DELIVERY OF GENETIC GAIN IN THE INTERIOR OF BRITISH COLUMBIA

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Cover: spruce conelets at the peak of receptivity

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Delivery of genetic gain in the interior of British Columbia

Proefschrift
ter verkrijging van de graad van doctor
op gezag van de rector magnificus,
van de Wageningen Universiteit
Prof. Dr. Ir. L. Speelman
in het openbaar te verdedigen
op dinsdag 29 mei 2001
des namiddags te half twee in de aula

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Delivery of genetic gain in the interior of British Columbia
Thesis Landbouwuniversiteit Wageningen
With summary in Dutch
ISBN 90-5808-394-2
Key words:
British Columbia, forest industry, drought stress, flower enhancement, gibberellin, seed and seedling size, nursery practices, progeny testing, genetic gain, realized gain.

The work presented in this thesis is the result of studies carried out in the interior seed orchards of the British Columbia Forest Service during 1985 - 1999

STELLINGEN

1. In bosbouw gericht op houtproductie leidt het gebruik van natuurlijke verjonging tot negatieve selectie.

2. Selectie voor groeikracht en concurrerend vermogen in populaties van Picea glauca, Picea engelmannii, en hun hybriden in het Zuidelijke binnenland van British Columbia leidt tot vermeerdering van het aandeel van Picea glauca.

3. Selectie en veredeling voor het verkrijgen van sneller groeiende bomen op de betere groeiplaatsen zal op de lange termijn nadelig blijken.

4. In British Columbia gaat boomveredeling evenzeer over mensen als over bomen.

5. Houtoogst per boom (in plaats van kaalkap) zal een toename van erosie veroorzaken.

6. Zaadproductie van klonen van geselecteerde bomen wordt voornamelijk bepaald door de locatie van de zaadtuin.

7. Paulus, in zijn brief aan de Romeinen, zei dat hij een wilde olijf heeft geënt op een geteelde. Dit bewijst niet dat hij niets van plantkunde afwist.

8. Enters, die veel praten, produceren minder overlevende enten.

9. Een overtuiging, die berust op geloof, is moeilijker te veranderen dan een die berust op redenering.

10. Het beschermen van kinderen door hun ouders zeggenschap over hen te ontnemen is niet meer dan een lapmiddel.

Stellingen behorende bij het proefschrift "Delivery of genetic gain in the interior of British Columbia" door Maarten Albricht.

Wageningen, 29 mei 2001.

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1. GENERAL INTRODUCTION

Harvesting of timber in the interior of British Columbia started in the beginning of the century. In 1913 lumber demands related to development in the prairie provinces declined. In 1940, with demands for lumber increasing the interior lumber industry recovered. The traditional style of timber harvesting in the interior, known as selection harvest (or high grading), removed single trees or small groups of trees. Reforestation was expected to take place naturally. Artificial reforestation in the interior, through raising of seedlings in nurseries and planting, did not start until the mid sixties. By that time there were large areas of forest land classified as "not satisfactorily restocked" (NSR). Artificial reforestation not only had to replace currently removed forest cover, but also had to bring back into production the backlog NSR lands, which had resulted from many years of neglect.

In an ideal world the entire productive forest area represents a situation where all age classes are present in about equal amounts. This allows harvesting of a portion of the mature timber available each year in such a way that by the time all mature timber had been removed the first segment of reforested areas has grown into maturity and is ready to be harvested. In British Columbia neglecting the reforestation aspect of the forest industry led to unequal representation of all age classes. In the early eighties it was estimated that the then current annual harvest of 70 million m^3 would not be sustainable much longer and would have to be reduced to 54 million m^3.

Expected productivity of forest land can be enhanced by an increased planting program, stand tending, thinning, fertilizing and by planting the best stock available. This involves a range of silvicultural activities including species selection, improving nursery practices, enhancing seedling survival by improving planting methods, proper site preparation and ensuring better survival and growth in forest plantations. It also involves using seed from the right location and selecting the best parents to provide seed for reforestation.

The delineation of seed zones is necessary to ensure adaptability of seedlings to the environment, in which they are planted. The selection of high quality parents is part of cone collection activities in natural stands. Cones are collected only from well formed trees showing good growth and health. This ensures that the mother trees are of good quality but little is known about the male parents. An improvement in this situation can be obtained by the use of seed production areas. These are good quality natural stands, in which the less desirable individuals can be removed. Taking this process one step further one can select and mark trees in the natural forest, collect pollen from the best parents only and apply this pollen to all selected trees. With the trees remaining where they are this system will eventually present logistical problems. Timing of events and activities and distances to be travelled make this a difficult, if not impossible proposition.

Since the genetic blueprint of every tree is present in each of its cells it is possible to bring all selected trees together in a common garden through grafting. These common gardens are known as seed orchards. In a seed orchard each selected parent tree is represented by a number of grafted individuals, which are genetically identical to the original tree (a clone). If a reasonable approximation of random mating can be attained there will be an expectation of progeny, which is genetically superior to that from seed collected in natural stands, in the characteristics selected for. Forest productivity can be expected to increase by using this progeny in reforestation. By testing the progeny of each tree selected and by removing clones from the orchard on the basis of the results form these progeny tests expected gains can be further increased. These are the basic ingredients of any tree improvement program. The interior tree improvement programs are explained in more detail in chapter 2, section 7.

In the following chapters, after a description of forestry in British Columbia (chapter 2), several studies are reported. These are studies, the results of which may lead to enhancing seed orchard productivity (chapters 3, 4 and 5), improved utilization of orchard seed (chapter 6) as well as enhancing genetic quality of the seed produced (chapter 7). With the exception of chapter 2 scientific names of tree species mentioned have been omitted throughout this thesis. They are presented in a separate list on page 84.

2. THE FOREST INDUSTRY IN BRITISH COLUMBIA

2.1. British Columbia

British Columbia, with a population of 3.1 million people, is Canada's westernmost province. It lies between 49° and 60° latitude (figure 2.1) and covers an area of 952 263 Km². The provincial government is responsible for the management of resources, which include forests. In 1995 the forest industry employed 265 000 people (106 000 directly). This is 15% of the total employment (Statistics Canada, 1995). In 1995 British Columbia accounted for the following share of Canadian output: 56% of softwood lumber, 58% of pulp, 16% of paper and 81% of softwood plywood (COFI, 1995). Nearly 50% of the province's income is generated by the forest industry.

British Columbia is characterized by a great variation in topography and climate. The main features are the Coast Mountains and the Rocky Mountains with the Interior Plateau between them. Almost all mountain ranges run from northwest to southeast and influence precipitation and vegetation. Climate conditions range from very wet on the coast and in the mountains in the east to very dry on the plateau in between the two. Annual precipitation at Prince Rupert is over 2500 mm, at Revelstoke 1000 - 2500 mm, at Williams Lake 300 - 500 mm and at Kamloops less than 300 mm (figure 2.1). The maritime climate of the coastal area is influenced by a relative warm gulf stream and is fairly mild. Mean daily temperatures at Prince Rupert range from 2°C to 14°C, extreme minimum temperature is - 21°C and there are 294 frost free days. The other extreme is the boreal climate of the plains east of the Rockies in the northeast corner of the province. Mean daily temperatures at Fort St. John range from - 17°C to 16°C, extreme minimum temperature is - 47°C and there are 74 frost free days. The Coast Mountains consist mostly of igneous rock, while the Rockies are largely made up from sedimentary rock. Glacial activity during and since the ice ages have contributed much to the land forms in British Columbia. A multitude of lakes, many of them created by hydroelectric projects, can be found throughout the province.

2.2. Forest area and administrative units

The total land area of British Columbia is 94.8 million ha. Areas designated as Provincial Forests cover 80.7 million ha (85%). Provincial Forests include 73.8 million ha in Timber Supply Areas and 6.9 million ha in Tree Farm Licenses. Not all land within the areas designated as provincial forest is productive forest land and some of it is not even forest land. These areas are owned by the province and are referred to as Crown land. Forest land, which is considered productive, amounts to 43.3 million ha (46%), but only 22.6 million ha (24%) is available and suitable for timber harvesting (Ministry of Forests, 1990). Every year approximately 0.2 million ha are harvested (table 2.1). This is equal to about 1% of the usable portion of the productive forest area. British Columbia has 60.6 million ha of forest land. Of this total 95% is owned by the province, 4% is privately owned and 1% is owned by the federal government.

A distinction is made between coast and interior. The dividing line runs along the Coast Mountains. The distinctly maritime climate of the coast is completely different from the climates in the interior. The coastal zone can best be described as encompassing the Coastal Western Hemlock, Coastal Douglas Fir and Mountain Hemlock biogeoclimatic zones (see section 2.3). The remainder of the province is referred to as the interior. The province is also divided into six management areas known as forest regions. A region can include five to nine forest districts. The regions are: Vancouver, Kamloops, Nelson, Cariboo, Prince Rupert and Prince George (figure 2.1). In addition to regions and districts the Forest Service also includes branches, based in Victoria with field offices throughout the province. The branches provide services to regions, districts and forest companies. The services provided are not related to any specific area in the province and are for that reason not a regional responsibility. Examples of such services are research and development, seed services, nurseries and tree improvement.

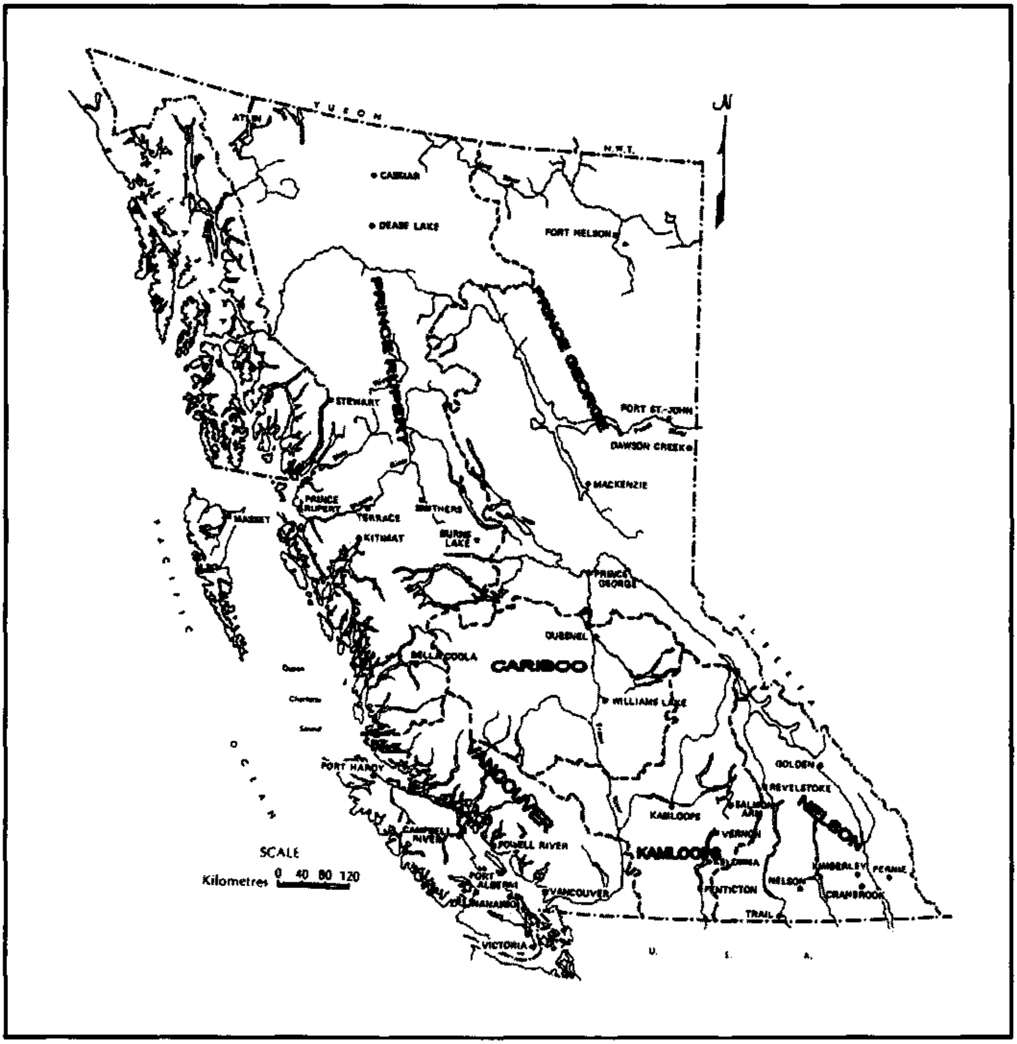


Figure 2.1. The Forest Regions of British Columbia

Inventory of standing timber, forecasts of sustainable yields and regulation of the harvest are done on the basis of Timber Supply Areas (TSA) and Tree Farm Licenses (TFL). A TSA is a regulatory area, which can consist of one or more districts. Companies, operating in a TSA, have standing timber assigned to them on the basis of a volume of wood but do not have any area based tenure. A TFL is a forest management area, based on an agreement between the province and a forest company. Under this agreement the company (often referred to as the licensee) has the right to harvest timber and the responsibility to manage the resource guided by very strict and well defined regulations. The amount of timber to be harvested in a TSA or a TFL is determined by the Chief Forester. A TFL can consist of privately owned land, Crown land or a combination of the two. It is an area based tenure providing the company with assurance of long term management.

2.3. Biogeoclimatic zones and tree species

About 15 000 years ago most of Canada was covered with a layer of ice, in some places over 1500 m. thick. When the ice began to recede some 10 000 years ago tree species started to migrate North. The present distribution of species reflects their ability to migrate and adapt. This process was regulated by natural selection (Hosie, 1973). The northwest to southeast alignment of the major mountain ranges made migration easier. The Pacific Northwest is therefore rich in species (Drushka, 1992). The main forest types, currently recognized and used in forest management in British Columbia, are based on the biogeoclimatic ecosystem classification, which was developed by Dr. V.J. Krajina on the basis of ecosystem studies carried out from 1750 to 1975 (Klinka et al., 1990). The biogeoclimatic ecosystem zones are briefly described below (Ministry of Forests,1988)

Coastal Western Hemlock: In this temperate rainforest western hemlock and amabilis fir are dominant; other species are Douglas fir, western red cedar, yellow cedar and Sitka spruce.
Coastal Douglas Fir: In this rain shadow forest Douglas fir is dominant; other species are grand fir, bigleaf maple and western flowering dogwood. Garry oak and arbutus are characteristic.
Mountain Hemlock: In this subalpine forest mountain hemlock and amabilis fir are dominant; it also contains yellow cedar.
Interior Douglas Fir: At lower elevations in the dry southern interior Douglas fir is dominant; other species are lodgepole pine and ponderosa pine.
Ponderosa Pine: In this, the warmest and driest forest zone, ponderosa pine is dominant; it also contains Douglas fir
Bunch Grass: This is a grassland zone in the driest and hottest valleys in the southern interior.
Sub Boreal Pine and Spruce: The dry and cold interior plateau is characterized by even aged lodgepole pine stands and minor amounts of white spruce.
Interior Cedar Hemlock: This is the most productive zone in the interior, with a cool and wet climate. Western hemlock and western red cedar are characteristic but white x Engelman spruce hybrids and subalpine fir are common. Douglas fir and lodgepole pine are found on drier sites.
Montane Spruce: In the south and central dry interior at mid elevations. Engelman spruce, Engelman x white spruce hybrids and subalpine fir are characteristic. Due to past fires successional forests of lodgepole pine, trembling aspen and Douglas fir are common.
Sub Boreal Spruce: On the gently rolling plateaus of the central interior. Engelman x white spruce hybrids and subalpine fir are characteristic. Extensive lodgepole pine forests occur in the drier parts.
Engelman Spruce Subalpine Fir: At high elevations throughout the interior. Engelman spruce, subalpine fir and lodgepole pine are dominant. In drier parts extensive forests of lodgepole pine and whitebark pine are common.
Boreal White and Black Spruce: The northern valleys west of the Rockies and the great plains east of the Rockies. White spruce, black spruce and trembling aspen as well as extensive stands of lodgepole pine are common.
Spruce Willow Birch: The severe climates of the north, above the boreal forest. At lower elevations white spruce and subalpine fir, at higher elevations scrub birch and willow.

Alpine Tundra: The treeless harsh climate of higher elevations throughout the province.

The species mentioned above are listed below in two groups; commercial and non commercial. Commercially important tree species are briefly described and non commercial species are listed below (Hosie, 1973; Houtzagers, 1954; Lyons, 1952; Forest Service, 1977).

Commercial species

Amabilis fir (*Abies amabilis* (Dougl.) Forbes): It grows in the coastal forest at mid elevations and can reach a height of 38 m and a diameter of 120 cm. It is a slender tree with a narrow, conical crown with drooping branches. The needles are dark green and come in varying sizes, the shorter ones pointing upward. The bark is smooth pale grey and turns scaly with age. The wood is not very strong and is mostly used for pulp and plywood.
Aspen (trembling aspen: *Populus tremuloides* Michx.): It grows throughout most of the interior and can reach a height of 27 m and a diameter of 60 cm. It has a straight stem with little taper and a short, rounded crown. The leaves are nearly round heart shaped and sit on a flat stem. The bark is smooth greenish to yellowish and becomes rough and furrowed with age. Although viable seeds are produced root suckers are the main method of natural regeneration, which leads to clonal grouping. The wood is mainly used for pulp and occasionally for boxes, matches and chopsticks.
Balsam (subalpine fir: *Abies lasiocarpa* (Hook.) Nutt.): It grows in the cold moist climate of higher elevations throughout the province and can reach a height of 30 m and a diameter of 76 cm. The crown is very narrow with a spire like top and drooping branches. The bark is smooth, ash grey with blisters and becomes greyish brown and scaly with age. The needles are greyish green, rounded or notched at the tip and curved upwards. The wood is used for general construction and pulp. It is also suitable for boxes and crates. It is often included in shipments of spruce.
Cedar (western red cedar: *Thuja plicata* Donn): It grows in the coastal and interior wet belts at lower elevations, but not in the north half of the province and can reach a height of 60 m and a diameter of 250 cm. It has a long, narrowly conical crown with drooping branches, which turn up at the end. The bark is thin, reddish brown and becomes fibrous and stringy with age. The leaves are scaly, blunt, pressed in two pairs against the twig. The wood is not strong but durable and very valuable. The Indians used cedar for building canoes and the bark for making rope.
Cottonwood (black cottonwood: *Populus trichocarpa* Torr. & Gray): It grows in the coastal and interior wet climates. It can reach a height of 24 m. and a diameter of 150 cm. It has a straight stem, large branches and an irregular crown. The bark is smooth, yellowish grey and becomes greyish and furrowed with flat ridges with age. The leaves are widely triangular or heart shaped, dark green on top and silvery on the underside. The wood is used for truck decking, furniture and soft tissue paper.
Engelman spruce (*Picea Engelmannii* Parry): It grows in the southern part of the subalpine forest at higher elevations and can reach a height of 40 m and a diameter of 100 cm. The crown is symmetrical and spire like and is difficult to distinguish from that of white spruce. The needles are bluish green, curved and four sided. The bark is thin, scaly and greyish brown. The wood is used in construction and pulp and paper. Compared to other construction wood it is light and is therefore cheaper to transport. Recently the building code has been amended so that the maximum span for spruce is greater than that for fir.
Fir (Douglas fir: *Pseudotsuga menziezii* (Mirb.) Franco): It grows in the coast and interior wet and dry climates at lower elevations, but not in the northern portion of the province. A height of 60 m and a diameter of 122 cm are possible. It has a long branch free stem with a short, flat topped and conical crown. The bark is smooth, greyish brown with blisters and becomes deeply furrowed and reddish brown with age. The needles are pointed and soft. The wood is very strong and used mostly for construction. The quality of fir lumber is well known throughout the world. This is the reason that in the pine growing areas in warmer climates there is concern about the quality of fast grown wood.

Grand fir (*Abies grandis* (Dougl.) Lindl.): It grows in the coastal forest and in the interior wet belt at lower elevations and can reach a height of 38 m and a diameter of 120 cm The crown is cylindrical or oval in outline and the branches hang down with the tips pointing up. The bark is a smooth greyish brown and becomes scaly with age. The needles are dark green, flat, lay in one plane and are of two sizes. The wood is of limited commercial value and used for lumber, pulp, plywood and boxes.

Hemlock (western hemlock: *Tsuga heterophylla* (Raf.) Sarg.): It grows in the coastal and interior wet climates at lower elevations and can reach a height of 50 m and a diameter of 120 cm. It has a long, branch free stem with a short, pyramidal and irregular crown. The bark is russet brown and scaly and becomes deeply furrowed with age. The needles are flat, blunt and of varying size. The wood is used in construction and for pulp. For a while it was sold as Alaska pine because customers had become used to the high quality of fir and the properties of hemlock were widely recognized as less desirable than those of fir.

Larch (Western larch: *Larix occidentalis* Nutt.): It grows in the dry and wet climates of the southern interior at low elevations and can reach a height of 60 m and a diameter of 120 cm. The stem is mostly branch free, with a short pyramidal and open crown. The bark is reddish brown and scaly becoming furrowed with age. The needles are pale yellow green and grown in spirally arranged clusters (short shoots). The wood is heavy, hard and strong. It is used in construction.

Lodgepole pine (*Pinus contorta* Dougl.var latifolia): It grows on well drained soils throughout the province from mid elevations to sub alpine. A height of 30 m and a diameter of 45 cm are possible. The coastal variety, known as shore pine (var. contorta), is much smaller and not very important commercially. The stem is tall and slender with a narrow rounded crown. The bark is greyish brown and finely scaled. The needles grow in pairs and are yellowish green. The wood is used in construction and for pulp, poles, mine timbers and railway ties. The Indians used lodgepole pine for building their wigwams, hence the name.

Sitka spruce (*Picea sitchensis* (Bong.) Carr.): It grows in a narrow strip along the Pacific coast at lower elevations and can reach a height of 60 m and a diameter of 200 cm It has a long, clean stem with a narrow crown. Characteristic are the branchlets drooping from the main, horizontal branches. The bark is thin and broken into reddish brown scales. The needles are flat and sharp. The wood is light and strong. It is used for general construction, ship building, airplanes, plywood, boxes, crates and sounding boards for musical instruments.

Western white pine (*Pinus monticola* Dougl.): It grows in the coastal forest and the interior wet belt and can reach a height of 40 m and a diameter of 90 cm. The stem is straight, slender and columnar. The crown is irregular. The bark is thin and greyish green. The needles are bluish green and grow in bundles of five. The wood is very valuable and used for indoor paneling.

White spruce (*Picea glauca* (Moench) Voss): It grows in the cold, moist climate of the boreal forest and can reach a height of 45 m and a diameter of 120 cm. The crown is uniform and conical. The bark is thin, scaly and pale greyish brown. The needles are bluish green and four sided. The wood is used in construction and for pulp.

Yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach): It grows in the coastal forest and in the interior wet belt at higher elevations. A height of 60 m and a diameter of 240 cm are possible. The stem is broad based and tapered and the crown is narrow conical with drooping branches. The bark is thin, greyish brown and papery. The needles are scaly and blunt. The wood is light, even grained and strong. It is used for boat building, greenhouses and is exported to Japan for floors.

Yellow pine (Ponderosa pine: *Pinus ponderosa* Laws): It grows in the dry and arid parts of the southern interior and usually grows in widely spaced stands, associated with bunchgrass and cattle grazing. It can reach a height of 30 m and a diameter of 65 cm The stem is straight and clear with little taper. The crown is short and irregular. The bark is orangy brown and deeply fissured into flat plates. The needles grow in bundles of three and are bluish green. The wood is used for sashes, paneling and boxes.

Non commercial species

Some of the commercially unimportant species are listed below. Western yew may become an exception. It is not important for its wood but for the bark, which is used for the production of taxol, which has been found to be effective against breast and ovarian cancer. Some companies are considering planting this species and there are even breeding programs underway.

Alpine larch (*Larix lyallii* Parl.), arbutus (*Arbutus menziesii* Pursh), black spruce (*Picea mariana* (Mill.) B.S.P.), broadleaf maple (*Acer macrophyllum* Pursh), Douglas maple (*Acer glabrum* Torr.), Garry oak (*Quercus garryana* Dougl.), jack pine (*Pinus banksiana* Lamb.), limber pine (*Pinus flexilis* James), mountain hemlock (*Tsuga mertensiana* (Bong) Carr.), pacific willow (*Salix lasindra* Benth.), paper birch (*Betula papyrifera* Marsh.), red alder (*Alnus rubra* Bong.), tamarack (*Larix laricina* (Du Roi) K. Koch), western flowering dogwood (*Cornus nuttallii* Audubon), western yew (*Taxus brevifolia* Nutt.) and whitebark pine (*Pinus albicaulis* Engelm.).

2.4. Forest Industry

Until 1848, when the first sawmill was built in Victoria, only spars, squared timbers and poles were exported (Dixon, 1956). Railway development in 1886 and the completion of the Panama Canal in 1914 have improved access to markets. Early markets were in Australia, Chile, China, the United States and later Japan. In 1995 major export markets were the United States, Japan and the European Union. Factors, that have affected the industry are: geographical isolation, market fluctuations, major disasters, competition from Sweden, dependence on foreign capital, shipping dominated by San Francisco based companies, prairie development, railway building, the Panama Canal, a small home market, dependence on the United States market and a scarcity of capital (Lawrence, 1957).

The total output of forest products of the province of British Columbia in 1995 was 33.7 million m^3 lumber, 1.7 million m^3 plywood, 7.6 million tonnes pulp and 2.9 million tonnes paper (COFI, 1995). Export products in order of value for 1995 were: Softwood lumber (42%), pulp (34%), newsprint (12%), paper and paperboard (4%) and other (8%). The total value of all exports in 1995 was $ 11 billion (Government Communications Office, 1995).

2.5. Timber Harvesting

Logging has progressed from falling trees with an axe to a highly sophisticated and mechanized industry and is characterized by development of hand tools and logging equipment. Transport of logs has evolved from using water and oxen to logging trucks and has been influenced by railroads and road building (Drushka, 1992). The principle of sustained yield is based on the notion that the annual harvest shall not exceed net annual increment. The annual allowable cut (AAC) calculation is based on an economical rotation. Culmination age is the age at which periodic annual increment equals mean annual increment and at which the latter reaches its maximum It is also the point, where the tangent through the origin meets the volume over age curve. This is the point in time where the rate of increase in volume starts to decline. Estimates of volumes available and growth rates expected are based on up to date inventories. A complete forest inventory by management units was done during the period 1960 - 1980 and is being updated annually. For mature timber in the unit the annual yield equals volume mature divided by rotation age. For immature timber the annual yield equals volume at culmination divided by rotation age. Yield for the unit equals the sum of volume mature timber and volume at culmination of immature timber. The cutting age equals yield divided by annual yield and does not necessarily equal culmination age. The annual yield is the indicated cut, which must be adjusted to take total depletion into account. Estimated losses over the rotation are used to adjust the indicated cut. They include: land alienation, logging roads, regeneration delays, fires, insects, diseases and wind damage. Losses in extraction must be taken into account as well. They include: leaving seed trees for natural regeneration, utilization standards and breakage (Young, 1972, personal communication). The adjusted indicated cut becomes the annual allowable cut, which is reviewed every five years. Annual harvesting averages are shown in table 2.1.

