to survival. Silviculturists should be aware that survival of interior spruce seedlings exposed to intense sunlight can be poor (Ronco 1975). Shallow, slow-growing root systems render spruce seedlings susceptible to drought stress, a problem that can be worsened by intense sunshine.

4.4.3 Effects of fire

Thin bark and a low-growing canopy with persistent dead flammable limbs make mature interior spruce particularly vulnerable to fire. Generally shallow rooting systems are easily damaged, predisposing trees to windthrow (Fischer and Bradley 1987). Rowe (1983) reports that white spruce may occasionally survive a single fire, but rarely do they double-scar and survive.

5 Silviculture

5.1 Natural Regeneration

Natural regeneration is the process of obtaining restocking using seed dispersed by trees growing on or adjacent to the site. The silviculturist may control the distribution of seed trees during harvesting to obtain adequate seed dispersal, and may prepare the site to improve seedbed conditions, but no artificial seeding or planting occurs. **Advance growth management**, a form of natural regeneration using seedlings and saplings that existed in the forest understory prior to harvesting, is discussed separately in a later section.

Natural regeneration offers a variety of advantages and disadvantages compared to artificial regeneration in the management of interior spruce. Table 11 summarizes these factors, providing an overview of the many ecological and economic considerations that influence the use and success of natural regeneration. This section describes the history and current status of the use of natural regeneration in the management of interior spruce, summarizes ecological factors affecting natural regeneration, and outlines management techniques that can be used to obtain natural spruce regeneration.

5.1.1 History

Until the early 1970s, when the interior spruce planting program expanded dramatically, there was almost total reliance on natural regeneration to regenerate interior spruce in British Columbia (Weetman and Vyse 1990). Large-scale logging of interior spruce started around 1914 in the SBS forests surrounding Prince George, and had expanded into the higher-elevation ESSF and MS zones of the southern interior by the 1940s (Smith 1955; Glew 1963). Early logging in spruce-fir stands involved selective removal of the best spruce trees to a diameter limit of 10 or 12 inches (25–30 cm). It was believed that release of the residual stand, along with gradual seeding-in of spruce and subalpine fir, would provide sufficient restocking to allow a second cut in approximately 120 years (Barnes 1937; Pogue 1949; Glew 1963). Before World War II most areas were horse-logged, with relatively little damage to the residual stand. The introduction of "cat" logging after the war substantially increased logging damage. There was also growing awareness that wind, insects and disease were causing excessive mortality of residual trees and that very few spruce seedlings were establishing in the understory, leaving a "battered and broken" stand consisting mainly of subalpine fir.

It was obvious that a different approach was required to assure successful spruce regeneration. Single tree selection and alternate strip cutting were introduced in an effort to improve regeneration success. However, loosely regulated diameter-limit cutting continued to be the norm in many areas throughout the 1950s and 1960s.

Single tree selection involving a diameter-limit restriction of 18 inches (46 cm), and, with crop trees marked for cutting (McKinnon 1940; Pogue 1949), was carried out operationally on approximately 30 000 ha of multi-aged spruce-fir stands in the Prince George District between 1951 and 1962 (Glew 1963) (Figure 32). Additional areas were treated using this approach in the Kamloops District (Smith 1955). Although single tree selection reduced injury to the residual stand, the incidence of damage was still high, and it did not successfully induce spruce regeneration. Average stocking of spruce on plots established by Glew (1963) was 2.7–6.3%, with the vast majority of spruce seedlings occurring on skid roads.

Alternate strip cutting was introduced into the central interior in 1954. Although this technique was intended for even-aged stands, its use soon spread to older uneven-aged stands as well. Strips measuring 50–100 m wide were laid out in a herringbone pattern oriented at right angles to the prevailing wind and parallel to the contour (Figure 33) (Glew 1963; Butt 1988a). Utilization standards were variable. Most cut strips were logged to a diameter limit of 11.1 inches (28 cm); often the largest trees were removed from the leave strips as well. To promote natural regeneration, both cut and leave strips were to be blade scarified to provide a mineral soil seedbed, with the leave strips winter logged once the regeneration was satisfactorily established. Where scarification was carried out, it was generally regarded as

TABLE 11. Natural regeneration of interior spruce: advantages and disadvantages

Factor	Advantages	Disadvantages
Regeneration delay/risk	Seeding-in over a period of years reduces the risk of regeneration being wiped out by unusual weather, pest outbreaks or other catastrophic events (Butt *et al.* 1989, unpublished; Weetman and Vyse 1990).	High degree of uncertainty caused by - sporadic seed crops (Zasada and Gregory 1969; Alexander 1987); - lack of control over ecological factors controlling germination and seedling establishment (Zasada and Gregory 1969; Stiell 1976; Braathe 1980); - high rates of seedling mortality for the first 5 years (Zasada and Gregory 1969; Fiedler *et al.* 1985). Slow rates of ingress delay reforestation decisions, allow non-crop vegetation to become well established, and cause longer rotations (Butt 1988b; Butt *et al.* 1989, unpublished).
Stocking and stem distribution	Clumped distribution and dense stocking allows selection of superior crop trees during thinning. Seedlings usually become established on appropriate microsites (Weetman and Vyse 1990).	Stocking is uneven, clumped and may require precommercial thinning (Zasada and Gregory 1969; Gardner 1980; Butt *et al.* 1989, unpublished; Weetman and Vyse 1990). Most large clearcuts will be insufficiently stocked. Often favours other conifer species (e.g., subalpine fir, western hemlock) over spruce (Beaudry and McCulloch 1989; Butt *et al.* 1989, unpublished).
Growth rate and tree form	Slower-growing natural regeneration may have better wood quality than rapidly growing plantation stock (Horvat-Marolt 1979; Butt *et al.* 1989, unpublished; Weetman and Vyse 1990). Clumped distribution may produce better stem form (narrower crowns with smaller branches) and earlier self-pruning (Horvat-Marolt 1979; Weetman and Vyse 1990).	Natural seedlings have slower initial growth rates than healthy planting stock (McMinn 1986; Butt 1988b, unpublished).
Tree damage	Roots less susceptible to deformation than those of planted seedlings (Horvat-Marolt 1979; Weetman and Vyse 1990). Seedlings better acclimated than newly planted nursery stock and less susceptible to cold stress injury (Herring 1987, unpublished). Clumped distribution may protect against damage from grazing, machines, wind, or snow (Horvat-Marolt 1979). Small mammal damage often less severe than on nursery stock.	Tiny seedlings are less able to withstand competing vegetation than large, healthy planting stock (Zasada and Gregory 1969). Leave strips and trees required to act as seed source are subject to blowdown (Glew 1963; Zasada 1978, unpublished). Harvesting of leave strips and seed trees may cause damage to natural regeneration (Zasada 1972).
Genetics	Maintains genetic diversity in regenerating forest (Butt *et al.* 1989, Butt 1990, both unpublished; but see Zasada 1986), and assures that regeneration is locally adapted.	Limits opportunities for tree improvement through selection of superior provenances or genetically improved stock (Zasada and Gregory 1969; Braathe 1980).
Site preparation		The need for costly and potentially environmentally damaging site preparation may be increased (Braathe 1980). Scarification practices needed to ensure adequate germination may encourage establishment of undesirable hardwoods (Zasada 1972; Wurtz and Zasada 1986).
Economics and management priorities	If successful, avoids costs and associated administrative, logistical and environmental constraints of planting (Weetman and Vyse 1990). Suited to remote areas where intensive silviculture is impractical or not cost-effective or to winter-logged areas where summer access for planting is difficult (Gardner 1980; Coopersmith 1990). Suited to areas where local provenances of seedlings are not available or where small-scale forest industry does not warrant a nursery program (Gardner 1980; Coopersmith 1990). Suited to areas where alternatives to large clearcuts are needed to maintain non-timber values (e.g., wildlife habitat or scenic views) (Weetman and Vyse 1990).	Requires alternatives to large clearcuts (e.g., shelterwoods, patch or strip cuts) to ensure a seed supply (Zasada 1972; Gardner 1980). These techniques tend to cost more than conventional logging. Requires that silviculturists exercise control over harvesting operations to ensure adequate seed supply and seedbed conditions (Zasada 1980).

FIGURE 32. A good example of single tree selection in a spruce–fir stand. The stand was not opened up so much that blowdown developed, but the residual stand has responded to the release (from Pogue 1949).

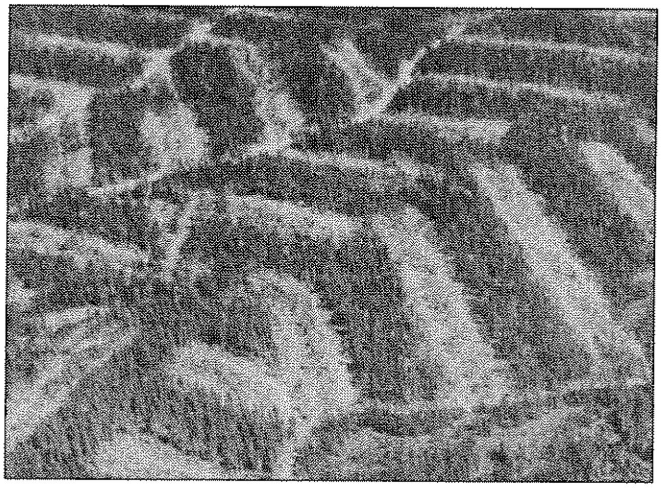

FIGURE 33. An aerial view of alternate strip cutting in the spruce–fir type near Prince George (from Glew 1963).

successful in achieving adequate spruce regeneration (Glew 1963; Gilmour and Konishi 1965), although some problems were encountered in wet and brushy areas (Arlidge 1967). However, only a small fraction of the strip-logged areas was scarified, and the second pass to remove the leave strips was rarely carried out. The result was that large areas were left in poor condition with low spruce stocking and numerous clumps of slow-growing residual subalpine fir interspersed with deciduous trees and shrubs. Strip cutting, like the earlier forms of partial cutting, also created optimum conditions for the build-up of spruce beetle populations in shaded slash and windthrow (Dyer and Taylor 1971).

By the early 1970s, diameter-limit logging and strip cutting had been replaced by large-scale clearcutting, the system that prevails today. The change was not primarily motivated by concern over inadequate reforestation, but it did have a tremendous impact on regeneration practices. Changes in sawmilling technology and the establishment of a pulp industry in the interior made it economical to greatly increase the utilization of all conifer species. Meanwhile, concerns over blowdown and recovery of bark beetle mortality, coupled with the introduction of highly mechanized logging operations, provided the justification for larger and larger clearcuts, usually averaging 40–100 ha in size, but often extending over much greater areas in order to recover windthrown and beetle-damaged timber.

Very poor natural regeneration on the large clearcut openings led to the expansion of the interior spruce planting program and to the virtual abandonment of natural regeneration as a deliberate management technique for regenerating spruce cutovers (Weetman and Vyse 1990). Throughout the 1970s many spruce-dominated clearcuts were left to regenerate naturally (Butt 1988a; Butt 1990, unpublished). Although some were scarified in an attempt to promote natural seedling establishment, most were left untreated. This practice resulted primarily from a failure of the planting program to keep pace with the rate of harvesting, not from a perception that such practices would lead to successful spruce regeneration (Butt 1988a).

Current estimates are that only 20% of spruce-dominated stands will become satisfactorily stocked through natural regeneration following clearcutting (Kuhnke 1989). Much of the regeneration on these areas is made up of species other than spruce. A series of problem analyses carried out to determine the causes of regeneration failure in various biogeoclimatic zones and subzones of interior British Columbia confirms the low rate of regeneration success in cutovers left for natural regeneration (Scagel 1987; Butt 1988a,b, unpublished, 1990, unpublished; Beaudry and McCulloch 1989; Butt *et al.* 1989, unpublished). For example, in the ESSFwc (formerly ESSFc) of the Nelson Forest Region, stocking of Engelmann spruce averaged just 918 seedlings/ha (390 well spaced) (Butt 1990, unpublished). Seven of the 56 openings surveyed had no natural spruce regeneration. The studies indicate that the success rate of spruce is lower than that of associated species such as western hemlock (Beaudry and McCulloch 1989), lodgepole pine (Butt 1988b, unpublished; Beaudry and McCulloch 1989), and subalpine fir (Butt *et al.* 1989, unpublished; Butt 1990, unpublished).

5.1.2 Biological factors

The biological requirements for successful natural regeneration of interior spruce are fairly well understood, having been intensively studied at various locations across North America. In Canada, intensive research on this topic began in the early 1920s and continued until the late 1950s and early 1960s when it was largely abandoned as the emphasis shifted to artificial regeneration. More recent research comes primarily from two areas in the United States, the central and southern Rocky Mountains, and interior Alaska near Fairbanks (Alexander 1987; Zasada 1980).

There are three main requirements for successful regeneration of interior spruce: 1) an adequate supply of viable seed; 2) a favourable seedbed for germination; and 3) a suitable microenvironment for subsequent survival and growth of the seedling (Rowe 1955; Roe *et al.* 1970; Lees 1972; Alexander 1987). These primary requirements have been arranged into a regeneration triangle (Figure 34). In the natural forest environment, the factors listed in Figure 34 fluctuate more or less independently of one another (Rowe 1955). Successful regeneration occurs when, by favourable coincidence, all of these factors come together at one time in one place. Under managed conditions, the silviculturist manipulates one or more of these factors to increase the likelihood of successful regeneration, but many factors remain beyond human control. Knowing which factors limit regeneration of interior spruce from seed and which can be successfully manipulated through silvicultural practice enables the silviculturist to decide whether natural regeneration is a feasible option and how best to achieve it.

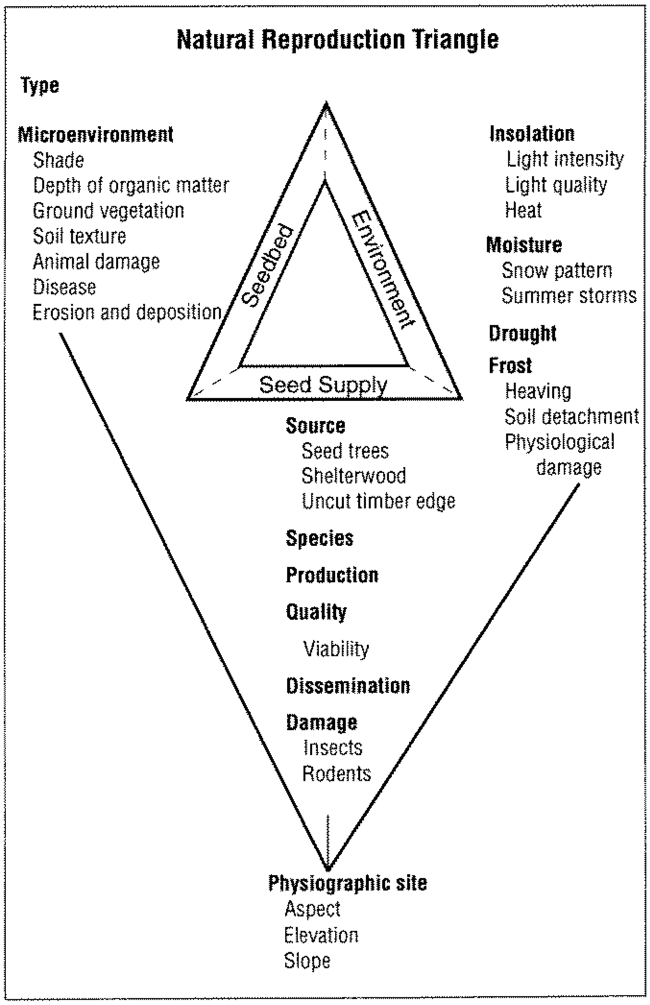

FIGURE 34. Factors affecting the success of spruce natural regeneration (from Roe *et al.* 1970).

Seed supply

Seed crop prediction The sporadic nature of interior spruce seed crops is one of the most important factors limiting the success of natural regeneration. Large variability in the amount of seed produced from year to year means that natural regeneration cannot be expected every year (Alexander 1987). In fact, with good spruce seed crops in British Columbia occurring on average only once every 4–12 years (Konishi 1985; B.C. Ministry of Forests 1990a), the risk of natural regeneration failing to occur within an acceptable regeneration delay period is very high. It is worth noting, however, that a heavy seed crop is not necessarily a prerequisite for successful natural regeneration. Where environmental conditions for seed dispersal and seedling success are exceptionally favourable, a poor or moderate crop may be all that is required to achieve restocking (Noble and Ronco 1978).

No reliable method for predicting or estimating spruce seed crops has yet been developed (Alexander 1987), but a variety of controlling factors has been identified. Table 12 summarizes possible methods of predicting spruce seed crops and indicates how they can be used to increase the effectiveness of natural regeneration.

The size, age and number of spruce trees in the stand have a major influence on cone and seed production. Significant seed crops are generally not produced in stands less than 45–60 years old (minimum 30 years), and widely spaced trees with large crowns produce earlier and better crops (Zasada and Gregory 1969; Owens and Molder 1984). In central Colorado, for example, dominant and codominant Engelmann spruce trees greater than 15 cm in diameter and 150–300 years old are the primary seed producers, with intermediate and suppressed trees producing few or no cones (Alexander

TABLE 12. Predicting spruce seed crops for natural regeneration

Type of information collected	Type of prediction made	Management application	References
Long term (>10-year timeframe)			
Climate – elevation – latitude – biogeoclimatic subzone – length and quality of growing season (growing degree-days, frost-free days)	Average periodicity of seed crops Average size of seed crops Average viability of seeds	Classifying elevation, climatic or biogeoclimatic (sub)zones according to their potential for natural regeneration. Developing silvicultural guidelines for natural regeneration. General planning of stand management treatments (harvesting, site preparation, planting, stand tending).	Zasada and Gregory 1969 Noble and Ronco 1978
Tree and stand characteristics – age – height – diameter – crown position – stem density	Long-term average seed production	Identifying stands with potential for natural spruce regeneration. Selecting appropriate stand management treatments for individual stands. Priorizing stands for treatment.	Alexander and Noble 1976 Alexander *et al.* 1982 Alexander 1987
Short term (±1-year timeframe)			
Weather – (May)June–July temperature – (May) June–July precipitation – late spring frosts – rainstorms during pollination	Time of occurrence of next heavy crop. Success or failure of next year's crop	Scheduling stand management treatments (especially site preparation). Selecting sites for natural vs. artificial regeneration.	Uskov 1962 Zasada and Gregory 1969 Dobbs 1972
Direct observations of cones and seeds – reproductive bud counts – immature cone counts – cone and seed pest survey – cone and seed sampling and evaluation – seed trap counts	Potential size of next year's crop. Actual size of this year's crop. Seed viability and quality. Seed dispersal patterns.	Finalizing harvesting, site preparation or planting decisions. Detailed information for research trials.	Eis 1967a Zasada and Viereck 1970 Dobbs 1972 Eis and Inkster 1972 Owens and Molder 1984 Eremko *et al.* 1989

1987). Researchers in Colorado have developed a mathematical equation to predict average annual seed production over a 10-year period from the size and number of dominant and codominant spruce stems in the stand (Alexander *et al.* 1982; Alexander 1987). These equations cannot be applied directly to British Columbia conditions, but the principle of using the volume and vigour of spruce trees in a stand as an index of its long-term potential for seed production is equally valid in this province.

Climatic conditions also determine the potential for viable seed production. Data for interior spruce and other coniferous species indicate that seed crops tend to be poor at high latitudes and at high elevations (Zasada and Gregory 1969; Owens and Molder 1984). In these environments the growing season is too short to provide trees with adequate resources to produce large seed crops. Seeds may also fail to mature completely in a short growing season, and there is a higher risk that extreme weather events will damage the seed crop. At the extreme limit of tree growth, the arctic or alpine timberline, trees often fail to produce a viable seed crop (Baig 1972, cited by Kearney 1982; Elliot 1979).

At any given latitude, high-elevation stands generally produce smaller seed crops and the interval between bumper seed crops is longer than at lower elevations (Owens and Molder 1984; J. Zasada, pers. comm., July 1990). The effect of latitude on seed production is more complex, probably because shorter growing seasons in the north are compensated for by longer daylengths, and because climate does not vary in linear fashion from south to north. In the taiga of Alaska, intervals between large seed crops of white spruce are on the order of 12–13 years (Zasada and Viereck 1970; Zasada *et al.* 1978); at low elevations in southern Canada, the interval is more on the order of 2–6 years (Fowells 1965; Waldron 1965). Yet when good white spruce seed crops occur in Alaska, they are among the largest recorded anywhere for the species (J. Zasada, pers. comm., July 1990). There are no data to indicate whether climate limits spruce seed production at the northernmost latitudes of the BWBS zone in British Columbia.

Year-to-year variation in seed crops is strongly controlled by weather conditions. Many authors, as summarized by Zasada and Gregory (1969), have shown that good seed crops are often correlated with warmer and drier than average weather during June and July of the previous year (i.e., the period of floral bud initiation).

However, these weather conditions do not guarantee a good seed crop. Frost during flowering can damage seed crops (Zasada 1971; Eis and Inkster 1972), and rain during pollination can cause a high incidence of empty, unfertilized seeds (Zasada and Gregory 1969). Weather data can thus be used to help predict the occurrence of bumper seed crops, but they must take into account the trees' internal rhythms and physiological condition. For example, bumper crops never occur 2 years in a row, regardless of weather conditions. Climate and weather data were used successfully by Uskov (1962; cited by Zasada and Gregory 1969) to predict Norway spruce seed production, but no similar models have been developed for white or Engelmann spruce.

In British Columbia, reproductive bud counts and sampling of immature cones are generally used for seed crop forecasting (Eis 1967a; Eis and Inkster 1972; Eremko *et al.* 1989). Cone crop forecasts are almost always made for the purposes of collecting seed for artificial regeneration (see Section 5.3.1, Seed procurement), but the same information can be used for natural regeneration management (Eis and Inkster 1972). Although this technique provides the most accurate predictions of seed supplies, its usefulness is limited by the short amount of lead time between when the information becomes available and when seeds are dispersed (up to 1 year, but often less than 2 months). Although good spruce seed years generally occur on a region-wide basis (Eis and Inkster 1972), Zasada and Viereck (1970) caution that there is a high degree of between-stand variation in cone production and they warn against making predictions about the cone and seed crop based on observations from only 1–2 stands. Eis and Inkster (1972) recommend sampling buds from three stands, (a total of 15–25 trees) to make general predictions of cone crops on a region-wide basis.

Predispersal seed losses Major cone and seed pests and pathogens of interior spruce are listed in Table 13. For additional information refer to Section 4, Pest Management, or Ruth *et al.* (1982).

TABLE 13. Major cone and seed pests and pathogens of interior spruce. Source: Ruth *et al.* (1982); Halvorson (1986); Eremko *et al.* (1989)

Species	Characteristics
Mammals	
Red squirrel (*Tamiasciurus hudsonicus*)	Harvests and caches whole, closed cones
Chipmunks (*Eutamius* spp.)	Cache and subsequently eat seeds from closed or open cones
Birds	
Red crossbill (*Loxia curvirostra*) White-winged crossbill (*L. leucoptera*)	Extract and eat seeds from closed or open cones
Chickadees (*Parus* spp.) Pine siskin (*Carduelis spinus*)	Take seeds from open cones and ground
Insects	
Spruce seedworm (*Cydia youngana*)	Larvae mine through cones, feeding on seeds
Spruce cone gall midge (*Dasineura canadensis*)	Larvae feed inside single seed
Spruce coneworm (*Dioryctria reniculelloides*)	Larvae feed on cone and shoots
Spiral spruce cone borer (*Lasiomma anthracina* = *Hylemya anthracina*)	Larvae bore inside cone, destroying seeds and scales
Spruce seed midge (*Mayetiola carpophaga*)	Each larva destroys one seed
Seed chalcid (*Megastigmus piceae*)	Larvae consume seed contents
Fungi	
Seed or cold fungus (*Caloscypha fulgens*)	Kills seeds, spreads in cold soil (often on forest floor)
Inland spruce cone rust (*Chrysomyxa pirolata*)	Attacks cone, causing poor cone and seed development and dispersal; alternate hosts are the herbs *Pyrola* spp. and *Moneses uniflora*

Red squirrels (*Tamiasciurus hudsonicus*) occur throughout the range of interior spruce and are the single most important seed predator (Halvorson 1986). Squirrels begin to harvest cones in early August, just before dispersal begins (Zasada and Viereck 1970). Streubel (1968, cited by Zasada and Viereck 1970), estimated that red squirrels consumed 58–88% of a white spruce cone crop at a site with active middens. In heavy seed years, however, there may be sufficient seed to satisfy squirrel populations and still leave plenty for regeneration. During a bumper seed crop in interior Alaska, squirrels reduced the numbers of cones only slightly, except at one stand where they caused more than an 80% reduction in seed production (Zasada *et al.* 1978). When cone crops are poor, the squirrels resort to eating reproductive buds, thereby damaging the next year's crop (Zasada and Gregory 1969) and accentuating fluctuations in seed availability. A variety of seed-eating bird species also removes seed from cones still on the tree. Fowells (1965) and Halvorson (1986) list chickadees (*Parus* spp.), pine grosbeaks (*Pinicola enucleator*), red and white-winged crossbills (*Loxia curvirostra*, *L. leucoptera*), pine siskins (*Carduelis spinus*), and red-breasted nuthatches (*Sitta canadensis*) as consumers of interior spruce seed.

