(Armson 1964, cited by Sutton 1969b). Alternatively, new buds laid down for the following year may expand prematurely. This is the phenomenon known as lamma growth. If normal seasonal growth is curtailed by lack of rain, a heavy rain later in the season is often followed by profuse lamma growth in young white spruce (Sutton 1969b). The incidence of lamma 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 (Arnett 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 560 m | end 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 | | June 28 | | Nienstaedt and Zasada (1990) |


TABLE 5. Time to breast height (1.3 metres)

<table>
<thead>
<tr>
<th>Location</th>
<th>Type of spruce</th>
<th>Natural or planted</th>
<th>Time (years)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pt. Rupert Region SBSmc subzone</td>
<td>interior</td>
<td>planted</td>
<td>10</td>
<td>Pollack et al. (1985)</td>
</tr>
<tr>
<td>ICHmc subzone</td>
<td>hybrid (Sitka x white)</td>
<td>planted</td>
<td>9</td>
<td>Pollack et al. (1985)</td>
</tr>
<tr>
<td>Cariboo Region</td>
<td>white</td>
<td>planted</td>
<td>approx. 8-9</td>
<td>Vyse (1981)</td>
</tr>
<tr>
<td>Prince George – Quesnel area</td>
<td>white</td>
<td>planted</td>
<td>9-10</td>
<td>Kis and Yeh (1988)</td>
</tr>
<tr>
<td>East of Prince George</td>
<td>white</td>
<td>advanced regeneration</td>
<td>15-16</td>
<td>Pogge (1946)</td>
</tr>
</tbody>
</table>

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 (1962,a, cited by Sutton 1969b) showed considerable variation in the duration of diameter growth in 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, thinnings, 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 above ground. 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 midway 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.

![Typical root forms of white spruce](http://example.com/roots.png)

**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).
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

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.
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 Craigallie 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, bining, 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 A₃ (GA₃) 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 GA₄ and GA₇ (GA₄/₇) have been used to induce cones of 17 species of the Pinaceae including the genus Picea. The best results have been obtained when GA₄/₇ 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](image-url)
spacing, and pruned regularly to produce a bushy form. After hardening-off for 1–3 months, the donor plants are destroyed to produce approximately 50–6 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 stocklings 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; Pate 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 (intraprovenance 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 (Jaquis 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 (Jaquis 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)

<table>
<thead>
<tr>
<th>Latitude/longitude range</th>
<th>Maximum transfer (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upward</td>
</tr>
<tr>
<td>45° - 53° (Nelson Forest Region only)</td>
<td>400</td>
</tr>
<tr>
<td>49° - 56°</td>
<td>300</td>
</tr>
<tr>
<td>56° - 58°</td>
<td>200</td>
</tr>
<tr>
<td>58° - 60°</td>
<td>100</td>
</tr>
</tbody>
</table>

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

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 bioclimatic 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 x 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 1972b, 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 Peralta (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 (Teich 1975). In Teich'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 bud set 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 reducing 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 testing² 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 ramets³ (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.

¹ A breeding arboreuma 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.