2.6. Reforestation

In the early days of timber harvesting the supply of wood seemed inexhaustible. Not much attention was paid to regenerating the forests. It was thought that somehow nature would take care of this. The principle that the province should retain ownership of all forest land was established in 1865 (Knight, 1990). The findings of the Royal Commission of Inquiry, chaired by F.J. Fulton, led to the passage of the Forest Act in 1912. The Forest Branch, which in 1945 would be renamed Forest Service, was established and given the responsibility for forest conservation, fire prevention and reforestation. On the coast high lead logging was the main method of harvesting timber. It was devastating and utilization standards were low. In the interior selection harvest or diameter logging was used. This method relies on natural regeneration. Diameter logging is more commonly known as high grading. The largest trees were removed and poorly spaced residual stands resulted. These stands often contained less commercially desirable species and inferior phenotypes to regenerate the area. In 1930 it was decided that 50% of the stumpage (government revenue from the sale of timber) should be reinvested in the resource and the first nursery was established at Green Timbers, near Vancouver. Planting on the coast commenced in 1932. Recommendations of the second Royal Commission of Inquiry in 1945, chaired by G. McSloan, led to cut control regulations through amendments to the Forest Act. The principle of sustained yield was introduced and resulted in calculation of the annual allowable cut (AAC). This meant that, in order to ensure harvesting of wood in perpetuity, annual cut could not exceed annual increment. In 1947 the Koksilah nursery was built at Duncan in order to deal with backlog reforestation of lands not satisfactorily restocked (NSR). In 1955 the third Royal Commission of Inquiry, again chaired by G. McSloan, reversed an earlier position on reforestation by means of planting and stated that this method can be economical. Following this statement nursery capacity was expanded in 1956 and the seed extraction plant was built at Duncan. A start was made with seed registration for the purpose of controlling transfer of tree seed and to ensure that trees would be adapted to environmental conditions at the location of planting. In the interior, where natural regeneration was still the norm, planting started in the early sixties and in 1967 the nursery at Red Rock, near Prince George, started production. Since almost all forest land is owned by the province (Crown land) and since therefore the Government and the Forest Service are responsible for reforestation the Forest Act was amended in 1964 to allow the use of credits to stumpage, owed by the licensees, to pay for all reforestation activities carried out by the forest companies. This meant that the work was not paid for until it had been completed and inspected. As a result of the work of the fourth Royal Commission of Inquiry in 1975, chaired by P.H. Pearse, the Forest Act was changed dramatically. Licensee responsibilities were redefined. Holders of a Tree Farm License, Timber License and a Forest License were required to submit a forest management plan, which includes a regeneration commitment. The Timber Sale License was retained for smaller sales under the small business forest enterprise program (SBFEP) and does not require a commitment to regeneration. Another requirement that was introduced is the pre-harvest silviculture prescription (PHSP). In the early seventies expansion of nursery capacity and planting programs was actively promoted by the Forest Service. In 1969 a goal was set to reach 75 million trees produced annually in 1975. In 1973 the Skimikin nursery was established near Salmon Arm. There were now eleven Forest Service nurseries throughout the province. The total number of seedlings actually produced in 1975 was 91 million. In 1987 the production of Forest Service nurseries was constrained to 100 million. The remaining requirement in planting stock would be produced by company and private nurseries. The development of four company and seven private nurseries was approved. In 1987 the combined annual production of all nurseries was 250 million seedlings. The average number of trees planted annually in the province is shown in table 2.1.

Table 2.1. Harvest and reforestation in British Columbia

period	harvest		reforestation - thousands of ha			planting
	thousands of ha	millions of m^3	planting	natural	total	millions of trees
1966-1970	111.3	44.5	25.2	32.5	57.7	23.5
1971-1975	151.8	61.3	48.7	63.4	112.1	53.4
1976-1980	176.7	73.1	60.2	78.1	138.3	67.3
1981-1985	193.3	70.9	96.9	55.3	152.2	102.4
1986-1990	234.0	83.1	167.5	55.1	222.6	196.5
1991-1995	199.8	76.5	199.3	48.6	247.9	234.8

In 1987 the Forest Act was amended to discontinue credit to stumpage as a means for the Government to pay for silviculture work carried out by the licensees. The reasoning behind this decision was that all silviculture activities, including reforestation, should be seen as a cost of timber harvesting and that the licensee should therefore be fully responsible for carrying the cost of such work. At the same time it can be argued that the province still pays by accepting lower stumpage rates for the timber harvested on Crown land (Knight, 1990). As a result of the transfer of financial responsibility for reforestation to the companies the estimated annual seedling requirements for the interior decreased dramatically. A survey, which requested input from all agencies in the interior and was done in 1983, showed a total estimated annual seedling requirement for the year 2000 and beyond for all species of 191 million. In 1990 this estimate was 161 million. This reduction may have been caused by declining lumber markets and an across the board reduction of the AAC. Another reason may have been a sudden increase in the use of natural regeneration to accomplish the required stocking standards after harvesting. With the new regulations natural regeneration would seem to be more attractive than planting. Planting contractors also noticed a change in the companies' interest in ensuring that the plantations would be successful so that costly replanting projects could be avoided. In the early nineties the number of seedlings, sown in nurseries, was on the rise again, presumably because natural regeneration does not always work and where it does work it represents a longer regeneration delay than planting. In the eighties significant progress was made on backlog reforestation, as shown in table 2.1, and intensive silviculture under federal-provincial shared funding agreements (Jones, 1990). In 1988 the government of the day felt that the Forest Service should not be in the business of producing trees for reforestation, with the exception of planting responsibilities in areas harvested under a Timber Sale License and backlog NSR planting, and that free enterprise should be allowed to take care of tree production. As a result eight of the eleven Forest Service nurseries were sold to private interests. In 1995 there were 3 Forest Service, 5 company and about 45 private nurseries with a total annual production capacity of over 250 million seedlings.

Methods currently in use for forest regeneration are briefly described below. They reflect the experience gained over many years of timber harvesting and reforestation. It has become abundantly clear that poor management practices led to loss of forest productivity and other resource values. During the past fifteen years values of the forest other than timber production have become more important. Considerations of protection of fish, wildlife and water resources as well as landscape integrity form part of the planning process for any timber harvesting and regeneration program.

Forest site quality (productivity) can be inferred from topography, soil characteristics and indicator plants. Sites with similar climate and soil characteristics can be expected to have similar vegetation and production potential. Forest regeneration can be achieved in any given site unit by the application of the ecological knowledge and experience relevant to that unit (Klinka et al., 1990). To identify these similarities the biogeoclimatic classification system is used. Site classification is based on biogeoclimatic zone, subzone and variant, and more specifically on site association, series and type. The biogeoclimatic zone, subzone and variant can be found on available maps. The site series is the basic unit to be used for preparing a pre-harvest silviculture prescription. Edatopic grids are available for all subzones and variants. The grid shows relative soil moisture regimes in eight classes, from very dry to extremely wet (xeric to super hydric), on the vertical axis and soil nutrient regimes in six classes, from very poor to extremely rich (oligotrophic to super eutrophic), on the horizontal axis. The intersect of moisture and nutrient regimes, found on the site, shows the site series. Indicator plants are a more reliable guide to soil moisture and nutrient regimes than site and soil characteristics (Klinka et al., 1990). For the major commercial tree species ecological suitability, silvical characteristics and regeneration implications are listed in the guidelines. Tree species selection is based on ecological suitability, management objectives, productivity, reliability and feasibility. In addition genetic variation and adaptability for the species selected, as reflected in the seed transfer guidelines must be taken into consideration when choosing an appropriate seed source.

The pre-harvest silviculture prescription (PHSP) is a framework for collecting information and making decisions about how best to use the natural productivity and potential of a site to serve specified management goals (Hadley et al., 1990). It is a legally binding document. It is based on careful examination of the site to be harvested and consideration of the effects of harvesting. Determination of the biogeoclimatic classification of the site and consideration of other resource uses and values assist in the formulation of a plan for harvest, site preparation and reforestation. Factors to be included are site damage, hazards, constraints, objectives, requirements and economics. The result of this planning process is a written statement of intent, actions and expected results, which can be used to monitor harvesting and forest regeneration activities. A cutting permit can be issued on the basis of an approved PHSP. For instance, if planting is the chosen method for reforestation the agency responsible must have ownership of a sufficient amount of seed from an appropriate source. Ultimately the expected result, which will be inspected, is a minimum requirement of a number of well spaced, free to grow (i.e. unencumbered by competing vegetation) seedlings per hectare within a specified number of years from harvesting. The acceptable number of seedlings, spacing and allotted time to reach the stated objective are site specific and are described in the PHSP. Whether the objective will be reached through natural regeneration or by planting is also agreed upon from the outset.

2.7. Tree improvement

2.7.1. General

Tree seed registration in British Columbia was started in 1956. This ensured that the origin of seed, used for reforestation, was known. No guidelines were available to assist the forest manager in deciding which seed source would be appropriate for a particular reforestation project. It was assumed that local sources would be best adapted to the environmental conditions. At that time not much was known about the geographic variation of the commercial tree species. Delineation of seed zones is essential where artificial regeneration is used on a large scale (Roche, 1970). Based on the ecological studies of Krajina 67 seed zones were identified in 1971 and revised in 1974. After several revisions during the period 1975 - 1985 there were 24 seed planning zones (figure 2.2). Seed for reforestation had to originate from within the seedzone in which planting was contemplated.

Figure 2.2. Seed Planning Zones and ▲ tree improvement sites

In order to be able to formulate guidelines for the movement of provenances in reforestation and to identify provenances outstanding in desired characteristics studies would have to be undertaken. Interior spruce provenance tests were established in 1965, when 39 different seed sources were planted at 5 sites in order to assess the effects of elevational and latitudinal displacement of white and Engelman spruce (Revel et al., 1966). Assessment of these plantations led to a better understanding of the plasticity of the species and resulted in the identification of two superior provenances. In 1968 153 lodgepole pine provenances were collected throughout the range of the species. Of these 117 were part of a collection sponsored by the International Union of Forest Research Organizations (IUFRO). Of these sources 140 were outplanted at 59 sites throughout the interior of British Columbia in 1974. Ten standard provenances were tested at all sites in addition to 50 regional provenances. At one location, the

Prince George Tree Improvement Station (PGTIS), all 140 provenances were represented (Illingworth, 1974). Seed transfer guidelines for lodgepole pine were based on observations in these plantations and are regularly reviewed and modified. Recently it has become clear that early results may not always be reliable. Certain provenances, which had shown superior growth for the first 10 years, were found to be more susceptible to disease than more local sources at some locations (e.g. needlecast; *Lophodermella concolor* (Dearn) Darker and western pine gallrust; *Endocronartium harknessii* (J.P. Moore) Y. Hirat). Initially it was assumed that it is safer to move seed down hill, i.e. to use seed from higher elevations than the planting site. Over the years it has become evident that lodgepole pine, when moved to lower elevations, displays a higher level of susceptibility to needlecast than local sources (Ying, personal communication). Most forest plantation diseases are caused by pathogens attacking trees on sites to which the trees are inadequately adapted (Heimburger 1962). In 1975 limited provenance testing of Douglas fir and Western larch was initiated with the establishment of 9 larch and 60 fir provenances on one site in the southern interior. When tree breeding programs were started in the late sixties and early seventies it was understood that more provenance research would be required to form a basis for the delineation of breeding zones. It was equally clear that resources, necessary for this work, were not available. As a result tree breeders have adopted a strategy for progeny testing which allows for learning more about seed transfer in addition to providing information on family performance. Most progeny tests include families from parent trees originating from outside the planning zone concerned as well as local controls, derived from seed originating from natural stands in the vicinity of the test site. Results from these tests indicate that the local sources are not always the best performers, e.g. spruce progeny testing in the East Kootenays showed that the high elevation families are not the most frost hardy and are outperformed by low elevation families in survival and growth (Kiss, personal communication). Provenance test results also have shown that there is a limit to seed transfer; e.g. lodgepole pine provenances from the coastal area and from the Yukon did not survive and grow well at Prince George. Superior provenances have been identified for spruce and pine in the interior. Generally the best sources are located in the transition zone between dry and wet climates in the interior.

2.7.2. Selection

Initial parent tree selection is based on growing vigour, stem form, crown shape, branching characteristics and apparent absence of diseases and insects on the tree as compared with other trees in the same stand. It is a purely phenotypical selection, which by itself can not be expected to produce much improvement (Albricht, 1969). The ranking of parent trees for their general combining ability is based on growing vigour of the progeny. The expected genetic gain is largely in volume production, although correlations have been found between growing vigour and insect resistance; e.g. high ranking families in spruce progeny tests consistently have a low incidence of leader weevil (*Pissodes strobi* Peck.) damage (Kiss and Yanchuk, 1991). There is concern about the quality of faster grown wood. All wood quality characteristics are positively and clearly correlated with wood density. It is expected that the shorter rotations of second growth forests will produce wood with a greater component of juvenile wood. Wood density is expected to be lower and therefore the quality of lumber will be lower (Bendtsen, 1978; Clayton and Kellogg, 1986; Megraw, 1986). Tree improvement will reduce rotations even further because the most economical way to profit from faster growing trees is to lower the rotation age. If the rotation age is kept the same for the production of a larger volume of wood the quality will not be affected very much; e.g. the strength properties of fast grown trees do not differ significantly from those of slower grown trees of the same age, but are significantly different from those of trees with the same diameter (Pearson and Gilmore, 1980; Barrett and Kellogg, 1984). The only end product which requires a low wood density is pulp for newsprint (Van Buijtenen, 1982). Specific gravity has been found to respond well to genetic manipulation (Gonzales and Kellogg, 1978). There is a weak but negative correlation between growth and wood density, but exceptions have been found. In all softwood species, for which it has been determined, heritability of wood density is moderate to high (Kellogg, 1982). Juvenile density has been included as a selection criterion in second generation breeding. The goal is to maintain wood density at the same level as in unimproved plantations. This will be done by selecting for growth in the first generation and to include wood density in the second.

2.7.3. Seed orchards

To have improved stands, genetically improved material must be used, i.e. improved seedlings should be planted. This material comes from seed orchards. Genetic gain is produced by selection and testing; delivery of genetic gain is done through seed orchards. All interior orchards except one are associated with an active breeding program. At present all seed orchards in the interior are clonal (i.e. selected parent trees are represented by their clones in the orchard), because the expected initial gains are greater (Zobel and McElwee, 1964; Wright, 1972). The orchard trees are grafts made from material collected from parent trees. Scion material (twigs) is collected in late winter and kept frozen till spring. Rootstock is sown two years prior to grafting. One year before grafting the rootstock is transplanted into pots (for pot grafting) or planted in the future seed orchard or a holding area (field grafting). Rootstock is of the same species as the scion and for optimal results should be from the same seed planning zone. Rootstock-graft incompatibility is virtually unknown in interior spruce, but some is suspected in lodgepole pine. In Douglas fir incompatibility is a serious problem. Special rootstock has been developed for this species. Trees, which have shown a general grafting compatibility in tests, are crossed and the offspring is used in Douglas fir grafting programs. Depending on the size of the orchard, which is determined by the seed requirements for the planning zone, each parent tree is represented by 10 - 100 ramets (for some reason a graft is called a ramet after it has been planted in a seed orchard). In interior spruce and lodgepole pine orchards, established earlier, i.e. 1974 - 1983, all selected parent trees are represented. Expected early gains are based on phenotypical selection and the elimination of inbreeding, which is known to take place in natural stands (Kleinschmit, 1979). When progeny test information becomes available the least desirable clones (parents) can be removed from the orchard. This process is known as roguing. These are the parent trees with a low general combining ability, i.e. they have produced poor offspring when crossed with a large number of male parents. Good correlations have been found between progeny performance (mean family height) at ages 5, 10 and 15, especially for the very low and very high ranked parent trees (Kiss, personal communication). Five year measurements are therefore considered adequate to base the removal of the lowest ranked clones (parents) on. As progeny test information becomes more reliable more clones can be removed. In orchards, which were established later, i.e. 1984 - 1990, only parents from the top 50% of the ranking (based on 10 year test results) or from the top 25% of the ranking (based on 15 year test results) are represented. In the final configuration of a clonal orchard only parent trees of known and superior general combining ability will be represented by their clones. This is known as backward selection, i.e. the progeny is assessed and the parents are selected. Parent tree ranking and therefore orchard roguing can be based on the results of open pollinated, i.e. seed is collected from the parent trees, or polycross progeny tests. Cone collection from parent trees must be done in good crop years because the amount of selfing and inbreeding in natural stands is greater in poor crop years, when there is less pollen available (Ying, 1978). Orchard size must be based on seed requirements, which are determined by the magnitude of planting programs. In 1995 three surveys had been done to determine annual seedling requirements in the interior. In 1995 there were eight seed orchard sites and three clone bank sites in the interior. A clone bank is a plantation containing grafts of all parent trees selected and serves as a backup system. In case of a disaster in the orchard material for replacement can be obtained from the clone bank. All breed arboreta are located at the Kalamalka Forestry Center near Vernon (figure 2.2). The purpose of these plantations, where clones of selected parent trees are maintained, is to allow controlled crossing. Selection of the best individuals in the best families, will lead to second generation seed orchards. This is called forward selection.

The objectives of the tree improvement programs are:

- promote the use of appropriate seed sources and superior provenances to ensure adaptability and to utilize gains available;
- provide the greatest possible genetic gain in the shortest possible time;
- ensure acceptable levels of adaptability;
- maintain adequate levels of genetic variability in production plantations;
- ensure preservation of genetic resources;

Activities carried out to reach these objectives include:

- defining of seed planning zones and identification of superior provenances;
- selecting parent trees and evaluating their breeding values through progeny testing;
- pairwise crossing of selected parent trees to produce a second generation breeding population;
- maintaining these breeding populations and preservation of gene resources;
- providing selected materials for the establishment of seed orchards;
- studying genetic variation, genotype by environment interactions, juvenile versus mature relationships, elevational transfer of seed, heritability of desirable characteristics and pest and disease resistance mechanisms;
- studying phenology, flower enhancement, pollen behaviour and identification, crown management in orchards and protection against insects and diseases.

Tree improvement in the interior involves the following species:

- Interior spruce. The two main commercial species, white and Engelman spruce, and their hybrids are collectively known as interior spruce; in the coast-interior transition zone there is evidence of introgression between white and Sitka spruce (Sutton et al., 1993), but these are not included in the interior spruce program;
- Lodgepole pine. The coastal form, known as shore pine, is not included in this program;
- Interior Douglas fir. This species is described by some taxonomists as a species different from coastal Douglas fir or at least a subspecies. In the arid climates of the interior a different form is recognized as dryland fir. This program is focused on the moist and wet climates;
- Western larch. The boreal and subalpine larches are not included;
- Western white pine. Selection in the white pine program is not aimed at volume gains, as is the case in all other programs, but the objective is to obtain resistance to the white pine blister rust (*Cronartium ribicola* J.C. Fish).

2.7.4. Interior spruce

Tree breeding in the interior started in 1966 with spruce. Parent tree selection was undertaken in 1968 and the first series of progeny tests, based on open pollinated seed collected from the original parent trees, were established in 1974. All selected parent trees were preserved in clone banks at Prince George and at Barnes Creek near Vernon (figure 2.1). The breeding plan includes selection of the best parents on the basis of progeny test results. The selected parent trees will be crossed with each other in a disconnected half diallel in order to generate material for second generation seed orchards (Kiss, 1966). Since little or no flower production was encountered at Prince George the breed arboretum was established at Kalamalka in 1976. It was (justifiably) anticipated that flower production would be more abundant in the warm and dry climate of the Okanagan. This represented a move of four degrees in latitude to the south so that the trees were also exposed to a shorter daylength during the growing season. In 1973 an additional parent tree selection program was started to provide material for seed orchards to ensure a steady supply of seed for reforestation. To date 4194 parent trees have been selected in 15 seed planning zones. In 1975 a number of planning zones, based on biogeoclimatic classification, were delineated (figure 2.2). Zone boundaries were revised a number of times because of refinements of the ecological mapping. In 1979 the first interior spruce seed orchard was established at Skimikin. As information on parent tree ranking in order of their general combining ability becomes available less desirable clones are removed from the orchards. Three types of seed orchards are recognized in this program. The first generation untested orchard, the first generation rogued orchard and the second generation orchard. In 1995 there were 12 spruce orchards producing, 4 established but not yet in production, 2 planned and 1 abandoned. With all spruce orchards in full production the average annual amount of seed delivered will be sufficient for the growing of about 64 million seedlings. For the planning zones included the total requirement is 76 million. Genetic gain predictions, based on progeny test results, must be substantiated by realized gain trials. Establishment of realized gain trials and demonstration plantations for spruce is underway.

2.7.5. Lodgepole pine

Until the late sixties lodgepole pine had been considered as a non commercial species. The introduction of close utilization standards led to a change in attitude. The range wide provenance test (section 2.7.1), started the breeding program. At the same time parent tree selection was undertaken in northern British Columbia and the Yukon in cooperation with the Swedish Cellulose Company (Fries and Lindgren, 1985). These selections were grafted to establish a breed population in Sweden and a clone bank at the Prince George Tree Improvement Station. Grafts in excess of these needs were made available for the establishment, in 1974 and 1978, of the first two lodgepole pine orchards at the Prince George Tree Improvement Station. There was concern about the validity of the Swedish progeny test results because these tests were established at higher latitudes than the planning zone of intended use for the orchard in British Columbia. A progeny test was established in the vicinity of Prince George, using open pollinated seed from the orchards. Parent tree selection continued till 1985. To date 1828 parent trees have been selected in seven seed planning zones. Open pollinated progeny testing commenced in 1984. The plan includes the following elements. Four test sites in each zone, 250 - 300 families from the zone, some from adjacent zones, some from superior provenances and some local controls from natural stand seed collections (Carlson, 1982). There are four types of seed orchard in this program, all of them clonal. First generation untested orchards, orchards based on the selection of the best individuals in the best families from identified superior provenances, orchards based on the selection of the best 15% of all parent trees tested and second generation orchards, which will include selections made in full sib progenies from the controlled crossing program. Currently there are 12 pine orchards producing, 5 established but not yet producing and 1 planned. With all pine orchards in full production the average annual amount of seed delivered will be sufficient for the growing of about 58 million seedlings. For the planning zones included the total requirement is 51 million. Genetic gain predictions, based on progeny test results, must be substantiated by realized gain trials. Establishment of realized gain trials and demonstration plantations for pine is underway.

2.7.6. Interior Douglas fir

Douglas fir breeding in the Interior was initiated in 1982 with selection of parent trees. This program concentrates on the more productive areas and aims to provide genetically superior planting stock for these areas. There will be no establishment of untested orchards. Seed orchard establishment will be done on the basis of progeny test results and will utilize the top 25% or better of the tested parent trees. No further roguing of these orchards is contemplated (Jaquish, 1982). Parent tree selection and progeny test establishment has been completed. To date 1794 parent trees have been selected in seven seed planning zones. In 1995 there were 4 orchards established and 2 planned. With all fir orchards in full production the average annual amount of seed delivered will be sufficient for the growing of about 7 million seedlings. For the planning zones included the total requirement is 8 million.

2.7.7. Western larch.

A larch program was initiated in 1987. It is considered a desirable species because of its rapid early growth, its relative resistance to root diseases and its high value wood. A chronic lack of sufficient amounts of quality seed, caused by spring frosts, insects and inadequate pollination, has reduced the larch planting program (Jaquish, 1987). Selection of parent trees was carried out in three seed planning zones. To date 383 parent trees have been selected. Progeny testing started in 1991. Field grafting started at Kalamalka in 1988 and two seed orchards were established in 1990 before selections were completed. This was done because the fast growth of the grafts made it impossible to keep them in the holding area much longer and because of the urgent need for seed. New crown management techniques, borrowed from the fruit growing industry, will keep orchard trees from becoming much taller than four meters. With all larch orchards in full production the average annual amount of seed delivered will be sufficient for the growing of about 7 million seedlings. For the planning zones included the total requirement is 5 million. More research will be necessary to establish protocols for pollen collection, extraction, storing and application. The study of flower enhancement techniques for larch will be continued.

2.7.8. Western white pine

White pine is a very desirable species, which has fast growth, good form, more than average resistance to root diseases and produces very valuable wood. Planting is minimal because of the widespread occurrence of the white pine blister rust (*Cronartium ribicola* J.C. Fisch), which was introduced in British Columbia in 1925 and had reached the Interior by 1930. The rust requires an alternate host (Ribes spp.), for the completion of its life cycle (Hunt, 1981). In the sugar pine and white pine areas of Oregon a Ribes eradication program was carried out with little success (Franc, 1988; Hoff, 1988). It was abandoned in 1966 (Thiesen, 1979). In 1983 a program was started for the genetic improvement of white pine. The objective of this program is to provide seed for rust resistant trees. A number of resistance mechanisms has been identified. Seed orchards will include parent trees, which carry resistance based on these mechanisms. Tolerance to the rust, especially bark reaction (Heybroek, 1980) will be included as well. Complete resistance, based on one mechanism (e.g. premature needle drop) has been found to be unsuccessful because the rust population appears to be able to adjust by changing through mutations and the obviously strong selection pressure (Franc, 1988). Surveys were carried out in Britisch Columbia to determine the location of natural stands where parent trees could be selected. Selection is aimed at finding apparently rust free trees in infected stands. Open pollinated seed is collected from the selected trees and progenies are inoculated with the rust. The seedlings are monitored for four years and those displaying rust resistance will be included in seed orchards (Meagher et al., 1993). Individual trees with the same type of resistance will be grouped together in order to reduce the possibility of losing the mechanism through cross breeding (Hunt and Meagher, 1990). To date 286 parent trees have been selected in the southern interior and seed for progeny screening has been collected from 234. Currently seed for reforestation is produced in two 19 year old plantations at the Skimikin seed orchard site. One of these plantations originates from seed obtained from the Idaho white pine blister rust resistance breeding program and the other from seed collected from apparently rust free trees in infected natural stands. An interim seed orchard, using material obtained from the Idaho rust resistance breeding program (Franc et al., 1992), has been established in 1994. The estimated annual production from these three orchards will be sufficient for the growing of 8 million seedlings. The annual requirement for the zones involved is 2 million seedlings. This requirement is expected to increase when rust resistant trees can be planted.