Seed dispersal Dispersal of interior spruce seed occurs mainly by gravity and wind. Seed can be blown for long distances across a crusted snow surface, or transported by water on floodplains (Rowe 1955; Zasada and Lovig 1983). Mammals and birds may transport some seeds, but their overall contribution to seed dispersal is considered negligible (Zasada and Gregory 1969; Alexander 1987).

The timing of seed dispersal appears to be consistent within both Engelmann and white spruce although there is some variation from year to year and from stand to stand (Alexander *et al.* 1982). Cones first open to release seed between late August and mid-September, depending on elevation and local weather conditions. Seed dispersal is greatest between mid-September and early November, with peaks occurring during periods of dry, windy weather. By January, only a small amount of seed (normally less than 10%) remains in the cone and this is gradually released throughout the following year (Crossley 1955a; Zasada and Viereck 1970; Bartlett 1976, unpublished; Dobbs 1976b; Zasada *et al.* 1978; Zasada 1985; Alexander 1986a, 1987; McCaughey *et al.* 1986; Walker *et al.* 1986). Zasada *et al.* (1978) noted that dispersal began about 99 days after pollination; other observers reported 97–108 days after pollination. In Manitoba, peak dispersal of spruce seeds occurs shortly before the peak period of aspen and spruce litterfall (Waldron 1966).

The spatial pattern of white and Engelmann spruce seed dispersal has been studied by several authors. Some have developed mathematical models to predict the amount of seed available at various distances from the stand edge. Seed dispersal patterns are influenced by seed and wing length, the height, basal area and physiographic location of source trees, size of the seed crop, humidity, and wind speed and direction (McCaughey *et al.* 1986).

Several studies of Engelmann spruce, carried out under differing experimental conditions, show that seed dispersal patterns follow a negative exponential curve (Figure 35) (Noble and Ronco 1978; Alexander and Edminster 1983; McCaughey and Schmidt 1987). These studies, all from the U.S. Rocky Mountains, conclude that 50–70% of seeds fall within 30 m of the windward stand edge, 95% within 100–120 m, and few or none beyond approximately 200 m.

White spruce has smaller, lighter seeds than Engelmann spruce, and available data suggest that its seeds may travel farther and have a slightly different dispersal pattern (Figure 36) (Dobbs 1976b; McCaughey *et al.* 1986). Near Prince George, white spruce seedfall decreased sharply with distance from the clearcut edge up to 100 m, but then tailed off very gradually (Dobbs 1976b). Even at 300 m the average dispersed seed density exceeded 3% of that recorded within the stand. Dobbs (1976b) suggests that this pattern indicates that significant quantities of seed were released in high winds. Zasada and Lovig (1983) followed white spruce seeds falling from an 18.5 m tall tree. Although there was only a slight breeze blowing, 4% of the seeds travelled more than 100 m. Mean dispersal distance was 33 ±24 m from the tree. Many of the seeds were buffeted about in various directions before landing, and actually travelled

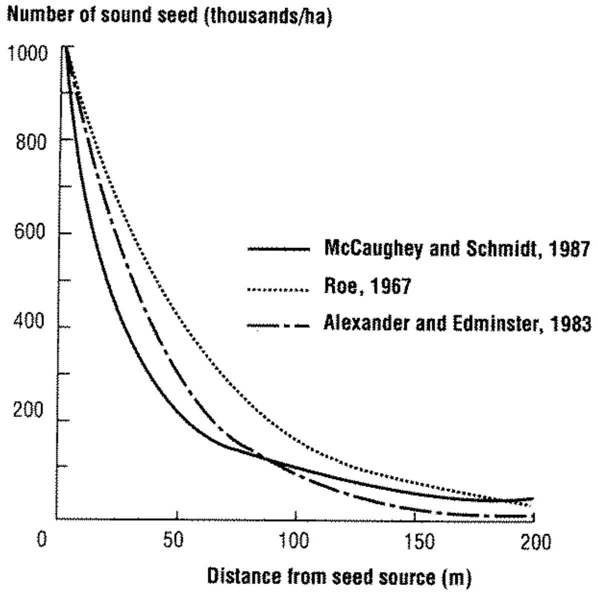

FIGURE 35. Seed dispersal curves from three studies of Engelmann spruce. All three models were calibrated to 1 million seeds per hectare at seed source (from McCaughey *et al.* 1986).

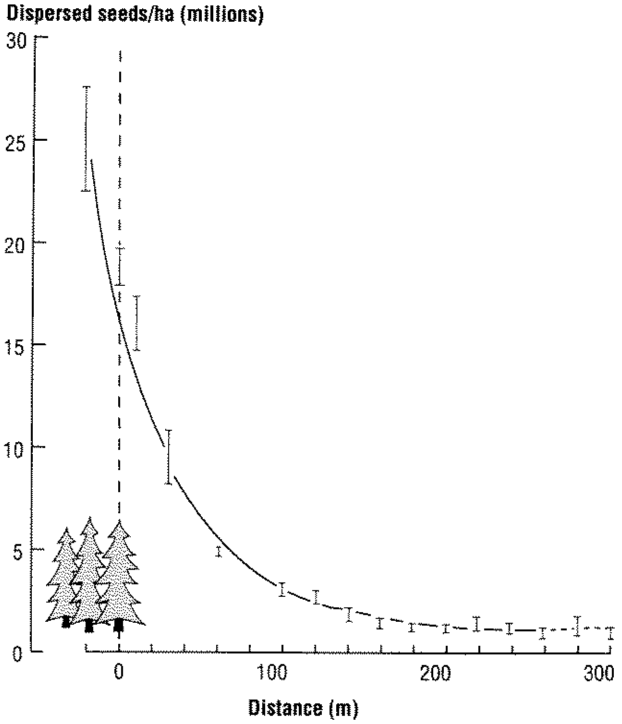

FIGURE 36. Seed dispersal curve for white spruce across a clearcut opening. Vertical bars represent ranges of the sample data (from Dobbs 1976b).

much farther than the measured distance. The average rate of fall for white spruce seeds is 0.5–0.6 m per second (Schlesinger 1970; Zasada and Lovig 1983).

In narrow openings such as strip clearcuts, seed dispersal follows a skewed U-shaped pattern (Figure 37), with much higher quantities of seed on the windward side of the cut than on the leeward edge (Dobbs 1976b; Noble and Ronco 1978; Alexander and Edminster 1983). On the leeward edge of the opening, Noble and Ronco (1978) did not observe any increase in seedfall until they got within 10 m of the stand edge.

These data illustrate how much influence the direction of autumn and early winter winds occurring during dry weather conditions can have on seed dispersal patterns. Strong winds accompanied by cold, wet weather will have relatively little effect on seed dispersal, as cones are normally closed under these conditions (J. Zasada, pers. comm., July 1990). The seed dispersal research also indicates how important it is to have an adequate spruce seed source on the windward side of the opening. Total numbers of seeds dispersed into an opening are strongly correlated with the density or basal area of mature spruce in the uncut, windward stand (Bartlett 1976, unpublished; McCaughey *et al.* 1986; Alexander 1987). The presence of large numbers of seed-bearing spruce trees on the leeward side of an opening will contribute relatively little to effective seed dispersal.

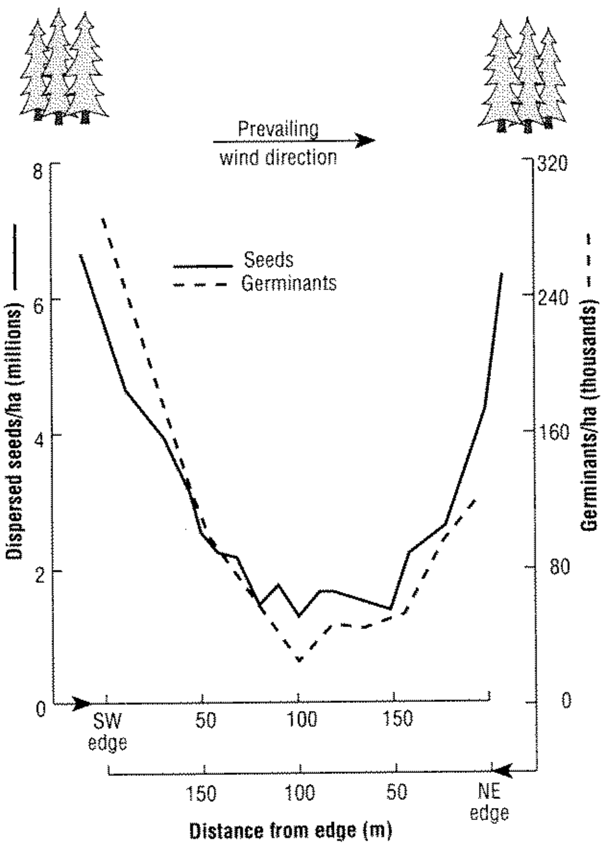

FIGURE 37. Distribution of dispersed white spruce seeds and germinants across a strip cut (from Dobbs 1976b).

On a year-to-year basis, there is a direct relationship between the size of the seed crop and the amount of seed that disperses into an opening (Noble and Ronco 1978; McCaughey and Schmidt 1987). The general pattern of seed dispersal is similar in both good and poor seed years, but with heavy crops there is a tendency for a higher percentage of the seed to land directly beneath or very close to the uncut stand (Noble and Ronco 1978; Alexander and Edminster 1983).

There is tremendous variation in the quantity of seed rain received at the forest floor. In interior Alaska, Zasada (1985) reported total seedfalls ranging from 21 to 4000 seeds/m^2 beneath uncut, mature white spruce stands with viable seedfall ranging from 13 to 2600 seeds/m^2. Near Prince George, Dobbs (1976b), recorded 660 and 2550 seeds/m^2 (48% sound) in stands with 77 and 205 stems/ha of mature spruce, respectively. After a medium to good seed year, Bartlett (1976, unpublished) reported 79 seeds/m^2 beneath a stand with 150–220 mature spruce per hectare, and 31 seeds/m^2 in an area with 60-100 spruce stems/ha.

Seed rain in high-elevation Engelmann spruce dominated forests of Colorado appears to be much lower than the rates reported by Zasada (1985) and Dobbs (1976b). Sound seedfall in one stand averaged just 7.9 seeds/m^2 (range 4.9–32.8) over a 10-year period (Alexander 1969), and during an exceptional crop total seedfall was on the order of 300–400 seeds/m^2. In the middle of clearcut strips, 40–60 m from the windward timber edge, Alexander (1969) found sound seed densities of 1.2–4.6 seeds/m^2 during good seed years. By comparison, at Dobbs' (1976b) Prince George sites there were more than 24 sound seeds/m^2 at a distance of 300 m from the windward edge. Zasada (1985) reported 9–80 sound seeds/m^2 at 50 m and 1–12 sound seeds/m^2 at 300 m into clearcut areas.

Under uniform spruce shelterwoods, the seed rain is quite evenly distributed, with densities of 300–350 sound seeds/m^2 reported for white spruce in Alaska (Zasada 1978, unpublished), and 61–100 sound seeds/m^2 recorded after a "poor" interior spruce seed year in the southern Alberta Rockies (Day 1970).

Seed viability Not all of the spruce seed that disperses from the tree is sound and capable of germinating. Engelmann spruce records from the Colorado Rocky Mountains, indicate that over a 14-year period, sound seed percentage ranged from 12–68%. Near Prince George, Dobbs (1976b) found that 40% of white spruce seeds were sound, 21% were empty, and 39% had deteriorated embryos. Most studies indicate that the highest percentage of viable seed occurs in good seed years (Dobbs 1972). Near Burns Lake, for example, seed viability was 68% during a good seed year, but only 12–15% during a series of poor seed years (Bartlett 1976, unpublished). Alexander (1987) reports that filled seed averaged 46% in good to bumper seed years. At one site near Fairbanks, Alaska, seed viability varied between 55 and 60% in years of good seed crops (Zasada 1980), while during a single good seed year (1970), filled seed percentage ranged from 38 to 77% over a wide range of sites (Zasada *et al.* 1978).

Across a clearcut opening, the percentage of sound seed generally varies with distance from the forest edge. Empty or decayed seeds, being lighter, tend to travel farther than sound seeds. Thus the farther one goes from the seed tree, the lower the percentage of sound seeds. Dobbs (1976b) reported 48% sound seed at distances less than 100 m from the stand edge, but only 31–32% sound seed at distances of 120–300 m.

Seed viability may also vary with the time of dispersal. In Dobbs' (1976b) study, seed viability ranged from a low of 23% for seeds dispersed in August (not fully mature) to a high of 55% for seeds dispersed in September. Interestingly, there was little deterioration in seed quality between October (32% viable) and June of the following year (31% viable). In contrast, Zasada (1985) reported a steady decline in seed viability throughout the dispersal period (Figure 38).

In general, spruce seed retains its viability for a relatively short period. In cold storage, seeds will keep for 10–13 years or more (Wang 1980), but at room temperature most will lose viability within a year. Under natural conditions seeds can survive for 1–2 years in the forest floor, but most germinate after the first winter (Rowe 1955, Walker *et al.* 1986). Those that do not, rapidly succumb to predators and pathogens.

Post-dispersal seed losses Once seeds are on the ground, small mammals are the most important source of seed losses (Smith 1955; Dobbs 1972; Radvanyi 1974; Alexander 1987). Arnott *et al.* (1979, cited by Gardner 1980) suggest that rodent activity is particularly heavy in the fall, shortly after seeds are shed. Deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionmys gapperi*), chipmunks (*Eutamius* spp.), meadow or field voles (*Microtus* spp.), shrews (*Sorex* spp.) and ground squirrels (*Spermophilus* spp.) are important seed predators. Rowe (1955) notes that losses are particularly severe when peak rodent years coincide with medium or poor spruce seed years. Radvanyi (1974) followed the fate of 2000 radio-tagged white spruce seeds placed in a western Alberta clearcut. Over a 17-week period, 49.3% of the seeds were destroyed, and, of those destroyed, 71.4% were consumed by mice and voles, 19.2% by chipmunks, 5.9% by shrews and 3.5% by insects. Laboratory studies indicate that a single white-footed deer mouse can consume approximately 2000 white spruce seeds nightly (Radvanyi 1974).

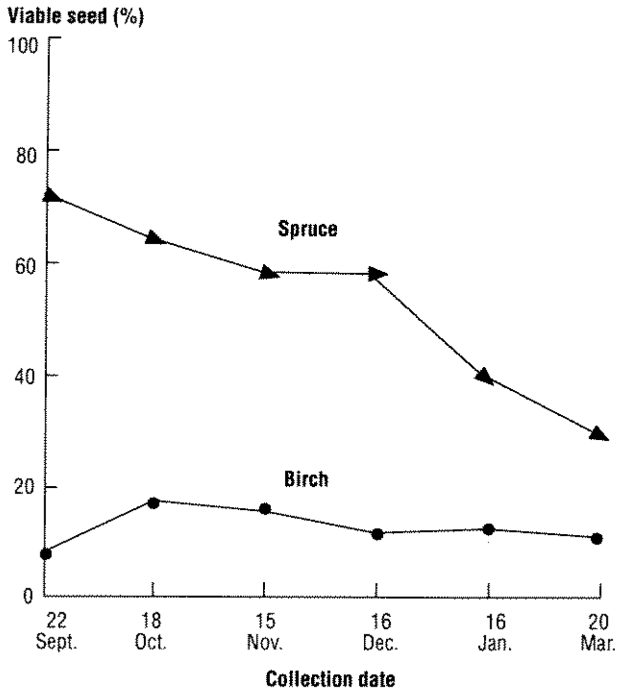

FIGURE 38. Decline in the viability of white spruce seed over the winter months. In contrast, paper birch seed has a lower initial viability, but retains its quality for a longer period of time (from Zasada 1985).

Ground-feeding birds such as dark-eyed juncos (*Junco hyemalis*), sparrows, and chickadees (*Parus* spp.) are also believed to consume a significant quantity of spruce seed; however, seed losses to birds were not of major consequence in any of the radio-tagging studies described by Radvanyi (1974).

A variety of fungi and invertebrates also attacks spruce seed on the forest floor, but most studies of these organisms have taken place in the nursery or seed laboratory rather than under field conditions (Harvey 1980; James

1986; Sutherland 1986). The best-known seed pathogen, *Caloscypha fulgens*, inhabits conifer duff and invades cones or seeds that contact the forest floor. Sullivan *et al.* (1984) found *C. fulgens* in squirrel caches in 25% of white spruce stands sampled near Prince George. These authors hypothesized that a mutualistic relationship exists between the fungus and the squirrel, with squirrels helping to disperse the fungus and the fungus preserving the squirrels' seed supply by preventing both germination and rotting of seeds. Soil-borne fungi of the genus *Fusarium* commonly cause seed decay and germination failure—known as "pre-emergence damping-off"—especially among seeds that spend prolonged periods in a damp environment (James 1986).

Seed germination Spruce seed has no special requirements to break dormancy, although chilling (stratification) and exposure to light have been shown to improve germination in some circumstances (Zasada and Gregory 1969; Wang 1974). In the natural environment, spruce seeds overwinter under the snow, absorbing moisture from snowmelt, and germinate the following spring or summer when conditions are moist and warm.

The timing of seed germination is very important because of its effect on subsequent seedling survival. In Manitoba, Colorado, and interior Alaska researchers have observed two basic patterns of seed germination, one occurring under favourable spring weather conditions (abundant moisture and warm temperatures ≥ 8°C), the other occurring under adverse weather conditions (extended cool temperatures, or droughty spring weather) (Waldron 1966; Zasada *et al.* 1978; Zasada 1980; Alexander 1987).

Under favourable conditions, seed germination is rapid, with 90% of total germination occurring over a 3–4 week period. The precise timing depends on the date of snowmelt and arrival of warm spring weather, but usually takes place between late May (interior Alaska [Zasada 1980]) and mid-July (Saskatchewan [Rowe 1955]; Colorado [Alexander 1987]). Peak germination normally occurs in mid-June. Under unfavourable conditions, there is usually a small amount of germination in the spring, but subsequent germination is sporadic and may be delayed until the onset of warm summer rains in late July or August. Low or irregular precipitation delays germination, and frequent showers produce more seedlings than infrequent, intense storms (Alexander 1987). The last germinants may appear as late as early September (Waldron 1966; Zasada *et al.* 1978).

Germination occurs earlier in open, early successional conditions than under a mature forest canopy (Walker *et al.* 1986). In the southern and central Rocky Mountains, the percentage of sound seed, protected from rodent predation, that actually germinates ranges from 0 to 28% (Alexander 1987). North of Prince George, Eis (1965a) reported an average germination rate of 33% of unprotected seed sown in June.

Seedbed conditions

Interior spruce seedlings are capable of germinating on a wide variety of substrates. From the wealth of research on this topic, it is evident that the physical properties of the substrate, particularly the way in which they influence moisture availability and temperature relations, are most important. Chemical and biological properties of the seedbed are also important, but less well understood.

Mineral soil Most research concludes that mineral soil is the most favourable seedbed for interior spruce (see Place 1955; Eis 1965a; Zasada and Gregory 1969; and Dobbs 1972 for summaries of early work), although a few studies have found mineral soil to be less favourable than certain types of organic seedbed or mixed mineral soil and humus (Day and Duffy 1963; Day 1964; Ahlgren and Ahlgren 1981; Knapp and Smith 1982; Fiedler *et al.* 1985; Geier-Hayes 1987). In undisturbed forests, spruce regeneration is common on hummocks of mineral soil produced by upturned trees (Rowe 1955; Smith 1955; Lees 1972; Van Cleve *et al.* 1980). Larger-scale natural disturbances such as flooding (Van Cleve *et al.* 1980; Krasny *et al.* 1984; Walker *et al.* 1986), wildfire (Garman 1929; Jarvis 1966; Zasada 1985), glacial retreat (Tisdale *et al.* 1966), avalanches and landslides also produce mineral soil seedbeds that promote spruce regeneration. Spruce also regenerates after artificial exposure of mineral soil occurring either incidently or intentionally during logging and road construction (Smith and Wass 1976, 1979, 1980; Herring and McMinn 1980), prescribed burning (Jarvis 1966; Stiell 1976; Zasada and Norum 1986; Butt *et al.* 1989, unpublished) or mechanical scarification (Griffith 1931; Lees 1963; Gilmour and Konishi 1965; Waldron 1966; Arlidge 1967; Zasada and Grigal 1978; Gardner 1980; Butt *et al.* 1989, unpublished).

A major benefit of a mineral soil seedbed is its ability to retain moisture and supply it to the seed and seedling. To quote Baker (1950) and Place (1955): "the infiltration capacity and aeration of mineral soil are good, yet the soil packs well around the seed, affording close contact with surface films of water." As moisture evaporates from the soil surface, capillary action continuously draws up new moisture to replace it. Not all mineral soils are alike in their ability to supply moisture for germination. Roe *et al.* (1970) found that germination was more than nine times greater on a heavy black loam soil that retained soil moisture than on a sandy loam soil subject to rapid surface drying. Similarly, Day (1964) rated an Ah mineral soil with incorporated humus much higher than a bare, coarse textured subsoil.

Another important property of mineral soil is its ability to store and transfer heat. Mineral soils heat up more slowly and cool down less quickly than organic material, so there is less risk of heat or frost damage, and optimal temperatures for growth are maintained for longer periods (Cochran 1969; Arnott 1973). Nutrient supplies are usually adequate for early seedling growth (Zasada and Gregory 1969). Freshly exposed mineral soil is also relatively free of inhibitory chemical leachates, pathogens or other biological agents that may prevent seed germination and seedling survival (Baker 1950; Daniel and Schmidt 1972).

Drawbacks of mineral soil seedbeds include a tendency for fine textured soils to frost heave when wet, or to form crusts or cracks when dry (Zasada and Gregory 1969; Gardner 1980; Krasny *et al.* 1984). They may also be more prone to flooding than elevated organic seedbeds, particularly where exposed mineral soil occurs mainly in ruts produced by logging or scarification equipment (Lees 1964a; Arlidge 1967). Some dense mineral soil seedbeds lack sufficient porosity to permit root penetration, and scalped or leached soils may be very low in essential nutrients (Zasada and Gregory 1969). On hot, sunny sites, mineral soil seedbeds often provide insufficient shade to protect seedlings from drought or heat injury.

Decayed (rotten) wood Numerous authors have observed that decayed wood is a preferred seedbed for interior spruce. In the undisturbed forest understory, spruce regeneration often occurs predominantly on decaying logs (Rowe 1955; Lees 1972). Knapp and Smith (1982) in Wyoming, Day (1964) in Alberta, Geier-Hayes (1987) in central Idaho, and Harvey *et al.* (1987b) in Montana all found that Engelmann spruce seedlings occurred on rotten wood in a larger proportion than would be expected from the area occupied by the seedbed. Wilford and Septer (1987, unpublished) noted that in wet topographic depressions of the SBS zone of central British Columbia, natural spruce regeneration was almost entirely confined to decaying wood. Lees (1970) observed a similar phenomenon on wet bottomland sites in the BWBS mixedwood of northern Alberta, as did Caza and Kimmins (1990a, unpublished) in ESSF clearcuts of the southern interior wet belt.

Like mineral soil, decayed wood provides a more stable moisture supply than organic materials such as litter and humus (Place 1950; Smith 1955). On dry sites, decayed wood lying beneath the mineral soil surface can act as a reservoir of soil moisture during periods of summer drought (Harvey *et al.* 1987b). Other suggested benefits of decaying log seedbeds include protection from flooding in wet depressions or on floodplains, improved light conditions, minimal competition and smothering from broadleaved vegetation, higher temperatures than on the forest floor, freedom from damping-off fungi and enhanced mycorrhizal development (Rowe 1955; Lees 1972; Geier-Hayes 1987; Harvey *et al.* 1987a,b). However, Smith (1955) reported high rates of damping-off mortality in spruce seedlings growing in rotten wood, and there are no experimental data to confirm that decaying wood enhances mycorrhizal development in interior spruce.