3. DROUGHT STRESS TO ENHANCE FLOWERING IN AN INTERIOR SPRUCE SEED ORCHARD

3.1. Introduction

The delivery of genetic gain in tree improvement is traditionally achieved through the establishment of seed orchards, management of these for maximum seed production and the encouragement of random mating. Immediate utilization of early gains can be achieved through vegetative propagation; e.g. rooted cuttings, tissue culture and somatic embryogenesis. Seed orchards can be clonal; i.e. the trees in the orchard are grafts from selected parent trees, or consist of seedlings. In the interior of British Columbia all seed orchards are clonal. The time lapse between inception of a program and full seed production is considerable. Assuming that provenance testing and ecological studies have led to the delineation of seed planning zones, the steps involved are as follows:

year 1 - 2	Phenological selection of parent trees and collection of open pollinated seed for progeny testing as well as scion material for grafting.
year 3 - 4	Sowing for progeny testing and grafting for clone banks as well as selection and preparation of test sites.
year 4	Establishment of progeny test.
year 8	Sowing rootstock for grafting.
year 9	Measurement and assessment of progeny tests as well as ranking of parent trees and preparing for grafting in year 10.
year 10 - 11	Grafting of selected parent trees (e.g. top 50% of the ranking) and preparation of orchard site.
year 14	Re-assessment of progeny test.
year 15	Adjustment of selected parents (e.g. top 25% of the ranking) and establishment of seed orchard.
year 21	First cone crop worth harvesting.
year 27	Full production.

In 1995 there were 16 interior spruce seed orchards established and 2 more under development in the interior of British Columbia. The required annual production from the total of approximately 60 ha of orchards is 292 kilograms of seed, which is sufficient to produce about 76 million seedlings. Flower enhancement, also referred to as cone induction, can speed up the delivery of genetic gain, lower the cost of seed production and improve panmixia.

Flowering in forest trees is affected by temperature, soil moisture, light intensity and daylength (Griffin et al., 1984). Since temperature, light intensity and daylength can not be manipulated it is obvious that the selection of the location is the most important factor in seed orchard establishment. Cone production can be enhanced by locating the seed orchard in a climate, where temperatures during the growing season are higher and the days are shorter than those of the area, where the parent trees have been selected and where the orchard seed will be deployed. A difference of 830 -1100 in accumulated degree days (based on 6° C) over the growing season is generally considered sufficient. The desired difference in accumulated degree days can be accomplished by locating the orchard two to three degrees latitude south of the seed planning zone or 600 to 700 m. lower in elevation. Climate has a profound effect on cone production of interior spruce (Kiss, 1979), but no clear relationship has been found between parent tree origin and flowering in lodgepole pine (Fleetham, 1981) and in interior spruce (Hewson, 1989). Cone production can also be enhanced by cultural practices, such as girdling, strangulation, rootpruning and manipulation of the water supply.

Girdling or banding by various means have long been practiced with success by horticulturists to reduce vegetative growth and to enhance production in fruit trees and has increased cone production in Corsican pine (Holmes and Matthews, 1951), loblolly pine (Bilan, 1960), Scots pine (Wesoly, 1985), radiata pine (Sweet and Hong, 1978) and Douglas fir (Ebell, 1971; Wheeler et al., 1985; Woods, 1989). Girdling may consist of one continuous or two overlapping semicircular incisions. Both girdling and strangulation result in accumulation of carbohydrates above the point of treatment (Bilan, 1960; Doorenbos, 1965) and may induce fruit production by altering the carbohydrate/nitrogen ratio in the crown of the tree (Pond, 1936), although sugar and starch content of shoots during bud development following girdling are not always consistently related to flower production (Ebell, 1971). Girdling increased the level of endogenous gibberellins in Scots pine (Wesoly, 1985) but not in Douglas fir (Ross and Pharis, 1976). This treatment should be done prior to bud differentiation and above at least one whorl (Ebell, 1971; Melchior 1960; Woods, 1989). Flowering response to girdling can be observed in the year following treatment. Some effect may be expected during the year of treatment as a result of improved nutrition of flower buds rather than a stimulation of flower bud initiation (Holmes and Matthews, 1951). Branch strangulation increases male flowering (Hare et al., 1977; Hare, 1979, Albricht and Walsh, unpublished).

Rootpruning has increased cone production in Douglas fir (Crown, personal communication) and in interior spruce (Cox, personal communication) and enhances the effect of girdling, but will affect tree health (Lindgren et al., 1977). Fertilizer application has increased cone production in loblolly pine (Wenger, 1952), slash pine (Barnes et al., 1968), eastern white pine (Schmidtling, 1983), radiata pine (Griffin et al., 1984; Sweet and Hong, 1985) and lodgepole pine (Ebell, personal communication). The effect of fertilizer application to enhance seed production to ensure natural regeneration after partial harvest is dependent on rainfall and is not likely to be effective on younger stands (Wenger, 1952). Response to fertilizer application in seed orchards is particularly effective when the trees have not been fertilized for a number of years prior to treatment. The effect of fertilizer can be direct nutritional or because of improved development of foliage. The role of nitrogen fertilizer is probably to increase crown size. This would only happen on sites where growth rate and crown size have been limited by a nitrogen deficiency (Sweet and Hong, 1985). Where extremely high amounts of fertilizer have been successful in enhancing flowering the treatment may be comparable to a chemical rootpruning. Fertilizing doubled female flowering in a slash pine orchard, but did not affect male flowering. The amount of nitrogen in the twigs was increased by the treatment and 60% of the increase was in arginine. Increase of arginine as a result of fertilizing has been reported earlier but is not indicative of flowering (Barnes et al., 1968). Timing of fertilizer application is important and may depend on species and location.

Large cone crops in natural stands are usually preceded by a dry and warm summer (pine) or a dry and warm spring (spruce). In Sweden the location of seed orchards for Norway spruce is based on the highest percentage of days with a maximum temperature of more than 15°C during the second half of June because this correlates well with a high probability of heavy cone crops (Lindgren et al., 1977). A period of soil water deficiency prior to bud differentiation is conducive to flowering in loblolly pine (Dewers and Moehring, 1970). Pinus species generally flower abundantly following a year with a wet spring (or irrigation) and a dry summer. In radiata pine in Australia heavy flowering and high rainfall in the previous summer are related (Griffin et al. 1984). In shortleaf pine in Arkansas irrigation early in the growing season increased the flower and cone crops dramatically (Schmidtling, 1985). The success or failure to promote flowering by the application of drought stress is dependent on timing (Owens and Simpson, 1988). Flower production of potted Engelmann spruce was increased by withholding irrigation during the period of rapid shoot elongation (Ross, 1985). This study was initiated to determine if drought stress could result in increased flower initiation in interior spruce seed orchards and what the optimal timing is for treatment. The experiment was prompted by the discovery that realized cone crops in some of the orchards were below expectations and by the need for a simple and cost effective technique to improve the situation. More encouragement for undertaking this study came from the results of a preliminary study, done in another spruce seed orchard on the same site.

3.2. Methods

The Central Plateau low elevation interior spruce seed orchard is located at Skimikin, near Salmon Arm, British Columbia, and produces seed for the Central Plateau seed planning zone northwest of Prince George. The 160 parent trees, represented by their clones in this orchard, originate from that zone at elevations below 840 m. In the design each of the 160 clones is represented once in each of 10 randomized blocks. At the time of this study there were 1520 trees in the orchard. Spacing is 5 x 5 m. The orchard was established in 1979 on a silty loam fluvial fan, overlaying a gravely glacial outwash. In 1981 a trickle irrigation system was installed to deliver an average of 9 -12 l of water per tree per day throughout the growing season. When rogued to produce maximum gain (25% of the clones left) the Central Plateau low elevation spruce orchard is expected to produce 4.0 Kg. of seed annually, an amount sufficient to produce over 1 million plantable seedlings.

Treatments for this study were carried out as follows. Treatments were applied to all trees over 2.5 m. in height, which had not been involved in previous studies; e.g. rootpruning. This height restriction was introduced to avoid comparing results on trees of very different size. Six of the randomized blocks in the orchard were selected. The treatments were given to two blocks each so that each clone observed would have two trees in each of the three treatments. This was not always the case because not all clones had a sufficient number of trees of the required height. Trees of each clone had been assigned to their position in each block randomly at the time of orchard establishment. Treatments were therefore given to different trees of each clone at random.

Treatments in 1985:
1. Withholding irrigation from May 22 to July 3 in blocks 1 and 6,
2. Withholding irrigation from May 22 to July 29 in blocks 2 and 5,
3. Regular irrigation from May 22 to September 15 in blocks 3 and 4.

Female and male flowers were counted in May 1986. No moisture stress measurements were taken during the treatment periods. A total of 381 trees of 88 clones were involved in the 1985 treatments. There were 127 sets of 3; one set receiving one of each of the three treatments. Only 39 of the 88 clones were replicated twice for all treatments. To determine whether or not the treatments had an effect a paired t test was done on all 127 sets of 3 and an analysis of variance was done on 2 x 39 sets of 3 (table 3.1).

Table 3.1. Number of trees and clones involved in the 1985 treatments

statistical analysis	sets of three	total clones	clones repl once	clones repl twice	total trees
paired t test	127	88	49	39	381
analysis of variance	78	39		39	234

treatments in 1986:
1. Withholding irrigation from May 22 to July 2 in blocks 2 and 5,
2. Withholding irrigation from May 22 to July 18 in blocks 1 and 6,
3. Regular irrigation from May 22 to September 15 in blocks 3 and 4.

Female and male flowers were counted in May 1987. Because of the large crop on all orchard trees in 1987 the number of flowers was estimated instead of counted. A total of 324 trees of 76 clones were involved in the 1986 treatments. There were 108 sets of 3; one set receiving one of each of the three treatments. Only 32 of the 76 clones were replicated two times for all treatments. To determine whether or not the treatments had an effect a paired t test was done on all 108 sets of 3 and an analysis of variance was done on 2 x 32 sets of 3 (table 3.2).

Table 3.2. Number of ramets and clones involved in the 1986 treatments

statistical analysis	sets of three	total clones	clones repl once	clones repl twice	total trees
paired t test	108	76	44	32	324
analysis of variance	64	32		32	192

The weather during the treatment periods was more or less normal for the area with a few exceptions. In 1985 the total precipitation for May, June and July combined was well below the ten year average. Precipitation in May was below average, June was somewhat dry and a July was particularly dry. The average temperature for May, June and July combined was above the ten year average. May and June were about normal but July was very hot. In 1986 the total precipitation for May, June and July combined was above the ten year average. May was relatively dry, but June and July were particularly wet. The average temperature for May, June and July combined was somewhat below the ten year average. May and June were about normal, while July was cooler than the ten year average. Weather data for the treatment periods in 1985 and 1986 are shown in table 3.3. The standard deviations of the ten year averages of monthly precipitation are fairly high. Since there is a great deal of variation in precipitation it is difficult to say what is normal. The variation in temperatures is less pronounced.

Table 3.3. Precipitation in mm and temperatures in °C
in two years and three months and the ten year averages at Skimikin

	May	avg	June	avg	July	avg	May-July	avg
precipitation								
1985	38.8	40.6	40.8	45.2	7.8	39.4	87.4	125.2
1986	22.8	36.8	59.0	45.9	47.0	40.5	128.8	123.2
temperature								
1985	11.5	11.4	14.8	15.1	21.5	17.8	15.9	14.8
1986	11.8	11.5	14.8	15.5	15.3	17.7	14.0	14.9

The timing of the treatments was based on the fact that flower enhancement treatments should be given during the period of rapid shoot elongation because that is the time when bud differentiation takes place. The short period of drought (treatment 1) was terminated when approximately 50% of the lateral shoots had ceased to grow. The long period of drought (treatment 2) was terminated when approximately 100% of the lateral shoots had completed elongation. Lateral shoot measurements were taken periodically between June 14 and July 24 in 1985 and between June 13 and July 18 in 1986 to determine when shoot elongation was terminated; i.e. when bud differentiation was theoretically completed. From six clones three trees were selected, one in each treatment. Current year shoot length was measured on the terminal shoot of four branches at weekly intervals (table 3.4).

Table 3.4. Lateral shoot development during treatment periods in 1985 and 1986

date	number of shoots that had ceased to grow		% of shoots that had ceased to grow	
	number	cumulative	number	cumulative
21 June 1985	11	11	16	16
28 June 1985	18	29	26	42
5 July 1985	29	58	41	83
12 July 1985	5	63	7	90
24 July 1985	7	70	10	100
13 June 1986	3	3	4	4
20 June 1986	16	19	22	26
27 June 1986	26	45	37	63
4 July 1986	17	62	23	86
18 July 1986	10	72	14	100

3.3. Results

The number of trees producing female flowers and the number of trees producing male flowers, the total number of female and male flowers (ovulate and staminate strobili), as well as the average number of female and male flowers per tree were all increased by drought stress treatments in both years (table 3.5). The response to the short drought period was greater than the response to the long drought period for both females and males in 1986 but only for females in 1987. The cone crop, resulting from the short drought period during the preceding year, was approximately 3.5 times that of the control in 1986 and approximately 1.4 times that of the control in 1987. For males the increase, resulting from the short drought period during the previous year, was approximately 1.6 times that of the control in 1986 and approximately 1.1 times that of the control in 1987. The long drought period resulted in smaller increases except for males in 1987. It is of interest to note that the short drought in 1986 resulted in a greater total number of females on fewer trees, while the long drought resulted in a smaller total number of females on more trees. For males the 1986 short drought resulted in a greater number of flowering trees with a smaller total number of flowers than the long drought.

Table 3.5. Flowering response to drought tress

	number of trees	flowering trees		flowering trees %		total flowers		average flowers/ tree	
		female	male	female	male	female	male	female	male
treatm. 1985 - results 1986									
short drought	128	35	30	27	23	1 045	1 306	8	10
long drought	128	27	26	21	16	602	1 026	5	8
control	128	13	15	10	12	299	809	2	6
treatm. 1986 - results 1987									
short drought	108	68	96	63	89	6 927	27 265	64	252
long drought	108	75	92	69	85	5 627	30 410	52	282
control	108	58	81	54	75	4 945	24 895	46	231

Since all clones involved in this study were represented in all three treatments at least once a paired t test was done to asses the differences between short drought and control, long drought and control as well as between short and long droughts. The results, shown in table 3.6, indicate that the short drought period resulted in significant increases in the number of females in 1986 and 1987. Increases in females related to the long drought period were not significant. Neither treatment resulted in significant increases in males in 1986 or 1987. The differences between treatments were not significant either.

Table 3.6. results of paired t test [1)]

year	results	short drought vs control	long drought vs control	short drought vs long drought
1985 - 1986	female	**	-	-
	male	-	-	-
1986 - 1987	female	*	-	-
	male	-	-	-

1) - not significant * significant at p = 0.05 ** significant at p = 0.01

An analyses of variance was done using only those clones, which were represented twice in each of the treatments. The results (table 3.7), indicate that treatment in 1985 had a significant (p=0.05) effect on female but not male flowering in 1986. The clonal effect was highly significant (p=0.01) for both female and male flowering. Treatment in 1986 had a significant (p=0.05) effect on female but not male flowering in 1987. The clonal effect was highly significant (p=0.01).

Table 3.7. Results of analysis of variance [1)]

source of variation	1985 - 1986		1986 - 1987	
	female	male	female	male
treatment	*	-	*	-
clone	**	**	**	**
treatment x clone	-	-	-	-

1) - not significant * significant at p = 0.05 ** significant at p = 0.01

3.4. Discussion

This study confirms the assumption based on earlier, preliminary trials, that drought stress can indeed enhance cone production in interior spruce seed orchards, but the effect on the production of pollen was not obvious. Earlier findings that timing of the treatment is important and that the critical period for flower enhancement in conifer trees is during the time of rapid shoot elongation (Owens and Simpson, 1988; Ross, 1985) were also confirmed. The short drought stress increased the number of female flowers, but when the drought period was prolonged the resulting increase diminished. While drought enhances differentiation of initiated buds into reproductive structures sufficient water must be available during bud development. Although all treatments increased the number of female as well as male flowers only the effect of the short drought on females was significant. It is of interest to note that the clonal effect in all cases was highly significant. With the very high clone to clone variation in flowering the differences caused by the treatments would have to be enormous in order to be identifiable.

The notion that flower enhancement treatments only increase flowering in clones, which have an inclination to flower, and that no results can be expected in clones, which do not, is not supported by the results of this study. When the results on flowers per tree are pooled over the two drought treatments and both years only 15% of the comparisons show increased flowering, where the controls were also producing; in 19% of the comparisons the treatment increased flowering, where the controls were not producing. The total number of female and male flowers, produced in 1986, was considerably lower than that in 1987. It is normal and expected that good cone crops are periodical. In this case it is surprising because the period of bud differentiation in 1985 was drier and warmer than the ten year average, while in 1986 the weather was more moist and cooler than the ten year average. 1987 was a good crop year in all the interior spruce orchards and 1986 was not. It seems, therefore, that predicting the cone crop from the weather during the previous spring and early summer is a losing proposition. However, while the monthly averages in temperature and precipitation may not be reliable predictors for future cone crops it may be the temperature and moisture of a few days during the period of bud differentiation that determine whether or not there will be a good cone crop in the following year. The timing of this event can not be defined as calendar days. If, for instance, development of new shoots is slow because of low temperatures the moment at which bud differentiation takes place will be later in the season. In this case the high temperatures required should be provided at a later date. The temperature seems to have more effect than precipitation on flowering in interior spruce, although the two are normally inversely related. The flowering response to drought is probably caused by reduced growing vigour in the new shoots. Vigorously growing shoots use all available endogenous gibberellic acid, which evidently not only acts as a flowering hormone, but also as a growth promoting substance. When the shoots are not growing very fast there will be more gibberellic acid available to promote flowering. Any treatment, which reduces growing vigour in the new shoots, can therefore be expected to increase flowering in the following year. In order for the induced flowers to develop properly irrigation must be restored after termination of the drought treatment. Providing a less than adequate water supply throughout the growing season does increase flowering, but this effect is not expected to be as dramatic as that of a well timed treatment, followed by restoration of normal irrigation.

The conclusion of this study is that drought stress, when applied from the beginning of the growing season to the date when approximately 50% of the new shoots have ceased to elongate, will increase cone production in interior spruce. With this treatment being effective in a relatively moist climate it may be expected to work even better in a dry climate.

4. THE EFFECT OF DROUGHT STRESS AND NITROGEN FERTILIZER ON FLOWERING AND HEIGHT GROWTH IN AN INTERIOR SPRUCE SEED ORCHARD

4.1. Introduction

Since withholding of irrigation during the first month of the growing season at Skimikin resulted in increased flower production it was decided to do a similar experiment at Kalamalka, where the climate is much warmer and drier. The optimal environmental regime for promoting flowering in Engelman spruce combines cool and dry conditions during early rapid shoot elongation followed by high temperatures and adequate soil water during the subsequent slow growth phase (Ross, 1988). In a greenhouse temperature can be controlled and heat treatment can be applied at the proper time. In a seed orchard the temperature in the crown can be increased to about 5°C above ambient temperature by enclosing the whole tree in a plastic tent. This was done at Skimikin and was found to be complicated and costly. At Kalamalka the local climate can be relied upon to provide high temperature. The purpose of this study was to determine if drought stress could result in increased flower initiation in interior spruce seed orchards in a warm and dry climate and what the optimal timing is for treatment. In addition an attempt was made to determine whether or not nitrogen fertilizer will enhance the response to drought stress. Because control of tree height becomes an issue sooner or later in seed orchard management the effect of drought and nitrogen fertilizer on height increment was also investigated. Heavy cone production may reduce vegetative growth (Todhunter and Polk, 1981). Treatments, which increase cone production, can be expected to reduce height growth during the crop year. In addition drought stress may reduce height growth during the year of flower initiation. However, stem diameter, but not height, was significantly correlated with the number of reproductive sites in black spruce (Smith, 1987) and heavy flowering reduced stem diameter by half in Douglas fir, grand fir and Western white pine (Eis et al., 1965), but had an even greater effect on growth of cone bearing shoots (Ebell, 1971). Early drought reduced shoot elongation and promoted cone production in potted Engelman spruce grafts (Ross, 1988). Shoot development is slowed down during periods of stress (Ross, 1985) by reducing the percentage of cells, which are dividing during the period of slow shoot elongation prior to vegetative bud burst (Owens and Simpson, 1987).

In seed orchards full participation of all clones in the production of female and male flowers as well as panmixia are assumed when gain predictions are made. In reality clonal contribution is generally incomplete. While some clones produce flowers in every crop year others do not. In addition there are clones in every orchard, which do produce little or no flowers at all times. Cone induction techniques must be directed to these recalcitrant clones in order to improve random mating amongst all clones in the orchard. Panmixia is encouraged by using a randomized block or permutated neighbourhood design. Parental balance is always a concern for the orchard manager and is influenced by cone crop size. In good production years the genetic base of the seed is much broader than in moderate or poor crop years (Matziris, 1992). Fortunately there is no relationship between flowering history of clones in an orchard and the geographic origin of the parent trees (Hewson, personal communication). Mineral fertilization and micro elements increase seed yield and improve clonal contributions (Danusevicius, 1987). Nitrogen fertilizer can increase cone production in Scots pine, especially when combined with herbicide treatment (Mikola, 1987). Two light applications two years apart produced better results than one heavy application and a heavy grass cover can cause a two year delay in the response (Wesoly et al., 1987). Fertilizer treatment should be given late enough to avoid excessive vegetative growth and early enough to encourage cone bud development (Schmidtling, 1983a). In Eastern white pine pollen cone production responded best to a late May application of fertilizer, while seed cone production responded best to a late June fertilizer application (Schmidtling, 1987b). In a lodgepole pine orchard the best formulation for promoting female flowering was ammonium nitrate and early July was the best time for treatment (Ebell, personal communication). For Douglas fir the best time for fertilizing coincides with the start of vegetative bud break (Ebell, 1988). Cone production response to nitrogen treatment can be inductive or direct nutritional and is generally weaker in cultured seed orchards than in nitrogen deficient natural stands (Ebell, 1988). Nitrogen fertilizer combined with irrigation increased basal area and reduced height in radiata pine (Griffin et al., 1984). The study reported here will determine the effect of drought stress and fertilizer application on flowering and height growth in an interior spruce seed orchard.

4.2. Methods

The Shuswap Adams low elevation spruce seed orchard is located at Kalamalka, near Vernon, British Columbia, and produces seed for the Shuswap Adams seed planning zone, which lies east of Kamloops in the transition zone between arid and wet climates in the interior of British Columbia. The 100 parent trees, represented in this orchard, originate from that zone at elevations below 1500 m. In the design each of the 100 clones is represented once in each of the 10 randomized blocks. At the time of this study there were 994 trees in the orchard. Spacing is 5 x 2.5 m. in the first two blocks and 5 x 5 m. in all other blocks. The orchard was established in 1981 with three year old grafts. At the time of the 1988 treatments the orchard trees where 10 years old from grafting. Tree height ranged from 1.3 m. to 4.0 m., with an average of 2.3 $\pm$ 0.5 m. The soil in the orchard is a sandy loam overlaying clay with exposed clay in a portion of the orchard. In 1981 a trickle irrigation system was installed to deliver an average of 10 liters of water per tree per day throughout the growing season. The orchard was designed to produce an average of 10 Kg of seed per year, which is sufficient for the production of 2.6 million plantable seedlings.

Treatments for this study were applied during the 1988 and 1989 growing seasons and consisted of different combinations of irrigation and fertilizer, which were either withheld or given. Treatments were given to the 20 long rows (A to T, each containing 35 tree locations) in the orchard, which include blocks 1 to 7, each containing 100 tree locations. This was done because it is easier to regulate irrigation and fertilizer by row than by individual tree. The inclusion of 7 blocks provides replication of the treatments and the orchard design (randomized blocks) ensures random selection of treatments to individual trees. Treatments were given to all trees in blocks 1 to 7, but trees with a total height of less than 1.5 m. at the beginning of the 1988 growing season were not included in the experiment in order to provide a measure of uniformity in tree size. In 1989 the treatments were modified. New trees were transplanted into the orchard in 1989. These trees received normal irrigation and fertilizer applications. Trees, carrying a good cone crop in 1989, were also given irrigation and fertilizer. The rows, receiving irrigation in 1989 received less water than was given in 1988 (see Irrigation I_1). The end of the drought stress period was earlier (see Irrigation I_0). The fertilizer treatments were included to determine if withholding N will affect height growth. In both years N fertilizer was reduced in the rows indicated. This means that also no S was given in these treatments because the N in the 21-0-0 fertilizer is in the form of ammonium sulphate.

Treatments in 1988.

1. I_1 N_0 : Water and reduced nitrogen, given to rows A, E, I, M and Q.
2. I_0 N_0 : No water and reduced nitrogen, given to rows B, F, J, N, and R.
3. I_1 N_1 : Water and nitrogen, given to rows C, G, K, O and S.
4. I_0 N_1 : No water and nitrogen, given to rows D, H, L, P and T.

Treatments in 1989.

1. $I_1 N_0$: Water and reduced nitrogen, given to rows B, F, J, N, and R.
2. $I_0 N_0$: No water and reduced nitrogen, given to rows A, E, I, M and Q.
3. $I_1 N_1$: Water and nitrogen, given to rows D, H, L, P and T.
4. $I_0 N_1$: No water and nitrogen, given to rows C, G, K, O and S.

Irrigation (I_1): In 1988 water was applied, through the drip irrigation system, in the amount of 20 - 48 liters of water per tree two times per week (i.e. 5.7 - 13.7 liters daily average). In 1989 the amount of water was reduced to 12 liters twice per week (i.e. 3.4 liters daily average). The amount of water applied in a given week was dependent on the weather during that week. Irrigation commenced on April 18 and was terminated on October 10.
No irrigation (I_0):.In 1988 water was withheld from April 18 to July 16. Water was turned on again about one month after completion of shoot elongation, which was observed to take place at different dates, depending on the clone, during the period June 15 - July 1. In 1989 the drought stress period was terminated on June 17, when shoot elongation was approximately 95% complete.
Full Nitrogen (N_1): Various fertilizers were given, using a Vicon spreader to apply fertilizer in bands along the tree rows (table 4.1). The fertilizer applications of a given year include those given in the fall of the previous year (October) because fall applications are not expected to have an effect until the following growing season. Late winter applications (March) of the same year are also included.
Reduced nitrogen (N_0): In both years all ammonium sulphate fertilizer (21-0-0) was withheld in the rows indicated with the exception of trees not included in the study; i.e. those with a total height of less than 1.5 m at the beginning of the 1988 growing season and those carrying a cone crop in 1989.

Table 4.1. Fertilizer applications during 1988 and 1989

		N	N & P	K
October 28	1987	100 Kg/ha 21-0-0		
March 18	1988			200 Kg/ha 0-0-50
April 29	1988		165 Kg/ha 11-55-0	
May 25	1988	70 Kg/ha 34-0-0		
June 10	1988		165 Kg/ha 11-55-0	
June 15	1988	100 Kg/ha 21-0-0		
June 21	1988	70 Kg/ha 34-0-0		
July 5	1988	100 Kg/ha 21-0-0		100 Kg/ha 0-0-50
November 15	1988	100 Kg/ha 21-0-0	100 Kg/ha 11-55-0	100 Kg/ha 0-0-50
May 30	1989		200 Kg/ha 12-51-0	
June 1	1989	100 Kg/ha 21-0-0		200 Kg/ha 0-0-50
June 15	1989	100 Kg/ha 21-0-0		
June 28	1989	100 Kg/ha 21-0-0		

The amounts applied are based on empirical observation over the years, on results of analysis of soil samples taken once every five years and on foliar samples taken every fall. The fall and late winter applications are done when the ground is frozen. Minerals will enter the soil in the spring when the snow melts. This is done so that nutrients are available at the time of beginning root activity and bud swell in the spring. Normally tractor access in the orchard is poor early in the spring because of snow and wet soils so that fertilizer application is not possible at that time.

Observations and analysis

In August 1989 cones were counted on all trees in the experiment. In August 1990 the number of cones on each tree in the experiment was estimated in five classes, namely N (none): 0 -20 cones, L (low): 20 -100 cones, M (medium): 100 - 500 cones, H (high): 500 - 1000 cones and X (extra high): 1000 + cones. For cone crop predictions flower counts are usually done in this manner. The ranges to be used for the estimates in each category are not the same each year but depend on the overall size of the cone crop. The ranges in the five classes are not the same for practical reasons. With larger numbers of cones per tree it becomes increasingly more difficult to estimate small differences. Tree heights were measured to the nearest cm for all trees in the fall of all years from 1987 to 1990. The year to year differences in height were used in the analysis as height increments for 1988 and 1989. Foliar analysis was done for all trees in the experiment for all years from 1988 to 1993. Foliar sampling is done every year in the fall. It is important to do this analysis on material gathered at a time of the year when the mineral content in the needles can be expected to be at a base level and not subject to fluctuations caused by weather and fertilizer applications throughout the growing season. Analyses of variance were done to determine whether or not there was an identifiable effect of drought in 1988 and 1989 on cone production in 1989 and 1990 and on height increment in 1988 and 1989 respectively. The analyses of variance were done with an unbalanced design to include all clones in the experiment and also in two balanced designs, one with two and one with three replications per clone. The reason for this is that the unbalanced design does not allow for estimating the interactions between the different sources of variation. Data from the different sets of observation were pooled to determine the effect of drought alone and the effect of fertilizer alone. The four treatments, which combine drought and fertilizer were also analyzed (table 4.2).

Table 4.2. Analyses of variance done and number of clones included in the unbalanced (UN), and in the balanced designs with 2 or with 3 replications (B2, B3)

Treatment	Cones				Height			
	year	UN	B2	B3	year	UN	B2	B3
1988: water vs drought: $I_1N_0 + I_1N_1$ vs $I_0N_0 + I_0N_1$	1989	98	64	19	1988	95	61	29
1989: water vs drought: $I_1N_0 + I_1N_1$ vs $I_0N_0 + I_0N_1$	1990	96	60	33	1989	95	58	28
1988: red. N vs full N: $I_1N_0 + I_0N_0$ vs $I_1N_1 + I_0N_1$	1989	98			1988	97		
1989: red. N vs full N: $I_1N_0 + I_0N_0$ vs $I_1N_1 + I_0N_1$	1990	98			1989	95		
1988: I_1N_0 vs I_0N_0 vs I_1N_1 vs I_0N_1	1989	95			1988	94		
1989: I_1N_0 vs I_0N_0 vs I_1N_1 vs I_0N_1	1990	94			1989	93		

4.3 Results

The effect of drought on cone production was highly significant ($p=0.01$) in 1989 and 1990. There was also a very strong clonal effect. There were no measurable interactions between the different sources of variation in 1989, but there was a significant ($p=0.05$) interaction between treatment and clones in 1990. The analyses also shows that the application of nitrogen by itself does not affect cone production or height increment significantly. The effect of drought treatment on height increment was highly significant ($p=0.01$) in 1988 and 1989. The four treatments, which were combinations of drought and fertilizer, had a highly significant ($p=0.01$) effect on number of cones in the year following treatment and on height increment during the year of treatment (table 4.3).

Table 4.3. Results of analyses of variance [1)]

source of variation	1988 - 1989 cones 1989	1988 - 1989 height 1988	1989 - 1990 cones 1990	1989 - 1990 height 1989
	drought alone (pooled data)			
drought	**	**	**	**
clone	**	**	**	**
drought x clone	-	-	*	-
	fertilizer alone (pooled data)			
fertilizer	-	-	-	-
clone	**	**	**	*
	drought and fertilizer combination treatments			
drought and fertilizer	**	**	**	**
clone	**	**	**	**

1) - not significant * significant at $p = 0.05$ ** significant at $p = 0.01$

In the following water means irrigation throughout the growing season; drought means irrigation was withheld during the period of shoot elongation; nitrogen means fertilizer was given as shown in table 4.1; and reduced nitrogen means that ammonium sulphate was withheld. The comparison of the means is shown in table 4.4.

A comparison of the means (pooled data) shows that drought increased the average number of cones per tree by 151 (256%) in 1989 and by 126 (280%) in 1990. Drought decreased the average height increment per tree by 12 cm (33%) in 1988 but increased this average by 3 cm (14%) in 1989. Differences related to drought were highly significant (table 4.3). Withholding of nitrogen fertilizer increased the average number of cones per tree by 34 (29%) in 1989 and by 12 (12%) in 1990. Withholding of nitrogen fertilizer decreased the average height increment per tree by 1 cm (3%) in 1988 but increased this average by 1 cm (5%) in 1989. Differences related to fertilizer were not significant.

The water and fertilizer treatments were compared with the controls, which received full irrigation and full nitrogen fertilizer (treatment 3). Water and reduced nitrogen decreased the average number of cones per tree by 64 (70%) in 1989 and by 18 (35%) in 1990. In 1988 this treatment produced no difference in height increment but there was an decrease of 4 cm (15%) in 1989. Drought and reduced nitrogen increased the average number of cones per tree by 182 (199%) in 1989 and by 137 (259%) in 1990. This treatment produced a decrease in average height increment of 14 cm (4%) in 1988 and an increase of 6 cm (24%) in 1989. Drought and nitrogen increased the average number of cones per tree by 57 (62%) in 1989 and by 88 (167%) in 1990. This treatment produced a decrease in average height increment per tree of 11 cm (32%) in 1988 but no difference in 1989. All differences in cone production related to the water and fertilizer treatments compared with the controls were significant.

Table 4.4 Comparison of means [1)]

water	fertilizer	1988 - 1989 average number of cones per tree in 1989		1988 - 1989 height increment 1987-1988		1989 - 1990 average number of cones per tree in 1990		1989 - 1990 height increment 1988-1989	
+		58.9	b	36.2	a	45.1	b	24.1	b
–		209.8	a	24.1	b	171.5	a	27.5	a
	+	117.2	a	28.7	a	99.6	a	24.1	a
	–	151.3	a	27.8	a	111.1	a	25.4	a
+	–	27.7	d	35.2	a	34.4	d	20.6	c
–	–	273.8	a	20.4	b	189.4	a	30.3	a
+	+	91.5	c	34.0	a	52.8	c	24.3	b
–	+	148.0	b	23.0	b	140.6	b	24.2	b

1) means followed by the same letter are not significantly different.

Results of the foliar analysis are given in percent of oven dry weight. Withholding of ammonium nitrate resulted in a decrease of nitrogen in the foliar samples of 1.76 - 1.60 = 0.16% in the non-clay part of the orchard and 2.33 - 1.75 = 0.58% in the clay part in 1988 and of 1.78 - 1.66 = 0.12% in the non-clay part and 2.03 - 1.74 =- 0.29% in the clay part in 1989. In all cases the amount of nitrogen was still sufficient for healthy growth (Ballard and Carter 1986). There were no differences in phosphorous and potassium quantities found but the sulphur quantity was reduced by the withholding of ammonium sulphate by 0.17 - 0.14 = 0.03% in the non-clay portion of the orchard and by 0.17 - 0.16 = 0.01% in the clay portion in 1989. The zinc and manganese content of the foliar samples was affected by the withholding of ammonium sulphate. The amount of manganese was reduced in both years and the amount of zinc was increased in both years. Other micro elements were not greatly affected.

4.4. Discussion

It has become abundantly clear that drought stress applied from the beginning of the growing season until the completion of shoot elongation increases the number of flowers and therefore the number of cones produced in the following year in interior spruce. The strong clonal effect is consistent with a great clone to clone variation in cone production. The results of this study also confirm the assumption, made at the end of chapter 2, that this treatment would have a greater effect in a warm and dry climate than in a relatively cool and moist one. The interaction in the cone crop of 1990 between drought and clone shows that the treatment does not have the same effect on all clones. With the large number of clones involved (table 3.2) this is not surprising because it takes only a few clones, where the effect of drought is clearly different or possibly negative to show interaction in the analysis. It will, however, have management implications if an appreciable number of clones behave differently. It may be necessary to identify these clones as well as tree locations and apply a different treatment to obtain the desired results. The effect of drought on height increment in 1988 is understandable. Drought stressed trees grow slower than those receiving regular irrigation. In 1989, however the drought stressed trees grew on the average faster than those receiving regular irrigation. This may be explained by the fact that the withholding of water was done by row and that the rows were switched in 1989 so that the trees receiving drought stress in 1989 had received regular irrigation in 1988. An ample water supply during the growing season ensures that buds are produced with the benefit of decent growing conditions. The number of needle primordia initiated in each bud will be larger than would be the case under poor growing conditions. The number of needle primordia affects the length of the shoot resulting from the bud during the following year (Pollard 1974). It is therefore not surprising that the height growth of the trees, which were under drought stress in 1989 could be greater than that of those, which were under drought stress in 1988. The differences in cone production, found between the four treatments which combine irrigation regimes and fertilizer applications, indicate that nitrogen fertilizer diminishes the effect of drought. It also indicates that withholding nitrogen fertilizer reinforces the effect of drought or vice versa. Fertilizer application can not be very effective if sufficient water is not available to allow normal uptake of nutrients. The reduction in nitrogen and sulphur content in the needles, caused by withholding ammonium sulphate, is not surprising. The reduced level of nitrogen is still well above the 1.45%, which is considered adequate for white spruce. This may explain the fact that fertilizer treatments alone did not have an effect on cone production or height growth. The conclusion from this experiment is that withholding water during the period of shoot elongation is an effective and easy method to enhance cone crops in interior spruce seed orchards. This should not be done in consecutive years. During the year following treatment the trees, which will be, in all likelihood, carrying a good cone crop must be given normal irrigation throughout the growing season. A sufficient amount of water is important during pollination to ensure that the ovules can form pollination drops of sufficient size. A lack of seed set can be associated with a lack of available water at this critical time.

5. PROMOTION OF FLOWERING IN A LODGEPOLE PINE SEED ORCHARD BY INJECTION OF GIBBERELLIN A4/7

5.1. Introduction

The Prince George Tree Improvement Station (PGTIS), about 15 Km south of Prince George, was established in 1973 to provide a secure land base for research plantations and lodgepole pine seed orchards.

Increased cone production is desirable for several reasons; it reduces the cost of seed, it allows earlier and more vigorous roguing and it meets the higher demand of seed production per tree when, after progeny tests, less desirable clones are removed and the required amount of seed has to come from fewer trees.

The onset of reproductive buds is affected by external (photoperiod, temperature and availability of water) and internal (growth regulators) factors (Longman, 1960). A photoperiod induced flowering hormone is produced in the leaves. After transport it causes the growing point to develop into a generative structure instead of a vegetative one (Thomas et al., 1956; Pharis, 1974; Evans, 1971). Evidence of transmission of the flowering stimulus has been found in lodgepole pine (Wheeler et al., 1980) and Douglas fir (Pharis et al.,1980). Gibberellic acids (GAs) have been found to have growth regulatory properties. They are involved in the control of growth and differentiation in conifer tree species (Pharis and Owens, 1966; Pharis et al.,1975).

Bud primordia can develop into aborted, latent, vegetative, pollen cone or seed cone buds. The number of reproductive buds depends on the number of buds initiated and the number of buds differentiated to become seed or pollen cones (Owens et al., 1986). The flowering response to exogenous GA is caused by the effect on differentiation of buds already initiated and not by a change in the total number of buds (Owens ,1969; Owens and Pharis,1971; Tompsett, 1977; Cecich, 1981).

In Douglas fir GAs, when applied to be available in the new shoots at the time of bud differentiation, promote flowering, otherwise they promote vegetative growth (Pharis et al., 1975). Buds for the following year are initiated about 6 weeks prior to bud burst. How they will develop is determined during the first 11 weeks after bud burst (Owens, 1969). The change from slow (cell division) to rapid (cell elongation) shoot elongation coincides approximately with the time of bud flush. Rootpruning at the time of bud flush did not affect cell division but reduced cell elongation and therefore retarded shoot growth by up to two weeks, thereby shifting the critical morphogenetic phase to a later date, when conditions are more conducive to flowering (Owens et al., 1985: Owens et al., 1986, Owens and Simpson, 1988).

In lodgepole pine the long shoot terminal bud contains a number of cataphyls or bracts, each of which can have one of the following axillary structures (from base to apex): none (sterile cataphyls), short shoot or pollen cone bud primordia, none, short shoot bud primordia, none, and near the apex lateral branch or seed cone bud primordia. The bud primordia in the proximal portion of the new shoot develop earlier than those in the distal portion. Pollen cone and short shoot buds differentiate in August, seed cone and lateral branch buds in September (Owens and Molder, 1975). Cone production takes place over a three year period. Bud differentiation takes place in year one, pollination and conelet development in year two, and fertilization in year three. Seeds develop and cones can be harvested at the end of the third growing season.

Foliar application of GA_3 has promoted flowering in sugi (Hashizume, 1959; Goo, 1966), Norway spruce (Chalupka, 1981), Arizona cypress and Western red cedar (Pharis and Owens, 1966; Pharis and Morf, 1967; Pharis et al., 1969; Owens and Pharis, 1971). Reproduction does not normally start until a juvenile phase has been completed. Aging may involve changes in synthesis or action of hormones (Doorenbos, 1965). Exogenous polar GA can terminate juvenility in Cupressaceae and Taxodineae (Evans, 1971; Pharis et al., 1975). Most cultural treatments, which promote flowering, reduce vegetative growth, thus making GA and assimilates available for flowering (Pharis, 1974; Webber et al., 1985; Owens et al., 1986). In Douglas fir and interior spruce (white and Engelman spruce and their hybrids) drought stress promotes flowering, leads to decreased levels of more polar GA (e.g. GA_3) and increased levels of less polar GA (e.g. GA_4 and GA_7) (Pharis, 1976; Webber et al.,1985). Flowering in conifer tree species can be promoted by cultural treatments such as rootpruning, girdling and drought stress. Increased levels of GA have been found in trees after flower enhancing cultural treatments. The amount of endogenous GA and flowering are positively correlated in Douglas fir (Pharis et al., 1975; Ross and Pharis, 1976), Norway spruce (Tompsett, 1977; Hall, 1988) and Scots pine (Wesoly, 1985). Flower induction through the application of exogenous GA suggests that endogenous levels of GA are insufficient (Tompsett, 1977).

Early attempts at cone induction with species in the Pinaceae through the application of plant hormones were not successful because GA_3 was used. In the Pinaceae $GA_{4/7}$ is correlated with flowering and GA_3 with vegetative growth (Pharis, 1974; Pharis et al., 1975). The application of exogenous $GA_{4/7}$ as a foliar spray has evoked a flowering response in Scots pine (Chalupka, 1981), jack pine (Cecich, 1981; Cecich, 1983), white spruce (Cecich, 1985; Marquart and Hannover, 1985), Engelman spruce (Owens and Simpson, 1988), black spruce (Hall, 1988), Western hemlock (Owens and Colangelli, 1989; Ross, 1989a) and tamarack (Eysteinsson and Greenwood, 1990). $GA_{4/7}$ applied to the bark, buds and injected in branches has promoted flowering in lodgepole pine (Pharis et al., 1975; Wheeler et al., 1980), Douglas fir (Ross and Pharis, 1976; Puritch et al., 1979; Pharis et al., 1980), longleaf pine (Hare, 1977), Sitka spruce (Tompsett, 1977; Philipson and Brown, 1987), slash pine (Hare, 1979), loblolly pine (Hare, 1979; Ross and Greenwood, 1979), radiata pine (Ross et al., 1984), Engelman spruce (Ross, 1985b) and white spruce (Pharis et al., 1986). These studies support the statement that $GA_{4/7}$ promotes flowering in a large number of species in the Pinaceae.

Concentrations of GA, used in the foliar spray experiments, range from 100 to 600 mg/l, dissolved in water or in 5 - 60% ethanol. Usually 0.05 - 0.10% of a surfactant is added. For larger trees this method is cumbersome and expensive. It is much easier to apply a more concentrated GA solution directly into holes drilled in the stem so that the sapstream can carry it to the branches. This method has been successfully used in Douglas fir (Ross et al.;1985a; Ross and Currell; 1989b, Ross and Bower, 1989c), Sitka spruce (Philipson, 1985a; Philipson,1985b; Philipson and Brown, 1987), white spruce (Pharis et al., 1986), Japanese and European larch (Philipson, 1995). The concentration of the GA solution used in these experiments ranges from 20 to 60 g/l in 0.5 to 95% ethanol. The dosage of actual growth regulator is controlled through the amount of solution applied and depends on the size of the tree. It is customary to use the diameter at breast height to determine the number of holes to be drilled. The amount of solution to be applied to each hole remains the same, but the concentration of the solution depends on the species.

The types of hormones required and the timing of application may be specific for each species (Owens, 1969). Whether there will be female or male flowering in response to GA application may depend on hormone concentration, age of graft and timing (Wheeler et al., 1980; Pharis, 1976). In one year old sugi seedlings male flowering was promoted by lower and female flowering by higher concentrations of GA. In older trees lower concentrations promoted especially female flowering. Application in June gave better results than those in August (Hashizume, 1959). In Scots pine male flowering was promoted by spray application of GA4/7 early in the growing season (Chalupka, 1981). The interaction between timing and concentration for female flowering in jack pine shows the importance of timing of the treatments (Cecich, 1983). In radiata pine GA4/7 application prior to bud flush enhanced shoot elongation, but after bud flush it reduced shoot growth (Ross et al., 1984). In Douglas fir GA4/7, when applied prior to bud burst, enhanced shoot elongation but not flowering, but when applied during rapid shoot elongation it enhanced flowering but not shoot length (Webber et al., 1985). In potted Engelman spruce grafts drought during rapid shoot elongation promoted flowering, but if given during late slow shoot elongation it inhibited flowering (Ross et al., 1985a). The effect of exogenous GA on shoot elongation is dependent on timing (Owens et al., 1985; Owens and Colangelli, 1989). In white spruce spray application of GA4/7 during shoot elongation produced more male and female flowering than spraying done after completion of shoot elongation (Cecich, 1985). For the promotion of male flowering in this species hormone applications must be given earlier in the growing season (Pharis et al., 1986). In Engelman spruce pollen cones are produced lower in the crown (where bud flush starts earlier) than seed cones so early treatments will favour male flowering (Owens and Simpson, 1988). In tamarack GA application at the beginning of shoot elongation gave the best results (Eysteinsson and Greenwood, 1990). Correct timing of flower enhancement treatments is essential and dependent on species. For practical use of growth regulators timing must be related to easy to recognize stages of bud and shoot development rather than calendar dates. GA combined with heat, drought or girdling resulted in better flowering than GA alone (Pharis, 1976; Philipson, 1985a; Philipson, 1985b; Philipson and Brown, 1987; Webber et al., 1985; Ross et al., 1985a; Marquart and Hanover, 1985; Pharis et al.,1986).

In Sitka spruce drilling holes in the stem for the injection of GA did not result in damage, but girdling caused dead foliage and stem breakage (Philipson, 1985a). The application of GA in an incision in the bark just below the terminal vegetative bud increased female flowering in white spruce, but also resulted in a number of dead branches (Pharis et al.,1986). GA application, especially when combined with girdling caused needle chlorosis in Douglas fir and interior spruce (Ross and Bower, 1989c). The phytotoxicity is typically confined to the year of treatment, but chlorosis can persist for another two years (Ross, personal communication).

Cone induction may result in a larger proportion of smaller seeds, which may be eliminated in the nursery (see also chapter 6). In sugi and metasequoia GA induced seeds were smaller and weighed less than non-induced seeds, but germinated normally (Puritch et al., 1979). GA induction caused a reduction in seed efficiency (number of filled seeds per cone) as well as an increase in conelet abortion in Douglas fir, but this loss was more than compensated for by the increase in number of cones (Puritch et al., 1979; Hall, 1988; Ross, 1988; Ross,1989a).

The study reported here was carried out in 1991 - 1993 in the Willow Bowron lodgepole pine seed orchard located at the PGTIS. Grafting for this orchard was done in 1976. It was established in 1978 and contains 110 clones. At the time of this study the grafts were 16 years old. Concern about productivity and clonal contribution led to the decision to try using growth regulators to promote flowering. In 1990, which was a good crop year, all clones in the orchard produced cones but only 22% of the clones produced 50% of the crop. Cone induction, if successful, will increase cone production, improve clonal contribution and enhance panmixia. Since the application of GA4/7 has been found very successful and reliable in interior spruce and in view of the results from earlier studies with a number of pine species it was deemed appropriate to try this method of flower enhancement in a lodgepole pine seed orchard. This study will evaluate the effectiveness of stem injections of GA4/7 as a single and double application at different times during the growing season.

5.2. Methods

Twenty three clones were selected for within clone uniformity in crown form and size in the spring of 1991. Five or six trees were selected per clone. For each tree an estimate of female and male flowers in 1991 was recorded. Also, with future damage assessment in mind, the number of shoot tips, damaged by cone harvest, was counted on each tree. One tree per clone was randomly assigned to receive one of six treatments. Only fourteen clones had a sufficient number of trees to receive all six treatments. For each of the remaining clones one of the treatments was omitted at random.

$GA_{4/7}$ applications were done in 1991 in: 1. None; controls, 2. Mid June, 3. End June, 4. Mid July, 5. Mid August, 6. Mid July and mid August. The objectives were to determine if $GA_{4/7}$ stem injections can promote flowering in mature lodgepole pine orchard trees and if different timing is required for the promotion of female or male flowering. In addition the double dose application was included to determine if repeating the treatment during the same growing season would increase the response.

Determination of the dosage for each tree was based on the standard developed for coastal Douglas fir and successfully used in interior spruce. The stem diameter of each tree was measured at approximately 10 cm below the live crown. Trees had been previously pruned to about 40 cm from the ground to facilitate stem injections. The dosage was then determined by deciding on the numbers of injection holes to be drilled in the stem (table 5.1). For the mid June and end June treatments 40 mg $GA_{4/7}$ in 0.5 ml of 95% ethanol was injected in each hole. By mid July it had become clear that the dosage given was high enough to be phytotoxic. Not much could be done for the trees, which had received the mid July treatment already, but for the remaining trees and for all subsequent treatments the dosage was reduced to one third of the original one. Even with the drastically reduced dosage there were signs of phytotoxicity. As a result some trees or entire clones were excluded from further treatments and or from the statistical analyses. This reduced the number of clones to 19 and the number of trees to 100 in 1992 and 93 in 1993.

Table 5.1. Original and adjusted dosages of $GA_{4/7}$ hormone application

		original dosage		adjusted dosage	
diameter (cm)	holes/tree	mg/hole	mg/tree	mg/hole	mg/tree
< 8	2	40.0	80.0	13.3	26.6
8-10	3	40.0	120.0	13.3	39.9
> 10	4	40.0	160.0	13.3	53.2

The application was done as follows. Each hole was drilled with a 6 mm drill bit to 35 mm deep at a slightly downward angle. All holes were placed approximately 10 cm below the lowermost live branch. The second hole was drilled at 180 degrees offset to the first one. The third and fourth holes were drilled at 90 degrees offset in relation to the first two and about 5 cm above them. After injection the holes were plugged with grafting wax as a protection against insects and diseases. The fertilizer regime for all study trees was the same as for the rest of the orchard throughout the growing seasons of 1991, 1992 and 1993. Types of fertilizer and amounts given each year were determined on the basis of an analysis of foliage collected in the fall of the preceding year. Since drought has been identified as an adjunct treatment, which will enhance the effect of $GA_{4/7}$ application, irrigation was withheld from the time of vegetative bud burst to the time of completion of shoot elongation.

It has been stressed by a number of authors that the timing of $GA_{4/7}$ application should be based on the stage of shoot development rather than on calendar date. There may be year to year differences in stages of shoot development by calendar date and there may be a clonal variation in timing of shoot development. Here it was decided to use calendar dates. This is a preliminary study to determine if $GA_{4/7}$ application has an effect on flowering and what approximate timing is most appropriate. Fine tuning of timing will be done in subsequent studies. To characterize the stage of shoot development for each tree at the time of treatment measurements were made on the terminal shoot of one representative first order branch in the upper crown and one in the lower crown. On the date of treatment the following was recorded for all study trees except the controls. Length of the current year's shoot measured from the basal bud scar to the base of the terminal bud, length of the new terminal bud and average length of needles within a single fascicle (short shoot) in the middle of the shoot. From these measurements the stage of phenology at the time of treatment(s) can be expressed as a percentage of final shoot, needle and bud length. These measurements can form the basis for further studies designed to determine if indeed there is a large year to year and/or clone to clone variation in shoot development. Timing of hormone application can then be based on a clearly defined stage of shoot development and would not be the same for all clones or all years.