Decaying wood appears to be a preferred seedbed mainly when seedlings establish under a forest canopy. In clearcut situations, high temperatures and more rapid drying will limit establishment on these seedbeds (Wagg 1964b, cited by Zasada and Gregory 1969), except perhaps in very moist microenvironments such as those described by Wilford and Septer (1987, unpublished) and Caza and Kimmins (1990a, unpublished). Another concern with decayed wood substrates is that seedlings may lack windfirmness, have stunted growth, and develop nutrient deficiencies if their roots fail to grow out into surrounding soil. Minore (1972) showed that decayed wood has very low levels of nutrients compared with humus. On active floodplains, Wagg (1964b, cited by Zasada and Gregory 1969) reported that decaying logs often act as a temporary, elevated substrate for white spruce establishment. Flooding buries the log and lower stem of the seedling in alluvium, and causes the seedling to produce adventitious roots, which then grow out into the newly deposited soil.

Litter and humus (duff) Although spruce seedlings will establish in litter and humus, most research indicates that germination and seedling survival rates are lower than in either mineral soil or decaying wood (see Place 1955; Eis 1965a; Zasada and Gregory 1969; and Dobbs 1972 for summaries). Lack of forest floor disturbance is frequently cited as a primary reason for failure of natural spruce regeneration (Noble and Ronco 1978; Krasny *et al.* 1984; McMinn 1986). Unstable moisture and temperature regimes appear to be the most important factors limiting seed germination and germinant survival in litter and humus. The loose, coarse textured organic matter dries quickly, and lacks capillary continuity, and moisture tends to be absorbed into the organic material rather than being available as surface films (Baker 1950; Eis 1965a). Seeds often fail to germinate because they are located in air pockets, and young germinants frequently die because their roots dry out before they can reach stable moisture supplies below the surficial layers of litter and poorly decomposed duff.

Temperatures of organic substrates fluctuate widely and, on sunny days, surface temperatures often become lethal to young germinants (Cochran 1969; Alexander 1984). In Alberta, Day (1963) found that exposed F and H humus seedbeds were typically 5 to 10°C hotter on the surface than exposed mineral soil and had the highest proportion of germinants injured by heat-girdling of the stem. Near Prince George, Eis (1965a) recorded a maximum temperature of 57°C in humus compared to 49°C in mineral soil.

Litter and humus layers may be favourable seedbeds for spruce in moist shady depressions where high temperatures and moisture stress are unlikely to occur (Rowe 1955; Day 1964). In droughty environments, the thickness of organic layers apparently affects whether spruce seedlings will germinate and establish successfully. Organic layers thicker than approximately 2.5–5 cm prevent spruce roots from reaching the mineral soil before the upper layers have dried (Place 1955; Zasada and Gregory 1969; Knapp and Smith 1982; Alexander 1984, 1987), but a shallow litter layer may be beneficial, particularly in dry years, because it reduces evaporation from the mineral soil (Place 1955; Waldron 1966). Fiedler *et al.* (1985) indicate that at high elevations, duff provides protection from frost heaving and lessens the impact of high-intensity rainstorms that can wash out or bury young seedlings.

The composition of organic layers is important (Place 1955). Coniferous and deciduous litters differ greatly in their physical structure and chemical and biological properties. A laboratory experiment by Daniel and Schmidt (1972) suggests that pathogens in spruce litter may inhibit spruce seed germination in the undisturbed forest floor. Spruce seed germination was dramatically reduced in unsterilized Engelmann spruce litter (3.5% germination) compared with a mineral soil substrate (82–86%) or litter from other tree species (73–87%). However, when the spruce litter was sterilized by autoclaving, germination rose to 84–85%. Captan fungicide produced similar results to autoclaving. Fungal hyphae were abundant in the untreated litter.

In contrast, Ahlgren and Ahlgren (1981) demonstrated that germination may sometimes be stimulated by substances found in leaf litter. White spruce seed germination was significantly higher in aspen, balsam fir and red and white pine litter than in a mineral soil control. White spruce litter was not tested. Waldron (1966) noted that a thin layer of aspen leaves over mineral soil enhanced white spruce germination, whereas a layer of conifer needles had either no effect or a negative effect.

Moss Moss seedbeds are similar to litter and duff, particularly in regard to their moisture and thermal properties. Most reports distinguish between two contrasting types of moss seedbed: 1) the feathermoss (*Pleurozium schreberi, Hylocomium splendens*) carpet that dominates the understory of most undisturbed spruce forests; and 2) the *Polytrichum* carpet that invades exposed mineral soil in clearcuts and other disturbed areas.

Feathermoss seedbeds are generally regarded as unfavourable, particularly after logging when they die back and become very dry and hot (Place 1955; Smith 1955; Zasada and Gregory 1969). However, Place (1955) notes that seeds can work their way down into the moss and thus obtain some protection from seed predators and fluctuating temperature and moisture levels. Day (1964) and Day and Duffy (1963) found more seedlings on moss seedbeds than on bare mineral soil, perhaps because moss tended to occur on moist, shaded microsites.

Polytrichum moss may also provide some protection from high temperatures and drought injury, but, when dense, it competes strongly for moisture and nutrients and may literally "choke out" young seedlings (Place 1955; Zasada and Gregory 1969; Zasada *et al.* 1978). *Polytrichum juniperinum* mats were a preferred seedbed for Engelmann spruce seedlings in central Idaho (Geier-Hayes 1987), but in the ESSF near Kamloops, where *Polytrichum* is abundant after burning or mechanical scarification, Butt *et al.* (1989, unpublished) observed that it appears to inhibit seedling establishment.

Burned seedbeds Burned seedbeds are not favourable for interior spruce, except where the burn is so severe that it completely removes soil organic layers (Zasada 1985; Zasada and Norum 1986; Butt *et al.* 1989, unpublished). Most fires leave some residual blackened organic matter and ash that has adverse temperature and moisture properties for seed germination and early seedling survival (Place 1955; Smith 1955; Waldron 1966). There is no evidence that ash chemically inhibits spruce seed germination, but Waldron (1966) notes that extreme soil surface temperatures may delay germination, and Alexander (1987) and Zasada (1985) report that seedling establishment is poor or nil on loose ash. Fiedler *et al.* (1985) found the lowest density of Engelmann spruce regeneration on burned seedbeds, but noted that seedbed conditions apparently ameliorated over time and that stocking increased dramatically between 5 and 10 years after burning. Butt *et al.* (1989, unpublished) observed poor regeneration on burned seedbeds, but found that spruce regenerated better than subalpine fir.

pH Seedbed pH does not appear to be an important factor affecting seed germination, except under unusually alkaline conditions. In a laboratory study, white spruce seed germination at pH 2.2 (85% germination) and 3.0 (83% germination) was not significantly different from that in distilled water (pH 6.5; 90% germination) but dropped markedly at pH 9.0 (48% germination) (Abouguendia and Redman 1979). It appears that the alkaline treatment was toxic rather than merely inhibitory, because germination failed to occur when the seeds were later washed in distilled water.

Other environmental factors affecting germination, survival and establishment

Aspect A variety of physical and biological factors interacts with the type of seedbed to affect the success of natural regeneration. Aspect appears to be one of the most important of these factors. The work of Alexander (1984, 1987) and others (Noble and Alexander 1977; Knapp and Smith 1981) in the U.S. Rocky Mountains, repeatedly shows that Engelmann spruce regeneration is much more successful on north aspects than on south aspects. Day (1964) also observed that spruce seedlings were most abundant on cooler northeast-, north-, northwest- and east-facing slopes of southern Alberta Rockies.

Aspect appears to affect spruce regeneration success in some areas of (southern) British Columbia, but not in others. In a survey of ESSF cutovers in the Kamloops Forest Region, Butt *et al.* (1989, unpublished) found that regardless of the subzone (very wet ESSFvc to dry ESSFdc) and the type of site preparation, north aspects had more natural regeneration than south aspects (Figure 39). Desiccation of organic seedbeds was thought to be the cause of poor stocking on south aspects. A similar survey in the Nelson Region found no significant stocking difference between north and south aspects (Butt 1990, unpublished). Clark (1969) also found no effect of aspect on spruce seedling establishment in a study carried out in the ESSF and ICH of southern British Columbia, and attributed this to a combination of gentle slopes and weather conditions throughout the major part of the growing season. No mention of the influence of aspect is made by Zasada or other Alaskan scientists or by researchers such as Dobbs and Eis in northern British Columbia.

Aspect can be important at the microtopographic level. Waldron (1966) examined differences in germination on four sides of a ridged seedbed (30 cm high, 30 cm wide). Germination was highest on north-facing surfaces, intermediate on east- and south-facing surfaces and lowest on west-facing surfaces.

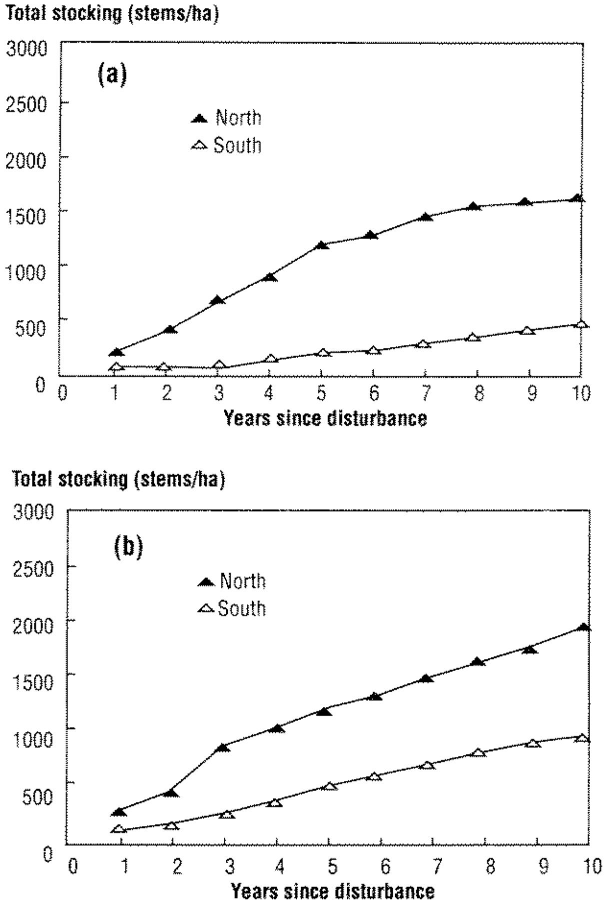

FIGURE 39. Density of Engelmann spruce natural regeneration on north- and south-facing clearcuts in (a) the Kamloops Forest Region, and (b) the Nelson Forest Region (from Butt *et al.* 1989 and Butt 1990, both unpublished).

Shade Light to moderate shade generally has a beneficial effect on germination and early survival of spruce seedlings (Day 1963; Clark 1969; Zasada and Gregory 1969). In the mountains of Colorado, shade is essential on south slopes to protect spruce germinants from heat injury and desiccation, even when sites are scarified (Noble and Ronco 1978; Alexander 1984). On north aspects, shading benefits seed germination and seedling survival, but is not essential for regeneration success. Waldron (1966) found that shading enhanced germination on scarified sites but had little impact on undisturbed seedbeds. In central Idaho, Engelmann spruce seedlings were most often found in heavy shade (≥66% cover) in the mid-elevation Grand fir–mountain maple habitat type, while in the higher elevation Grand fir–black huckleberry habitat type, they were most often found in light shade (≤33% cover)(Geier-Hayes 1987). Alexander (1987) recommends 40–60% shade as optimum for spruce seedling survival in the central and southern Rocky Mountains. Clark (1969) found that seedspots shaded by logs and stumps had significantly better seedling survival than seedspots in the open or shaded by vegetation.

The need for shade is probably greater in hot, dry climates than in cooler, northern environments. In a comparison of shelterwood and clearcutting systems in the Tanana Valley of interior Alaska, there was no evidence that the shelterwood system provided more favourable microclimatic conditions for germination and seedling establishment than clearcutting (Youngblood and Zasada 1991). However, the clearcuts in this Alaska study were only 1 ha in size. Results from the SBS zone near Prince George and Burns Lake indicate that young seedlings may have difficulty surviving in exposed large clearcuts. Eis (1965a) recorded higher survival rates of spruce seedlings in plots located at 0 and 22 m from the forest edge (25 and 60% of full sunlight, respectively) than in plots located 62 m from the forest (85–90% of full sunlight). Bartlett (1976, unpublished) found that seedling survival was poor away from the protection of the timber margin.

Moisture regime Waldron (1966) observed higher germination rates on more or less mesic ecosystems than on very moist to very wet sites. However, he felt that in a dry year, the pattern could be reversed. In the ESSF of southern British Columbia, natural stocking of spruce tends to be greater on mesic than on either submesic or subhygric sites (Butt *et al.* 1989, unpublished; Butt 1990, unpublished). In the Nelson Region, spruce stocking on subhygric sites is particularly low (Butt 1990, unpublished). Clark (1969) observed higher seed germination and seedling survival on fresh and moist sites (29% stocking after 3 years) compared with dry sites (16% stocking).

Flooding is a common cause of seedling mortality in depressional areas that fill with water in the spring. However, Lees (1970) observed that some of the best seedlings were found around the margins of depressions. On river floodplains, spruce seedlings generally fail to become permanently established until terraces are raised above the level of yearly sediment deposition, erosion, and potential oxygen limitation to root systems (Van Cleve *et al.* 1980; Walker *et al.* 1986).

Frost Naturally regenerated seedlings are often thought of as being more resistant to frost damage than planted seedlings because they are phenologically attuned to their environment (see, for example, Herring 1989). While this may be true, frost damage is a major cause of mortality among naturally regenerated spruce seedlings, especially during the first growing season when seedlings are succulent and have insufficient carbohydrate reserves to permit shoot regrowth after frost damage occurs. Temperature data from southern British Columbia indicate that potentially damaging frost can occur at any time during midsummer on a wide range of site types in the MS, IDF and ESSF zones (Stathers 1988; Steen *et al.* 1990). Seedlings that germinate late in the growing season are particularly susceptible to the killing frosts of fall (Alexander 1987).

Many seedlings die as a result of frost heaving (Alexander 1987). Young seedlings with poorly anchored root systems, and especially new germinants, are at highest risk. Frost heaving occurs primarily when daytime temperatures are warm but nights drop below freezing and soils are saturated but not covered with snow. Seedlings on open, scarified ground are most susceptible, while those under a full or partial tree canopy are less susceptible. Frost heaving can also be alleviated by maintaining a light covering of duff over mineral soil (Fiedler *et al.* 1985; Orlander *et al.* 1990). Arlidge (1967) observed frequent frost heaving on scarified seedbeds with heavy textured soils near Prince George, but did not consider it a serious concern. Many of the seedlings had exposed "hockey stick" roots, but their growth and vigour seemed unaffected.

Vegetation (See Section 3.3, Vegetation Interactions, for additional discussion.) Vegetation has both beneficial and negative effects on the establishment of spruce seedlings. For young germinants, overtopping vegetation prevents desiccation and heat injury, and may protect against frost damage. However, conditions favouring high rates of seed germination and early seedling survival may not be beneficial in the long run (Zasada and Gregory 1969; Noble and Ronco 1978; Krasny *et al.* 1984). For example, Clark (1969) observed much higher rates of seed germination under vegetation than on fully exposed plots, but after 2 years the shaded plots had only slightly higher stocking because of losses due to leaf smothering. Day (1964) reported that while seedlings were most abundant in moderate to heavy shade, the largest seedlings were found in light shade, and Zasada (1972) notes that although white spruce can germinate and survive for a few years beneath an undisturbed mature spruce stand, the seedlings eventually die because adequate growth is not maintained.

Competition for light, moisture and nutrients, inhibitory chemicals and physical damage from plant litter are the main potential negative effects of vegetation on young seedlings (Zasada *et al.* 1978). In northern environments, lower soil temperatures beneath overtopping vegetation can also inhibit subsequent seedling growth (Krasny *et al.* 1984).

Where deciduous or herbaceous vegetation is abundant, leaf smothering may be the most important cause of spruce seedling mortality (Rowe 1955; Zasada and Gregory 1969). Crushing under aspen leaves caused 36–45% of total mortality in a mixedwood stand in Manitoba (Waldron 1966). Spruce beneath an Alaska paper birch stand took 4 years to become large enough to outgrow the negative impacts of leaf fall (Gregory 1966, cited by Zasada and Gregory 1969). Rowe (1955) suggests that 3 years are required to overcome this problem. Raised hummocks and ridges of mineral soil or decaying wood provide some degree of protection from leaf smothering.

A lush growth of grasses, sedges or forbs can severely inhibit spruce regeneration (Noble and Ronco 1978; Eis 1981; Alexander 1987; Geier-Hayes 1987). The dense growth causes seeds to become suspended above the ground (Eis 1981). Those germinants that do reach mineral soil are either shaded out, smothered by dead foliage, or face strong competition for soil moisture. Alexander (1987) believes that shrubs with sparse foliage can be beneficial to growth of spruce seedlings where they cast shade without seriously depleting soil moisture. Butt (1990) recorded less natural regeneration under fireweed or white rhododendron than other vegetation types sampled. Lees (1972) noted that an aspen shelterwood creates a favourable environment for establishment of spruce seedlings, and Geier-Hayes (1987) found that Engelmann spruce seedlings were more common under thimbleberry cover than beneath forbs, grasses or sedges.

Surveys in the ESSF of southern British Columbia showed that total stocking of spruce seedlings was unaffected by vegetation density until cover exceeded 80%; then stocking dropped off sharply (Butt *et al.* 1989, unpublished). Seedling establishment was poor on sites with undisturbed *Rhododendron-Menziesia* shrub communities and on wet sites with abundant *Equisetum*, *Pleurozium*, and *Brachythecium*. However, in this study, the vegetation may have served more as an indicator of unfavourable seedbed conditions (thick organic layers, wet ground prone to flooding) than as a direct impediment to spruce establishment.

Disturbances such as mechanical scarification and fire that create favourable seedbeds and growing conditions for spruce also create an ideal environment for a variety of other species that may subsequently interfere with spruce growth (Zasada and Gregory 1969; Zasada 1972). Many of these competing species are capable of rapid vegetative regrowth from surviving rootstocks or rhizomes, which gives them a considerable advantage over the slow-growing spruce. Competing plants may also have an advantage over spruce in terms of regeneration from seed. Species such as birch, cottonwood and willow produce more abundant seed, and have wider seed dispersal and more rapid seedling growth rates than spruce.

Animal damage Damage by mammals and birds can be an important cause of mortality in young spruce seedlings. Noble and Shepperd (1973) reported that cotyledon clipping by dark-eyed juncos (*Junco hyemalis=J. caniceps*) caused 28% of first-year mortality at an experimental site in the central Colorado Rocky Mountains. This type of damage is commonly observed and had previously been attributed to rodents. While it now appears that mice and other rodents seldom consume seedlings in the cotyledon stage (Alexander 1987), winter damage to older seedlings is common, especially during peak periods in the animal's population cycle. Debarking and stem clipping are typical forms of damage (Zasada and Gregory 1969; Alexander 1987; Finck *et al.* 1989). Snowshoe hares (*Lepus americanus*) are a major cause of spruce seedling mortality (Radvanyi 1987). Although spruce seedlings are not a preferred food item, hare browsing can be heavy when rabbit populations are high (Rowe 1955; Walker *et al.* 1986), or preferred species are absent (Smith *et al.* 1988). The hares feed mainly on buds and smaller twigs during the winter months. Damage is most severe in aspen-covered or brushy areas that offer cover to the hares.

Grazing or browsing of interior spruce seedlings by ungulates and livestock is usually negligible (McLean and Clark 1980; Alexander 1987). Numerous studies indicate that most of the damage from these larger animals is caused by trampling. Damage is often exacerbated in mechanically prepared areas because the animals prefer to walk in the prepared trails where seedlings are concentrated (Waldron 1966; Alexander 1987).

Fungi A variety of pathogenic fungi can damage or kill young seedlings. Damping-off fungi (*Fusarium* spp.) are a common cause of post-emergence mortality on moist seedbeds. Ronco (1967) reported 17% mortality due to damping-off fungi. Lees (1970) suspected that snow mold (*Phacidium* spp.) was the primary cause of overwinter mortality in a spruce-aspen shelterwood in Alberta. On high-elevation sites where the snowpack lingers well into the spring, the black felt fungus (*Herpotrichia nigra*) can cause major seedling damage or mortality (Alexander 1987).

Rates of recruitment, survival and growth

Seedbed receptivity and rates of ingress Numerous investigators have examined the rate at which spruce seedlings become established on a seedbed following a disturbance. Interest in this topic is motivated by several concerns: 1) establishing the timing of harvest and site preparation treatments in relation to spruce seed years; 2) determining regeneration delay or length of time before an area becomes stocked; and 3) deciding on the appropriate time to carry out a regeneration survey to determine stocking.

The length of seedbed receptivity is related to the degree of vegetative competition. Exposed mineral soil is considered a "receptive" seedbed, while one that is overgrown with vegetation or covered with plant litter is no longer receptive. Mesic and drier ecosystems will remain receptive longer following site preparation than moist productive ecosystems where vegetative regrowth is rapid (Eis and Inkster 1972). Arlidge (1967) investigated the effective life of machine-scarified seedbeds on 17 moist spruce ecosystems in strip cut and clearcut areas within the SBS zone around Prince George. Seedbeds were artificially seeded 0, 1, 2, 3 and 4 years after scarification. There was a marked reduction in stocking between seedbeds sown in year 0 (50.5% stocking after 4 years) and year 1 (32.8% stocking after 4 years). Stocking was mostly unsatisfactory if seeding occurred more than 1 year after scarification. Large seedbeds had better seedling survival and remained receptive longer than small patches. Seedbeds on Devil's club ecosystems remained receptive for shorter periods than Aralia-Oakfern ecosystems owing to rapid regrowth of competing vegetation, particularly thimbleberry and birch. Although Bunchberry-Moss ecosystems were not tested in his study, Arlidge (1967) thought that they would remain free of vegetation for 4–5 years.

A similar study was conducted by Lees (1970) on less productive ecosystems in the mixedwood forest of northern Alberta. There was a marked reduction in seedling establishment 3 years after scarification, and by the fourth year, the seedbeds were no longer receptive. In this case, seedbed receptivity declined most rapidly on a dry upland ecosystem where grass competition for moisture was a problem, and most slowly on a mesic ecosystem. The wet bottomland site (a horsetail ecosystem) was intermediate.

Zasada *et al.* (1978) reported that seedbeds in an interior Alaska study remained receptive to spruce for 3–5 years following mineral soil exposure. By the fifth growing season, exposed mineral soil had decreased from 85 to 3% of the soil surface, due mainly to increases in plant litter and moss.

Other investigators have taken a retrospective approach to the question of seedling recruitment, by looking at the age distribution of naturally regenerated seedlings some years after harvesting or site preparation. These studies of "ingress" paint quite a different picture from what would be expected from the seedbed receptivity studies summarized above.

Butt *et al.* (1989, unpublished) and Butt (1990) looked at ESSF sites up to 15 years after disturbance, and concluded that regeneration surveys conducted 5 years post-logging would substantially underestimate the amount of natural stocking. In the Kamloops Forest Region, increases in stocking levelled off after about 7 years, but on some south-facing and untreated sites it could take as long as 10–12 years to get a good estimate of the amount of ingress. In the Nelson Forest Region there was no significant levelling off in ingress rates after 7 years. Seedling establishment continued to rise for 10 or more years.

Similar results have been obtained outside British Columbia. In the Yukon, stocking levels on naturally seeded areas were still on the increase five seasons after logging or scarification (Gardner 1983). In west central Alberta, Johnstone (1976a) found that ingress continued for 13 growing seasons after scarification, and recommended that surveys be delayed until 8 years after final disturbance to get a good estimate of stocking levels. Johnstone (1976a) observed that the rate of ingress in white spruce is slower than that in lodgepole pine, and that ingress patterns on partially cut areas are similar to those on clearcut areas, except that the former have higher seedling densities.

Rowe (1955), Day (1964), and Lees (1970) all commented on the strong periodicity of spruce seedling establishment. In their studies, a very high percentage of the total ingress resulted from 1 or 2 good years. These results suggest that a coincidence of exceptional seed years and weather conditions may be just as important as, or more important than, the timing of site preparation and the seedbed condition.

Patterns of seedling survival Spruce seedlings are most susceptible during the first year following germination (Zasada 1980). Alexander (1987) estimates that 50% or more of seedling mortality occurs during the first growing season. Mortality is also very high during the first winter, when seedlings are subjected to freezing damage, frost heaving and erosion, and smothering beneath litter. Those seedlings that germinate late in the growing season are particularly vulnerable (Waldron 1966; Zasada 1978, 1980; Alexander 1987), because they are not fully hardened-off, and because of their small size.