The number of fully developed and aborted ovulate strobili (females) as well as the number of pollen clusters (males) were counted in 1992 and in 1993. The average number of staminate strobili per cluster was determined for all study trees in 1992. Also in 1993 fully developed cones, resulting from the 1992 flowers, were counted to allow comparison between female flower production in 1992 and the resulting cone production in 1993. By mid July 1991 it had become obvious that $GA_{4/7}$ application was phytotoxic to some trees. In order to assess the extend of the damage tree condition was recorded in September 1991, August 1992 and again in July and October 1993. Each tree was rated according to the degree of chlorosis, needle drop and the number of dead shoot tips, branches and stems (or parts thereof) on a scale of 1 to 13 as follows. 1. no chlorosis, healthy tree; 2. minor chlorosis and/or brown old needles in lower crown; 3. minor chlorosis and/or brown old needles in upper and lower crown; 4. moderate chlorosis and/or brown old needles in entire crown; 5. heavy chlorosis and/or brown old needles in entire crown; 6. as 5 but more pronounced; 7. as 6 but browning including current year's needles in upper crown; 8. dead branch tips and/or sparse crown; 9. dead leader and/or some dead lateral branches; 10. upper crown dead, old and current needles chlorotic; 11. upper crown dead as well as some lower branches; 12. tree three quarters dead, only a few live branches in lower crown; 13. tree dead.

Analyses of variance were done for total, aborted and net females as well as for males counted in 1992 and in 1993. The actual flower counts were adjusted to eliminate a possible bias from the inherent propensity of each tree to produce flowers. The actual flower counts were reduced by the percentage of potential flowering sites occupied in 1991. An unbalanced design was used for these analyses because using the same number of observations for all treatments would have severely reduced the total number of observations available. Since an unbalanced analysis of variance is only valid if the variances in all populations are approximately equal a test of equality of variances (Bartlett's) was done for all of the above. Because there were no replications within treatments and clones the significance of interaction between treatments and clones could not be assessed. Correlation coefficients between total, aborted and net females as well as males counted in 1992 on the one hand and shoot, bud and needle length at the time of $GA_{4/7}$ application expressed as a percentage of their final length on the other hand were calculated and checked for significance. In addition the correlation coefficients between total females and males in 1992 on the one hand and the percentages of female and male flowering sites occupied in 1991 on the other were calculated.

5.3. Results

The 1992 observations clearly show that the application of GA4/7 influenced female flowering in the year following treatment. There was a highly significant (p = 0.01) treatment effect for total, aborted and net females (table 5.2). Application of GA4/7 did not have a significant effect on male flowering. The clonal effect was highly significant (p = 0.01) in all instances.

Table 5.2. Results of analysis of variance of observations in 1992 [1)]

	total females	aborted females	net females	males
treatment	**	**	**	-
clones	**	**	**	**

1) - not significant * significant at p = 0.05 ** significant at p = 0.01

A comparison of the 1992 means (table 5.3) shows that GA4/7 application in mid July was the best treatment for promoting total and net females (i.e. total minus aborted females) with increases over the controls of 77% and 71% respectively. The mid August GA4/7 application resulted in fewer female flowers than the controls, but this difference was not significant. All treatments resulted in significantly higher numbers of aborted females than the controls. For males (total number of clusters) there were no differences between the means.

Table 5.3. Comparison of means in 1992 [1)]

		total females			Aborted females			net females			males		
tr	n	means	SE		means	SE		means	SE		means	SE	
mid jul	18	225.2	39.8	a	12.8	2.2	a	212.2	39.1	a	192.6	32.4	a
end jun	19	167.6	24.9	ab	24.2	5.7	a	143.1	21.8	ab	179.8	28.6	a
mid jun2	18	158.2	25.6	ab	15.8	3.6	a	141.9	24.8	ab	214.4	34.2	a
jul & aug	11	141.7	20.9	ab	13.7	3.4	a	127.9	18.8	ab	180.7	29.6	a
control	18	126.7	16.2	b	3.1	0.7	b	123.7	16.1	b	187.8	18.2	a
mid aug	16	108.4	15.2	b	10.5	3.4	a	97.8	14.5	b	161.8	26.4	a

1) n = number of observations
SE = standard deviation of the mean
means followed by the same letter are not significantly different

The 1993 observations clearly show that the application of GA4/7 did not influence female flowering two years after the treatments (table 5.4). There was no significant treatment effect for total , aborted, net females or for males. The clonal effect was highly significant in all instances (p=0.01).

Table 5.4. Results of analysis of variance of observations in 1993 [1)]

	total females	aborted females	net females	males
treatment	-	-	-	-
clones	**	**	**	**

1) - not significant * significant at p = 0.05 ** significant at p = 0.01

A comparison of the 1993 means (table 5.5) shows that there were no differences between the means of any of the treatments for total, aborted and net females as well as for males. The mid July application (treatment 4) was the only treatment resulting in more females than the controls, but this difference was not significant.

Table 5.5. Comparison of means in 1993 [1)]

		total females			aborted females			net females			males		
tr	n	means	SE		means	SE		means	SE		means	SE	
mid jul	18	131.3	18.6	a	8.1	3.4	a	123.1	19.2	a	162.8	38.3	a
control	18	121.5	12.6	a	3.6	1.0	a	117.7	12.4	a	145.8	29.0	a
end jun	17	116.2	15.6	a	5.9	2.5	a	110.6	15.0	a	187.4	71.9	a
jul & aug	9	102.2	19.0	a	3.8	0.9	a	98.4	18.5	a	137.7	32.5	a
mid jun	16	100.3	17.1	a	4.3	1.9	a	96.1	17.1	a	204.7	51.0	a
mid aug	15	86.1	17.2	a	3.2	1.1	a	82.9	16.8	a	183.2	33.8	a

1) n = number of observations
SE = standard deviation of the mean
means followed by different letters are significantly different

There were no significant correlations between shoot phenology and flowering response to treatment The correlations of females (total, aborted and net) and males, produced in 1992, with the shoot, needle and terminal bud length at the time of treatment in 1991 were all not significant. The correlations between females and males (number ovulate and staminate strobili) produced in 1992 on the one hand and the percentage of potential flowering sites occupied in 1991 on the other hand were positive and significant ($p = 0.05$) but rather weak ($r = 0.45$ and $r = 0.41$ respectively).

In the description of methods it was mentioned that a number of trees were excluded from this study because of early signs of phytotoxicity. Of the original 129 study trees (107 treated) 6 were dead and 11 were severely damaged, with more than half of the crown dead. Of the trees, which received treatment 15% were either dead (5%) or severely damaged (10%). Many other trees sustained less damage but still showed signs of a phytotoxic effect of GA4/7. Of the 17 trees seriously affected 9 had been given a high dosage (40 mg GA4/7/hole), 8 received the reduced dosage (13.3 mg GA4/7/hole) and one tree, which was dead in September 1991, did not receive any GA4/7.

5.4. Discussion

Lodgepole pine appears to be more sensitive to exogenous GA4/7 than interior spruce. Similar, but less dramatic, symptoms of phytotoxicity caused by GA4/7 application have been encountered in white spruce (Pharis et al., 1986), Douglas fir (Ross and Bower, 1989c) and interior spruce (Ross and Cox, personal communication). In the spruce orchards at Skimikin chlorosis in parts of the crown above the point of application was fairly common, but not serious. The damage was greater when GA4/7 was combined with girdling. This adjunct treatment does increase the effect of GA4/7 but has been discontinued because of the increased amount of damage and cost. The fact that in this study about equal numbers of trees seriously affected were in the high and low dosage categories seems to indicate that even the low dosage was too high and that a greater reduction of the dosage must be contemplated in further studies and/or operational application.

Possible interactions between treatments and clones could not be assessed due to the lack of replications. Similarly, the effect of drought treatment on flowering, possible synergisms and interactions with GA4/7 application and clones, could not be determined because this adjunct treatment was given to all study trees.

The correlations between 1992 female and male flowering on the one hand and the percentage of potential flowering sites occupied in 1991 on the other indicates that there is a linear relationship between response to GA4/7 treatment and flowering history. Past experience in the lodgepole pine seed orchards shows that the flowering performance of individual clones is fairly consistent over the years (Fleetham, personal communication). Response to GA4/7 application appears to be greater in clones with a good flowering history. In Douglas fir exogenous GA4/7 promoted flowering in families with a good flowering history, but promoted vegetative growth in families with a poor flowering history (Webber et al. 1985).

Attempts to relate flowering response to shoot phenology did not meet with success. All correlation coefficients were very low and not significant so no conclusion can be drawn from this. On the basis of this study no recommendation can be made for the use of shoot development stage for timing of treatment. Further studies will be necessary to determine if there are large year to year differences in shoot phenology. If there are no significant year to year changes in the dates of completion of shoot elongation, as was found in white spruce (Cecich, 1985), calendar dates can be used to determine timing of GA4/7 application. This would eliminate the need for phenological observations to determine the stage of shoot, bud or needle development. Treatments must be timed to ensure that the hormones are available in the current year's shoots at the time of bud differentiation. In lodgepole pine differentiation takes in place in August for males and in September for females (Owens and Molder, 1975).

The results of this study support the following conclusions about the efficacy of GA4/7 application, timing and dosage for the promotion of flowering in lodgepole pine seed orchards.

1. The application of GA4/7 definitely had an effect on female flowering and the abortion rate in the year following treatment, but the timing and dosages used did not significantly affect male flowering.
2. For the promotion of female flowering in the year following treatment mid July was the best application time. This is about two months prior to the time of bud differentiation.
3. For the promotion of male flowering in the year following treatment, although there were no significant differences, mid June appeared to be the best application time. This is about two months prior to bud differentiation.
4. For the best treatment the losses, caused by abortion, were more than made up for by the increase in total females. This was also demonstrated in Douglas fir (Puritch et al., 1979).
5. There was no carryover effect; i.e. flowering (female and male) two years after treatments was not affected by the treatments.
6. The number of dead and severely damaged trees resulting from the treatments was not affected by dosage. A loss of 15% dead or severely damaged of all treatment trees is too high to consider the application of GA4/7, at the rates used in this study, on a regular basis for the promotion of flowering in an operational seed orchard.

Considering all of these conclusions the application date of mid July is recommended for the promotion of female flowering. A single application date should be used because it is easier and cheaper. For the promotion of male flowering the mid June application date is recommended. It will be best to carefully select individual trees within each clone, which require treatment for the promotion of female, and others for male flowering. Drought as an adjunct treatment requires further study. Timing and duration of the drought period are important. It is also important that the treated trees are well irrigated before and after the drought period. Treatment should not be given every year. Once every four years seems reasonable. This will provide a year of rest and recovery after the crop year. With some refinements of timing and dosage (which will have to be lowered) the application of $GA_{4/7}$ can be used operationally in lodgepole pine seed orchards for the promotion of flowering to increase cone crops and to improve panmixia.

6. THE EFFECT OF CROP SIZE ON CONE AND SEED CHARACTERISTICS AND OF SEED SIZE ON GERMINATION AND SEEDLING SIZE IN INTERIOR SPRUCE

6.1. Introduction

The need to maximize seed production in seed orchards and the success of flower enhancement techniques can lead to very large numbers of cones per tree. Although developing cones seem to have a high priority in terms of being supplied with photosynthates and nutrients there is concern that excessive numbers of cones can not be fully supported by the tree. Good crop years are almost always followed by poor cone crops because there is not enough energy available for the differentiation of reproductive buds when large numbers of cones are developing. In black spruce bud initiation and reproductive bud development is restricted by development of the current year's cones (Caron and Powell, 1987a). In Douglas fir cone production reduces carbohydrate concentration in shoots, reduces growth and number of new shoots and reduces the number of developed buds per shoot (Ebell, 1970). Casual observation in interior spruce has shown that a very heavy cone crop on an individual tree often leads to smaller cones, which produce smaller seeds. Good correlation between cone size and seed size has been found in black spruce (Caron and Powell, 1987b) and in several pine hybrids (Righter, 1945). In white spruce, however, seed weight varies by year but is not related to crop size (Hellum, 1977).

Because seed size seems to affect seedling size many nurseries have adopted the practice of seed grading. Seedlots are segregated by seed size or weight and only the larger or heavier fractions are used for sowing. This leads to larger and more uniform seedlings. Morphological seed grading provides the silviculturist with more uniform planting stock, which allows matching stock size with site conditions (Dobbs 1976). Larger stock survives and grows better than small stock especially on planting sites with heavy weed and brush competition. Seedlings with a large caliper at outplanting had higher survival rates especially on sites where heavy snowfall is common (Hines and Long, 1986). In Douglas fir seedling size is not affected by seed size but heavier seeds produce more living two year old seedlings (Lavender, 1958). Seed size affects seedling size in white spruce (Burgar, 1964), in eastern white pine (Demeritt and Hocker, 1975), western white pine (Perry, 1976), radiata pine (Griffin, 1972), Japanese larch (Logan and Pollard, 1978), Douglas fir (Sorensen and Campbell, 1985) and several pine hybrids (Righter, 1945). The effect of seed size on seedling size is temporary and diminishes with age (Demeritt and Hocker, 1975; Jenkinson, 1975). Differences in early growth related to seed characteristics are unlikely to last much beyond four years (Rohmeder, 1962). Seed size has an effect on germination capacity (total germination) and vigour (speed; defined as germination percent in a given number of days). Growth variation caused by seed size will have only a small effect on time to stand closure and rotation length unless seedlings from large seed have inherently faster growth rates (Sorensen and Campbell, 1985).

There is a strong maternal effect on seed size. The seedcoat and endosperm are maternal tissues and make up most of the weight of the seed. The embryo contributes less than ten percent of the total weight. Differences in germination are consistently related to the female parent in Virginia pine (Bramlett et al., 1983). Maternal and genetic factors could affect seed size and long term seedling growth differently (Sorensen and Campbell, 1985). Seed size influences seedling growth for the first few years only whereas genetic factors determine growing vigour throughout the life of the tree. Nurseries use bulk seedlots, consisting of seed collected from varying numbers of open pollinated parent trees in natural stands or seed orchards. Bulk seedlots therefore contain a number of half sib families. Segregation of bulk seedlots by seed size or weight, followed by the preferential use of large seed for sowing, leads to the elimination of smaller seeds. Genotypes, associated with small seeds, are removed from the population. If there is a relationship between female parent and seed size the practice of using only large seeds could virtually remove entire families from the population. There is no reason to believe that segregation of genes and random assortment during meiosis, which takes place before the seedcoat and endosperm are formed, will happen in a different fashion in different sizes of seed. Embyonic or inherent vigour can therefore be considered to be distributed randomly among all seed sizes. Thus the seedling with the greatest inherent vigour is just as likely to originate from a small as from a large seed (Righter, 1945).

It is of interest to note that studies, resulting in the conclusion that seed size has an effect on seedling size, are based on bulk seedlots segregated in size or weight classes. Where seed from single families was used no such relationship was found. In a study with Ponderosa pine it was found that the relation between family growth and family seed weight was poor after one year ($r=0.44$) and worse after two years ($r=0.32$). Although seed weight varies widely among families from the same origin the influence of family seed weight on seedling growth is weak and quickly lost (Jenkinson, 1975). This seems to suggest that differences in seedling growth are not only caused by seed size but by family differences as well. Each tree produces cones and seed of characteristic size. Sorting seed prior to sowing and using only the heaviest fraction will result in a population which is genetically different from a natural population (Hellum, 1977). In a study on the effect of seed weight on height growth of seedlings in Douglas fir seed weight differences were found to have an effect on culling outcome; i.e. if seed weight differences were 50% or more most of the culled seedlings started out from lighter seeds (Sorensen and Campbell, 1985). In a study with a number of Douglas fir families it was found that culling by seed weight would remove entire families and that retaining the heaviest one third of the seed would result in sowing only fifty percent of the families, none of which ranked high in a ten year progeny test (Silen and Osterhaus, 1979).

In the nurseries in British Columbia planting stock is graded at the time of lifting and prior to storage or shipping. There is a morphological as well as a physiological component to the culling rules. Seedlings of a specific stock type must conform to strict height and diameter guidelines. For instance an interior spruce seedling, grown in one season in a PSB 313B (plug styro block, 160 cavities per block, each cavity 3 cm wide and 12.7 cm deep, with a volume of 65 cm^3 filled with a peat perlite mix), must have a height of 12 to 25 cm, with a target of 17 cm, and a minimum rootcollar diameter of 2.4 mm, with a target of 3.0 mm (Scagel et al., 1993). All seedlings must be in good health and free of damage. Genetically improved seed from seed orchards is not treated differently. Resulting seedlings must conform to the same standards. Since there is no reason to believe that inherent vigour is related to the size of one or two year old seedlings it can be argued that seedling populations are genetically altered during the sorting process. Thus morphological sorting leads to the use of larger seedlings in field plantations whereby families with small seeds and therefore small initial seedling size may be eliminated. Sorting of planting stock in the nursery will have the same effect as eliminating small seed prior to sowing.

The objectives of the study reported here are to determine for interior spruce whether:

- two trees of the same clone produce cones and seeds of different size when one is allowed to develop all conelets while the other is forced into a light crop situation by removing approximately 75% of its conelets,
- two trees of the same clone produce cones and seeds of different size when one is carrying a large cone crop while the other is carrying a small cone crop,
- seed size affects germination capacity and vigour,
- seed size affects the size of one year old seedlings.

6.2. Methods

This study was done in the Prince George (PG) and Prince Rupert (PR) breed arboreta at the Kalamalka Forestry Center near Vernon, British Columbia, Canada. These breed arboreta were established in 1976 using four year old interior spruce grafts moved to Vernon from Prince George. For each clone four trees were planted in a clonal row design; i.e. the four trees belonging to the same clone were planted adjacent to each other in a row. This design is different from the random block design used in seed orchards. The reason for this is that the purpose of this plantation is to allow the carrying out of controlled crossing and not the production of seed for reforestation. If seed production is considered in a breed arboretum controlled crossing or mass pollination with isolation of female flowers must be used to ensure panmixia (random mating among all desired clones) and to eliminate or minimize self pollination. The clones represent parent trees selected in the McGregor (PG) and the Bulkley Valley (PR) seed planning zones. Two PG clones and three PR clones were selected in 1987. The criteria used were: there must be two trees in the clone about equal in size and vigour and each one must be bearing a heavy cone crop (at least 1000 conelets) and there must be a third tree bearing a light crop (less than 1000 conelets). In the spring of 1987 thinning (removal of approximately 75% of the conelets) was done on one of the two heavy crop trees in each clone. This created a situation where there was one tree with a heavy cone crop, one with a thinned (artificial light) cone crop and one with a natural light cone crop in each of the five clones used for this study. In August 1987 cones were collected from each of the 15 trees included in the study (three treatments and five clones).

From each tree 25 cones were randomly selected for measurement of cone width, length and weight. For cone width and length there were 25 individual observations for each treatment and each clone. Cone weight was determined by weighing 25 cones and using the total weight to calculate the average weight per cone for each tree included in the study. Seed was extracted and the 100 seed weight was determined by weighing 400 seeds and dividing the total by four for each tree included in the study. Germination and nursery tests were only done for the seed from trees with a heavy and trees with a light cone crop. Trees with a heavy crop that had been thinned were not included in the germination and nursery tests because by this time it had become obvious that thinning had not had much of an effect on seed size (tables 6.1 and 6.3).

Germination capacity (% germination after 29 days) was determined in December 1988. On 1 December two samples of 50 seeds each were placed in a petri dish on blotter paper, moistened with distilled water, on a layer of perlite. The petri dishes were placed in an incubator and kept at 25 - 30 °C. Germinants were counted and removed on December 5, 8, 13, 20 and 29.

Nursery performance was determined in 1992. For each treatment and clone 80 seeds were sown in PSB 313B (160 cavities per block, each cavity 3 cm wide and 12.7 cm deep with a volume of 65 cm^3 filled with a peat, perlite mix) on March 30. Seedlings were grown in a greenhouse under normal nursery culture and growing conditions for one growing season. They were grown under natural daylength with two hours of supplemental light in the middle of the night till June 10, when the supplemental light was discontinued. Fertilizer was applied two or three times weekly (once every three days); i.e. a highly soluble fertilizer (20:20:20) was injected in the water supply in the amount of 100 ppm N. The fertilizer used contained 20% N, 20% P_2O_5 and 20% K_2O. The amount of fertilizer used to apply 100 ppm of N was 100/20 x 100 = 500 grams per 1000 liters. The amount of P applied was 500 x 0.44 x 0.20 = 44 ppm and the amount of K applied was 500 x 0.83 x 0.20 = 83 ppm. Watering was done when required, depending on moisture conditions. On June 10 the polyethylene cover of the greenhouse was removed and the fertilizer was changed to 8:20:30 in the amount of 50 ppm N to start the hardening off process (lignification and budset). The fertilizer used contained 8% N, 20% P_2O_5

and 30% K_2O. The amount of fertilizer used to apply 50 ppm N was 100/8 x 50 = 625 grams/ 1000 liters. The amount of P applied was 625 x 0.44 x 0.20 = 55 ppm and the amount of K applied was 625 x 0.83 x 0.30 = 155 ppm. These conditions were maintained till October when the seedlings were lifted and stored at -2°C. For each treatment and clone 50 seedlings were randomly selected in September prior to lifting. Seedling height was measured in cm and root collar diameter in mm. Treatments and observations are summarized below.

Treatments:
1. Heavy cone crop not thinned (h),
2. Heavy cone crop thinned (t),
3. Light cone crop (l).

Observations:
1987: Cone width; 375 observations (3 treatments x 5 clones x 25 cones),
1987: Cone length; 375 observations (3 treatments x 5 clones x 25 cones),
1987: Cone weight: 15 observations (3 treatments x 5 clones),
1987: 100 seed weight; 15 observations (3 treatments x 5 clones),
1988: germination; 20 observations (2 treatments x 5 clones x 2 lots),
1992: nursery performance; 500 observations (2 treatments x 5 clones x 50 seedlings).

6.3. Results

The averages per tree of the 25 observations on cone width and length, the average cone weight as determined from a sample of 25 cones, and the average 100 seed weight as determined from a sample of 400 seeds are shown in table 6.1.

Table 6.1. Cone and seed characteristics by clone and treatment [1)]

clone	treatm	cone			100 seed
		width mm	length mm	weight g	weight g
PG 170	heavy	28.96	51.28	1.94	0.21
	thinned	30.44	55.56	2.67	0.25
	light	28.88	50.52	2.11	0.23
PG 130	heavy	22.44	50.64	1.63	0.20
	thinned	26.12	51.48	1.88	0.21
	light	33.92	58.28	3.12	0.31
PR 50	heavy	19.76	48.48	1.28	0.16
	thinned	21.20	51.04	1.85	0.18
	light	22.88	51.68	2.18	0.20
PG 75	heavy	20.76	49.64	1.56	0.17
	thinned	20.28	46.00	1.45	0.15
	light	26.76	58.04	2.90	0.24
PR 54	heavy	23.16	55.64	2.10	0.20
	thinned	23.76	60.44	2.80	0.22
	light	23.76	60.60	2.68	0.22

1) heavy = heavy crop not thinned
thinned = heavy crop thinned (artificially light)
light = light crop (naturally light)

The light cone crop produced generally larger and heavier cones as well as heavier seeds than the heavy cone crop. Results from the thinned crop were less clear. Size and weight of cones and seed from the thinned crop were not much different from either the light or the heavy crop. The four characteristics were found to be positively correlated. Strong relationships were found between cone length and cone weight (r = 0.92), between cone width and 100 seed weight (r = 0.91) as well as between cone weight and 100 seed weight (r = 0.87).

Table 6.2. Results of analyses of variance for cone and seed characteristics [1)]

	source	sum sq	df	mean sq	F
cone width	treatment	1 164	2	582	3.39
	clones	3 555	4	889	5.18 *
	tr x cl	1 372	8	172	35.69 **
	error	1 730	360	5	
	total	7 823	374		
cone length	treatment	1 631	2	815	2.81
	clones	3 671	4	918	3.16
	tr x cl	2 323	8	290	16.85 **
	error	6 202	360	17	
	total	13 825	374		
cone weight	treatment	2.00	2	1.00	5.15 *
	clones	1.00	4	0.25	1.29
	residual	1.56	8	0.19	
	total	4.56	14		
seed weight	treatment	0.007	2	0.004	4.46 *
	clones	0.008	4	0.002	2.55
	residual	0.006	8	0.001	
	total	0.022	14		

1) * = significant at p = 0.05 ** = significant at p = 0.01

Table 6.2. shows the results of analyses of variance for the four characteristics studied. The treatment effect was significant only for cone and seed weight (p=0.05). One clone (PR 54) did not show much of a treatment effect on cone width, but still had a lower value for the heavy crop. In one of the clones (PG 170) cone width and length were greater for the heavy crop (table 6.1). This suggests a treatment by clone interaction, which was indeed found. The interaction could not be tested for cone weight and seed weight because instead of individual measurements only averages were determined. Without the individual measurements the possible interaction variances and the error variance cannot be separated and form together the residual variance. Where a significant interaction was found the mean squares of the interaction was used as the denominator for the calculation of F. For cone and seed weight the measures were expressed in grams. Three of the clones (PG 130, PR 50 and PG 75) clearly showed a treatment effect, with all cone and seed characteristics observed consistently lower for the heavy crop than for the light crop. This was confirmed by paired t tests done to compare treatments for each individual clone.

Table 6.3. Cone and seed characteristics by treatment [1]

treatm	cone						100 seed	
	width mm		length mm		weight g		weight g	
	mean	SE	mean	SE	mean	SE	mean	SE
heavy	23.02	0.35a	50.74	0.41 a	1.70	0.14 a	0.19	0.01 a
thinned	24.36	0.37a	52.90	0.57 b	2.13	0.26 ab	0.20	0.02 ab
light	27.24	0.41b	55.82	0.54 c	2.60	0.20 b	0.24	0.02 b

1) SE = standard deviation of the mean
means followed by the same letter are not significantly different.

Table 6.3. presents the treatment means of the four characteristics. The light crop was always larger than the heavy crop with the thinned crop in between. This was not always the case for each clone due to a strong clone by treatment interaction (tables 6.1. and 6.2.). This interaction was also the reason why the treatment effects for cone width and cone length were not statistically significant (table 6.2.).

Cone and seed weight means were progressively larger for heavy, thinned and light cone crops. However, the differences in seed weight between light and thinned as well as between thinned and heavy were not considered large enough to justify including seed of the thinned crop in the germination and nursery performance trials (table 6.3). For this reason the germination and nursery performance trials were done with seed from the heavy crop and seed from the light crop, so that there were only two treatments, namely small and large seed.