After the first growing season, the rate of mortality declines sharply, but losses continue to be high for several years (Figure 40). Zasada (1980) considers a seedling to be "established" when it enters its third growing season, whereas Alexander (1987) prefers 5 years. Noble and Ronco (1978) concluded that after seedlings reach 4–5 years or 8–10 cm in height, only unusual factors such as snow mold, fire, trampling, or predation by gophers or snowshoe hares could seriously affect regeneration success.

Evaluating the overall regeneration environment: seed:seedling ratios and regeneration probabilities The number of seeds required to produce one first-year or established seedling is often used as an index of the overall regeneration environment. Favourable environments have a low seed:seedling ratio, while hostile environments have a high ratio.

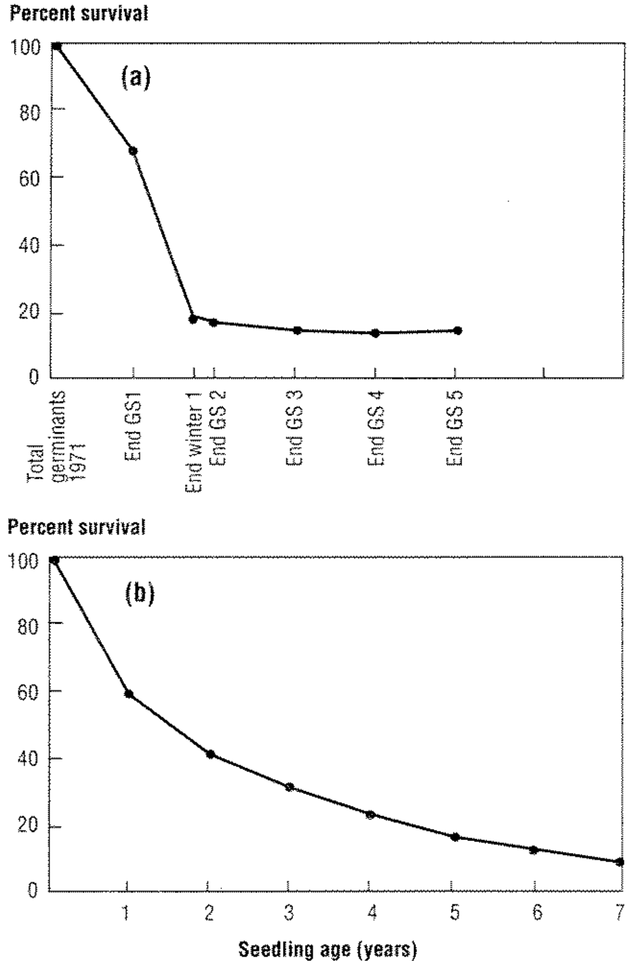

FIGURE 40. Survival rates of (a) white spruce seedlings in Alaska (GS = growing season), and (b) Engelmann spruce seedlings in the Rocky Mountains of Colorado (from Zasada 1980 and Noble and Ronco 1978).

In central Colorado on shaded, north-facing, mineral soil seedbeds, seed:seedling ratios averaged 18:1 at year 1 and 32:1 at year 5; while unshaded, unprepared seedbeds averaged 750:1 at year 1 and had no surviving seedlings at year 5 (Alexander 1984, 1987). Near Prince George, seed:seedling ratios averaged 26:1 at the end of the first growing season, ranging from 21:1 on the shaded southwest (north-facing) side of the opening to 33:1 in the centre and on the northeast side (Dobbs 1976b). Zasada *et al.* (1978) used seed:seedling ratios to measure the decreasing receptivity of a scarified seedbed over time. In 1971, the seed:seedling ratio on a freshly exposed seedbed was 4:1, but by 1973 it had increased to 16:1 as the seedbed became covered with plant litter and moss.

A major Colorado study that included five sites and extended from 1961 to 1975 found that seed:seedling ratios varied by geographic area, with distance from the timber edge, and from year to year according to weather conditions (Noble and Ronco 1978). The lowest seed:seedling ratios were 60:1 after the first year and 926:1 for established seedlings (4–13 years old). The highest ratios were 2066:1 at year 1 and 20 809:1 for established seedlings. Low seed:seedling ratios in the first year did not necessarily lead to low ratios later on. In fact, the authors cited several instances where seedbeds that were highly favourable in the first year were rapidly invaded by dense vegetation that reduced survival in subsequent years.

As an alternative to seed:seedling ratios, the overall success of the regeneration environment can be summarized as a regeneration probability. In this approach, the probability that an established seedling will be regenerated is estimated through a stepwise procedure that assesses the likelihood of success at each phase in the regeneration process, from seed production and seed dispersal, through seed viability, predation and germination, to successful survival and establishment. Table 14 presents a hypothetical situation in which the likelihood of successful natural regeneration is compared under two different silvicultural regimes applied to the same site (clearcutting vs shelterwood). The technique could just as well be used to compare the suitability of two different sites (e.g., south vs north aspect) for natural regeneration.

Growth rates of natural regeneration Under field conditions, the early growth of spruce seedlings is very slow. One of the important reasons why artificial regeneration is favoured is that it may take 5–10 years for an average naturally regenerated seedling to equal the size of 1-year-old nursery stock. Subsequent growth to reach a "free growing" state may also be unacceptably slow.

TABLE 14. Sample natural regeneration probabilities for interior spruce. This hypothetical example compares the expected regeneration on a large clearcut with that of a shelterwood on the same site, following a heavy seed year. The probabilities are derived from this literature review.

			No. of seeds or seedlings		
Regeneration system	**Regeneration phase**	**Probability**	**/m^2**	**/ha**	**Reference**
large clearcut (±300 m from edge)	seed production (uncut stand)	1.0	1000	10 000 000	Dobbs 1976b; Zasada 1985
	seed dispersal	0.02	20	200 000	Dobbs 1976b; Zasada 1985; Figure 36
	seed viability (sound seeds)	0.3	6	60 000	
	seed predation	0.5	3	30 000	Radvanyi 1974
	germination	0.3	0.9	9 000	Eis 1965a
	1st-year survival	0.1	0.09	900	Figure 40; Eis 1965a
	established seedling (5 years)	0.4	0.036	360	Figure 40; Eis 1965a
shelterwood	seed production (uncut stand)	1.0	1000	10 000 000	Dobbs 1976b; Zasada 1985
	seed dispersal	0.75	750	7 500 000	Day 1970; Zasada 1985
	seed viability (sound seeds)	0.4	300	3 000 000	Dobbs 1976b
	seed predation	0.6	180	1 800 000	Radvanyi 1974
	germination	0.4	72	720 000	
	1st-year survival	0.4	28	280 000	Figure 40
	established seedling (5 years)	0.5	14	140,000	Figure 40

The pattern of shoot and root growth of interior spruce seedlings during the first growing season was recorded by Eis (1965a) near Prince George (Figure 41). Height growth of shoots ceased by early August, but root growth continued well into September. Data from a wide geographic area indicate that a typical, healthy seedling at the end of the first growing season has a stem measuring 1–3 cm and a sparsely branched root system 4–10 cm long (Rowe 1955; Smith 1955; Eis 1965a; Noble 1973b; Zasada *et al.* 1978) (Figures 41–43). Noble (1973b) and Eis (1965a) both note that the amount of root growth in the first year is crucial because it determines whether the seedlings will be able to gain access to soil moisture and because overwinter survival depends on the seedling's ability to withstand frost heaving and soil erosion.

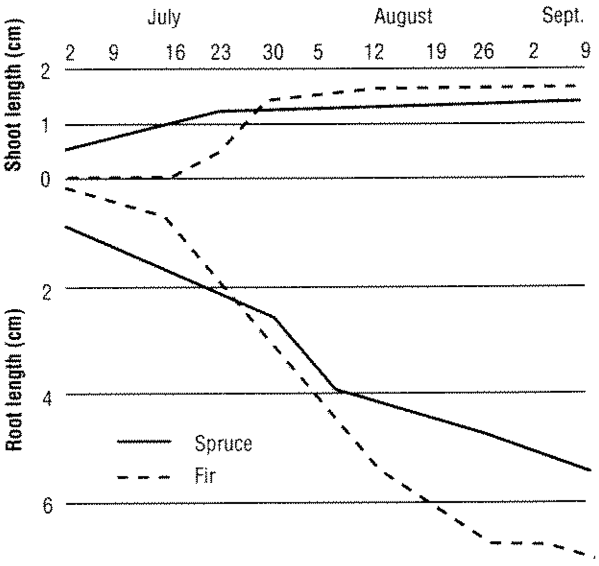

FIGURE 41. Shoot and root development of interior spruce and subalpine fir during the first growing season in the SBS zone near Prince George (from Eis 1965a).

After 3–5 years, seedlings are no longer so vulnerable, and those still alive are considered "established." However, they are still quite tiny and growth rates continue to be slow. In the ESSF of southern British Columbia, five-year-old spruce seedlings are 10–20 cm tall, 10-year olds average 40–50 cm, and at 20 years most are still below 100 cm (Butt *et al.* 1989, unpublished; Butt 1990, unpublished). Similar growth rates are reported outside British Columbia. In northern Alberta, 3-year-old white spruce seedlings averaged 3.8–7.3 cm in height (Day 1970). On floodplain sites in the Yukon, spruce seedlings averaged 5 cm in height at year 3 and 12 cm at year 5 (Gardner

1983), while in Alaska, seedlings ranging in age from 3 to 13 years averaged 5–5.5 cm tall (Krasny *et al.* 1984). Zasada *et al.* (1978) reported that the most vigorous 5-year-old seedlings averaged 18.5 cm tall. The best growth rates found are from Manitoba, where the height of dominant seedlings averaged 18–30 cm at 6 years and 111–120 cm at 14 years (Waldron 1966). The slowest growth rates are reported from a harsh dry site in south-eastern Alberta where seedlings 15 years of age were only 20 cm tall and had roots extending only 25 cm into the soil (Day 1964) (Figure 44).

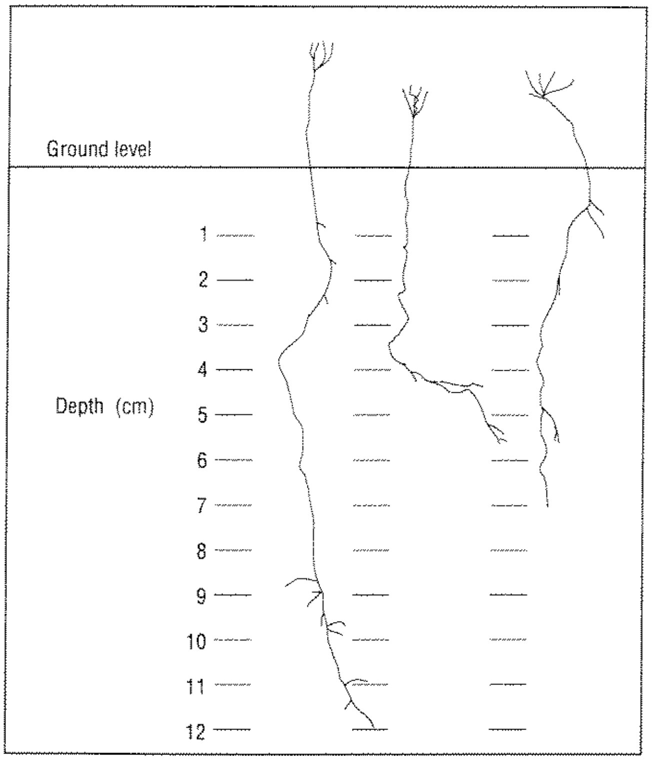

FIGURE 42. Rooting depths of 3-month-old Engelmann spruce seedlings in Colorado (from Noble 1973a).

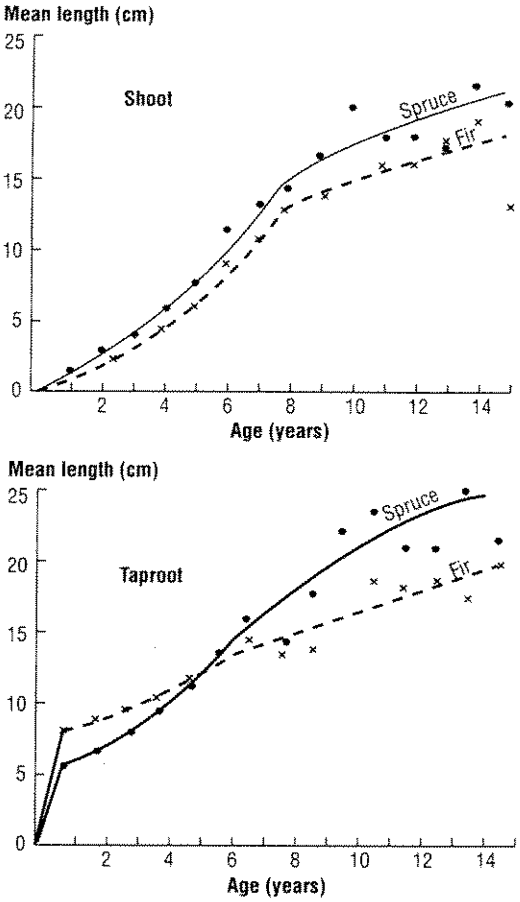

FIGURE 44. Mean shoot and root growth of interior spruce and subalpine fir seedlings aged 0 to 15 years in the Crowsnest Forest, Alberta (from Day 1964).

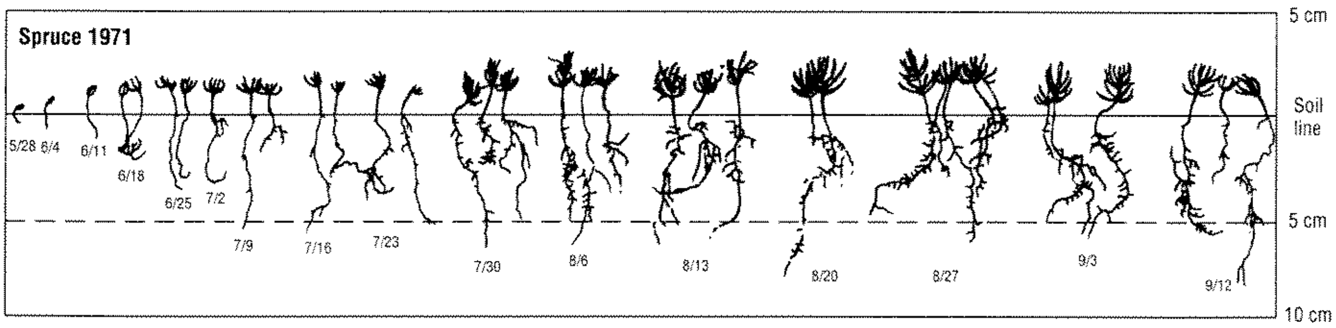

FIGURE 43. First growing season development of white spruce seedlings in interior Alaska as indicated by weekly excavation of vigorous individuals. Numbers indicate month/day of excavation (from Zasada *et al.* 1978).

Some studies suggest that growth rates begin to accelerate somewhere after 5–10 years if growing conditions are satisfactory (Alexander 1987; Butt *et al.* 1989, unpublished). However, juvenile height growth curves developed by Johnstone (1976b) suggest that there is a steady rather than an abrupt increase in height growth over the first 20 years of seedling growth (Figure 45).

Comparing growth of planted and natural seedlings There are few studies that directly compare the growth rates of natural vs planted seedlings; however, available data suggest that growth of naturals is considerably below what can be achieved in planted seedlings over the same period. McMinn (1986) contrasted the growth of natural regeneration with that of planted seedlings on three clearcut sites east of Prince George. Eight to 13 years after site treatments, the naturally regenerated seedlings ranged from 56 to 189 cm in height and had diameters of 0.9–2.5 cm., while the planted seedlings were 202–536 cm tall and 3.2–10.3 cm in diameter (data adjusted to correct for age differences). In the Yukon, planted seedlings averaged 40 cm at 5 years (26 cm increment since planting) compared to 7–12 cm for naturally or artificially seeded stock (Gardner 1983).

An indirect way of comparing the growth rates of natural and planted seedlings is to superimpose the juvenile height growth curves (Day 1964; Eis 1970; Johnstone 1976b; Butt *et al.* 1989, unpublished) over curves of average plantation performance (Vyse 1981; Eis and Craigdallie 1983; Pollack *et al.* 1985) (Figure 46). As Vyse (1981) observes, such an assessment also indicates that there are substantial growth gains to be made by planting early rather than relying on natural regeneration. It is not clear whether natural seedlings will follow the same growth curve as planted seedlings once they reach the initial height of the planting stock (Figure 47: curve A), or whether the initial size advantage gives planted seedlings superior growth rates (curve B). The growth lag will be accentuated if there is a significant regeneration delay period before natural seeding occurs (curves C and D).

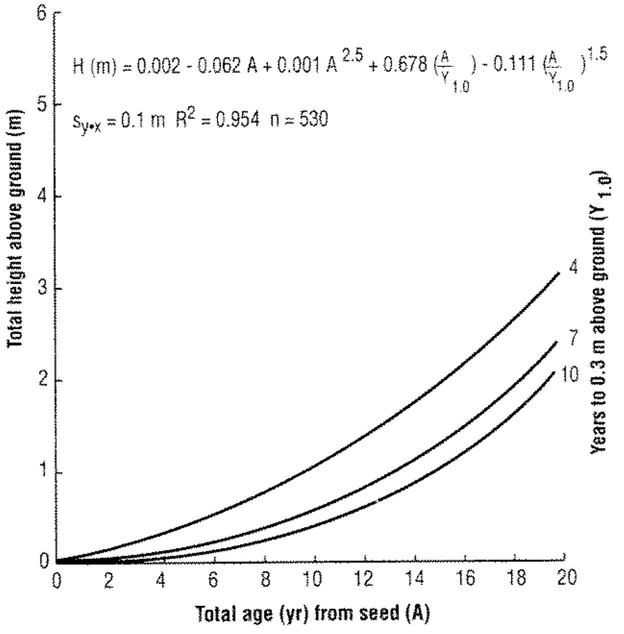

FIGURE 45. Juvenile height growth curves of dominant, naturally regenerated white spruce in west-central Alberta (from Johnstone 1976b).

Effects of environmental factors on growth A variety of studies has been carried out to determine how environmental factors such as climate, site preparation and the degree and type of vegetative competition affect the early growth of naturally regenerated spruce. Butt *et al.*

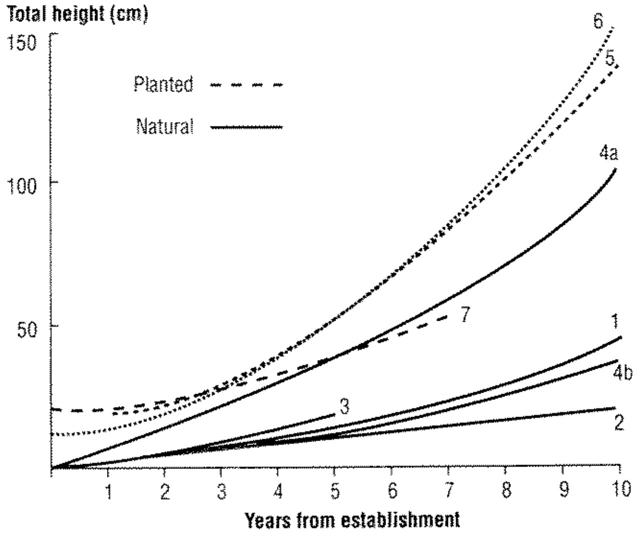

FIGURE 46. Comparison of height growth curves of naturally regenerated (solid lines) and planted (dashed lines) interior spruce seedlings updated from Vyse 1981): (1) average growth of naturals, ESSF zone, Kamloops Forest Region (Butt *et al.* 1989, unpublished); (2) average growth of naturals, Alberta Rockies (Day 1964); (3) average growth of B.C. naturals (Vyse 1981); (4a) most rapidly growing dominants, (4b) slower growing dominants, western Alberta (Johnstone 1976b); (5) average plantation performance, SBS zone, Prince Rupert Forest Region (Pollack *et al.* 1985); (6) "acceptable" plantation performance, Cariboo Forest Region (Vyse 1981); (7) average growth of planted seedlings under heavy brush competition, SBS zone, north of Prince George (Eis and Craigdallie 1983).

(1989) compared growth rates in various subzones of the ESSF in southern British Columbia. Spruce height growth in the mild subcontinental ESSFwm subzone west of the Fraser River was superior to that in the dry climate of the ESSFdc (Kamloops/Okanagan area) as well as that in the wet but cold ESSFvc and wc subzones (Clearwater/Salmon Arm area). Height growth in the Nelson Forest Region was similar to that observed in the ESSFwm (Butt 1990, unpublished). Elevation (range 1270–1810 m) and site moisture regime (submesic, mesic, subhygric) had no apparent effect on average height growth (Butt *et al.* 1989, unpublished; Butt 1990, unpublished).

The impact of site preparation on growth performance is variable. Some studies such as those of Waldron (1966), Butt *et al.* (1989), and Youngblood and Zasada (1991) show that growth is substantially greater on scarified surfaces than on unscarified sites. Others, including Day (1970), Herring and McMinn (1980) and McMinn (1986), indicate that scarification can reduce growth. These conflicting results seem to depend on the harshness of the site and the severity of scarification. Negative impacts of scarification apparently take place when inherent site fertility is low and/or removal of surface organic layers and soil layers exposes a compacted or nutrient-poor subsoil. In McMinn's (1986) study, seedlings on deeply scalped ground grew more slowly than those on lightly scalped ground, and seedlings on mixed mineral soil and organic seedbeds grew best of all. Site preparation had little effect on spruce height growth in the Kamloops Forest Region until trees were over 10 years of age (Butt *et al.* 1989, unpublished). Trees 11–14 years old were significantly taller on burned and mechanically treated sites than on untreated sites. In the Nelson Forest Region, Engelmann spruce grew faster on burned sites than on unburned sites (Butt 1990, unpublished).

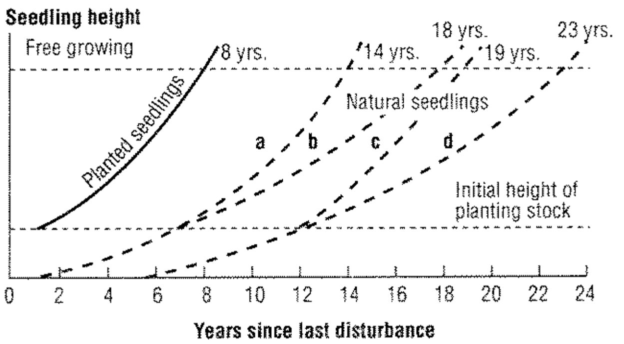

FIGURE 47. Hypothetical height growth scenarios for natural vs planted interior spruce seedlings. In this example, the planted stock reaches free growing height 8 years after the last disturbance (logging or site preparation). Natural seedlings take 7 years to reach the initial height of planted seedlings and may follow any one of four different growth curves: a) naturals grow at the same rate as planted seedlings after reaching the initial height of the planted trees (14 years to free-growing); b) naturals continue to grow more slowly than planted trees after reaching the initial height of the planted trees (18 years to free growing); c) growth rate is the same as in A, but there is a 5-year regeneration delay before seedlings appear (19 years to free growing); d) growth rate is the same as in b, but with 5-year regeneration delay (23 years to free growing).

Krasny *et al.* (1984) compared growth of spruce seedlings in the open with those under willow, alder and spruce stands. The seedlings ranged in age from 3–13 years (oldest under spruce stand). There were no differences in total height among the four vegetation types, but the seedlings under spruce were older (average age 10 years) and were growing much slower (height growth 0.4 cm/year) than those in the young seral stages (average age 4–5 years; height growth 2.0–2.4 cm/year). Root:shoot ratios were highest in the open (0.5) and lowest beneath spruce (0.24) and alder (0.20). In Alberta, Day (1970) found that 3-year-old seedlings averaged 3.8 cm in clearcut openings compared with 5.5–7.3 under a spruce-aspen shelterwood. But Waldron's (1966) results indicate that height growth of 7-year-old seedlings diminishes as the basal area of the residual stand increases (see Figure 48). At 14 years, the dominant 14-year-old seedlings averaged 111–120 cm in height in stand openings, but only 19–36 cm under partial shade.

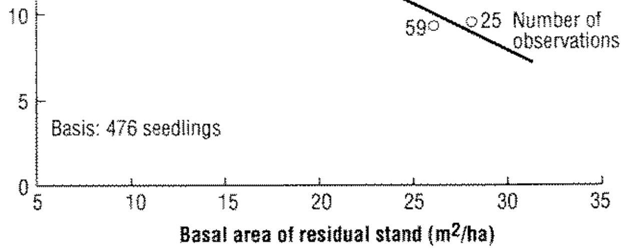

FIGURE 48. Effect of stand density on the total height of 7-year-old white spruce seedlings on scalped seedbeds (from Waldron 1966).

Comparisons with other species Several researchers have compared the early growth of spruce with that of subalpine fir, its most common associate in the west. Subalpine fir has a larger seed than spruce, and produces a sturdier germinant with a larger, faster-growing taproot (Smith 1955; Day 1964; Eis 1965a; Knapp and Smith 1982) (Figure 44). It is therefore more resistant to desiccation than spruce, establishes better on undisturbed litter and humus, and is generally less sensitive to environmental stresses during the first growing season. The size advantage of subalpine fir germinants may aid establishment and survival, but it does not confer a growth advantage. Day (1964) showed that after 5–6 years, spruce taproots were longer than those of subalpine fir. At his study site in the Crowsnest Pass, Alberta, shoot growth of spruce was slightly higher than that of subalpine fir over the first 15 years. Similarly, in naturally regenerated clearcuts of northwest Montana (*Abies lasiocarpa–Clintonia uniflora* habitat type), the tallest Engelmann spruce seedlings averaged 76–107 cm tall and were growing at a rate of 4.3–5.8 cm/yr, compared to 61–67 cm height and 3.6–4.3 cm/yr increment for the subalpine fir (Shearer 1988). The superior growth of spruce was consistent over hot, dry (*Xerophyllum tenax*), medium (*Clintonia uniflora*) and cool, moist (*Menziesia ferruginea*) phases of the habitat type. Age of the trees was not determined but the sites were prescribed burned 16–17 years before sampling. In British Columbia, survey data from a wide range of ESSF sites suggest either that the average growth rates of these two species over the first 10 years from seed are very similar (Butt *et al.* 1989, unpublished), or that subalpine fir has significantly slower growth (Butt 1990, unpublished). However, these studies did not compare spruce and subalpine fir growth under specific site conditions. Herring and McMinn (1980) measured height growth of subalpine fir and Engelmann spruce 21 years after blade scarification on three ESSF sites northwest of Clearwater. There was no significant difference in mean total height (77 cm for spruce; 62 cm for subalpine fir) or current annual increment (7 cm/yr for both species).

Early growth of naturally regenerated lodgepole pine is substantially greater than that of spruce. Juvenile height growth curves developed by Johnstone (1976b) for west central Alberta indicate that lodgepole pine grows at approximately twice the rate of white spruce, taking, on average, only 3.5 years to reach 30 cm height, compared to 7 years for white spruce. In northwestern Montana, the tallest lodgepole pine seedlings on a naturally regenerated clearcut averaged 201–393 cm in height and 2.1–5.2 cm dbh compared with 76–110 cm height and 0.15–0.30 cm dbh for Engelmann spruce, and were putting on 2–4 times as much annual height increment as the spruce (Shearer 1988). Other results from this same Montana habitat type suggest that western larch also has substantially greater initial growth rates than spruce, while Douglas-fir is just slightly greater (Shearer 1988).

5.1.3 Management practices

There are three steps involved in obtaining successful natural regeneration of interior spruce:

1. securing an adequate seed supply;
2. preparing a suitable (mineral soil) seedbed; and
3. ensuring that environmental conditions are suitable for seedling survival and growth.

Silvicultural procedures required to accomplish these three steps may involve some or all of the following activities (Waldron 1966; Lees 1972; Zasada 1972; Alexander 1987; Weetman and Vyse 1990):

- determining whether the site is an appropriate candidate for natural spruce regeneration and/or priorizing the site for artificial regeneration;
- deciding on an appropriate silvicultural system (i.e., clearcutting versus some form of partial cutting) and harvesting method;
- laying out the cutting area and/or marking cut and leave trees;
- monitoring cone and seed crops;
- scheduling and carrying out harvesting and site preparation (note: site preparation may precede harvesting);
- surveying the area to determine the adequacy of site preparation;
- surveying the area to determine stocking and condition of natural regeneration;
- harvesting leave strips or residual trees; and
- carrying out additional stand treatments such as fill planting, brushing, or spacing.

Securing a seed supply Seed trees for natural regeneration may either be left as residuals on the site, or left on the perimeter of the area to be regenerated (Alexander 1987). In either case, the seed trees must be healthy, phenotypically desirable, dominant or codominant stems, at least 40–60 years old, with a well-developed crown capable of producing a large seed crop. Unmerchantable, small diameter, damaged or deformed residual trees do not constitute an adequate seed source.

Blowdown hazard assessment A key concern with interior spruce is that the seed trees are windfirm. Cutting patterns designed to enhance natural regeneration will normally increase the risk of blowdown compared to large clearcuts (see, for example, Zasada and Grigal 1978). Table 15 (adapted from Alexander 1987) identifies characteristics of windfirm trees and windfirm stand boundaries that can be used to minimize windfall potential.

TABLE 15. Characteristics of windfirm trees and stand boundaries

Windfirm trees:

- healthy dominants or codominants
- full, symmetrical crown
- no signs of decay or injury
- rooted in deep, well-drained soils
- widely spaced
- straight stem

Windfirm boundaries:

- valley bottoms not parallel to direction of prevailing winds
- flat areas
- long boundaries located parallel to contour or road
- long boundaries located perpendicular to prevailing wind
- leeward boundary in protected location
- deep, well-drained soils without root-restricting layers
- absence of windblown trees in stand
- open-grown, poorly stocked stands *
- immature stands *
- avoid ridgetops
- avoid gaps or saddles that funnel wind through ridges

* these may not provide an adequate seed supply

Within any specific geographic area, it is essential to become familiar with local wind patterns, and topographic and soil conditions that create a high risk of blowdown. One example might be extensive areas of soils with a compacted root-restricting layer just below the surface (e.g., Trowbridge *et al.* 1980, unpublished).

Clearcutting: size and shape of openings Either small patch clearcuts or narrow strip cuts oriented perpendicular to prevailing winds can be used to facilitate natural regeneration. The cutting unit must be designed so that seed from the surrounding timber margin reaches all parts of the opening (Alexander 1986b). Recommendations for the maximum distance that any point on the opening may be from a seed source range from 60–90 m (Wurtz and Zasada 1986) to 200 m (Butt *et al.* 1989, unpublished). Other authors provide recommendations for the maximum width of the opening: Noble and Ronco (1978) suggest 100–160 m, Dobbs (1976b) recommends 300 m, and Squillace (1954, cited by Geier-Hayes 1987) suggests 350–400 m. Bartlett (1976, unpublished) recommends long, narrow, contour cuts, 100 m wide. For square clearcuts, Dobbs (1976b) recommends a maximum opening size of 35 ha, while Butt *et al.* (1989, unpublished) suggest 20 ha. In determining opening size and shape it is important to remember that seed sources will not be uniformly distributed around the perimeter, and that seed travel from the leeward side of the opening is often quite limited.

The size and shape of the clearcut must reflect not only seed dispersal patterns, but the environmental conditions for seed germination and seedling survival. There is abundant evidence that spruce seedlings establish poorly in open, exposed environments. After 20 years of studying seed production and dispersal and seedling survival in the central Rocky Mountains, Alexander (1986a,b, 1987) has developed guidelines for the size of clearcut openings that are based on the principle that the more unfavourable the environment, the more seeds are required to obtain adequate stocking. Because it is substantially more difficult to successfully regenerate a hot, sunny slope with an undisturbed seedbed than a cool, moist slope with freshly exposed mineral soil, openings on the former site must be much smaller than those on the latter to ensure an adequate seed supply.

Alexander's (1986b, 1987) guidelines for producing approximately 2000 5-year-old Engelmann spruce seedlings per hectare are as follows:

Environmental conditions	Maximum opening width (m)	Tree height (m)
North aspect, shaded, scarified	122–137	5–6
North aspect, unshaded, scarified	91–107	4–5
North aspect, shaded, unscarified	91–107	4–5
South aspect, shaded, scarified	15–30	1–1.5
North aspect, unshaded, unscarified	clearcutting and natural regen. unsuitable	
South aspect, unshaded or unscarified	clearcutting and natural regen. unsuitable	

Readers evaluating these guidelines for British Columbia conditions should consider that: 1) environmental conditions for spruce establishment are harsher in the central Rocky Mountains than they are in most of British Columbia; and 2) available data suggest that seed production and dispersal rates in British Columbia may be substantially higher than those observed by Alexander(1986b, 1987) and his coworkers. Alexander (1987) himself notes that similar guidelines developed for the Intermountain Region of the United States (north of his study area) suggest that somewhat larger clearcuts than indicated here can be successfully restocked on both north and south aspects (Roe *et al.* 1970, cited by Alexander 1987).

Day (1970) suggested progressive strip cutting as an economically feasible option for obtaining natural regeneration. Strips should progress into the prevailing wind and sun to remain windfirm and to provide seed and shelter for reproduction.

Partial cutting The seed-tree, shelterwood, and selection systems, or variations of them, can all be used to create conditions under which white spruce will regenerate naturally (Zasada 1972).

Little information on the success of **seed-tree** systems is available. Quaite (1956, cited by Lees 1970) suggested that as few as six spruce seed trees per acre constitute an effective seed source, but Zasada (1972) recommended a minimum of 25 seed trees per hectare (0.7–1.4 m^2 basal area/ha). Geier-Hayes (1987) recommends seed-tree cuts that have been lightly scarified, but still have plenty of brush to provide shade, for regenerating Engelmann spruce in the Grand fir/mountain maple habitat type of west central Idaho.

Shelterwood systems are regarded by many researchers as one of the most efficient options for achieving natural regeneration of interior spruce. Alexander (1987) provides guidelines for a variety of shelterwood cutting systems for different stand types, most involving three or more entries at 10–20 year intervals. However, most other researchers describe a simpler 2-cut uniform shelterwood with an initial regeneration (seed) cut, followed by final harvest cut. Zasada (1972) suggests that a 3-cut system, including a light preparatory cut, may be required in stands less than 100 years old.

From a purely ecological perspective, the shelterwood system provides ideal conditions for natural spruce regeneration: the regeneration cut ensures that a well-distributed spruce seed source is left and undesirable trees are removed and it creates an optimum, partially shaded microenvironment that provides sufficient light for survival and growth, yet protects the young seedling from desiccation and frost and prevents excessive competition from deciduous and herbaceous species. Final removal of the overstory is carried out when the young spruce are well established and poised for rapid juvenile growth, giving them a competitive edge over invading species.

From an operational or economic perspective, however, there is a variety of disadvantages to the shelterwood system, including: higher harvesting costs; damage to residual trees during the regeneration cut; a higher risk of blowdown and spruce bark beetle attack; damage to young seedlings when the residual stand is removed; and more difficult site preparation compared to clearcutting (Day 1970; Zasada 1972; Alexander 1973, 1987; Baldwin 1977).

Shelterwood trials with white and Engelmann spruce have been carried out across North America. The volume of timber removed in the regeneration cut varies considerably, depending on factors such as stand composition, density and age, windthrow hazard, and economic concerns. Alexander *et al.* (1982) recommend that between 50 and 110 dominant and codominant spruce trees/ha left at the time of the seed cut should be an adequate seed source. They note that a greater number of stems generally have to be left to protect against windfall than would be required strictly for seed production. However, leaving too many trees will prevent satisfactory development of regenerating seedlings (Waldron 1966). Waldron (1966) and Zasada (1972) recommend reducing the total stand basal area to 9–14 m^2/ha, retaining no less than 5.7 m^2/ha of spruce. Baldwin (1977) removed 20 and 40% of the basal area in a 40–50-year-old mixedwood stand with an initial basal area of 42 m^2/ha. Windfall was not a problem at either density, and spruce regeneration was best under the 40% removal treatment. Blum (1973) reported favourable results after an initial cut that removed 34% of the original basal area of 39 m^2/ha. In Saskatchewan, development of seedlings and saplings was found to be best under a residual basal area of 17 m^2/ha (Waldron 1959b, cited by Waldron 1966).

Trees selected for the residual stand should have a good cone crop or show evidence of having been good cone producers in the past (e.g., piles of cone scales at the base) (Zasada 1972; Alexander 1987).

Shelterwood removal takes place once the area is adequately restocked with spruce, but before the overstory begins to have a significant adverse effect on seedling growth and development (Day 1964; Zasada 1972). The length of time depends on the regeneration delay and on the shelterwood density. Blum (1973) reported that regeneration occurred 2–6 years after the first cut, peaking in year 4. Waldron (1966) suggested removing the residual stand after seedlings are 2–3 years old and recommended waiting no more than 5 years, since seedbeds are no longer receptive beyond this period. Overstory removal is best carried out in winter, when snow cover protects young seedlings from damage. Some researchers, such as Lees (1972) stress delaying overstory removal until seedlings are large enough to withstand logging damage and outgrow the heavy vegetative competition that is invariably brought about by overstory removal. Following a summer harvest, Baldwin (1977) observed that most mortality occurred in seedlings less than 15 cm tall, and recommended that the final harvest should not be carried out until regeneration averages 30 cm in height. However, Zasada (1972) noted that summer logging damage may not be undesirable if there is a need to reduce overstocking.

Selection systems are generally less effective than shelterwoods for obtaining spruce regeneration. They can be used where an uneven-aged stand structure is desired, particularly where the need to retain continuous forest cover for aesthetic or environmental reasons outweighs the silvicultural objective of obtaining rapid spruce growth. Weetman and Vyse (1990) consider selection logging as more feasible than shelterwood for regenerating old-growth ESSF stands in southern British Columbia. In most areas, this system will favour regeneration of the more tolerant subalpine fir over spruce (Glew 1963; Alexander 1987), but, equally, there are other ecosystems where selection logging should favour spruce over less tolerant hardwood species (Zasada 1972) or lodgepole pine.

Seedbed preparation Regardless of the reproduction method used, seedbed preparation will increase the success of spruce regeneration. Scarification to expose mineral soil is almost universally regarded as essential for obtaining adequate natural regeneration of spruce (Clark *et al.* 1954; Smith 1955; Glew 1963; Gilmour and Konishi 1965; Waldron 1966; Arlidge 1967; Zasada and Gregory 1969; Lees 1972; Bartlett 1976, unpublished; Johnstone 1976a; Noble and Ronco 1978; Alexander 1987; Gardner 1980, 1983). An exception may be the situation where abundant seed is available, environmental conditions are highly favourable and minimizing exposure of mineral soil may help to prevent overstocking and inhibit regeneration of hardwood species (Wurtz and Zasada 1986). Scarification may also be undesirable and/or unnecessary on exposed, dry, infertile sites with very thin humus layers (Day 1964) or in wet ecosystems where it is likely to cause soil damage and encourage competing vegetation (Waldron 1966; Arlidge 1967; Lees 1972).

The size, type and distribution of scarified patches directly influences the distribution of seedlings and the length of time the seedbed remains receptive. Arlidge (1967) and Waldron (1966) recommend producing wide scarification trails to retard vegetation regrowth and minimize animal trampling. While Arlidge (1967) found that seedbeds with a rough surface had more seedlings than smooth seedbeds, Waldron (1966) produced better results with a straight blade than with a soil disc. Butt *et al.* (1989, unpublished) recommend medium- to high-impact site preparation that exposes 30–50% mineral soil, except on south-facing slopes where light impact is recommended. Zasada and Grigal (1978) experienced overstocking and heavy deciduous invasion on their 1 ha scarified openings, and recommended small scalped patches to reduce these problems. On larger openings, it may be possible to control stocking density by scarifying more intensively near the centre of the block and less intensively near the forest edge (McCaughey and Schmidt 1987).

Timing of seedbed preparation is critical (Noble and Ronco 1978) because the relatively short period of seedbed receptivity (usually 3–5 yrs) must coincide with an adequate seed crop (Zasada and Gregory 1969). Zasada *et al.* (1978) and Bartlett (1976, unpublished) recommend scarifying before September to get maximum benefit from a particular seed crop. However, in an excellent seed year, even areas scarified during the winter may get enough late seedfall to adequately restock the site (Zasada *et al.* 1978). It is not always necessary to have an excellent seed year in order to get adequate spruce regeneration; even a poor to fair seed year may suffice if seed distribution is good and environmental conditions are highly favourable for seedling survival (Noble and Ronco 1978).

Eis and Inkster (1972) recommend carrying out as much site preparation as possible during good seed years and concentrating efforts on mesic and drier ecosystems during poor seed years, as these will remain receptive longer and have a higher chance of successful natural regeneration. There is considerable flexibility in timing site preparation to coincide with cone crops, because the treatment can be carried out either before any logging takes place, between cuts if a partial cutting system is used, or after logging if clearcutting is chosen. Where alternate cut and leave strips are created, seedbed preparation can be carried out simultaneously on both areas by pre-scarifying the leave strips and post-scarifying the cut strips (Gilmour and Konishi 1965). Pre-scarifying during a good seed year is also recommended on Devil's-club ecosystems with clayey soils because they have poor trafficability following logging and tend to brush in quickly (Gilmour and Konishi 1965).

When the early studies of natural regeneration were carried out in the 1950s and 1960s, a straight blade mounted on a crawler tractor was virtually the only equipment available for mechanical site preparation. Today, a much wider choice of equipment is available (Coates *et al.* 1987; Hunt and McMinn 1988), with the capability to prepare seedbeds to match specific site requirements and to minimize site degradation and residual tree damage. Although in British Columbia most of this modern, specialized equipment has been used only to prepare sites for planting, it is also effective for natural regeneration (Orlander *et al.* 1990).

Broadcast burning is not recommended as a method of preparing sites for natural spruce regeneration because it rarely exposes enough mineral soil to facilitate natural regeneration, and charred organic layers are a poor seedbed for spruce (Bartlett 1976, unpublished; Zasada 1985, 1986; Zasada and Norum 1986). Piling and burning of logging slash may, on the other hand, create the desired level and distribution of exposed mineral soil.

Regeneration surveys In British Columbia, stocking levels on areas left for natural regeneration are normally assessed 2–5 years after harvesting or site preparation to determine if the area is satisfactorily restocked (B.C.

Ministry of Forests 1990a). Surveys by Johnstone (1976a) in Alberta, and Butt *et al.* (1989, unpublished) and Butt (1990, unpublished) in southern British Columbia indicate that such early surveys give a poor indication of eventual spruce stocking because of the combination of heavy early mortality and the prolonged period of ingress. Johnstone (1976a) recommended conducting surveys 8 years after logging, and indicated that even then they would catch, on average, only 50% of the expected spruce regeneration. In the Kamloops Forest Region, Butt *et al.* (1989, unpublished) concluded that regeneration surveys conducted approximately 7 years after the latest disturbance will capture most of the ingress, except on untreated sites and south aspects.

5.1.4 Summary and conclusions

- Interior spruce is a difficult tree species to regenerate naturally because it has sporadic seed crops, limited seed dispersal, a short period of seed viability, fairly exacting requirements for seedling establishment, and slow initial growth rates.
- During the 1970s, natural regeneration was largely abandoned as a means of regenerating spruce in British Columbia because of the failure of large clearcuts to restock adequately. However, there is a renewed interest in this option because of poor plantation performance in some biogeoclimatic subzones and ecosystems, a need to rationalize silvicultural investments in low-yield forest types, and accelerating public demand for alternatives to short-rotation clearcut forestry.
- The biological requirements for successful spruce regeneration are well understood but often difficult to achieve. Good seed crops occur at 4–12-year intervals with moderate crops in between. Adequate regeneration can be achieved on more or less mesic sites if a good seed source is maintained and a mineral soil seedbed is exposed shortly before seed dispersal. Seed predation and early seedling mortality are very high. Survival of seedlings requires shelter from desiccation and temperature extremes, but also control of excessive competing vegetation. Early growth of seedlings is very slow; it typically takes 5–10 years for a healthy seedling to reach the size of 1-year-old nursery-grown stock.
- Silvicultural systems for naturally regenerating interior spruce will have to be adapted to local ecological conditions. In general, spruce does not regenerate well in large clearcuts. Small patch clearcuts, narrow strip clearcuts, or shelterwood systems, used in conjunction with mechanical site preparation, have the best chance of producing adequate stocking in most biogeoclimatic subzones where spruce is abundant. Modified prescriptions that provide greater protection to young seedlings will probably be required in dry climate subzones where spruce occurs mainly as a late successional species or under atypical site conditions (e.g., frost-prone sites).
- Silvicultural standards and growth and yield projections for naturally regenerated spruce stands must take into account the long delay period before full stocking is achieved and the slow initial growth rates of this species. In most cases, naturally regenerated spruce will not meet the free growing performance standards currently established in British Columbia.

5.2 Advance Growth Management

Advance growth management is the term used to describe the use of suppressed trees existing in the understory of a stand (i.e., advance regeneration) to restock the stand following harvesting. Advance growth management can reduce reforestation costs and rotation lengths, and it provides an immediate tree cover, which may be desirable for aesthetic, wildlife, and watershed management purposes (Johnstone 1978; McCaughey and Schmidt 1982). However, species composition, anticipated logging damage, the potential for growth following release, and stem distribution are some of the important factors that must be considered before managing for advance regeneration.

In most mature and old-growth interior spruce stands in British Columbia, spruce is far outnumbered by subalpine fir in the understory. As a result, reports and management guidelines applicable to interior British Columbia conditions have tended to focus on subalpine fir (Smith and Craig 1968, 1970; Herring 1977; Monchak 1982, unpublished). There is relatively little information describing how advance spruce regeneration is affected by logging disturbance and how it responds to release.

Available information from British Columbia (Stettler 1958; Smith and Wass 1979), Alberta (Crossley 1976; Johnstone 1978) and the Intermountain Region of the United States (McCaughey and Schmidt 1982; McCaughey 1983; McCaughey and Ferguson 1988) suggests that interior spruce does respond well to release from suppression and that its ability to respond is relatively independent of the age of the tree. However, it appears that spruce may take longer to release, and may grow more slowly following release than subalpine fir.

Smith and Wass (1979) found that average height growth of released Engelmann spruce advance regeneration ranged from 4.3 to 12.7 cm/yr on seven ESSF study sites in southeastern British Columbia. On all sites, average height growth of subalpine fir was greater than that of Engelmann spruce.

McCaughey and Schmidt (1982) studied spruce-fir stands at four locations in Idaho, Wyoming and Utah. Significant increases in spruce height growth began from 1 to 7 years after release with an average of 3–4 years. In contrast, subalpine fir averaged 1–2 years. In the 6–10-year period after clearcutting, spruce trees grew an average of nearly four times faster than before treatment. In partial cuts, trees grew an average of 2.5 times faster. Response was less during the 0–5-year period. On most of the study areas, subalpine fir response was greater than that of Engelmann spruce. Height growth of spruce was still accelerating 10 years after treatment on both partial cuts and clearcuts. Response was essentially missing in uncut (control) stands.

An Alberta study indicated that although the growth of subalpine fir advance regeneration was initially greater than that of white (and black) spruce, the spruce eventually surpassed the subalpine fir (Johnstone 1978). Height and diameter growth of residual trees did not increase until after the crowns had expanded. The growth response was characterized by a rapid diameter growth throughout the stem and relatively slow height release, suggesting that released trees will develop quite different stem forms and height-diameter relationships than forest-grown trees.

Berry (1982) reported the results of a long-term experiment in which white spruce had been spot-seeded in the understory of an aspen–red pine stand. When the overstory was removed 27 years later, the suppressed spruce understory was just 70–80 cm tall with annual increments of approximately 3 cm. The advance regeneration responded dramatically to release. Height growth increased to 30 cm per year, and 30 years later the trees averaged 11 m tall.

Destructive sampling has shown that it is impossible to predict the age of advance regeneration by its size (height or diameter). In general, studies have found no relationship between the age of the advance regeneration and its potential for release (Johnstone 1978; McCaughey and Ferguson 1988). Trees that have been suppressed for 27 years (Berry 1982), more than 40–50 years (Baker 1949, Lees 1966, Steneker 1967, all cited by McCaughey and Ferguson 1988) or for more than 100 years (McCaughey and Schmidt 1982) were all capable of rapid growth following release. There is some evidence that the size of the tree may affect its rate of release, but results are inconsistent. McCaughey and Schmidt (1982) found that the greatest height growth increases occurred in taller spruce. In New Brunswick, Baskerville (1961, cited by McCaughey and Ferguson 1988) observed just the opposite. In Alberta, taller trees grew more rapidly than shorter trees immediately after logging, but the differences diminished with time (Johnstone 1978).

The potential for decay is a serious concern in advance growth management, particularly where the regeneration is damaged during logging, or where the trees have reached an advanced age before they are released. In McCaughey and Schmidt's (1982) study, Engelmann spruce seedlings averaged 68 years old (range 5–195 years) and there was some logging damage to the sample trees, but no evidence of decay was found 10 years after logging. The authors felt that 10 years might have been insufficient for rot to become apparent. Crossley (1976) also found no sign of incipient decay in residual white spruce trees 10 years after logging. McCaughey and Ferguson (1988) recommend that all trees 70 years or older be examined for evidence of decay before they are saved to become the next crop.