Table 6.4. Results of analyses of variance for germination and seedling height [1]

	source	sum sq	df	mean sq	F
% germination	treatment	22	1	22	0.76
	clones	1 721	4	430	14.81 **
	tr x cl	203	4	51	1.74
	error	291	10	29	
	total	2 236	19		
seedling height	treatment	260	1	260	6.80
	clones	1 951	4	488	12.76 *
	tr x cl	153	4	38	4.48 **
	error	4 183	490	9	
	total	6 547	499		

1) * = significant at p = 0.05 ** = significant at p = 0.01

Results of the analysis of variance for germination and seedling height are shown in table 6.4. The treatment effects were not significant. The clone effects for germination (p=0.01) and seedling height (p=0.05) as well as the clone by treatment interaction for seedling height (p=0.01) were significant.

Table 6.5 Mean germination percentage and its standard deviation [1)]

clone	small seed				large seed				all seed			
	n	mean	SE		n	mean	SE		n	mean	SE	
PG 170	2	99.00	1.00	a	2	96.50	1.50	a	4	97.75	1.03	a
PG 130	2	97.00	1.00	a	2	94.50	1.50	a	4	95.75	1.03	a
PR 50	2	90.00	4.00	ab	2	86.00	3.00	ab	4	88.00	2.35	b
PG 75	2	71.00	7.00	bc	2	82.50	1.50	b	4	76.75	4.42	b
PR 54	2	71.50	2.50	c	2	79.50	7.50	b	4	75.50	3.97	b
all clones	10	85.70	4.25		10	87.80	2.55		20	86.75	2.43	

1) n = number of observations
SE = standard deviation of the mean
means followed by the same letter are not significantly different

In accordance with the results of the analysis of variance no significant differences in germination between small and large seed were detected in a comparison of the means, but the clonal effect was clearly visible in this comparison (table 6.5). In the nursery performance trial seedling height was greater for large seeds than for small seeds, but the analysis of variance did not show a significant treatment effect. A comparison of the means and their standard deviations (table 6.6.) suggests that nursery height was greater for large seed than for small seed in three of the clones, namely PR 50, PG 75, and PR 54. This was confirmed by paired t tests ($p = 0.01$). For the other two clones there was no significant difference. A comparison of the means for all small seed and all large seed and their standard deviations, as well as the results of paired t tests, strongly suggest that seedling height is greater for large than for small seed. The clonal effect on seedling height, found in the analysis of variance, can also be seen in table 6.6.

Table 6.6 Mean seedling height in cm and its standard deviation [1)]

Clone	small seed				large seed				all seed			
	n	Mean	SE		n	mean	SE		n	mean	SE	
PG 170	50	19.26	0.43	a	50	19.34	0.49	a	100	19.30	0.32	a
PG 130	50	16.73	0.39	b	50	16.89	0.40	b	100	16.81	0.28	b
PR 50 *	50	15.37	0.54	b	50	17.99	0.35	ab	100	16.68	0.35	b
PG 75 *	50	13.05	0.32	c	50	15.49	0.40	c	100	14.27	0.28	c
PR 54 *	50	12.88	0.34	c	50	14.80	0.41	c	100	13.84	0.28	c
All clones	250	15.46	0.24		250	16.90	0.21		500	16.18	0.16	

1) n = number of observations
SE = standard deviation of the mean
means followed by the same letter are not significantly different
* = indicates clones which showed significant differences between small and large seed

A summary of the results of the analyses of variance (table 6.7) shows that the size of the cone crop significantly affects the weight of cones and the weight of seed. It does not significantly affect cone size, germination percentage or seedling height. The analyses show significant clonal effects for cone width, germination and seedling height as well as clone by treatment interaction for cone width, cone length and seedling height.

Table 6.7. Summary of results of analyses of variance [1)]

source	width	cone length	weight	seed weight	germ [2)] percent	seedling [2)] height
treatment	-	-	*	*	-	-
clones	*	-	-	-	**	*
tr x cl	**	**	not done	not done	-	**

1) - not significant * significant at $p = 0.05$ ** significant at $p = 0.01$
2) germination and nursery tests done with small (heavy crop) and large (light crop) seed only

Planting stock standards, currently in use in British Columbia, specify that PSB 313B interior spruce seedlings must have a minimum rootcollar diameter of 2.4 mm and a height between 12 and 25 cm. Of all the seedlings in this study only 46% was acceptable under these stock standards. The low number of acceptable seedlings was largely caused by small diameters (table 6.8). The percentage of acceptable seedlings was low for all clones. However, the results of this study did not show that entire families (clonal seedlots) would have been removed by the nursery culling process.

Table 6.8 Mean seedling diameter in mm and its standard deviation [1)]

Clone	small seed				large seed				all seed			
	n	Mean	SE		n	mean	SE		n	mean	SE	
PG 170	50	2.36	0.06	a	50	2.33	0.05	a	100	2.34	0.04	a
PG 130	50	2.30	0.06	ab	50	2.35	0.06	a	100	2.33	0.04	a
PR 50	50	2.51	0.08	a	50	2.34	0.06	a	100	2.42	0.05	a
PG 75	50	2.19	0.05	b	50	2.20	0.06	a	100	2.20	0.04	b
PR 54	50	2.35	0.06	a	50	2.31	0.06	a	100	2.33	0.04	a
All clones	250	2.34	0.03		250	2.31	0.03		500	2.32	0.02	

1) n = number of observations
SE = standard deviation of the mean
means followed by the same letter are not significantly different

As can be seen in tables 6.6 and 6.8 seedling heights were consistently larger for large seed, but the diameters were not. The large seed produced seedlings with slightly smaller diameters, but the difference was not significant.

6.4. Discussion

The fact that a heavy crop produced smaller seeds than a light crop suggests that an artificially light crop could be expected to produce larger seeds. That this was not the case in this study was probably caused by the fact that thinning was not done till mid June. By this time much of the cone and seed development had already taken place. It follows that any impact on seed size can only be expected when removal of conelets is done as soon as they become visible.

Germination percentage was higher for large seeds. That this difference was not significant may be explained by the fact that the seed size differences between treatments were not large enough; i.e. the range of possible seed sizes may have been greater if more clones had been included in the study. A larger sample may be required to detect differences.

The nursery performance test was judged by seedling heights only because root collar diameters were very similar in the two seed size categories as well as in the five clonal lots used. The lack of difference in diameters may have been caused by competition for space in the PSB 313B. This effect was slightly more pronounced in the large seed category, where heights were larger and diameters were smaller than in the small seed category (tables 6.6 and 6.8). The large percentage of seedlings with a rootcollar diameter below the standard could have been caused by the late sowing date and the container type. The PSB 313B (160 cavities per block) has been discontinued for spruce because diameters are often too small. It has been replaced by other container types such as the PSB 410 (120 cavities) and the PSB 415B (77 cavities). Cavity spacing can affect seedling diameter. The interaction between seed size and female parent indicates that if small seed grows into small seedlings in one family it will not necessarily grow into small seedlings in another family. The strong relationship between female parent and nursery performance means that it is entirely possible that nursery culling will virtually remove entire families and that the genetic composition of a population can be affected by this practice. It is interesting that in three of the families (clonal lots) seedling height was significantly larger for large seed, but in the other two it was not (table 6.6).

Estimates of the percentage of a seedling crop removed by culling vary widely among nurseries and range from 5% to 30%. Since inherent vigour of trees and therefore their long term growth potential are not related to seed or seedling size a concern about the application of standard nursery practices to genetically improved seedlots is still valid. It is possible, but not proven by this study, that seedlings produced from small seeds can have large inherent vigour but are not capable to reach a sufficient size in one growing season. Thus there may be a danger that individual trees or indeed entire families, which contain good growing vigour potential throughout the rotation, are removed from the population by the nursery culling process, which applies a selection process on the basis of first year growth only and does not consider long term growth potential. In addition it is common practice in British Columbia nurseries to double sow (two seeds per cavity) when the germination percentage of a seedlot is below 95%. This is done because it reduces the cost per seedling produced. One of two seedlings in each cavity will have to be removed early in the growing season. This process, known as thinning, will favour early germinants (El-Kassaby, 1992). It is not known if there is a relationship between germination vigour and long term (i.e. throughout the rotation) growth potential. The effect of seed size on seedling growth is only expressed in the first few years and the inherent capacity for vigorous growth may not be fully expressed till after outplanting. However, the decision to retain or remove a seedling is made at the nursery after one growing season (container stock) or after two growing seasons (bareroot stock). In order to minimize the consequences of the nursery culling system for genetically improved seed it may be best to grow seedlings in segregated lots, apply different culling standards to each, and mix the seedlings prior to outplanting.

It is highly unlikely that conelet thinning will be considered as a practical method of ensuring the production of large seeds because of the enormous amount of work involved. If under specific circumstances thinning is found necessary it will be advisable to do it as early as possible.

Although the intent of the study reported here was more to find out if conelet thinning, to increase cone and seed size in a heavy crop year, would be appropriate the relationships found indicate that it will be worth while to carry out another study to follow up on relationships between families, seed size and seedling size. The effect of nursery culture and culling standards on the genetic composition of a seedlot after outplanting as compared to the original seedlot must be thoroughly investigated. Gains, obtained during the breeding and selection cycle, could be affected by what happens in the nursery. This study, if undertaken, should include a larger number of female parents and preferably only those for which ten year progeny test information is available so that predictions about the effect of culling and recommendations about optimal nursery practices for genetically improved seed can be made.

7. PROGENY TESTING IN INTERIOR SPRUCE IN BRITISH COLUMBIA TO INCREASE GENETIC GAIN

7.1. Introduction

7.1.1. Genetic variation

It is essential to acquire some knowledge about the genetic variation of the species before embarking on a tree improvement program. Some basic questions need to be answered first. Is it always best to use local seed for reforestation ? What is the definition of local seed ? How will trees behave when they come from seed from different locations ? Are populations within the species strongly adapted to local environments ? Does elevation of the seed source play an important role ? How far can the seed source be removed from the planting site ? Is the between population variation large compared to the tree to tree variation within a population ? Is the variation clinal or ecotypical ?

If environmental factors follow a gentle gradient the variation is likely to be clinal. If the gradient is very steep, or if environmental factors exerting selection pressure are discontinuous, the variation will be ecotypical (Nienstadt, 1975). In the interior of British Columbia environmental gradients are gentle with a few notable exceptions. A typical steep gradient is formed by the Rocky Mountains east of the Finlay and Parsnip Rivers. On the west side are the Engelman Spruce Subalpine Fir, the Sub Boreal Spruce and the Spruce Willow Birch biogeoclimatic zones and on the east side the Boreal White and Black Spruce biogeoclimatic zone. The variation in interior spruce is mostly clinal. Another example is the transition from the coastal region to the interior. Transfer of seed from the coast to the interior is not recommended. A good illustration of this can be seen in the lodgepole pine interior provenance test plantation at the Prince George Tree Improvement Station. Here 153 lodgepole pine provenances, from locations throughout the natural habitat of the species, were planted in 1973. Provenances from coastal British Columbia have shown high mortality and poor growth. Provenances from central interior British Columbia have shown good survival and growth.

Perennial species, and especially trees which live very long, are exposed to fluctuating living conditions (weather and its interactions with soil and topography). Tree populations must be able to adjust to climate changes in order to maintain their fitness through many generations. At the same time tree populations must have immediate fitness, which is the ability to survive and reproduce during the current generation. Maintaining flexibility, which is the ability of the population to adjust to changing living conditions, comes at a cost. The population must retain genetic variability for future fitness. This tends to go at the expense of maximum immediate fitness (Nienstaedt, 1975). Pioneer species are the first to establish themselves following a catastrophe. Pioneer populations have apparently sacrificed some of their immediate fitness for an increase in variability (the sum of existing genetic variation and the potential of genetic variation hidden in not yet realized gene combinations and heterozygosity). Successionally advanced species have sacrificed some of their variability for some specialization to specific site conditions (Rehfeld and Lester, 1968). Some pioneer species however, such as red pine, are exceptional in that they are highly adapted and have a low variability (Nienstaedt, 1975). Interior spruce, which is considered a successionally advanced species, is another exception in this regard. It shows greater variation in height growth within than between populations. This does not seem to indicate a high degree of specialization (Kiss, personal communication).

7.1.2. Seedzones

Tree improvement started with seed registration to ensure use of appropriate seed sources so that planting stock could be expected to be adapted to the environment in which it was planted. This can only be done if guidelines for seed transfer have been established. Seed transfer over long distances is impossible if there is site specific adaptation (Kleinschmit, 1979). The use of seed from locations with dramatically different growing conditions can lead to poor survival and growth. The following example illustrates this. Interior spruce progeny from high elevations (1600 m and more) invariably shows less vigorous growth than progeny from lower elevations when planted at lower elevations. It is entirely possible that natural selection at low elevations (or generally in areas with better growing conditions) is based on competitive vigour, whereas at higher elevations (or generally in areas with poor growing conditions) it is based on survival of harsh growing conditions (Illingworth, personal communication). Transfer of seed can be restricted by the delineation of certain areas and the stipulation that within each of these only seed from within the boundaries of that area can be used for reforestation. These areas are known as seed planning zones. Originally these zones were delineated according to biogeoclimatic classification, which defined areas in accordance with climate, soils and natural vegetation (see section 2. 3). Refinement of the biogeoclimatic classification has led to changes in seed planning zone boundaries. Provenance testing, which involves testing of seed from many different origins in a number of locations, has led to an increase in knowledge about the limits of seed transfer, which led to modification of seed planning zone boundaries and seed transfer guidelines.

7.1.3. Selection

The collection of cones in natural stands must be guided by the principle that the best phenotypes, in terms of desired characteristics, should be used. Poorly formed and slow growing trees must be avoided. Squirrels gather cones in late summer and fall in order to have a food supply in the winter. It has been noticed that they only gather healthy cones and that seed from squirrel caches generally has a higher germination percentage than seed gathered by people. However, squirrels do not pay attention to the growing vigour or form of the tree they gather cones from. For this reason collecting cones for reforestation from squirrel caches is not recommended.

Using the best phenotypes in natural stands to collect cones from guarantees only the superiority of the female parents. Male participation is provided by pollen from neighbouring trees, which were not selected. Collecting pollen from superior parents and applying it to others is impractical. The selected parent trees can be vegetatively propagated through grafting. This creates a clone for each parent tree. Each individual in one clone is genetically identical to the parent tree. These clones can be planted in a common garden where they can be encouraged to produce flowers and to engage in random mating. These gardens are known as seed orchards. One method for delivering genetic gain to the operational plantation is the establishment of seed orchards.

Parent trees were selected within stands because within population variation is larger than between population variation in interior spruce. Phenotypically superior individuals were selected in a stand and a good geographical representation within the seed planning zone was obtained. The criteria used to select individual parent trees included: growing vigour (greater height and diameter than neighbouring trees of the same age), straightness (straight stem without defects such as crooks, forks, curves or twists), stem cleaning (a relatively large portion of the lower stem without branches), branch form (small diameter branches at an angle of 90° with the stem), crown form (narrow and pyramidal) and resistance (apparently free from disease and insects).

In interior spruce most seed orchards are based on phenotypical selections. For each seed planning zone all selected parent trees were included in the orchard. At the time the first objective was the production of seed per se. Progeny from seed orchards is generally superior to progeny from natural stands because of selection and reduction of inbreeding (Kleinschmit, 1979). Genetic improvement would come later through progeny testing, using open pollinated progenies. Roguing (removal of less desirable parents on the basis of progeny test results) of existing orchards would then be carried out. This meant that, in addition to collecting scion material for grafting to create seed orchards and clone banks (plantations for the preservation of genotypes), cones had to be collected from the selected parent trees. This should be done in a good seed year when sufficient amounts of pollen are available. This maximizes cross pollination (Silen, 1966). Selecting trees in a poor seed year may result in inbred or selfed progeny because of a general lack of pollen and most of it coming from nearby trees, which are in all probability at least somewhat related to the selected tree. Neighbouring white spruce trees in natural stands appear to be related at about the half sib level (Park and Fowler, 1984). Self pollination in white spruce not only increases the percentage of empty seeds but also reduces germination and subsequent growth (Ying, 1978; Fowler and Park, 1983). In addition selection in a poor seed year may bias the selector in the direction of flowering trees. High fecundity is heritable and trees with a good flowering history may not assign as much of their resources to the production of wood. Selection for abundant flowering is a dubious venture since cones and pollen require a significant portion of the metabolites otherwise available for vegetative growth (Libby et al., 1969). On the other hand the selection of parent trees, which do not produce many flowers may create problems in the seed orchard. One of the difficulties in selecting a sufficient number (e.g. 250 per breeding zone) of parent trees and collect open pollinated seed is crop periodicity in natural stands of interior spruce.

Vegetative propagation can be used directly for reforestation. This includes the use of rooted cuttings (stecklings) or somatic embryogenesis (emblings). The risks of clonal forestry increase with the size of the plantation and with the heterogeneity of the planting site (Kleinschmit, 1979, 1983). Plantations based on selected clones tend to be more productive than plantations based on seedlings derived from seed orchards because clonal selection gives greater genetic gain than the half sib family selection on which seed orchards are based. Clonal selection is more efficient (Morgenstern, 1980) because all genetic variance is selectable. With half sib family selection only a small part of the genetic variance is selectable. In addition vegetative propagation takes less time. If gain is to be realized at year 20 (from commencement of the tree improvement program) selection of ortets for vegetative propagation can be based on progeny test results from 15 year measurements. To realize gain through seed orchards at year 20 selection of parent trees must be based on 3 year progeny test measurements. Gains from 15 year measurements are likely to be greater than gains from 3 year measurements (Matheson and Lindgren, 1985).

7.1.4. Progeny testing

The use of progenies, obtained through open pollination, to test parent trees has been a standard procedure in the interior of British Columbia. The advantage of this method of testing is that it brings results in terms of parent tree ranking sooner than controlled crossing, which involves a waiting period of up to 15 years before all intended crosses have been made in a clone bank or breed arboretum. A disadvantage may be that each parent tree to be tested receives pollen from a different group of trees and that therefore the comparison of progeny performance is not as good as in a controlled crossing or in a polycross. However, good estimates of general combining ability can be obtained, provided that seed collection is done in a good seed year. Parent tree selection in the interior has been much less intensive than in the coastal Douglas fir program. The reasoning for this was that it is better to spend time and effort on progeny testing than on elaborate phenotypical selection. That testing is more important than initial selection was shown by poor rank correlation between phenotypically superior parent trees in interior spruce and their offspring (Kiss, personal communication). Similar results have been found in Norway spruce (Rohmeder and Schönbach, 1959) Ten year results of open pollinated Douglas fir progeny tests showed that family performances of the phenotypicaly best, second best and randomly selected parent trees were not sufficiently different. This indicates that phenotypical selection by itself is not efficient (Silen and Mandel, 1982).

Progeny testing is essential for the development and improvement of seed orchards. Testing can be done immediately after selection. Orchard establishment can be deferred until information about the ranking of parent trees is available. This information can then be used to include only the better parent trees in the orchard. For the Shuswap Adams seed orchards this was not done. The orchards were established after selection had been completed and all selected parent trees were included.

Further enhancement of the expected genetic gain from these orchards through roguing was considered desirable. Open pollinated seed had been collected from a limited number of parent trees. Therefore another method of progeny testing had to be found. Controlled crossing, increased efforts to obtain open pollinated seed, use of individual seedlots as produced under normal orchard management practices (i.e. open pollinated orchard seed) and using a polycross were considered. In the context of this report the polycross test is defined as a progeny test to assess general combining ability, in which a mixture of pollen is artificially applied to each parent to be tested (the expression topcross is used in British Columbia to indicate controlled crossing between top ranked parents). In a polycross the male contribution is exactly the same for all females. This promotes the fairness of the test (Park, 1987). Polycross matings have the same advantages and disadvantages as open pollination but ensure that the number of pollen parents (of the half sib families) is not limited (e.g. during a poor seed year in a natural stand) or biased (Bridgewater and Ledig; 1986, Libby et al. 1969). Financial constraints limited the options available and the polycross was chosen.

7.1.5. Breeding

In the long term productivity of forest lands can be enhanced considerably by tree improvement programs. In agriculture even slight genotypic improvements in yield are desirable since they may be expected to recur again and again in the progeny of the improved variety (Sinnott et al., 1958). In forest trees even a small genetic improvement in growing vigour can become quite significant if the planting program is large and is carried out over a considerable number of years. Genetically better trees must be used in conjunction with proper site preparation and the best silvicultural methods for stand establishment and maintenance in order to realize the optimum benefit (Weir and Zobel, 1975). The objectives of a tree improvement program can include achieving of an increase in adaptability, in resistance to pests, in growth rate, in tree form and in wood quality (Zobel, 1974). Tree improvement aims to find or create and mass produce genetically superior trees, which have the desired characteristics and are adapted to the environments in which they will be utilized (Khalil, 1975). A dilemma in breeding is that using genetic variation implies its destruction in the long term (Namkoong and Koshy, 1995). The inclusion of adaptation to poor and marginal growing sites becomes important with increasing pressure for other land use (Zobel, 1974). Selection for growth rate equals selection for competitiveness. Gains in agriculture have largely come from changes in harvest index and to a lesser extend from changes in total biomass. In forest trees there may be less scope for increasing harvest index because a large proportion of the total biomass is in stemwood (Burden, 1995; Silen, personal communication). Selection criteria should be based on the end product (Faulkner, 1981).

7.2. Methods

In the Shuswap Adams (SA) seed planning zone a total of 226 parent trees were selected during 1975 - 1980. Of these 114 were at lower elevations (460 - 1470 m) and 112 at higher elevations (1500 - 2000 m). Scion material (twigs) was collected from all of these trees and grafting was substantially completed in 1981. Two clonal seed orchards were established during 1981 - 1983 at Kalamalka near Vernon, one each to produce seed for use at low (< 1500 m) and high (> 1499 m) elevations. Of the selected parent trees only 99 and 97 were represented in the low and high elevation seed orchards respectively because for some parent trees grafting failed. The word elevation is used here to indicate altitude and is given in m above sea level.

A polycross program was initiated in 1986. This program, together with drought stressing to promote flowering where deemed necessary, was carried out in the existing seed orchards. Pollen was collected from 20 trees selected in natural stands at lower elevations within the Shuswap Adams seed planning zone. These trees were selected to be representative for the zone and were average or better in the stand in which they were selected. At the time the age of the orchard trees was 8 years or less from grafting and they were not producing much pollen. It is typical for interior spruce grafts to produce female flowers at an earlier age than pollen. After drying and extraction 8.5 grams of pollen from 12 of the 20 trees was mixed. Of the other 8 trees not enough pollen was available. A large amount of pollen was required because it was estimated that not all crosses could be made in one year and because pollination would have to be done several times to ensure that pollen was applied at the right time, i.e. at maximum receptivity. Female flowers were isolated by tying a paper bag with a plastic window around them as soon as they could be visually identified, which was well before receptivity. This ensured that no other pollen could participate in this mating. The pollenmix was applied at least twice to a total of 211 ramets from 105 clones (69 in the low and 36 in the high elevation orchards) in May 1986. On each ramet 20 to 50 conelets were pollinated. The remaining pollen was tested for moisture content, which was found to be within the 4 - 6% range recommended for storage, and stored at -18°C. Clones, which had not produced any female flowers, were given drought stress treatment (no irrigation during June) in order to promote flowering in 1987. The polycross program was continued during 1987 and was considered substantially complete in 1988, when 97 of the 99 low elevation clones and 92 of the 97 high elevation clones to be tested had produced sufficient amounts of seed for a progeny test. All seed was extracted, dewinged, cleaned, checked for the recommended moisture content (4 - 6%), dried where necessary and stored at - 18°C.

In May 1989 the seed was sown in PSB 415 B containers (112 cavities per styro block, each cavity 3.5 cm wide and 14.9 cm deep) at the Skimikin nursery. Seedlings were grown in a greenhouse under normal nursery culture and growing conditions for one growing season. They were grown under natural daylength with two hours of supplemental light in the middle of the night till June 10, when the supplemental light was discontinued. Fertilizer was applied two or three times weekly; i.e. a highly soluble fertilizer (20:20:20) was injected in the water supply in the amount of 100 ppm N (see also section 6.2) and watering was done when required, depending on moisture conditions. On June 10 the polyethylene cover was removed from the greenhouse and the fertilizer was changed to 8:20:30 in the amount of 50 ppm N to start the hardening off process (lignification and budset). These conditions were maintained till October when the seedlings were lifted and stored at -2°C. Planting was done in the spring of 1990.

Two plantation sites had been selected for this test. Traditionally more than two test sites have been used to meet a wider diversity of site conditions. Previous experience with interior spruce seemed to indicate that genotype by environment interaction is negligible in this species, which has shown a high level of adaptability to varying environments. It was therefore decided that two sites would be sufficient to obtain a reliable parent tree ranking on the basis of family performance (general combining ability). An earlier conclusion that family ranking in interior spruce is not significantly affected by test site elevation was based on comparison of family performance on nine test sites in the East Kootenays. The elevational differences between these test sites was not very large; i.e. they were all within an elevation range of about 300 m (1200 - 1500). For that reason the two sites for this test were selected at a low and a high elevation. Interior spruce planting is done over an elevation range from 500 m to 2000 m (low elevation: 500 - 1499 m and high elevation: 1500 - 2000 m). One test site was located at Skimikin at an elevation of about 600 m and one at Gold Creek (east of Adams Lake) at an elevation of about 1600 m. These sites were thoroughly prepared in the spring of 1990. The site at Skimikin had been used for transplant beds and was well prepared already. It was cultivated prior to planting. The site at Gold Creek had been logged in 1989 and was scarified with a bulldozer equipped with a brush blade to create a uniform planting site. All half sib families as well as the control populations were planted at both sites. This was done to evaluate the ability of progenies of maternal parent trees from low elevation to survive and grow at high elevation in addition to being tested at their own elevation, and vice versa.

A total of 295 families were included in this test as well as 6 control populations originating from seed collected in natural stands and currently in use for reforestation in the Shuswap Adams (SA) seed planning zone (table 7.1). Duplicated sets of families with the same female parent, generated from polycross (polyX) seed and open pollinated (OP) seed, were included to compare the two tests. Also included were families generated exclusively from seed created through polycross. Progenies of parent trees not represented in the orchards were included to allow incorporation of the best of these in future controlled crossing programs to provide material for selection for a second generation seed orchard. Thompson Okanagan (TO) families, generated by a similar polycross program for an adjacent seed planning zone and for a different seed orchard, were included to check performance of these families in another seed planning zone. Also included were 6 populations from natural stand seedlots, originating from elevations 1000 - 1820 m (low: 1000 - 1440 and high: 1500 - 1820) and collected in the Shuswap Adams seed planning zone, as controls to allow comparison between the parent tree progenies tested here with seedlots currently in use for reforestation in the seed planning zone. Also included were 26 families, obtained from open pollinated seed collected from individual parent trees from the well known Birch Island provenance. This provenance originates from an elevation of 425 m and is known to outperform most other seedlots in growth at the nursery. This was done to find out how the Birch Island source would perform in terms of survival and growth at a high elevation planting site. The Shuswap Adams controls are populations (not families) because they originate from commercial collections in natural stands and therefore their parentage is unknown, but in this test they were treated as families in the same way as all other sources.