Information comparing the growth of advance regeneration with that of post-logging natural or artificial regeneration on the same site would be of interest in assessing the potential of advance growth management for reducing rotation lengths. The few studies on this topic suggest that advance regeneration grows more rapidly than post-logging regeneration, at least during the first few decades following logging. Smith and Wass (1979) reported that Engelmann spruce advance regeneration averaged 40–157% greater height growth than post-logging regeneration (Table 16). In the ESSF zone near Clearwater, Herring and McMinn (1980) reported that 21 years after treatment, the height increment of Engelmann spruce advance regeneration averaged more than five times that of natural spruce regeneration. The advance regeneration averaged 6.3 m in total height while the post-logging natural regeneration averaged 0.8 m. A significant factor in this latter study was that most of the natural regeneration established on seedbeds where the soil had been degraded by excessive blade scarification.

TABLE 16. Comparison of average rates of annual height growth since logging of Engelmann spruce (post-logging) and advance regeneration on undisturbed surfaces at seven ESSF sites in southeastern British Columbia (from Smith and Wass 1979)

Area	Years since logging	Avg. annual ht. growth (cm) Post-logging regeneration	Avg. annual ht. growth (cm) Advance regeneration	Difference (%)
Russell Cr.	13–16	5.67	7.92	40
Batys Cr.	9	3.06	4.31	41
Templeton Cr.	18	2.82	4.87	73
Templeton Cr.	19	4.39	7.69	75
Wildhorse Cr.	15	4.93	12.69	157
Shuswap Cr.	13	3.54	7.12	101
Inlet Cr.	15	5.69	13.37	135

5.3 Artificial Regeneration

Artificial regeneration, by planting of nursery-grown seedlings, is the predominant method used to reforest interior spruce in British Columbia today. Artificial (direct) seeding, while popular in some other regions, notably Alberta, is virtually unknown in British Columbia. A very comprehensive review of white spruce artificial regeneration in Canada was prepared by Stiell (1976). This section serves as an update of that review, highlighting those topics thought to be of greatest interest to British Columbia silviculturists.

5.3.1 Seed procurement

Current cone and seed collection and processing procedures for interior spruce in British Columbia are fully described in Eremko *et al.* (1989).

Cone crop and seed evaluation Accurate prediction of cone crops facilitates the planning of seedbed preparation for natural regeneration (see Section 5.1.2, Biological factors, Seed supply), and seed collection for artificial regeneration (Eis and Inkster 1972).

A collectible spruce cone crop is not an annual event, but occurs sporadically, at intervals of approximately 4–12 years (Figure 49; Konishi 1985). Early cone crop forecasting is generally accomplished through bud sampling. Reproductive buds are differentiated in the year before seed release (see Section 2.6, Sexual Reproduction) allowing cone crops to be predicted the previous winter. Reproductive buds can be identified without a microscope after about the middle of September and become progressively easier to identify as the buds develop (Eis and Craigdallie 1981). Reproductive buds are much larger than vegetative buds, and have chaffy, brown inner scales that protrude and cover the upper portion of the bud (Eis and Inkster 1972). The female (ovulate) buds are usually broadest near the base while male (staminate) buds are broadest in the central portion (Figures 11 and 12). In contrast, vegetative buds are dome-shaped and covered completely by green outer scales.

Bud sampling involves collecting a branch from the cone-bearing portion of the crown of several well-distributed dominant or codominant trees in each stand being surveyed (Eremko *et al.* 1989). To confirm the occurrence of heavy crops, Eis and Inkster (1972) suggest that only four trees need be sampled and for nil crops only six trees need be sampled. However, to distinguish between ratings of light to heavy cone crops, it can be expected that, on average, nine or ten trees will be needed.

Because early crop forecasting gives only a general indication of prospective cone crops, quantitative assessments of the developing cone crop are usually made in late June or early July of the year cones mature. Cone crop rating involves locating likely stands and visually

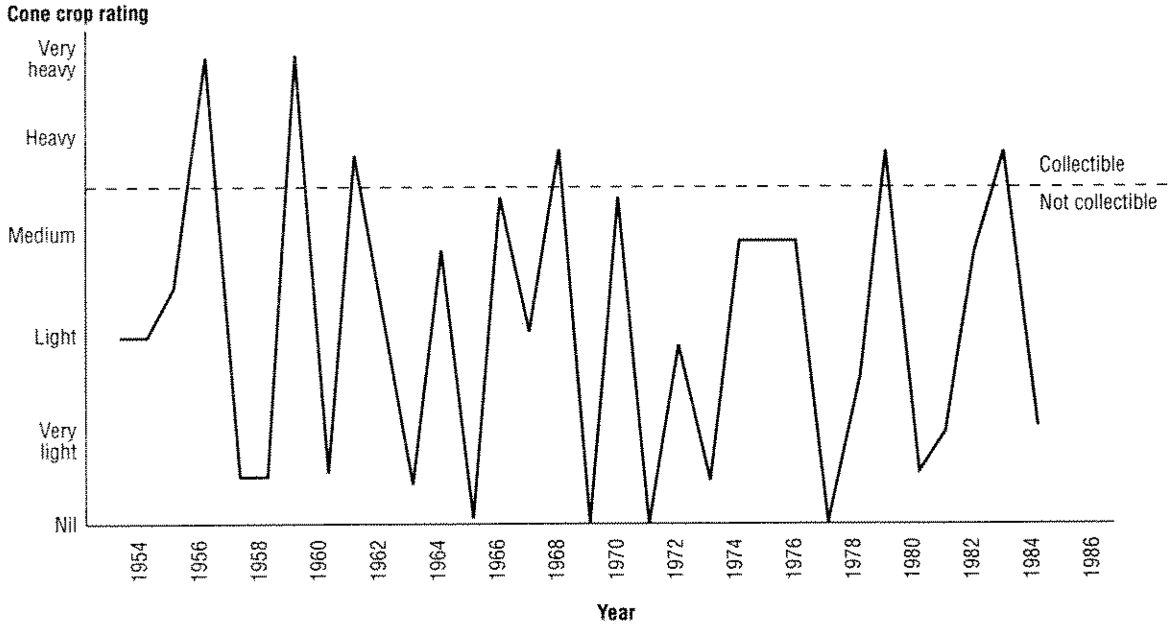

FIGURE 49. Periodicity of collectible spruce cone crops in the central interior of British Columbia, 1953–1984 (from Konishi 1985).

assessing the relative number of cones in the upper, cone-bearing portion of well-distributed dominant and codominant trees (Eremko *et al.* 1989). Crops are rated according to the scale on Table 17.

TABLE 17. Cone crop rating (from Eremko *et al.* 1989)

Crop rating		Definition (refers to dominant and codominant trees only)
1	None	No cones
2	Very light	Few cones on less than 25% of the trees
3	Light	Few cones on more than 25% of the trees
4	Light	Many cones on less than 25% of the trees
5*	Medium	Many cones on 25–50% of the trees
6*	Heavy	Many cones on more than 50% of the trees
7*	Very heavy	Many cones on almost all of the trees

* Crops rated as 5 or more are generally considered collectable. Where crops rated as 4 or 5 are considered for collection, seed evaluation should be intensive to ensure adequate yields.

Subsequent, detailed evaluation of cone and seed quality is usually made during August, shortly before cone and seed maturation. Cone samples are collected from representative trees and split longitudinally to expose the seeds. The number of exposed, filled seeds in one half-section is counted and used to estimate the total number of filled seeds per cone using the following equations (Eremko *et al.* 1989):

Engelmann spruce $WC = 6.3S + 6.0 \quad r^2 = 0.89$
white spruce $WC = 6.3S + 4.0 \quad r^2 = 0.73$

WC = filled seeds per whole cone; S = filled seed count per half cone.

For both species a minimum standard of seven filled seeds per half cone is normally used to determine whether or not the cone crop is collectable. The presence and extent of insect and disease damage is also assessed at this time. For collectable crops, additional seed cutting tests and other assessments may then be carried out to determine when seed is fully mature and ready for collection.

Seed collection and processing For optimum seed quality, interior spruce cones should not be collected until all maturity criteria are met (Table 18). However, under controlled conditions, it may be possible to artificially ripen cones and seeds. White spruce cones collected 4 weeks before natural seed dispersal and stored on open, screened trays for 12 weeks at 5°C and 75–95% relative humidity yielded seeds with approximately 85% germinability (Winston and Haddon 1981). Seeds extracted from cones immediately after this collection and not subjected to artificial ripening failed to germinate. The required storage period for artificial ripening decreased at later collection dates.

TABLE 18. Criteria used to assess cone and seed maturity for collecting interior spruce cone crops (from Eremko *et al.* 1989)

Feature	Recommended collection standard
Cone colour	lustrous light brown
Cone opening	some of the cones in the stand should have already begun to open
Storage tissue	opaque, firm and resembling coconut meat
Seedcoat	glossy, pale to dark brown
Seedwing	light brown, with a dark stripe along one edge
Embryo	should occupy 90% of the cavity; yellowish, firm

One situation where artificial ripening may be required is in the collection of high-elevation spruce provenances where the seed may not be fully mature by the end of the growing season. In interior Alaska, for example, Zasada (1988) reported that at low elevations, embryos filled 95% of the cavity at the end of the growing season, while at higher elevations the embryos filled only 75% of the cavity. He found that seed collection can be started when embryos fill 75% of the embryo cavity but collecting seeds when embryos are more mature will result in better quality seeds.

A new seed-processing procedure involving seed Incubation, Drying, and water Separation (known as IDS) is being introduced in British Columbia to improve the quality of interior spruce seedlots (Edwards and Banerjee 1989). IDS can be used to either increase the percentage of viable seed in poorly germinating seedlots to an acceptable level, or to boost germination rates of good seedlots to the point where single-seed sowing of nursery containers is feasible.

Seed storage Wang (1980) reported that white spruce seed can be effectively stored for 10–13 years with low seed moisture content in airtight plastic or glass containers at -18°C. Spruce kept better when stored at -18°C than at +2°C. Altmann *et al.* (1981) reported that seed is stored at -18°C and 50% relative humidity. However, Carlson (1983) suggests that spruce seed is best stored at 0°C to -5°C with a seed moisture content maintained between 5 and 10%. At the British Columbia Ministry of Forests Seed Centre in Surrey, interior spruce seeds are stored at -18°C in airtight polyethylene bags within waxed cardboard containers (H. Rook, pers. comm., July 1990).

Seed testing Seed testing involves determining the physical and physiological qualities of a seedlot and is carried out primarily at two stages in the artificial regeneration process: immediately after processing and immediately before sowing (Bonner 1974). The Surrey Seed

Centre tests its seeds when they first arrive and at roughly 2-year intervals thereafter (H. Rook, pers. comm., July 1990).

Standard testing procedures for interior spruce seedlots are described by Edwards (1987). The physical quality of the seedlot can be tested for its purity, weight, moisture content and the number of seeds per kilogram. Viability of the seedlot is determined quickly by immersing the seed in tetrazolium stain, or directly by carrying out a germination test. Germination tests should be carried out on both pre-chilled (21 days at 1–5°C) and unchilled seeds. Alternating night/day temperatures of 20/30°C with 8 hours or more of light per day are prescribed. The first germination count is made at 7 days and the final count at 21 days.

Stratification The degree of dormancy in white spruce seed varies with seed source, and both Zasada *et al.* (1978) and Edwards (1987) recommend that all white spruce seedlots have stratified and non-stratified germination tests performed to evaluate the need for stratification. In the Prairie provinces, stratification of white spruce is not normally required (Hocking 1972) but a cold, moist treatment in peat for 3 weeks at 4.5°C will ensure more uniform germination (Carlson 1983). Wang (1974) found that pre-chilling for 21–28 days resulted in maximum germination in the lab. All seedlots had better nursery germination and seedling survival after pre-chilling at 3–5°C for 21 days. Wang (1974) recommends pre-chilling for 21 days as a standard practice to obtain optimum germination. This stratification procedure is used for all spruce seed at the Surrey Seed Centre (Bowden-Green 1988).

Longer stratification of Engelmann spruce generally improves the rate and, in some cases, completeness of germination more under a cool temperature regime (15°C days/5°C nights) than under a warm temperature regime (30/20°C) (Tanaka *et al.* 1986). This phenonmenon may be important when seeds are sown outdoors, in early spring, under suboptimal germination temperatures. It may also explain why field germination rates are often higher than those reported in the laboratory (Daniels and Simpson 1990). Stratification periods of 6 weeks or longer at 2°C were generally most effective. Tanaka *et al.* (1986) also found that, for a given stratification period, surface-drying of the seed for half an hour at the end of stratification was at least as effective as surface-drying at the beginning or during stratification. The authors recommend a 6- to 8-week stratification with seeds surface-dried at the end of stratification for nursery sowing of Engelmann spruce.

5.3.2 Direct seeding

In British Columbia, many research and field foresters have concluded that direct seeding of interior spruce is not a viable operational technique (Caldicott 1989, unpublished). Most trials have not been successful and the risk of failure is considered too great. Climatic conditions often discourage successful seedling establishment and seed is subject to destruction by small mammals, birds, and insects. In addition, there are substantial differences in the early growth rates of seeded and planted trees.

A Canada-wide summary of 79 white spruce seeding trials carried out between 1969 and 1972 indicates that 98% of these areas failed to restock successfully (Waldron 1974, his Table 1). By comparison, success rates for species such as jack or lodgepole pine and Douglas-fir are considerably higher. Between 1983 and 1986, just 54 hectares were direct seeded to interior spruce in British Columbia (Kuhnke 1989). Alberta, on the other hand, seeded a total of 23 703 hectares to mixtures of white spruce and pine over the same period, and expects an 80% rate of successful restocking.

In the past, chemical seed treatments were widely used to protect seeds from predators and disease. Combinations of endrin, arasan, aluminum flakes and latex were most widely used (Waldron 1974; Stiell 1976). However, these treatments were generally found to be unsatisfactory, as they tended to reduce germination, were not durable enough to withstand adverse weather conditions (Sullivan *et al.* 1990), and had potentially toxic effects. The biocide endrin has been banned in Canada because of its potentially harmful effects on humans (Fraser 1974). A concerted effort to find a safe and effective combination of repellents for white spruce was carried out in the late 1960s and early 1970s, but no satisfactory formulation was found (Radvanyi 1974). More recently, it has been demonstrated that rodent predation of Douglas-fir and lodgepole pine seeds can be successfully reduced by providing an alternative food source (sunflower seeds and oat kernels) along with the conifer seeds, but this approach has not been tested on interior spruce (Sullivan and Sullivan 1984; B.C. Ministry of Forests and Lands 1986).

Direct seeding research indicates that mineral soil or mixed mineral-organic soil seedbeds result in the best survival rates (Clark 1969; Zasada and Gregory 1969; Gardner 1980; Putman and Zasada 1985). In a greenhouse study, the highest white spruce germination rates resulted from sowing the seed on mineral soil and covering the seed with a thin layer of aspen leaf litter (Cayford and Waldron 1962, cited by Arnott 1974). Some protection against predation and desiccation can be afforded white spruce seeds by covering them with a layer of soil (Richardson 1974). However, because of the small size of spruce seeds, only a thin layer of soil can be used as opposed to larger pine seeds, which can safely be sown deeper. Thus, white spruce would be subjected to higher evaporation stress, larger fluctuations in soil moisture, and more extreme surface temperatures than pine.

Direct seeding is not appropriate on sites with dense vegetation competition. Broadleaf litter may form a continuous, thick mat over the seedspots and either inhibit germination or kill the germinants (Dominy and Wood 1986). Such sites also require seedlings capable of rapid initial growth to outgrow the competition. McMinn (1986) reported that of the 10 tallest trees in each treatment, planted stock produced more than 80 times the volume per tree than seeded trees after 13 growing seasons.

Timing of seed application does not appear to be a consistent or significant factor in the success of direct seeding of spruce. In Maine, more seedlings usually resulted from fall-sown seed than from spring-sown seed but the results were not significant (Griffin 1977). Gardner (1980) found the reverse to be true, and Putman and Zasada (1985) found no significant effect of early, middle, and late season sowing. In northern Alberta, direct seeding is carried out both in February–March (on fresh snow) and in May–June (Caldicott 1989, unpublished). The mixtures of white spruce and pine seed are usually aerially applied at a rate of 430 000 viable seeds/ha.

Cone-shaped seed shelters are sometimes placed over seedspots to protect seed and improve the microenvironment for germination and subsequent growth. In Alaska, seed shelters appeared to benefit germination and survival of spruce but site preparation, or the lack of it, accompanying the shelter treatment seemed to have a greater overall effect (Putman and Zasada 1985). Dominy and Wood (1986) found that, generally, growth was not improved by sheltering the seed.

5.3.3 Stock production

Detailed procedures for growing interior spruce nursery stock are beyond the scope of this report as they are primarily of interest to growers rather than to silviculturists. Instead, readers are referred to the excellent chapters on container and bareroot seedling production in the recently published text, *Regenerating British Columbia's Forests* (Daniels and Simpson 1990; Van Eerden and Gates 1990).

5.3.4 Stock quality testing

A variety of tests has been developed to evaluate the quality of nursery stock before outplanting. Some of these same tests can be used to monitor the status of seedlings in the field.

Morphological criteria are used to ensure that the seedling has the appropriate size, sturdiness and shoot:root balance to withstand the physical stresses of the outplanting site. Among the the most common morphological indices are the shoot:root ratio (usually measured in terms of dry weight, but also as volume) and height:root collar diameter (RCD) ratio. Good balance for most container-grown species and sites in British Columbia is an RCD of less than 80 and a shoot:root ratio (dry weight) of less than 2.0 (Mitchell *et al.* 1990).

In one study, Burdett *et al.* (1984) measured height:diameter (RCD) in planted trees. At planting, the ratio for container stock was 73:1. This ratio was reduced to 43:1 by the end of the third growing season, which was similar to the ratio maintained by bareroot stock throughout the 3 years of observation. Initially, the container stock appeared to allocate dry matter production largely to diameter growth. Better balanced planting stock may produce more rapid early height growth.

Physiological tests used to predict outplanting survival and growth performance include root growth capacity (RGC; also called root growth potential [RGP]), stress tests, dormancy release index, frost-hardiness and variable chlorophyll fluorescence (Duryea 1985; Vidaver *et al.* 1988). Of these, RGC is by far the most widely used test, but its reliability has recently been called into question (Binder *et al.* 1988; Landis and Skakel 1988), and it is recommended that RGC only be used as a general guide to seedling vitality in combination with other sources of information about the stock and the planting environment.

A field test by Simpson *et al.* (1988) showed that interior spruce seedlots with an RGC of more than 10 roots per plant generally had high survival when planted on a wide range of sites in the ICH, ESSF and MS zones of southern B.C. Seedlots with RGC below the 10-root threshold were far more variable; some had very poor survival, but many others had excellent survival rates.

5.3.5 Stock characteristics and outplanting performance

A variety of interior spruce stock types has been used both operationally and for research purposes in British Columbia and elsewhere in North America. These include BC-CFS styroblock plug (PSB), bareroot (BR), transplant, bullet, paperpot, sausage container, and Spencer-Lemaire (Stiell 1976; Daniels and Simpson 1990; Van Eerden and Gates 1990). For most of these stock types, a range of stock sizes, age classes and cultural practices (including the growing medium, water, nutrient, light, temperature and pesticide regimes, and root pruning techniques) is possible. Any or all of these factors may have a major influence on outplanting performance.

Outplanting performance can be assessed in a variety of ways, including seedling survival, height, diameter or other measures of aboveground growth, and root development. Several authors have cautioned that a single measure of success is not adequate for evaluating the performance of different stock types. For example, plantation survival figures may not be a reliable index because of potential differences in subsequent height growth (Walker and Ball 1981) and height measurements alone may be a poor indicator of biomass accumulation because of differing rates of caliper (diameter) growth between seedlings (Burdett *et al.* 1984).

Stock size Stock size at the time of planting appears to be one of the most consistent indicators of long-term success of interior spruce plantations. Many studies have found that larger stock has higher survival and growth rates after planting (Dobbs 1976a; Walker and Johnson 1980; Vyse 1982; McMinn 1985b; Hines and Long 1986; Walker and Ball 1987; Payandeh and Wood 1988), and a few longer-term studies now suggest that these differences may be maintained for extended periods. At SBS sites near Prince George, benefits of larger stock were still evident 15 years after planting (Thomson and McMinn 1989b) and large stock planted in favourable site treatments should reach merchantable size years before less successful options (McMinn 1985b). Moreover, the higher survival rates of large stock types may mean the difference between a fully stocked and a partially stocked plantation.

Several studies indicate that the growth rates of seedlings in the field may be proportional to their size at planting. McMinn (1978) found that after five growing seasons PSB415 stock (415 refers to plug top diameter of about 4 cm and plug length of about 15 cm) had maintained a twofold mass and size advantage over PSB211 stock (2 by 11 cm plug). This ratio was similar to differences when planted. Sutherland and Newsome (1988) carried out a study with five stock types of interior spruce: 1-0[7] CBR1010 (container-grown bareroot from a 10x10x10 cm boxed container), 1-0 PSB615, 1-0 PSB415 (with and without copper root pruning treatment), and 1-0 PSB313. The larger stock types (1-0 CBR1010 and 1-0 PSB615) had an initial height and caliper advantage and outgrew the others in total seedling height and caliper after five growing seasons. Relative growth rates were similar for all stock types, indicating that the larger stock types were maintaining their initial advantage.

A key benefit of larger planting stock appears to be its ability to withstand competing vegetation (McMinn 1985a). Dobbs (1976a) suggests that the more intense the competition from surrounding vegetation, the greater the advantage of using large stock. Planting large stock without site treatment may be a feasible alternative to planting small stock with site treatment (McMinn 1982b). Alternatively, McMinn (1985a) suggests that PSB313 seedlings planted immediately following site preparation may exhibit similar growth performance to PSB415 stock planted following a delay.

Although reclaim transplant stock (seedlings that did not meet 2-0 standards and were subsequently planted as 2-1 stock) could be assumed to be of poor genetic quality, it had an advantage over smaller plug stock in the presence of competing vegetation (Thomson and McMinn 1989a). However, in the absence of competition, this stock type performed relatively poorly. These results illustrate the benefits of planting large stock in brushy areas. Smaller stock (e.g., 1-0 PSB211) planted on untreated sites suffered from vegetation press, and the growth of survivors was generally slow (McMinn 1982b). However, Vyse (1981) cautions against placing too much importance on seedling size. He points out that although the performance of small plug stock was poor on some brushy sites, larger bareroot stock also performed poorly.

Shoot:root ratio Although the optimal container shoot:root ratio is thought to be between one and two (see above), Walker and Johnson (1980) reported that seedlings with ratios as high as 7:4 exhibited excellent performance to the third year after planting. Stock that retains or develops high shoot:root ratios may be less windfirm in later years (Hellum 1978).

Stock type The BC-CFS styroblock plug has evolved as the dominant stock type for interior spruce in British Columbia (Johnson 1982; Van Eerden and Gates 1990). Institutional and economic factors related to nursery practice and planting were partly responsible for this trend, but it also reflects the superior outplanting per-

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[7] This notation indicates the age of stock at planting time. The number before the dash indicates the number of growing seasons the seedling spends in its original container or planting bed. The number following the dash indicates the number of growing seasons in a transplant bed. Adding the numbers together gives the total age of the seedling. For example, 2-1 bareroot stock spends 2 years in the original planting bed, 1 year in a transplant bed, and is 3 years old at the time of planting.

formance of this containerized stock type, especially when compared to the 2-0 BR stock that was widely used in British Columbia in the late 1970s. Numerous comparative trials have been carried out over the past decade. These studies have often produced contradictory results that reflect a variety of uncontrollable factors including constantly evolving stock types, and differences in site and stock quality.

Table 19 indicates the shift from sowing dominantly bareroot stock in 1981 to the more successful styroblock plug stock in 1990. Also evident is a trend towards larger-sized plug stock.

TABLE 19. Sowing requests for the most common interior spruce stock types in British Columbia for the period 1981–1990. Source: British Columbia Ministry of Forests' Sowing Request Allocation Report.

Sowing year	Stock type/size					
	Bareroot[a]	Transplant	PSB211	PSB313	PSB415	PSB615
	(thousands of trees ordered)					
1981	42 946	3 778	14 246	4 845	257	0
1982	42 449	9 938	12 180	10 951	633	0
1983	40 736	11 217	12 561	14 943	433	9
1984	24 754	0	3 967	46 203	454	2
1985	15 070	0	3 915	66 264	1 127	0
1986	7 964	5	606	99 949	1 490	0
1987	6 057	0	32	72 896	6 599	0
1988	4 245	3 505	82	85 814	15 239	0
1989	1 550	12 858	7	87 946	28 060	128
1990	262	8 106	0	55 682	41 008	105

[a] includes bareroot-to-bareroot transplants

In British Columbia, both Dobbs (1976a) and Vyse (1982) judged interior spruce plug stock to be superior to bareroot and transplant stock of greater initial size. Plugs suffered less mortality than BR or transplant stock on similar sites and, although the plug stock was initially smaller, after five growing seasons the mean height of plug stock plantations surpassed that of bareroot plantations (Vyse 1982). Based on height growth at 2 years, 2-0 BR stock was least successful when compared to a variety of plug and transplant stock types (McMinn 1985b). Vyse (1981) found that plug stock grew more rapidly in the first year than bareroot stock, and that both plug and bareroot stock grew more rapidly than natural seedlings. Gardner (1982) found insignificant survival differences after 10 years but the trend (from highest to lowest survival) was PSB211, 2-0 and 2-1 BR, bullet-plugs, and bullets. The BR seedlings had an initial height advantage and generally had faster growth rates and were tallest by the tenth year.

Where stock is of good quality, the performance of different stock types may be closely related to their size. McMinn (1985b) suggests that 1-year-old PSB415 stock may be interchangeable with 2-1 transplants. Similarly, Dobbs (1976a) observed that performance of 2-1 transplants was only marginally better than that of large 2-0 BR seedlings, and suggested that grading 2-0 BR stock by size categories could negate the need for producing transplants to regenerate brushy or untreated sites.

Container stock Carlson and Endean (1976) reported that both container diameter and volume affect seedling growth. White spruce produced significantly more roots in the top quarter of the container than lodgepole pine, indicating that for optimum growth these two species require containers of different configurations. For spruce, a 1:1 height:diameter container configuration produced significantly more total dry weight than 3:1 or 6:1 configurations. Total dry weight and shoot length increased as container volume increased. These results concur with those reported by Hocking and Mitchell (1975).

There are cost implications to modifying container configuration. Increases in the volume and diameter of containers decreases the number of seedlings produced per unit area and increases the cost of production per seedling (Carlson 1976). Large stock is also more costly to plant. Clearly, the optimum characteristics of planting stock represent a compromise between outplanting performance and production and planting costs.

Vyse (1981) suggested that rapid first-year growth after outplanting may be a result of the successful control of growing conditions in the nursery, which control bud formation and needle development (Pollard and Logan 1977, 1979) as well as the ability of the root plug to supply moisture after planting.

One advantage of containerization is that the seedling root system is protected from disturbance and drying (Phipps and Noste 1976). A disadvantage of container stock is that it is more prone to mortality resulting from short-term flooding than bareroot stock (Rauscher 1987). Frost-heaving of spruce seedlings is more common in container than bareroot stock (Walker and Johnson 1980) and is most common on sites with exposed, heavy textured mineral soil (Revel *et al.* 1990).

5.3.6 Storage, handling and lifting of seedlings

Options for the storage of spruce seedlings include fall or spring lift followed by cold storage (generally -1 to -4°C); fall or spring lift followed by cool storage (generally 0 to 5°C), and hot-lift (lifting trees in a dormant or active state and planting soon after).

Mullin and Parker (1976) studied the effect of storage temperature on seedling survival. At -18°C almost all seedlings died, while a temperature of -4°C was judged a success. Sutton (1984a) suggests that there are no advantages to storing seedlings at temperatures below -2°C.

Trees in storage will become dessicated unless protected (Sutton 1982). Ideally, relative humidity should approach 100% (Sutton 1984a). Seedling stock is damaged more by root exposure than by shoot exposure. Even partial drying of bareroot seedlings during lifting, handling, and planting can lower subsequent growth and survival (Sucoff *et al.* 1985).

Extended cold storage can cause deterioration or damage to seedlings. Day (1985) reported that as the length of cold storage was increased, bud burst was poorer, but height growth differences were minimal among frozen, conditioned, and fresh stock. For spring planting, freshly lifted stock had the greatest number of abnormal terminal buds and shoots, followed by spring-lift, cool-stored, stock, followed by fall-lift frozen-stored stock (McDonald *et al.* 1983). Silim and Lavender (1992) suggest that storage of stock should start no earlier than December.

Spruce stock should not be lifted and planted while it is actively growing. Actively growing stock perform poorly compared to cold-stored stock (Mullin and Forcier 1976; Mullin and Reffle 1980). In Ontario, at 48°N latitude, Mullin and Reffle (1980) suggested cut-off dates for planting of May 31 for spring hot-lift and June 15 for spring-lift cold-stored stock. This cut-off date should vary according to latitude and geographic location. Near Prince George, British Columbia, McMinn (1978) reported that, provided seedlings were lifted at the proper time, both hot-lift and cold-stored white spruce gave comparable results when planted to mid-June. Fall-lift cold-stored stock generally grew as well as, or better than, spring-lift cool-stored stock especially when planted late in the season (end of June) (McDonald *et al.* 1983).

Blake (1983) compared fall-lift, cold-stored and spring hot-lift stock, and found that cold-stored seedlings appeared better able to avoid transplanting shock and an early drought despite delayed root growth. In response to drought, the cold-stored stock displayed delayed flushing of new shoot growth and increased stomatal resistance, which resulted in decreased transpiration. The spring-lift stock lacked this response. Stomatal opening and photosynthetic potential of cold-stored stock was not reduced when moisture was adequate.

Field storage Optimally, thawed stock should be stored at 1–2°C with relative humidities over 90% (Ronco 1972). For periods of a week or less, storage temperatures around 4.5°C and humidities near 50% can be tolerated. After 100 days of storage at 4.5°C, dry weight losses in bareroot spruce averaged 4–4.5%, and were as high as 6% (van den Driessche 1977). Following cold storage, seedlings in boxes should not be exposed to temperatures above 10°C (Binder and Fielder 1988). The refrigerated vans commonly used for transportation and on-site storage typically maintain seedlings at 2–4°C (Mitchell *et al.* 1990).

Dry ice (solidified carbon dioxide) should not be used to cool seedlings (Ronco 1972). High concentrations of gaseous carbon dioxide disrupt the physiological processes of respiration and water transport and may be toxic to seedlings at extremely high concentrations.

5.3.7 Planting season

Planting in cold soils is not desirable for white spruce (Day 1985). Planting should not commence before soil temperature reaches 5°C (Lyr and Hoffman 1967, cited by Mullin and Parker 1976), and should be terminated in the fall when soil temperature drops below 6°C, if some root development is to occur (Revel 1985). For more information on soil temperature effects on spruce performance refer to Section 3.2.3, Temperature relations.

In most references, the following criteria pertain to different planting seasons.

- Spring planting usually begins when soil temperature exceeds 5°C and continues until late June–early July.
- Summer planting extends from late June to early August.
- Fall planting extends from early August until soil temperature drops below 5–6°C.

In the Prince George Forest Region, cold-stored 2-0 or 2-1 stock can be planted up to July 15 (Revel 1985). After this date, the seedling may not complete its growth cycle before damaging autumn frosts and cold soil result in abnormalities. Prolonged cold storage may also result in poor seedling performance (LePage and Pollack 1986). Mitchell *et al.* (1990) recommend that no stock should be cold stored beyond 8 months. In most parts of interior British Columbia, this means that planting should be completed by mid-June. However, in the far north, the late arrival of spring dictates that the spring planting season often extends beyond this date—at some risk to seedling condition.

In Ontario, the preferred planting season for bareroot stock is the 3- to 4-week period in the spring after the soil temperature reaches 5°C and before the stock flushes (seedlings are hot-lifted while dormant in the spring) (Arnup *et al.* 1988).

In British Columbia, summer planting of hot-lifted containerized seedlings is an increasingly popular alternative to late spring planting on northern or high-elevation sites with short growing seasons. The seedlings (normally 2+0 PSB stock) are artificially conditioned in the nursery to complete shoot growth and set bud before being lifted. Sutton (1984a) and Revel (1985) indicate that hot-lift planting of good quality white spruce stock on suitably prepared sites can be successful throughout the growing season. However, Revel *et al.* (1990) recommended that hot-lift planting be completed before mid-August in the BWBS and SBS zones. In July and early August, on mesic to subhygric sites, soil temperatures were 8–12°C, which promoted active root egress. By late August, soil temperatures were marginal for root growth, particularly on subhygric sites.

Container stock is better adapted to planting throughout the season than bareroot stock. Interior spruce container stock (plug and sausage) were successfully planted in June, July, and August whereas plantation failures occurred with bareroot stock planted after June (Walker and Johnson 1980).

5.4 Stand Management Treatments

5.4.1 Growth and yield information

Given the importance of white and Engelmann spruce as timber-producing and plantation species in North America, there is relatively little growth and yield information available to guide stand management activities. This lack of data stems largely from the fact that current logging still takes place almost entirely in unmanaged (usually mixed species) stands of natural origin, and that most plantations are still very young (less than 20 years).

There are three primary sources of growth and yield information on interior spruce.

Sampling of established natural stands and plantations Traditional site index curves and yield tables are developed from a large pool of sample-plot data collected from unmanaged stands of varying ages and site productivity classes (Farr 1967; Kabzems 1971; Johnstone 1977; Hegyi *et al.* 1981; Quenet and Manning 1990). These empirical data sets are increasingly being supplemented by data from plantations and naturally regenerated stands that have received some silvicultural treatment. Sampling natural stands and plantations has the advantage of allowing a wide range of sites, stand types and genotypes to be sampled inexpensively and efficiently. However, the database lacks precision, and without repeated sampling there is no way of knowing the history and conditions of stand development, and whether such conditions will exist in the future.

In the interior of British Columbia, site index curves were developed from 3212 individually measured spruce trees (including black spruce) (Hegyi *et al.* 1981). The curves were used to define site classes (good, medium, poor, low) for trees at a reference age of 50 years (Figure 50). Viszlai (1983) used the British Columbia Ministry of Forests inventory database to prepare variable-density yield projection equations for pure stands of interior spruce. The equations enable stand volume to be determined from the site index, stand age and stand density (measured either as basal area or crown closure). Separate equations were developed for three geographic regions: the southern interior, the central interior, and the far north. (See Table 20 for sample equations and coefficients for the central interior.)

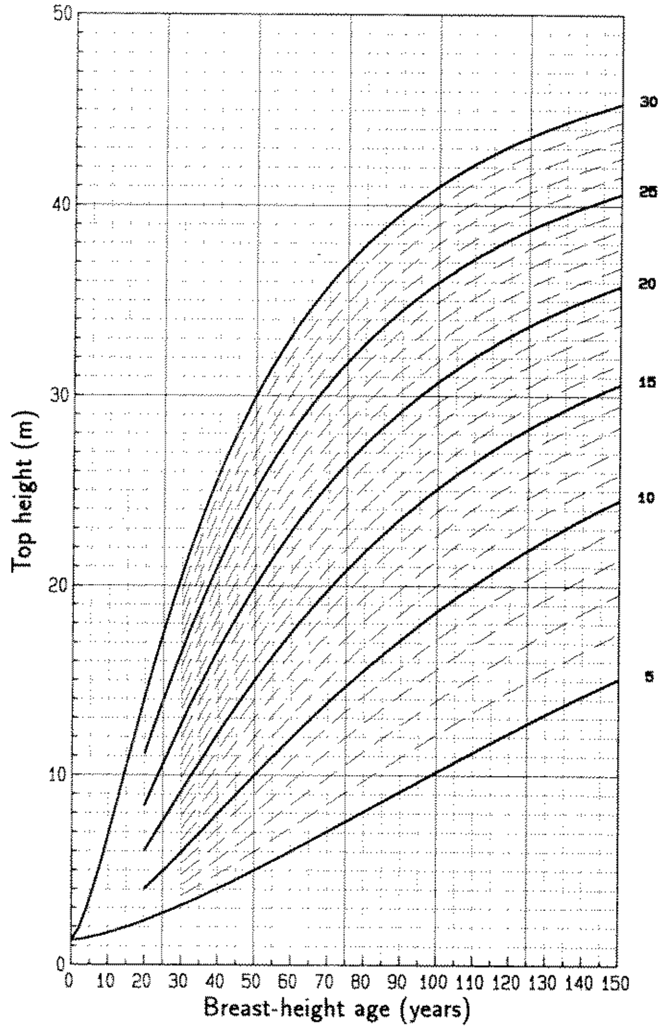

FIGURE 50. Site index curves for interior spruce in British Columbia, developed by the B.C. Ministry of Forests Research Branch (from Thrower *et al.* 1991).

TABLE 20. Variable density yield projection coefficients for pure stands of spruce in the central interior[a] of British Columbia. Volumes are determined for three different diameter limits/utilization standards: (a) whole stem volume for all trees > 7.5 cm dbh; (b) close utilization standards[b] less decay volume for all trees > 17.5 cm dbh; (c) close utilization standards less decay volume for all trees > 27.5 cm dbh (from Viszlai 1983).

$$\text{Volume} = b_1{*}SI_{(100)}{*}BA{*}D{*}(1 - e^{b2{*}Age^{b3}}){*}e^{b4{*}SI(100) + b5{*}BA + b6{*}D}$$

	Diameter limits		
Coefficients	**>7.5 cm**	**>17.5 cm**	**>27.5 cm**
b1	0.04872158	0.03678087	0.03600000
b2	-0.02784562	-0.04540562	-0.01541438
b3	0.96250120	2.14099323	0.29143472
b4	-0.02005648	-0.02078555	-0.01936027
b5	0.00091505	0.00102732	0.00103631
b6	-0.02402621	-0.01972938	-0.02041430
Statistics			
N	985	984	985
R^2	0.97443	0.97587	0.96821
SE	24.347	22.184	27.074

Where:
BA = stand basal area (m^2/ha)
D = stand mean diameter (cm)
$SI_{(100)}$ = site index (100 yr base age)
b_1 to b_6 = regression coefficients obtained by Marquardt's algorithm
N = number of samples
R^2 = coefficient of determination
SE = standard error of estimate

[a] the central interior includes Forest Inventory Zones H, I and J, encompassing the Chilcotin Plateau, the southern part of the Prince George Forest Region and southern interior portion of the Prince Rupert Forest Region. Note that a similar set of coefficients has been prepared for the southern interior and the far north.

[b] close utilization standards include all stem volumes above a 30 cm tall stump and below a 10 cm top diameter.

Eis *et al.* (1982) collected age, dbh and height data from 454 even-aged groups of interior spruce and lodgepole pine in the SBS zone of central British Columbia to compare the growth of these two species on three site types (Alluvium, Aralia and Cornus-Moss). Stem analysis was also carried out on 166 dominant and codominant spruce and pine trees and 87 suppressed spruce trees. A similar comparative study of the growth of spruce and subalpine fir was carried out on Alluvium and Aralia sites in the same area, involving 132 paired spruce and fir trees, and stem analysis of 86 spruce and 38 subalpine fir (Eis and Craigdallie 1983). Growth curves from the two studies are presented in Figure 51 (spruce and pine) and Figure 52 (spruce and fir).

Figure 51 illustrates that when both species are free growing, lodgepole pine initially outgrows spruce, but that the spruce overtakes the pine at between 88 and 130 years, depending on site productivity (Eis *et al.* 1982). The highly productive Alluvium sites are best suited to growing spruce on relatively long rotations, while Cornus-Moss sites are better suited to pine. When spruce are initially overtopped by pine, height growth is approximately half that of trees that developed without suppression. Diameter growth is more sensitive to suppression by pine than is height growth.

Subalpine fir initially outgrows spruce, but spruce overtakes fir at approximately 70 years on Alluvial sites and 82 years on Aralia sites (Figure 52; Eis and Craigdallie 1983). Mature spruce were always at least 10% taller than mature fir. Spruce reached mature height at 200–250 years, whereas height increments of fir were insignificant after about 150 years. Diameter and volume growth show similar patterns to height growth except that spruce diameter increment overtakes subalpine fir at a more advanced age (120–130 years). Up to about 100 years, subalpine fir produced somewhat greater volume per tree than spruce. Additionally, the authors felt that it may be possible to grow subalpine fir at greater densities than spruce because of subalpine fir's greater shade tolerance and narrower crown.

Operational spruce plantations provide growth and yield information for young stands. Pollack *et al.* (1985) prepared height-over-age and height increment curves for interior spruce plantations up to age 11 or 12 in two biogeoclimatic subzones of the Prince Rupert Forest Region (ICHmc=ICHg and SBSmc=SBSe), while Vyse (1981) produced similar curves for plantations up to 5 years after outplanting in the Cariboo Forest Region (Figures 53 and 54). These curves show height increments on the order of 15 cm/yr at 5 years, increasing to 20–25 cm/yr at 10 years. Plantation height averaged approximately 50 cm at 5 years and 130–150 cm at 10 years. Neither study provided information on diameter or volume growth.

Experimental installations with trees planted at a range of densities (espacement trials) or in which naturally regenerated stands are thinned to varying densities (spacing or thinning trials) The advantages of this approach are that data are collected under highly controlled conditions and that the actual development of the stand is followed through time. The major disadvantage is that such installations are extremely costly and labour intensive, restricting the database to very few sites and genotypes, and limiting the potential for extrapolation to "real world" conditions.

For white spruce, the oldest and largest espacement trial, at Petawawa, Ontario, was first established in 1922. Yield tables have been developed for unthinned plantations at six different spacings (1.25, 1.50, 1.75, 2.00, 2.50 and 3.00 m) and on four site index classes (15, 18, 21 and 24 m at 50 years) showing dbh, basal area, total and merchantable volume for trees aged 20–50 years by

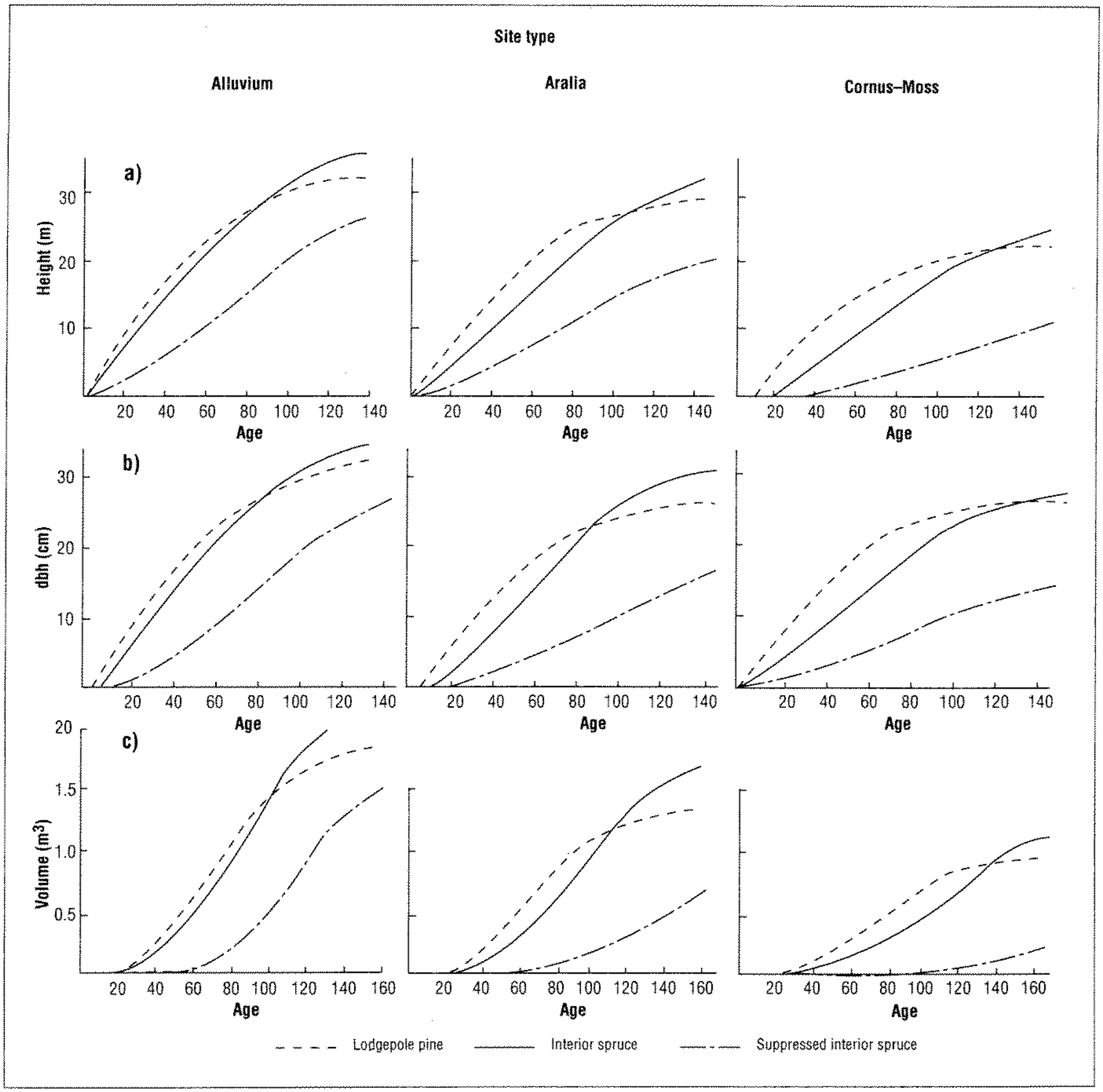

FIGURE 51. Comparative growth of free growing lodgepole pine and interior spruce, and suppressed interior spruce on three site types (Alluvium, Aralia, Cornus-Moss) in the SBS zone of central British Columbia: (a) height growth; (b) diameter growth (dbh inside bark); and (c) volume growth (from Eis *et al.* 1982).

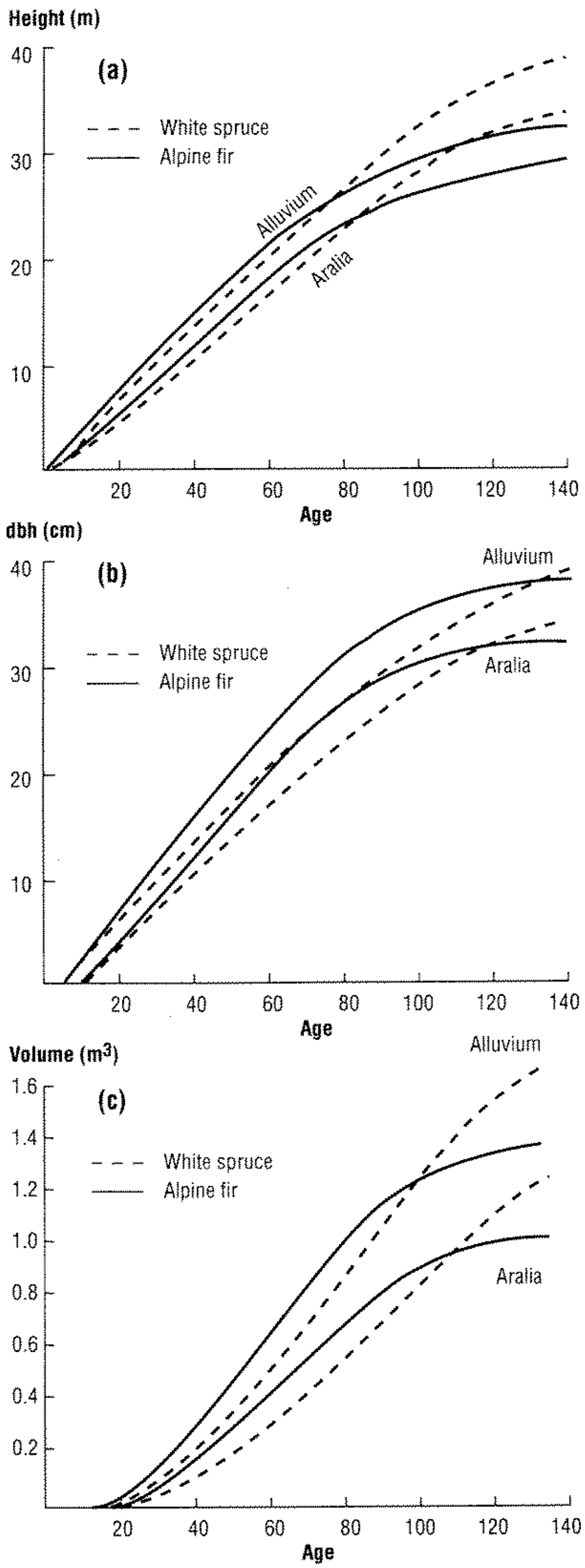

FIGURE 52. Comparative growth of interior spruce and subalpine fir on two site types (Alluvium, Aralia) in the SBS zone of central British Columbia: (a) height growth; (b) diameter growth (dbh inside bark); and (c) volume growth (from Eis and Craigdallie 1983).