Table 7.1. Families in Shuswap Adams progeny test [1)]

Female parents	Male parents	Number of Families	remarks
Shuswap Adams low	polycross	29	part of duplicated set
Shuswap Adams low	open pollinated	29	part of duplicated set
Shuswap Adams low	polycross	68	polycross only
Shuswap Adams low[2)]	open pollinated	8	not in orchard
Shuswap Adams high	polycross	22	part of duplicated set
Shuswap Adams high	open pollinated	22	part of duplicated set
Shuswap Adams high	polycross	70	polycross only
Shuswap Adams high[2)]	open pollinated	4	not in orchard
Thompson Okanagan low[3)]	polycross	14	different pollenmix
Thompson Okanagan high[3)]	polycross	3	different pollenmix
controls low[4)]	open pollinated	4	currently used in zone
controls high[4)]	open pollinated	2	currently used in zone
Birch Island low[5)]	open pollinated	26	currently used in zone
all sources		301	

1) low: elevation of origin <1500 m, high: elevation of origin >1499 m
2) families from parent trees selected in the Shuswap Adams zone, but not included in the orchards
3) from polycross done in a different orchard with a different pollenmix
4) populations from seed collected in natural stands in the Shuswap Adams seed planning zone
5) families from low elevation good provenance, none represented in Shuswap Adams orchards

In each of the two plantations there were eight replications (blocks). In each block there was one plot, consisting of four trees, for each of the 295 families and 6 control populations involved (a total of 301 entries). A randomized block design was used. Close spacing (1x1m) was used in both plantations. In other interior spruce progeny tests it has been found that correlations between family rank based on 3, 6, 10 and 15 year results are fairly good with r values ranging from 0.80 to 0.90 (Kiss, personal communication). These high correlations were found when only the highest or the lowest 25% of the ranking were considered. In other words, families that perform very well or very poorly at an early age generally seem to do the same at later measurements. Close spacing is expected to lead to earlier crown closure and between tree competition so that useful ranking information can be obtained at an earlier date. It was anticipated that initial orchard roguing could be done on the basis of three year measurements and that further roguing would be based on five and ten year ranking. In order to avoid any edge effects a double row of surround trees was added to both plantations. Height measurements were done in 1992 at plantation age three, in 1994 at plantation age five and in 1999 at plantation age ten.

Statistical analyses were done for low (<1500 m) and high (>1499 m) elevations, for the two test sites (Skimikin and Gold Creek) and for the three dates of measurement (1992: age 3 years; 1994: age 5 years and 1999: age 10 years) and included the following.

- Comparing the levels of mortality of all sources: SA polycross, SA open pollinated, not in orchard open pollinated, TO polycross, Birch Island open pollinated and control populations (301 entries).
- Ranking of SA families, obtained through polycross, in order of mean family height (189 entries; 97 low and 92 high elevation families).

- Comparing the collective mean heights of families selected in this ranking, at different selection intensities, with the mean heights of the polycross and the mean heights of the control populations (low and high elevation).
- Comparing mean heights of families obtained through polycross with those obtained through open pollination (51 entries; 29 low and 22 high elevation families in the duplicated sets).
- Comparing mean family heights of the entire test population with the elevation of origin of their maternal parent trees (301 entries).
- Analyses of variance to determine the between family variance contribution to the total variance (189 entries; 97 low and 92 high elevation families).
- Analyses of variance for the two test sites combined to evaluate genotype by environment interaction (301 entries).
- Estimating narrow sense family heritabilities for the polycross populations based on the ratio between genetic between family variance (which is 1/4 σ_A^2) and the total variance since: $h^2_{fam} = \sigma_A^2/\sigma_P^2$, where σ_A^2 is the additive variance and σ_P^2 is the total variance.
- Estimating expected genetic gains using: $\Delta G = h^2_{fam} \times SD \times 2$, where ΔG = expected gain in height growth in cm, h^2 = narrow sense family heritability and SD = selection differential (mean of the selected families - mean of the controls). SD replaced $i \times \sigma_P$, where i represents the selection intensity expressed as a coefficient of the phenotypical standard deviation (σ_P), which represents the phenotypical variation. Gain does not result from the progeny test alone, but is realized through seed production in a seed orchard where the selected parents are represented by their clones. Since each clone in the orchard provides male and female gametes the factor 2 is used in the formula above.
- Expressing the expected gains at 3, 5 and 10 years as a percentage of the appropriate polycross and the appropriate control populations.

The objectives of the Shuswap Adams progeny test were:

- Determine the general combining abilities of the parent trees represented in the two Shuswap Adams seed orchards to provide guidance for upgrading through roguing.
- Estimate expected genetic gain at different roguing levels.
- Compare family ranking of progeny generated from open pollinated seed with that of progeny derived from polycross mating.
- Assess family performance by parent tree elevation at both test sites.
- Compare family performance of the same families planted at low elevation (600 m) with that at high elevation (1600 m).
- Provide information for the selection of parent trees to be included in controlled crossing to provide material for a second generation seed orchard.

7.3. Results

Overall survival was very good at the Skimikin test site but rather poor at Gold Creek for the three, five and ten year assessments (tables 7.2. and 7.3). Sources were ranked in descending order or survival. At Skimikin survival was high and differences between sources were small. Low and high elevation families survived equally well. Survival and ranking of sources by survival did not change much over time.

Table 7.2. Survivals at Skimikin, expressed as percentage of each subpopulation

Sources	No of fam planted	age 3 years % Surv	age 5 years % Surv	age 10 years % Surv
TO high polycross	3	100.0	100.0	100.0
TO low polycross	14	99.8	99.8	99.8
SA low polycross	97	99.0	98.9	98.9
SA high polycross	92	99.0	98.9	98.9
Birch Island	26	98.7	98.7	98.7
SA low open pollinated	37	98.7	98.6	98.6
SA high open pollinated	26	98.3	98.2	98.3
control population low	4	98.4	97.7	97.7
control population high	2	96.9	96.9	95.3
all low elevation	178	99.0	98.9	98.8
all high elevation	123	98.9	98.8	98.8
overall survival	301	98.9	98.8	98.8

At Gold Creek survival was poor and there were larger differences between sources. The lowest survival was observed in the Birch Island families, which originated from a low elevation (425 m). Shuswap Adams high elevation families, especially the open pollinated ones, and the control populations survived well. Generally high elevation families survived much better than the low elevation families. Survival became progressively lower over time. Ranking of sources by survival remained essentially the same.

Table 7.3. Survivals at Gold Creek, expressed as percentage of each subpopulation

Sources	No of fam planted	age 3 years % Surv	age 5 years % Surv	age 10 years % Surv
SA high open pollinated	26	93.5	91.8	86.3
control population high	2	93.8	89.1	81.3
control population low	4	91.4	87.5	80.5
SA high polycross	92	86.8	82.5	75.9
SA low open pollinated	37	82.5	78.8	72.6
SA low polycross	97	79.8	74.0	66.0
TO high polycross	3	60.4	58.3	50.0
TO low polycross	14	50.2	45.5	32.8
Birch Island	26	33.8	24.8	19.5
all low elevation	178	71.6	65.7	58.3
all high elevation	123	87.7	84.0	77.5
overall survival	301	78.2	73.2	66.2

Overall height growth at Skimikin was about double that at Gold Creek (tables 7.4 and 7.5). Sources were ranked in descending order of mean height. The mean height of all low elevation sources combined was significantly larger than that of the high elevation sources at Skimikin. However, at Gold Creek the opposite was true. Notable exceptions to this general trend were the Thompson Okanagan high elevation families, which performed quite well at Skimikin, and the Shuswap Adams low elevation open pollinated families, which grew quite well at Gold Creek. There was a highly significant source by site interaction. e.g. Birch Island was significantly better than all other sources at Skimikin and was significantly poorer than most sources at Gold Creek. Control high was significantly poorer than Birch Island and several others at Skimikin, while it was significantly better than these sources at Gold Creek.

It is of interest to note that there was a strong negative relation between survival percentage at Gold Creek and height growth at Skimikin. Using the source means (tables 7.3 and 7.4) at plantation age 10 the value of $r = -0.94$ (significant at $p=0.01$). It is also interesting that the ranking of sources by mean tree height did not change between 3 and 10 years at both sites (one exception at Gold Creek).

At Skimikin height growth at three, five and ten years was best for Birch Island and worst for Shuswap Adams high elevation open pollinated families (table 7.4). The Shuswap Adams low elevation polycross families were significantly better than the low elevation controls, but the Shuswap Adams high elevation polycross families were significantly better than the high elevation controls only at age three. Low elevation polycross families were significantly better than high elevation polycross families at all ages. The ranking of sources in order of their mean heights did not change over time.

At Gold Creek height growth at three, five and ten years was best for the high elevation controls and poorest or almost poorest for the Birch Island families (table 7.5). The Shuswap Adams high elevation polycross families were poorer than the high elevation controls, but the difference was significant only at age five. The Shuswap Adams low elevation polycross families were not significantly different from the low elevation controls. The ranking of sources did not change from five to ten years.

Table 7.4. Mean tree heights in cm at Skimikin at plantation ages 3, 5 and 10 years [1]

	age 3 years					age 5 years					age 10 years			
Sources	Fam [2]	Mean	SE [1]		Sources	Fam [2]	Mean	SE [1]		Source	Fam [2]	Mean	SE [1]	
Birch Isl	26	87.6	2.1	a	Birch Isl	26	145.4	3.4	a	Birch Isl	26	293.3	6.5	a
TO lo poly	14	76.8	1.8	b	TO lo poly	14	130.7	2.2	b	TO lo poly	14	273.3	6.4	a
TO hi poly	3	73.6	3.9	bc	TO hi poly	3	125.5	4.9	bcd	TO hi poly	3	271.2	12.2	ab
SA lo poly	97	72.9	0.8	b	SA lo poly	97	124.6	1.2	bc	SA lo poly	97	257.1	2.6	b
SA lo OP	37	68.2	1.4	c	SA lo OP	37	118.8	2.5	ce	SA lo OP	37	249.5	5.2	bc
SA hi poly	92	66.5	0.6	c	SA hi poly	92	115.8	1.0	de	SA hi poly	92	239.9	2.4	c
control lo	4	61.8	1.9	d	control lo	4	110.4	3.1	e	control lo	4	237.0	6.9	c
control hi	2	59.5	2.5	d	control hi	2	106.0	4.8	e	control hi	2	232.6	9.1	cd
SA hi OP	26	55.9	2.1	d	SA hi OP	26	100.0	3.2	f	SA hi OP	26	210.9	7.1	d
all lo elev	178	74.1	0.8	a	all lo elev	178	126.6	1.2	a	all lo elev	178	261.6	2.3	a
all hi elev	123	64.3	0.8	b	all hi elev	123	112.5	1.2	b	all hi elev	123	234.4	2.6	b
overall	301	70.1	0.6		overall	301	120.8	0.9		overall	301	250.5	1.9	

1) values followed by the same letter are not significantly different
2) Fam = the number of families measured
3) SE = standard deviation of the mean

Table 7.5. Mean tree heights in cm at Gold Creek at plantation ages 3, 5 and 10 years [1]

Sources	age 3 years Fam [2]	Mean	SE [1]		Sources	age 5 years Fam [2]	Mean	SE [1]		Source	age 10 years Fam [2]	Mean	SE [1]	
control hi	2	39.3	0.8	a	control hi	2	62.6	0.2	a	control hi	2	142.9	7.7	a
SA hi OP	26	37.9	0.8	a	SA lo OP	36	59.2	1.1	b	SA lo OP	36	134.8	2.1	a
SA hi poly	92	37.5	0.4	a	SA hi poly	92	58.3	0.5	b	SA hi poly	92	131.7	1.2	a
SA lo OP	37	37.5	1.1	ab	SA hi OP	26	57.5	1.2	b	SA hi OP	26	130.0	2.7	ab
SA lo poly	97	35.5	0.4	bd	SA lo poly	97	55.4	0.6	c	SA lo poly	97	125.6	1.4	b
control lo	4	35.0	0.7	bd	control lo	4	54.6	1.0	ce	control lo	4	123.8	2.0	b
TO lo poly	14	31.2	1.2	c	TO lo poly	14	50.4	1.6	d	TO lo poly	14	110.1	5.2	c
TO hi poly	3	30.2	2.9	cd	Birch Isl	25	48.1	1.8	d	Birch Isl	22	106.1	4.9	c
Birch Isl	26	27.5	1.2	c	TO hi poly	3	47.3	3.5	de	TO hi poly	3	99.0	7.8	c
all lo elev	178	34.4	0.4	a	all lo elev	176	54.1	0.7	a	all lo elev	173	120.2	2.0	a
all hi elev	123	37.5	0.3	b	all hi elev	123	58.0	0.5	b	all hi elev	123	130.7	1.2	b
overall	301	35.6	0.3		overall	299	55.7	0.5		overall	296	126.6	0.9	

1) values followed by the same letter are not significantly different
2) Fam = the number of families measured
3) SE = standard deviation of the mean

The response, in terms of survival and growth, of sources to being planted at elevations different from the elevation of their origin is illustrated in table 7.6. This table brings together information from tables 7.2 - 7.5 for three sources from different elevation ranges. At Skimikin survival percentages were not different, but growth became progressively less with increasing elevation of origin. At Gold Creek both survival and growth became progressively better with increasing elevation of origin. At Gold Creek adaptation to high elevation is expressed in both height growth and survival.

Table 7.6. Survival % and growth in cm of sources from three elevation ranges at Skimikin and Gold Creek at plantation age 10

Source	elevation of origin	Skimikin elev 600 m survival	growth	Gold Creek elev 1600 survival	growth
Birch Island	425 m	98.7	293.3	19.5	106.1
SA low polyX	500 - 1500 m	98.9	257.1	66.0	125.6
SA high polyX	1500 - 2000 m	98.9	239.9	75.9	131.7

The polycross and open pollinated families in the duplicated sets (see table 7.1.) were compared as follows. The 29 polycross low elevation families were ranked in order of mean family height. This ranking was compared with that for the 29 open pollinated families. This was done for the results at three, five and ten years (table 7.7). The same comparison was made for the 22 high elevation polycross and open pollinated families (table 7.7). The two sets of paired measurements (29 low and 22 high elevation families) were also ranked in order of family number and paired t tests were done for the two sites and the three dates of measurement. Correlations between polycross and open pollinated families in these two sets were also calculated (table 7.8).

The ranking using polycross family mean heights was very different from the ranking based on open pollinated family mean heights (table 7.7). This was true for low and high elevation at both sites and for all three dates of measurement and was confirmed by a paired t test at Skimikin (differences all significant at p = 0.01). At Gold Creek the differences in ranking were confirmed by a paired t test only for low elevation families at five and ten years (p = 0.01 and 0.05 respectively). For high elevation the considerable differences between polycross and open pollinated family means were positive or negative so that the paired t test did not provide a confirmation of the differences.

Table 7.7 Comparison [1] of polycross and open pollinated rankings [2] for family mean tree height at plantation age ten

Low elevation families at Skimikin

polycross mean	polycross fam	open pollinated fam	open pollinated mean
324.5	1364	1364	361.2
318.8	3079	3079	301.7
292.0	1285	3173	297.3
279.9	2721	3186	274.6
279.8	3011	1284	271.5
278.2	3173	573	268.8
276.4	3009	3011	264.5
273.7	1352	2721	263.8
267.9	3015	3246	258.1
267.8	1295	3001	252.9
267.2	1284	2719	248.4
264.1	573	3009	243.8
257.7	3225	1352	241.7
256.0	3250	3015	236.5
255.7	2719	3169	236.2
253.3	3001	3048	234.7
251.5	3146	3250	232.6
249.8	1194	1285	232.3
248.4	3186	3146	230.0
244.8	3169	3225	224.5
243.3	3018	3258	224.4
240.8	3246	3221	222.7
240.5	3057	1295	221.3
240.5	3258	3061	218.4
236.9	3221	1194	218.2
229.7	3061	3046	212.8
227.2	3046	3018	212.0
226.0	1296	3057	211.6
217.8	3048	1296	208.0

High elevation families at Gold Creek

polycross mean	polycross fam	open pollinated fam	open pollinated mean
152.5	1196	3301	159.0
148.9	3301	3309	148.0
145.3	3270	3132	141.5
144.5	3298	3293	138.1
143.6	3222	3270	136.3
143.0	3263	3298	135.7
142.6	1199	3160	134.1
138.7	1358	3278	132.9
135.5	3252	1358	132.6
134.6	3268	1196	132.3
134.3	3304	3268	131.5
133.8	3293	3263	131.0
133.4	3247	1199	129.2
127.7	3235	3006	127.2
127.6	3006	3247	126.8
127.3	2708	3077	123.9
122.5	3278	3235	121.9
122.3	3160	3252	120.0
121.1	3132	3304	117.6
120.6	3309	1298	116.1
110.8	3077	3222	113.4
109.8	1298	2708	103.4

1) polycross and open pollinated families with the same number were connected to show difference in ranking
2) all families ranked in order of family mean heights

All coefficients of correlation between the two sets of measurements, except for high elevation at Gold Creek at five and ten years and at Skimikin at ten years, were significant, but not very high (table 7.8). Even for low elevation at three years at Skimikin, where the correlation coefficient was the largest, only 69% of the variation between polycross family mean heights was accounted for by the variation between open pollinated family mean heights. There was a linear relationship for all sets, except for high elevation at Skimikin at ten years and at Gold Creek at five and ten years. Almost all r values mentioned here became consistently smaller with increasing age. These observations did not support the notion that the two methods of selection give similar results in ranking of families by their mean heights.

Table 7.8. Coefficients of correlation between open pollinated and polycross families [1)]

plantation age		Skimikin		Gold Creek	
		low elev	high elev	low elev	high elev
3 years	r	0.83 **	0.45 *	0.59 **	0.46 *
	r^2	0.69	0.20	0.35	0.21
5 years	r	0.81 **	0.49 *	0.50 **	0.31
	r^2	0.66	0.24	0.25	0.10
10 years	r	0.75 **	0.41	0.39 *	0.23
	r^2	0.56	0.17	0.15	0.05

1) * = significant at p = 0.05 ** = significant at p = 0.01

The coefficients of variation of the means (CV in Table 7.9) were consistently smaller for the polycross than for the open pollinated families at Skimikin and at Gold Creek (with one exception, namely at Gold Creek for high elevation at three years). The overall means of the polycross families were consistently larger than those of the open pollinated families at Skimikin. At Gold Creek, where the differences were much smaller than at Skimikin, this was only true for the high elevation families. For low elevation the polycross means were smaller than the open pollinated means.

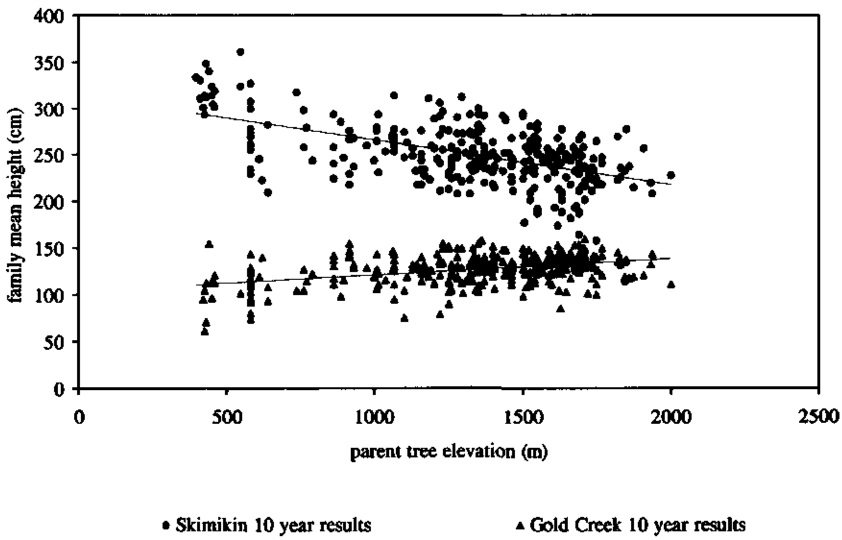
Table 7.9. Tree height means for polycross and open pollinated families in the duplicated sets [1)]

plantation age		Skimikin				Gold Creek			
		low elev		high elev		low elev		high elev	
		polyX	OP	polyX	OP	polyX	OP	polyX	OP
3 years	mean	72.3	67.0	66.3	55.2	35.7	37.3	37.6	37.6
	CV	10.2	13.8	8.0	19.1	12.1	18.7	11.3	10.8
5 years	mean	125.1	116.6	116.1	99.0	56.8	59.4	58.7	57.2
	CV	9.9	13.9	5.7	16.4	9.8	11.2	9.7	10.1
10 years	mean	259.0	245.7	241.4	208.1	128.6	133.9	132.7	129.7
	CV	9.8	13.6	8.2	16.8	7.6	9.5	8.9	9.3

1) These means are different from those in tables 7.4 and 7.5 because here only the families in the duplicated sets were used.

Family mean heights at three, five and ten years showed a negative correlation with the elevation, from which the female parents originated, at Skimikin (r = -0.63, -0.60 and -0.56 respectively) and a positive correlation at Gold Creek (r = 0.51, 0.39 and 0.38 respectively). In both cases the correlations were significant but weak (Figure 7.1). As shown already in tables 7.4, 7.5 and 7.6 these correlations again show that the lower elevation sources perform better at the low elevation site, but the high elevation sources perform better at the high elevation site.

Figure 7.1. Family mean tree heights in cm at ten years versus parent tree elevation in m



Correlations between polycross family mean heights at Skimikin and at Gold Creek were very low and not significant. No linear relationship between the results on the two sites was detected at plantation ages three, five or ten years. The r values for low elevation were -0.06, 0.01 and -0.03 and for high elevation -0.15, -0.13 and -0.14 respectively.

On the other hand correlations between three and five year as well as between five and ten year measurements at the same site were very high and clearly significant ($p=0.01$). The r values at Skimikin were 0.90 and 0.92 for low elevation and 0.90 and 0.89 for high elevation. The r values at Gold Creek were 0.88 and 0.76 for low elevation and 0.85 and 0.75 for high elevation. The ranking of sources by mean tree height remained the same between three and ten years at Skimikin and almost so at Gold Creek.

As shown already in tables 7.4 and 7.5 there were strong source by site interactions. This was confirmed by an analysis of variance for both sites combined. The family by site interaction effects were highly significant ($p = 0.01$) at three, five and ten years.

Analyses of variance were also done using plot means for the two sites and the three dates of measurement. These were done for low elevation and high elevation separately using the polycross families only. The results of these analyses were used to estimate heritabilities, which are shown in table 7.10. These are narrow sense family heritabilities, calculated in accordance with: $h^2_{fam} = \sigma_A^2/\sigma_P^2$, where σ_A^2 is the additive variance and σ_P^2 is the total variance.

The heritabilities at Skimikin were considerably larger than those at Gold Creek (table 7.10). At Skimikin the heritabilities remained more or less the same from three to ten years for low elevation and increased somewhat for high elevation. At Gold Creek the heritabilities became smaller from three to ten years for low and high elevations. It is of interest to note that at Skimikin the percentage of the total variance attributable to families did not change very much from three to ten years for low elevation (9.9, 11.6 and 9.9) and increased for high elevation (7.3, 8.2 and 9.1). At Gold Creek this percentage declined steadily for low elevation (4.0, 3.5 and 2.5) and for high elevation (3.2, 2.9 and 1.47). The fact that at Gold Creek the between family contribution to the total variance was quite small was reflected in the lower heritabilities.

Table 7.10. Heritabilities for tree height

plantation age	Skimikin		Gold Creek	
	low elev	high elev	low elev	high elev
3 years	0.78	0.72	0.50	0.48
5 years	0.81	0.74	0.45	0.43
10 years	0.79	0.78	0.35	0.26

The average polycross family heights at three different levels of roguing were calculated as the average of the family means of the group of parents selected (i.e. retained in the orchard) for Skimikin and for Gold Creek (tables 7.11 and 7.12). The controls, shown in this table, are the averages of the means of the control populations. There were two control populations. One for low elevations (<1500 m), which included four populations, and one for high elevations (>1499 m), which included two populations. These populations were obtained from seed, collected in natural stands, which is currently in use for reforestation in the seed zone. The average family heights at the different levels of roguing must be compared with these control populations in order to estimate the operational genetic gain expected from roguing and with the means of the polycross population to show the results from selection with the polycross population.

Gain expectations in height growth were calculated on the basis of these comparisons and the estimated heritabilities (table 7.10): i.e. $\Delta G = h^2_{fam} \times SD \times 2$, where ΔG = expected gain in height growth in cm, h^2 = narrow sense family heritability and SD = selection differential; the difference between the mean of the selected families and the mean of the controls. The factor 2 is used here because during the realization of the genetic gain each parent tree (clone in the orchard) acts as a female as well as a male parent. The estimated gain was then expressed as a percentage of the average height of the controls (tables 7.11 and 7.12) and as a percentage of the average height of the polycross population (i.e. 100% retained). In this case it was not really the families that were selected. This was a backward selection, whereby the parents were selected on the basis of the height growth of their offspring. The clones, representing the selected parent trees, would then be retained in the orchard after roguing. The seed, resulting from random mating between the retained clones, would then provide the gains expected. For low elevations heritability and selection differential found at Skimikin were used and for high elevation those found at Gold Creek were used. Retention of the top 25% of the clones in the Shuswap Adams low elevation seed orchard would lead to an expected height growth in an operational plantation resulting from the orchard seed, which would be 36.6% faster than the controls at age ten (table 7.11). Similarly the expected gain over the controls for the Shuswap Adams high elevation seed orchard with retention of the top 25% of the clones would be 0.8% (table 7.12). When height growth was compared with the overall mean height of the polycross population, in which the selections were made, the low elevation gain would be 21.4% and the high elevation gain would be 5.3%.