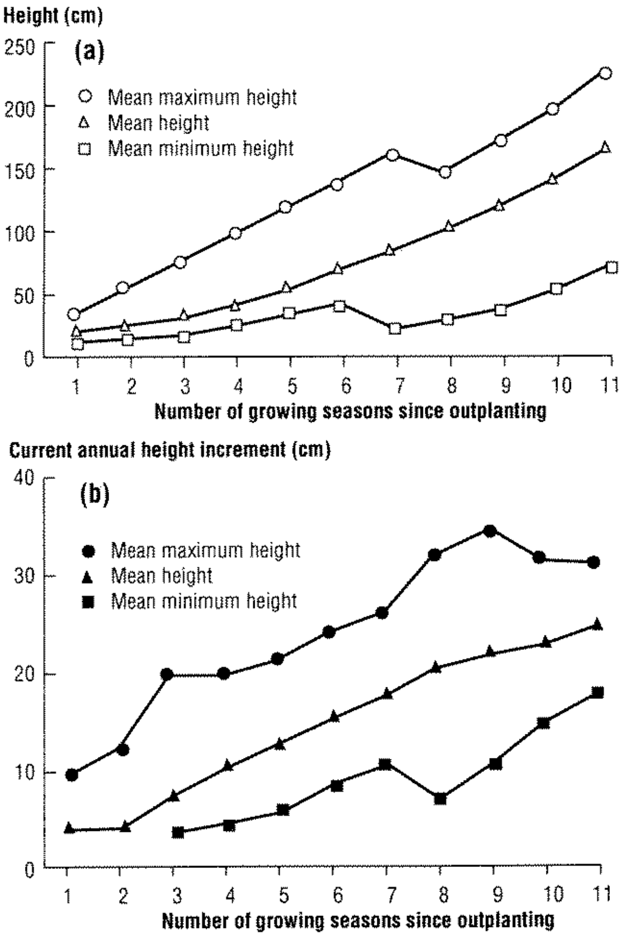

FIGURE 53. Height (a) and height increment (b) performance of operational spruce plantations in the SBSmc (formerly SBSe) subzone of the Prince Rupert Forest Region. Percentage values on the vertical scales indicate relative performance compared to the average for the subzone. The curve connecting the 100 percentile points represents the average performance of 90 plantations (from Pollack *et al.* 1985).

5-year age classes (Stiell and Berry 1973; Berry 1978). In British Columbia, site indices within this range would be rated as Medium to exceptionally Good (Hegyi *et al.* 1981).

A smaller espacement trial was established in 1951 on a Thunder Bay, Ontario site with site index at 50 years of 18 m for white spruce (Ontario Ministry of Natural Resources 1989). This site would be rated as Good in British Columbia (Hegyi *et al.* 1981). White spruce, black spruce, and red pine were each planted at spacings of 1.8, 2.7 and 3.6 m (2900, 1300, 730 sph). Total stand and individual tree volume growth are shown in Figure 55. At 37 years, mortality caused by intraspecific competition was occurring at the closest spacing (1.8m) but was not yet apparent at the two wider spacings. White spruce grew much more slowly than red pine, and slightly more quickly than black spruce (due primarily to greater diameter growth). Based on the 37-year results, the authors recommend 2.0–2.2 m spacing (2500–2270 sph) for white spruce with commercial thinnings beginning at about age 40 to maintain high growth rates and recover maximum volume.

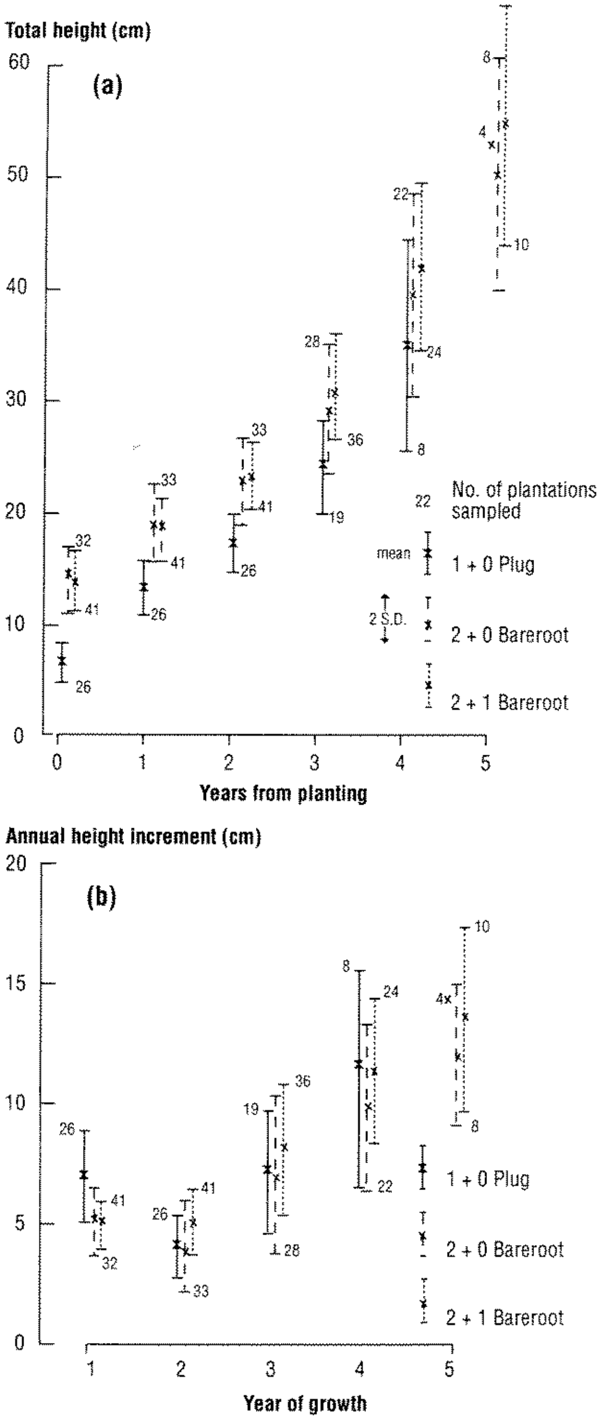

FIGURE 54. Height (a) and height increment (b) performance of operational spruce plantations in the Cariboo Forest Region (from Vyse 1981).

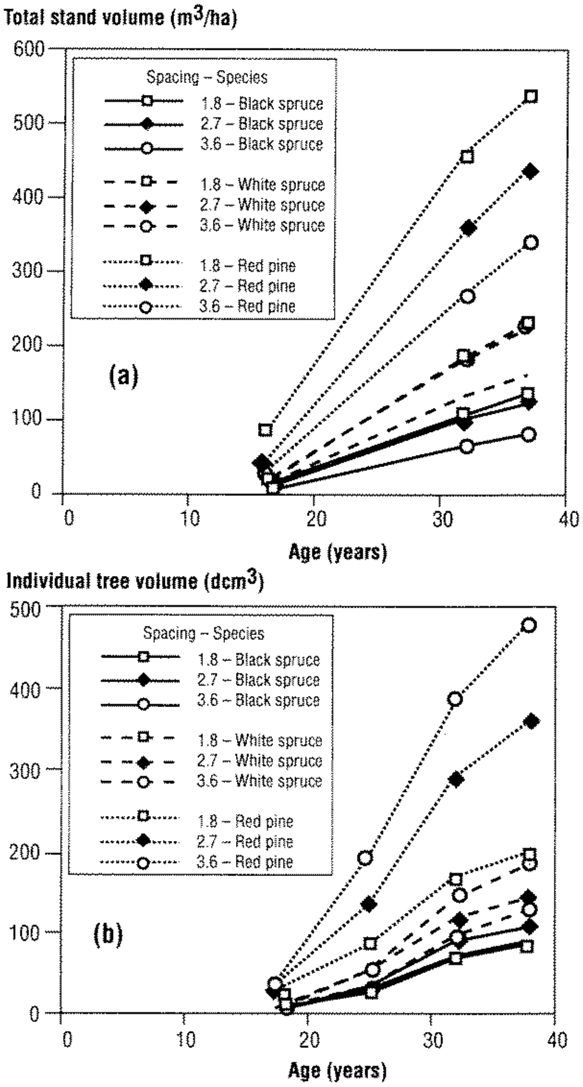

FIGURE 55. Total stand volume (a) and individual tree volume (b) for white spruce, black spruce and red pine planted at three initial espacements (1.8 m, 2.7 m, 3.6 m) near Thunder Bay, Ontario (from Ontario Ministry of Natural Resources 1989).

The oldest interior spruce espacement trial in British Columbia, established in 1959, is located near Houston in the Prince Rupert Forest Region. There, spruce seedlings were planted at 420, 747, 1329 and 6727 stems/ha. The experiment was measured at 6, 12, 16, 26 and 30 years from planting. Pronounced growth differences among espacements were evident 30 years after planting (Pollack *et al.* 1992). Wider espacements produced trees with larger diameters, crowns, and branches. Basal area and total volume per hectare were greatest in the closest espacement (Table 21). Of the four densities tested, the 1682 stems per/ha treatment provided the best compromise between individual stem growth and overall stand production (Pollack *et al.* 1992). Pollack *et al.* (1992) present predictive equations for 19 tree and stand characteristics for the density range of 420–6727 stems/ha. In the Prince George Forest Region, at three locations near Prince George or Vanderhoof, interior spruce, lodgepole pine, subalpine fir and Douglas-fir were established at four espacements in 1967. The espacements were 637, 1076, 2196 and 4306 stems per hectare. Not all espacements were established at each site. The plantations were measured every 5 years post-planting. The most recent measurement in fall 1986 (20 years) is currently being analyzed (D. Coopersmith, pers. comm., September 1990). Table 21 provides some interim results from this study.

Because of the slow juvenile growth of interior spruce and the length of time required to achieve crown closure, plantation espacement may not appreciably affect growth early in the rotation. In a Manitoba study, 16 years after planting, density had no effect on white spruce growth, even at spacings as low as 1.2 m (Bella and De Franceschi 1980). Similarly, in the Prince George Forest Region trials (Table 21a) no differences in height growth of the trees were evident after 11–14 growing seasons. Information on diameter growth, which would presumably be more sensitive than height to intertree spacing, was not provided. The Houston data set (Table 21b) and Ontario results suggest that effects of stand density on tree growth are quite apparent by age 30.

TABLE 21. Interim results of interior spruce espacement trials in the Prince George and Prince Rupert Forest Regions

(a) Mean total height (m) of interior spruce after 11–14 growing seasons in spacing trials in the Prince George Forest Region. No statistically significant height differences due to spacing are yet apparent (from B.C. Ministry of Forests 1981).

	Location and age				
Stems/ha	**Buckhorn 1 (11 yrs)**	**Cluculz (11 yrs)**	**Chilco Cr. (11 yrs)**	**Buckhorn 2 (13 yrs)**	**Anzac (14 yrs)**
637 (4 × 4 m)	0.63	1.33	1.51	1.73	2.26
1076 (3 × 3 m)	0.68	1.19	1.34	1.78	2.12
2196 (2 × 2 m)	0.82	1.25	1.34	1.73	2.20

(b) Growth response of interior spruce near Houston, Prince Rupert Forest Region, thirty growing seasons after planting (from Pollack *et al.* 1992).

Stems/ha	**Mean height (m)**	**Mean diam. (cm)**	**Mean BA (m^2/ha)**	**Mean volume[a] (m^3/ha)**
420	5.9	10.1	3.8	11.3
747	5.7	9.5	4.9	14.9
1682	5.9	8.9	10.2	31.6
6727	4.9	6.1	20.9	63.7

[a] total stem volume, not merchantable volume

Single-tree or stand-level computer models simulate the growth and yield of spruce trees at varying ages, densities and site qualities These models make use of the databases described above to either develop the model or to test and refine it. Stand management models used in the interior forests of western North America are reviewed by Johnson (1988). In British Columbia, the single-tree model known as TASS (Tree and Stand Simulator) (Mitchell 1969; Mitchell and Cameron 1985) is being used to develop new yield tables for interior spruce. When completed, a program called TIPSY (Table Interpretatiion Program for Stand Yields) will be available to enable users to calculate stand yields from the TASS output (K. Mitchell, pers. comm., September 1990).

Other models have also been developed or modified for Engelmann or white spruce, including the Prognosis model widely used in the western United States (Wykoff *et al.* 1982; Wykoff 1985), RMYLD from the United States Rocky Mountains (Edminster 1978), and STEMS from the northeastern United States (Belcher *et al.* 1982; Holdaway 1984).

Advantages of simulation models are their flexibility and their ability to fill in gaps in the database. Unlike the traditional yield tables, simulation models also have the potential to adapt to changing circumstances, such as climatic or silvicultural regimes that may not have existed in the past. However, they can be quite cumbersome or complex to use, and their accuracy and reliability is always in dispute.

5.4.2 Juvenile spacing

There is little information available describing the effect of juvenile spacing on the growth of interior spruce. Although several spacing trials have been established in British Columbia (Kelly 1988, unpublished; Revel 1990, unpublished), none of these is yet producing meaningful results.

In eastern Oregon, a 10-year-old naturally regenerated Engelmann spruce–western larch stand was spaced to 2.7 × 2.7 m and 4.6 × 4.6 m. Ten years after treatment, diameter growth was greater at the wider spacing but total basal area and volume growth were greater at narrower spacing (Seidel 1984). Within species, there was no significant difference in height growth at the different densities, although larch grew approximately twice as quickly as spruce.

In the Lakes States, dense 15- to 20-year-old white spruce plantations are spaced to provide 5.6–6.5 m^2 of growing space per tree (approximately 2.4–2.5 m spacing or 1600–1700 sph) (Rauscher 1987). In British Columbia, intertree spacings of 3–4 m (700–1300 stems/ha or 7.7–14.3 m^2/tree) are typical for juvenile spacing of interior spruce, but there is considerable flexibility depending on local conditions and stand management objectives (B.C. Ministry of Forests 1990).

5.4.3 Pruning

Dead branches of interior spruce are extremely persistent (Stiell 1976), and compared with other conifers this species produces relatively little clear, knot-free lumber. Spruce trees whose lower boles are exposed to sunlight by thinning and heavy pruning often develop epicormic branches (Berry and Innes 1967).

Pruning of interior spruce is rarely carried out on an operational basis, although Berry (1964) concluded that it could be a profitable investment. Most operational pruning of conifer stands involves pruning to a height of 17 feet to create a 16-foot clear log. In Berry's (1964) study, carried out in a 30-year-old experimental plantation at Petawawa, Ontario, this procedure averaged 9.9 minutes per tree using a sectional curve-bladed pole. There are no comparable data on this topic from British Columbia. Additional information on pruning interior spruce is provided by Stiell (1976).

5.4.4 Thinning

Objectives of thinning include reducing mortality, increasing sawlog potential by concentrating growth on fewer trees (Stiell 1980), altering species composition, and increasing the merchantable volume that can be extracted from an area (Frank 1973, 1977; Stiell 1980).

Potential detrimental impacts of thinning include damage to the residual stand during falling and skidding, wind damage and reductions in growth caused by excessive thinning, and soil damage from machine traffic (Frank 1973; Froehlich and Berglund 1979; Stiell 1980). To maintain stand integrity and reduce the potential for wind damage, only 20% of the total volume should be removed in a single operation on wet and steep slopes and up to 50% on well-drained sites (Frank 1973). Excessive thinning can also impair total and merchantable growth, presumably by decreasing the quantity of foliage available for photosynthesis (Stiell 1980). In closely spaced plantations in the Upper Great Lakes Region of the United States, it is common to remove every third row at 30–50 years of age. Subsequent thinnings (at approximately 20-year intervals) reduce the residual basal area to between 18.4 and 25.3 m^2/ha (Rauscher 1987).

Thinning can affect tree growth by altering radiation, temperature, nutrient, and water regimes (Van Cleve and Zasada 1976). In their study near Fairbanks, Alaska, basal area growth started earlier in the year and ended later in thinned, and thinned and fertilized plots, than in fertilized or untreated plots. These results agree with those reported by Frank (1973) for the northeastern United States.

In Ontario, 10-year results after crown thinning 30-year-old white spruce plantations (the removal of large competitors from around crop trees) were reported by Berry (1974). Stands were spaced to basal areas of 32.1, 25.3, and 18.4 m^2/ha, with the control having 37.2 m^2/ha. Over the 10-year period after thinning, periodic annual increment was 9.59 m^3/ha at 18.4 m^2/ha and increased with increasing density to 14.48 m^3/ha on the control. Growth of individual trees was greatest at 18.4 m^2 basal area/ha and decreased with increasing density. Berry (1974) recommended that spacing in this type of stand should not reduce residual basal area below 25.3 m^2/ha so that both growth per tree and growth per hectare are kept near the optimum.

In a similar study in a 33-year-old white spruce plantation, basal areas were reduced by thinning from below to 18.4, 25.3, and 32.1 m^2/ha (the control was 35.3 m^2/ha) (Stiell 1980). The heaviest thinning resulted in considerably less total and merchantable volume production than the other three treatments. The 25.3 and 32.1 m^2/ha thinnings differed mainly in the volume removed and 20-year standing volumes. Clearcutting these latter two areas 20 years after the initial thinning could increase merchantable volume by 80 and 12.8%, respectively, compared to the control.

The ability of interior spruce over 70 years of age to release after thinning is uncertain. Nine to 10 years after releasing 75- to 100-year-old spruce, neither total nor merchantable volume production increased significantly in stands where up to 40% of the stand basal area was removed. Increment response of individual spruce trees was only slight (Steneker 1974). The author concluded that spruce greater than 70 years old is too old to significantly respond to release.

The ability of older interior spruce to respond to release may depend less on age than on site-specific factors such as the degree of release, the degree of competition, and site potential (i.e., moisture and nutrient availability). Frank (1973) found that 70- to 75-year-old white spruce will respond to release and recommended that competing stems be removed on at least three and preferably four sides of the crop tree. Ten years after treatment, the mean annual circumference increment was 0.56 cm (control), 0.61 cm (one side released), 0.62 cm (two sides released), 1.04 cm (three sides released), and 1.12 cm (four sides released).

In Alaska, thinned plots in 70-year-old white spruce stands had significantly greater basal area increment than controls, although the greatest increment was achieved by thinning combined with fertilization (Van Cleve and Zasada 1976).

5.4.5 Fertilization

Fertilization trials have been carried out at various stages of tree and stand development, ranging from the nursery to 100-year-old spruce stands. These studies usually report growth and survival responses. Because application costs and product values change, the economic feasibility of fertilization is generally not included in the literature and is not considered in this report. Nevertheless, operational fertilization programs should not be undertaken without some form of cost-benefit analysis.

Fertilization – nursery Nursery fertilization regimes are complex and vary between nurseries. They are not dealt with in detail in this report. A general discussion of fertilization regimes in British Columbia nurseries is provided by Daniels and Simpson (1990) and Van Eerden and Gates (1990).

One objective of regulating nutrient and moisture levels in the nursery is to govern the rate and duration of seedling growth (McClain and Armson 1975). For seedling growth after outplanting, adequate nutrient content at lifting may be as important as, or more important than, maximum growth in the nursery (van den Driessche 1988). Use of slow-release fertilizers and nutrient-loading (adjusting the late-season fertilizer regime to increase nutrient levels to luxury levels) in the nursery may be cost-effective alternatives to fertilizing at the time of planting (Brockley 1988).

Significant increases in dry weight production are attainable with additions of fertilizer (McClain and Armson 1976). Both the form and amount of fertilizer affect outplanting growth and survival (van den Driessche 1988).

Fertilization – at planting There has been considerable interest in fertilization of newly planted white spruce seedlings as a means of minimizing the duration and severity of "planting check" (Burdett *et al.* 1984). The topic has recently been investigated by Brockley (1988); readers are referred to that publication for a detailed review of the relevant literature. Review of a variety of studies suggests that fertilization has the potential to decrease seedling survival and that the best growth response occurs when early fertilization is combined with intensive site preparation and vegetation control.

Although most fertilizer applications include nitrogen, phosphorus and potassium, Brockley (1988) found little evidence to indicate that interior spruce seedlings on most forest sites respond to nutrients other than nitrogen.

High rates of fertilization can reduce the survival of planted seedlings, particularly if they are under stress, because of the osmotic effect of high salt concentrations (Sutton 1982). Brockley (1988) reported that the application of soluble inorganic fertilizers at the time of planting generally reduces survival. Also, the early growth performance of interior spruce seedlings is often not improved by fertilization although the severity of planting check can be reduced in some cases.

Seedling condition can significantly affect the response to fertilization. The application of slow release NPK fertilizer (Osmocote®) produced large increases in shoot growth by low root growth capacity (RGC) barerooot spruce stock, especially in the second season after planting, and by high RGC container-grown stock in both the first and second seasons (Burdett *et al.* 1984). Burdett *et al.* (1984) hypothesized that, as root establishment proceeds, shoot growth tends to be limited first by the supply of water, then by the availability of mineral nutrients. More rapid response to slow-release fertilizer could be achieved by planting stock with high RGC or other adaptations to drought.

The application of 40 g/tree of Osmocote® (18-6-12) increased spruce height growth and groundline stem diameter (Burdett *et al.* 1984). After 3 years, percent stem volume growth of fertilized container stock was 88% greater than unfertilized container stock. Sutherland and Newsome (1988) found that Osmocote® fertilization (40 g/tree placed in a 15-cm radius) produced an irregular response and, overall, did not significantly improve seedling height or diameter growth.

Fertilization may not produce a significant growth response if factors other than soil nutrient availability are limiting seedling growth. In a study in Ontario using 3-0 BR stock, low soil temperature was the most important factor affecting white spruce growth followed by vegetation competition, and then fertilization (Brand and Janas 1988). On sites with cold soils, fertilization and brush control produced little benefit, possibly because of soil temperature-induced moisture stress. In another study, near Prince George, fertilization had virtually no impact on seedling growth because factors such as small mammal damage, frost injury and competing vegetation were far more important (McMinn 1989, unpublished). Commonly, the growth of competing vegetation is enhanced by fertilizer application, resulting in a net negative impact on the seedling (Stephens 1965; Sutton 1972).

Fertilization of interior spruce does not appear to increase the incidence of fall frost damage significantly (except possibly at high elevations) and it may decrease the incidence of winter injuries (Brockley 1988).

Fertilization – established stands Many factors may affect the cost-effectiveness of fertilizing stands of interior spruce. Among these are inherent site productivity, site history, and dosage and type of fertilizer applied.

The average growth response to fertilizers by white spruce has been less than the response by pine and Douglas-fir, and, because many spruce sites are inherently nutrient-rich, fertilization may have little impact on growth (Foster and Morrison 1983). Mullin (1978a) found no apparent benefits from the addition of sulfur and NPK fertilizer (10-10-10) on an old-field spruce plantation and Timmer (1979) found that breast height diameter growth did not change significantly 3 years after fertilizing with urea, triple superphosphate, or muriate of potash.

Stocking levels may affect growth response after fertilization. Salonius and MacKay (1980) found no apparent increase in growth 10 years after urea fertilization in stands with over 2500 stems/ha (lower density stands were not treated).

Combining fertilization with other stand improvement treatments may produce the best results. Improved rates of basal area growth resulted more from thinning and fertilization than from fertilization alone (Van Cleve and Zasada 1976). This was attributed to improved moisture, nutrient, light, and soil temperature regimes.

In a plantation in Ontario, potassium was the major limiting nutrient and there was a significant relationship between K_2SO_4 fertilization rates (0, 50, and 100 kg K/ha) and basal area and total volume growth (Phu and Gagnon 1975). They reported that a foliar potassium level above 0.60% is required for good growth.

Adding one nutrient may cause another to become limiting. For example, on many British Columbia spruce sites, sulfur could become growth limiting if nitrogen deficiencies were alleviated by nitrogen fertilization (Ballard 1985). Timmer (1979) found that additions of nitrogen decreased foliar concentrations of phosphorus, calcium, and magnesium, whereas additions of phosphorus were associated with increased concentrations of nitrogen, phosphorus, and potassium.

The form in which the fertilizer is delivered can affect the degree and duration of growth response in spruce. Plastic-coated urea resulted in higher foliar nitrogen concentrations than "conventional" forestry-grade urea, presumably because losses through volatilization and leaching were reduced (Salonius 1978).

Growth response of spruce to fertilization has been measured in a variety of ways over differing time periods. Over a 10-year period, growth increments of 12.6 – 27.8 m^3/ha were achieved with varying amounts and combinations of potassium sulfate and urea (Gagnon *et al.* 1976b). After the addition of urea (224 kg N/ha), Foster and Morrison (1983) reported an average 5-year growth rate of 4.5 m^3/ha. Thinning and fertilizing with NH_4NO_3, KCl, and triple superphosphate increased diameter increment 3.6 times over a control within one summer (Van Cleve and Zasada 1976). Other studies (Mullin 1978a; Timmer 1979; Salonius and MacKay 1980) found an insignificant, or no, increase in spruce growth after fertilization.

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