Table 7.11. Average family tree heights in cm at Skimikin and expected gains as % of the controls and as % of the polycross population mean height at different levels of roguing [1)]

	Skimikin plantation age 3 years					
	low elevation			high elevation		
clones retained	mean hgt cm	gain % over control	gain % over polyX	mean hgt cm	gain % over control	gain % over polyX
top 25%	82.9	53.5	21.3	73.5	33.7	15.2
top 50%	78.8	43.1	12.5	71.2	28.2	10.3
top 75%	75.9	35.7	6.2	69.2	23.4	6.0
100%	72.9	28.3	0.0	66.5	16.7	0.0
controls	61.8			59.5		

	Skimikin plantation age 5 years					
	low elevation			high elevation		
clones retained	mean hgt cm	gain % over control	gain % over polyX	mean hgt cm	gain % over control	gain % over polyX
top 25%	141.0	44.8	21.2	127.3	29.7	14.8
top 50%	134.1	34.8	12.4	123.0	23.7	9.3
top 75%	129.2	27.6	6.0	119.7	19.1	5.1
100%	124.6	20.8	0.0	115.8	13.6	0.0
controls	110.4			106.0		

	Skimikin plantation age 10 years					
	low elevation			high elevation		
clones retained	mean hgt cm	gain % over control	gain % over polyX	mean hgt cm	gain % over control	gain % over polyX
top 25%	291.9	36.6	21.4	266.9	23.0	17.5
top 50%	277.8	27.2	12.7	257.9	16.9	11.7
top 75%	267.1	20.1	6.2	249.7	11.5	6.4
100%	257.1	13.4	0.0	239.9	4.9	0.0
controls	237.0			232.6		

1) Roguing is removal of lower ranked clones in the orchard to increase gain. It is a backward selection where the parents are selected on the basis of the performance of their offspring.

Table 7.12. Average family tree heights in cm at Gold Creek and expected gains as % of the controls and as % of the polycross population mean height at different levels of roguing [1)]

Gold Creek plantation age 3 years

clones retained	low elevation mean hgt cm	low elevation gain % over control	low elevation gain % over polyX	high elevation mean hgt cm	high elevation gain % over control	high elevation gain % over polyX
top 25%	40.7	16.6	14.8	41.8	6.2	11.0
top 50%	38.7	10.7	9.1	40.4	2.8	7.4
top 75%	37.3	6.8	5.2	39.2	-0.3	4.2
100%	35.5	1.5	0.0	37.5	-4.3	0.0
controls	35.0			39.3		

Gold Creek plantation age 5 years

clones retained	low elevation mean hgt cm	low elevation gain % over control	low elevation gain % over polyX	high elevation mean hgt cm	high elevation gain % over control	high elevation gain % over polyX
top 25%	62.9	13.5	12.2	64.8	3.0	9.5
top 50%	60.1	9.0	7.6	62.6	0.0	6.2
top 75%	58.0	5.5	4.2	60.6	-2.8	3.3
100%	55.4	1.3	0.0	58.3	-5.8	0.0
controls	54.6			62.6		

Gold Creek plantation age 10 years

clones retained	low elevation mean hgt cm	low elevation gain % over control	low elevation gain % over polyX	high elevation mean hgt cm	high elevation gain % over control	high elevation gain % over polyX
top 25%	141.9	10.3	9.1	145.1	0.8	5.3
top 50%	136.1	7.0	5.9	140.9	-0.7	3.6
top 75%	131.5	4.4	3.3	137.0	-2.2	2.1
100%	125.6	1.0	0.0	131.7	-4.1	0.0
controls	123.8			142.9		

1) Roguing is removal of lower ranked clones in the orchard to increase gain. It is a backward selection where the parents are selected on the basis of the performance of their offspring.

7.4. Discussion

The traditional wisdom that families from low elevation perform better than those from high elevation was confirmed at Skimikin but not at Gold Creek, where high elevation sources survived and grew better (table 7.6). This traditional wisdom may be true within a restricted elevation range, but appeared invalid if a wider elevation range is considered, as was done in this study (figure 7.1). The very obvious source by elevation (site) interactions made that clear. Parent trees, to be selected for the production of high quality seed for use at higher elevations must therefore be tested in the environment where their offspring will be grown for the production of wood. Since the ranking of families was quite different for the two sites a high breeding value at one site is meaningless for the other. In view of the above and the necessity to deliver genetically improved seed, which not only leads to enhanced growth but also must be well adapted to the environment in which it will be utilized, it is recommended that parent trees to be retained in the low elevation (< 1500 m) Shuswap Adams seed orchard are selected on the basis of results at Skimikin while parent trees to be retained in the high elevation (> 1499 m) Shuswap Adams seed orchard are selected on the basis of results at Gold Creek.

Since the ranking of polycross and open pollinated families were far from similar (table 7.7) the question arises which is the better approach. Because height growth of the polycross families was generally better than that of the open pollinated families the polycross appears to be the better test. This conclusion is supported by the following:

i. The polycross test gives a better estimate of the breeding value of the mother tree than the open pollinated test because the male contribution does not vary.
ii. The variable pollen contribution in the open pollinated test comes to a large extend from neighbouring trees, which tend to be related to the test tree and to each other. The relationship within the family resulting from open pollination will therefore be greater than half sib (Libby et al., 1969). A certain amount of selfing can be expected as well, especially in a poor seed year.
iii. The coefficient of variation of the means in the polycross was consistently smaller than that in the open pollinated test (table 7.9). This could have been expected since the variation between half sib families in the polycross test is caused by the female parents only, while in the open pollinated test there is an additional component from the different male parents involved. This strongly supports the theory that open pollination is not at random, which leads to a less reliable test.

For improvement of an existing orchard the best and cheapest way to do a progeny test is to use open pollinated seed from within the orchard. Seed is collected separately from each clone (each one representing one of the parent trees to be tested). Progenies, thus created, are the result of all female parents receiving the same pollenmix because of the randomized design of the orchard. After outplanting and measuring of the progenies clones can be removed or retained in the orchard on the basis of their progeny performance. This method not only will provide a better comparison of the tested trees but will also allow a better estimate of the end product of the orchard because the seed used in the test is produced in the same way as that which will be delivered for operational reforestation. It will also ensure that for high elevation test plantations pollen from high elevation parent trees is used because the pollen has come from within the high elevation orchard. The cost advantage of this method is that it does not require expensive cone collection expeditions (to collect open pollinated seed), which includes the effort to find the original parent tree and the need to be there at the right time in a good crop year. The obvious disadvantage is that the date of selection on the basis of test results will be much later, since there will be a waiting period of about ten years before there is the abundance of flowering required for random mating in the orchard.

The famous Birch Island source, which traditionally outgrows almost anything at low and mid elevations, did not survive or grow well in the severe climate at the higher elevation, but it did quite well at Skimikin, where 21 of the 26 Birch Island families were in the top 25% and 16 in the top 10%. At Gold Creek, on the other hand 22 of the 26 Birch Island families were in the bottom 25% and 13 in the bottom 10%. This compares well with earlier observations made in an interior spruce progeny test near Fort Nelson, at 59° latitude compared to 53° latitude for Birch Island, where Birch Island spruce was not surviving and growing well (Kiss, personal communication) and with observations from spruce provenance trials in the Kamloops, Prince Rupert and Nelson Regions, where Birch Island sources survived and grew well at lower elevation sites but poorly at high elevation sites (Clark, 1983; Ying, personal communication).

The very strong relationships between the results of different years of measurement at both sites suggests that family ranking has become fairly stable very early in the test. Past experience (Kiss, personal communication) has shown that this is likely to be true only for the very high and very low ranked families. Nevertheless roguing on the basis of early measurements should be conservative. Expected genetic gain from a timid roguing is modest (tables 7.11 and 7.12). It is better to base even timid roguing (removal of 10% of the lowest ranked clones) on five year results and serious roguing (removal of 25% of the clones) should not be contemplated until ten year results are available. Final roguing (which leaves only 25% of the clones in the orchard) should have the support of progeny test measurements at fifteen years or more. This is especially true for the high elevation site, where everything happens at about half the speed of that at the low elevation site. Ideally a progeny test will be for half the rotation age (40 - 60 years) but measurements at an earlier age can lead to gains. Additive genetic variance seems to be fully expressed after competition starts (Ledig, 1983). This happens at the time of crown closure, which will come at a later date in a harsh (high elevation) climate. Close spacing is generally used in progeny tests to hasten the onset of competition.

At Skimikin heritabilities were considerably larger than at Gold Creek (table 7.10). At the slower rate of growth and the environmental insults the trees had to suffer in this harsh climate it is understandable that family differences take much longer to be clearly expressed. While at Skimikin the heritabilities did not change much over time at Gold Creek they declined steadily. This can perhaps be explained by what happened at the Gold Creek site during the early years of growth. The planting shock was more severe at this elevation and the damage done to many individual trees by snow press was formidable. At ten years many trees had recovered and were beginning to look near normal again. At this time trees that had been placed in a horizontal position by the heavy snow load were beginning to catch up to those that had remained upright. It is possible that the early snow damage had created artificially high family to family differences. At the time of the second and third measurements these differences had become smaller because of the recovery. High mortality has also contributed to diminishing family to family differences because many of the slower growing individuals were removed (died) from the test population. It is obvious from these results that even ten year measurements are not sufficient as a basis for rigorous selection and that a longer period of growth is required for proper assessment of family differences at a high elevation site or in otherwise disagreeable climates.

Gain predictions can be influenced by the method of comparison. In this study the average height of the group of selected families was compared with that of the control populations, but also with the overall mean of the polycross population. Predicted gains based on using these two comparisons were quite different (table 7.11 and 7 12). At Skimikin gains were lower when using the polycross population mean and at Gold Creek they were higher. Using the polycross mean for the comparison would never lead to predicted losses because all gains are greater than zero. For operational purposes the comparison with the controls is useful because it shows the difference with what is currently used for reforestation. For theoretical purposes the comparison with the population mean is useful because it shows the result of selection within that population. It also allows comparing the results at the two sites. Based on ten year measurements at Skimikin retention of the top 25% of the clones in de low elevation orchard would lead to an estimated gain of 21.4%. For the high elevation orchard, based on the ten year measurements at Gold Creek, this would be 5.3%. The fact that the high elevation polycross families were consistently poorer than the high elevation controls at Gold Creek (table 7.5) may have been caused by the fact that a low elevation pollenmix was used.

A small amount (2 - 3%) of gain can be provided by an unrogued orchard (i.e. all original clones remaining in the orchard). The absence of relationships between the clones ensures that there is no inbreeding, such as may be expected in natural stands. Self pollination is not a problem in seed orchards because in 95% of selfed seeds the embryo will abort (Kiss, personal communication). Moreover, progenies resulting from selfing are less vigorous than those resulting from outcrossing (Orr Ewing, 1957) so that most of these seedlings will be removed from the population through nursery culling. In addition there are several archegonia in each ovule and it seems that embryos resulting from outcrossing survive better than the selfed ones so that a filled seed still results in spite of self pollen being present (Owens, personal communication). In addition some gain can be expected in an unrogued orchard from the phenotypical selection of the parent trees.

It must be emphasized that the gains predicted on the basis of ten year results are just that. There is no indication from the data in this test that these gains will be maintained, increased or decreased over the duration of a full rotation. The gain predictions are based on the assumption that all clones in the orchard contribute equally to the production of male and female gametes. This never happens in a real (as opposed to a theoretical one) seed orchard. It must also be stressed that these results predict gain on a per tree basis. For the prediction of volume gains on a per ha basis realized gain tests will be necessary. These tests should use 100 tree blocks properly replicated and established on a number of different sites representing the varied growing conditions in the seed planning zone. Without the luxury of confirmation from a realized gain test it is best to view these gain predictions with the utmost caution.

It is recommended for future progeny tests that stock types and nursery culture chosen are such that short and thick seedlings are produced. This would alleviate some of the snow damage problems at high elevations. It is also recommended that more control populations are used.

Investment in selection and breeding for areas with marginal growing conditions, such as high elevation or extremely dry areas, is a waste of time and money. Since the expected gains in these areas are lower than in more productive areas and since these gains will be applied to a slower growing population the resulting gains will be very low. Available funding for tree improvement must be concentrated on the more productive areas. This will bring a better return on the investment in terms of the production of additional wood. In the marginal areas reforestation should be done through natural regeneration or through planting, which uses seed collected in local natural stands. The economies of harvesting and reforestation in these areas should be carefully considered.

8 GENERAL DISCUSSION

The forest industry in British Columbia has evolved from exploitation of available wood supplies in natural forests to management of a renewable resource based on long term sustainability. The loss of forest land to other uses is a continuing concern. Productivity of remaining forest lands must be increased. This can be accomplished through enhanced reforestation programs to reduce regeneration delays, proper choices of species and stock types as well as through stand management and protection. Above all productivity can be enhanced by using genetically improved seedlings as shown in table 7.11. Genetic gains, obtained through selection, can be implemented year after year and, unlike the effects of thinning and fertilizing, the improvements will last throughout the rotation.

Tree planting must include appropriate site preparation and the use of healthy, well adapted and improved planting stock. Trees must have characteristics required for the production of maximum amounts of high quality wood. In areas not conducive to plantation forestry, such as the arid regions in the interior, where plantations are likely to fail, or at high elevations, where the growing season is very short, harvesting methods must encourage natural regeneration with special attention to the selection of seed trees to avoid genetic impoverishment. Retention of the best phenotypes, which will provide seed for the next generation, is a form of positive mass selection, which may very well lead to improvement in the long run.

Plantation forestry using genetically improved trees can lead to the production of the required amount of wood on a smaller land area. Tree improvement programs are important because the resulting production plantations will include higher levels of desired characteristics, such as faster growth, than in the case of non-improved stock. Faster growing trees will alleviate the forest land alienation problem and will allow increasing amounts of forest land to be set aside for conservation.

The considerable investments in selection, progeny testing and breeding, which lead to the procurement of genetically improved trees, would be wasted if there is no system to deliver the gains to the production plantation. Clonal forestry is potentially risky (see section 7.1.3) and not socially acceptable. In forestry plantations must be able to successfully deal with changing growing conditions over a long period of time. Plantations, consisting of clones representing a limited number of genotypes, may not have the required amount of buffering against unforeseen calamities such as introduced diseases. Small, but very vocal, groups of conservationists foster a very strong sentiment against clearcut as a wood harvesting method and against plantation forestry. In their view monocultures, and some consider even mixed plantations as monocultures, are unnatural and undesirable and must be avoided at all cost. Clonal forestry will be seen as even more of an abomination. Seed orchards are therefore an essential link between breeding and the realization of genetic gain.

Seed orchards, where the best parents are represented by their clones, must be managed to maximize panmixia and seed production. If only a limited number of the clones in an orchard participate fully in the production of seed the realized gains will be lower than the expected gains. Moreover there will be a reduction in the genetic variability. The objectives of the tree improvement programs (see section 2.7.3) include maintenance of adequate levels of genetic variability. Gain expectations are based on the assumption that random mating takes place in the orchard and that all clones contribute equally to the production of male and female gametes. Deviation from this ideal situation will result in lower gains and lower genetic variability. Even with careful selection of orchard sites, in climates conducive to flowering, this ideal situation will often not occur. Flower enhancement techniques can therefore improve this situation as shown in chapters 3, 4 and 5. Drought stress and hormone application are relatively cheap and efficient methods to increase cone crops in seed orchards. Since the two are synergistic they can be used in combination for greater results. Timing of the treatments and dosage of hormone applications must be checked out in each individual orchard, because they will not be the same for different species and locations. These techniques can also be used in seed orchards to improve clonal balance. The treatments can be given preferentially to clones with a poor flowering history (see section 3.4). To enhance random mating and full participation of all clones in the production of male as well as female gametes protocols need to be worked out for the encouragement of not only female but also male flowering. For each orchard, where these techniques are used, decisions about the frequency of the treatments need to be made. It would be best to have a year of treatment, followed by a year of cone production, followed by a year of rest and recovery. For pine species, which have a three year reproductive cycle, there would be a year of treatment, a year of flowering, a year of cone production followed by a year of rest. The result of improving panmixia in a seed orchard will be that the realized gains can be expected to be closer to the predicted gains. The result of increasing seed production will be that roguing, which leads to increased gain expectations, can be done at an earlier date.

There is a legitimate concern about the loss of genetic variability caused by the use of genetically improved planting stock. However, the production plantation can hardly be considered as a method of preserving genetic variability since its only purpose is to produce wood. Furthermore genetic variability can be maintained in parks, in ecological reserves, through natural regeneration and in clone or seed banks. To date no appreciable differences have been found in genetic variability (as measured by levels of heterozygosity) between plantations containing genetically improved stock and natural stands (Lester, personal communication). Since seed orchards combine parents from widely varying locations random mating within the orchard can be expected to produce new gene combinations. This may help to offset a possible reduction in genetic variability by selecting a relatively low number of parent trees to provide seed for reforestation in the seed planning zone.

There is also a legitimate concern about the effect of nursery practices on the genetic make-up of plantations. There is a good possibility that, if small seeds are eliminated or if small seedlings are culled at the nursery, the genetic composition of the resulting plantation will be altered. There is reason to believe that there is no relationship between seed or seedling size and inherent growth potential (see section 6.1 paragraph 3). If crop uniformity at the nursery is important genetically improved seedlots can be sown in two or more different lots segregated by seed weight and combined again prior to planting. Different culling standards should be used for each lot. Since genetic gains, obtained through selection, could be affected by nursery practices more studies will be necessary to determine if nursery culling indeed removes entire families from the population. Female parents, for which progeny test information is available, should be used in such a study.

In interior spruce progeny testing it has long been assumed that there is no genotype by environment (family by site) interaction. This implies that the results of the test in terms of ranking parent trees according to the performance of their progeny are not expected to be influenced by the test location. However, when two test sites are sufficiently different in growing conditions considerable interaction effects, as demonstrated in chapter 7, can be observed. That families originating from low elevation grow better than those from high elevation is only true at low elevation planting sites (table 7.6 and figure 7.1). If seed from the best parents, as selected at a low elevation test site, is used for planting at high elevation the resulting trees will be outperformed in survival and growth by trees with high elevation parents. This was clearly demonstrated in chapter 7. It is therefore abundantly clear that progeny testing must be done in the climate zone of intended use.

Tree improvement for areas with marginal growing conditions is not a good investment. All efforts in selection and breeding should concentrate on productive areas. At test sites with marginal growing conditions such as high elevation sites (chapter 7) heritabilities and therefore expected gains will be low. The reduced growth rates experienced under such conditions reduce the financial gains even further. The results of chapter 7 show this. When using seed from the best parents, as selected at a high elevation test site, for production plantations at high elevations low gain and slow growth will combine to produce very low realized gains. On the other hand gene preservation in areas with marginal growing conditions, e.g. high elevation or extremely dry regions, is highly recommended. Competition with other land uses is very high in productive areas. With increasing demands for other land uses, such as agriculture, urban expansion, hydroelectric power projects, parks and ecological reserves, in the more productive areas the forest industry may in the long term become more and more dependent on areas of low productivity for the production of wood. It will be necessary to have an arrangement for the preservation of genotypes, which include adaptation to the marginal growing conditions of these areas (see section 7.1.5). This does not mean that gene preservation for the more productive areas is unimportant. A reduction in these areas means that the best possible use must be made of the remainder.

On theoretical grounds one may assume that the polycross progeny test provides a better comparison of the breeding value of parent trees than the open pollinated test because the male contribution for all of the female parents in the test is the same (see section 7.1.4). For open pollination it would be naive to assume a similar equal male contribution. Chapter 7 clearly shows that this is indeed not the case (table 7.9 and section 7.4) and that the rankings of the two tests are very different (table 7.7). It would be unwise to use the results of one test to predict the outcome of the other. Since in the seed orchard all female parents receive the same pollenmix open pollination within the orchard would be a good basis for a progeny test (see section 7.4)

Once genetic gain has been delivered to the production plantation the forest manager must decide on the length of the rotation. An increase in annual increment can be utilized by shortening the rotation and producing the same volume of wood in a shorter time or by producing a larger volume of wood by keeping the rotation the same. Shortening the rotation will negatively affect wood quality. A larger component of juvenile wood in the end product will reduce wood density (specific gravity), which has a positive correlation with all strength characteristics (Kellogg, 1982). This can significantly affect the value of the end product. The long and the short term financial aspects of these two different approaches must be considered. With faster growing trees one may expect marketable products to result from thinning at an earlier date. Thinning at a later stage in the rotation can be expected to result in a more vigorous release (i.e. the increased growth of the remaining trees). Shortening the rotation, in addition to affecting wood quality, also means removal of organic material from the growing site at a faster pace. This can result in a reduction of site quality in the long term (Kimmins, 1974). The long term consequences of the method chosen to utilize genetic gain must be carefully considered.

9. SUMMARY

British Columbia is characterized by a great variation in topography and climate. There are 43 million ha of usable productive forest land. About 1% of that is harvested annually. Almost all of the forest land is owned by the province. Forest management is done by the Forest Service through six regions in B.C. and a number of Victoria based branches. Biogeoclimatic zones have been identified and are used for reforestation decisions. There are 16 commercial and at least as many non commercial tree species. Major export markets include the United States, Japan and the European Union. In 1995 the value of all exports (lumber, plywood, pulp and paper) was $ 11 billion (Canadian). Sustainability of yield is ensured by the annual allowable cut, based on volumes of available mature and immature timber, expected growth rates and losses over the rotation. Natural regeneration was relied upon for forest renewal until the thirties on the coast and the sixties in the interior, when planting programs started. In 1987 the responsibility for reforestation was shifted from the Forest Service to the forest companies. In 1995 there were 3 Forest Service, 5 company and about 45 private nurseries with a total annual production capacity of over 250 million seedlings. All harvesting of timber must have prior approval, based on harvesting and reforestation plans. In 1956 seed registration started and in 1971 seed zones were identified. In the sixties provenance testing was started for interior spruce, interior Douglas fir and lodgepole pine. Parent tree selection in the interior was carried out during 1968 - 1992 for interior spruce, lodgepole pine, western white pine, interior Douglas fir and western larch. A total of about 8500 trees were selected. Seed orchard establishment started in 1974 and is still ongoing. In 1995 there were 8 seed orchard sites, 42 seed orchards established and 5 planned in the interior. When all interior orchards are in full production the average annual amount of seed produced will be sufficient for some 144 million seedlings.

The effect of drought stress on flowering was studied in the Central Plateau low elevation interior spruce seed orchard during 1985 - 1987. Drought stress, when applied from the beginning of the growing season to the date when 50% of the new shoots had ceased to elongate, increased the number of female, but not male, flowers in the year following treatment. A longer drought period resulted in a smaller increase in female flowers. Drought stress increased flowering also in clones with a poor flowering history.

The effect of combinations of drought stress and application of N fertilizer on flowering and height growth was studied in the Shuswap Adams low elevation interior spruce seed orchard during 1988 - 1990. Drought stress, applied from the beginning of the growing season until the completion of shoot elongation increased the number of female flowers in the year following treatment and also reduced height growth during the year of treatment. The effect was greater in the warm and dry climate at Kalamalka than in the relatively cool and moist climate at Skimikin. A reduced amount of N fertilizer by itself did not affect flowering or height growth, but reinforced the effect of drought.

The effect of the application of flowering hormones on the production of flowers was studied in the Willow Bowron lodgepole pine seed orchard during 1991 - 1993. The application of $GA_{4/7}$ through stem injection increased female, but not male, flowering in the year following treatment. Dosages used must be lower than those used in interior spruce because lodgepole pine was found to be more sensitive to phytotoxic effects. Optimal timing for best results is later in the growing season than for spruce. The mid July treatment was found to be the most effective for the promotion of female flowering. Optimal timing for the promotion of male flowering is probably mid June.

In a study on the effect of cone crop size on cone and seed size and on the effect of seed size on seedling size there was a strong indication that small seeds result in small seedlings. The difference was significant for three of the five families used. The effect of seed size on seedling growth is only expressed in the first few years. Seed grading and nursery culling may therefore have an effect on the genetic composition of the resulting plantations. Trees with large inherent vigour are just as likely to have started from small as from large seed.

Tree improvement programs should start with provenance testing to establish the extend to which improved populations can be transferred so that breeding zones can be delineated. Phenotypical selection of parent trees in a zone is followed by progeny testing to establish their genetic worth (general combining ability). The best parent trees are included in a seed orchard, where panmixia can be encouraged by cultural practices to allow maximum delivery of genetic gain to the production plantation. Seed orchards, containing all phenotypical selections, can be improved by roguing on the basis of the breeding value of parent trees. Progenies can be obtained through open pollination, controlled crossing between parent trees or by a polycross. A progeny test, using the first and the last mentioned methods, was established in 1990 for the Shuswap Adams interior spruce low and high elevation seed orchards on a low and a high elevation test site. Measurements at plantation ages 3, 5 and 10 years allowed the following conclusions. There was a strong genotype by site interaction. Breeding values of parent trees based on the results of their open pollinated progenies and on their polycross progenies were not well correlated. The parent tree ranking differed considerably, indicating that open pollination does not result in a similar genetic contribution to the selected mother trees, i.e. in a clear deviation from random pollination. Survival and growth at the low elevation site were much better than at the high elevation site. Heritabilities were much higher at the low elevation site. Roguing of seed orchards must be based on results of the appropriate test sites. Progenies must be tested in the environment where the orchard seed will be deployed. Predictions of expected gains should be based on comparison with control populations. Gain expectations mentioned here are somewhat too high because they assume random mating in the orchard with full participation of all clones in the production of male and female gametes. The gain expectations are based on single tree performance. Realized gain trials will be necessary to obtain estimates of volume gains per unit of area. At high elevation test sites much more time must be allowed for progeny growing than at low elevation test sites before conclusions are drawn.

Enhanced reforestation and stand management, in combination with plantation forestry using genetically improved planting stock, can improve productivity and allow increased amounts of natural forests to be preserved in parks. Investments in tree improvement would be wasted without seed orchards to deliver the gains to the production plantation. Cultural practices in seed orchards must be used to maximize panmixia and seed production. Flower enhancement techniques that can be used include drought stress and hormone application. To date a reduction in genetic variability in plantations using improved trees has not been confirmed. Since seed grading and nursery culling may affect the genetic composition of plantations resulting from orchard seed nursery practices must be reviewed. When progeny test sites are sufficiently different family by site interactions can be expected. It is imperative that parent trees are tested in the environment of intended use. Tree improvement for areas with marginal growing conditions is not a good investment. Low heritabilities and low gain predictions, combined with slow growth in production plantations, will lead to very low gains. Tree improvement efforts should concentrate on productive areas. Results from polycross and open pollinated progeny tests can not be expected to be similar. The polycross provides a better comparison of the female parents because they all receive the same pollenmix. The best way to do a polycross for existing seed orchards is to use progenies resulting from open pollination in the orchard. Utilizing genetic gains by shortening the rotation may have serious consequences for wood and growing site quality.

10. SAMENVATTING

British Columbia heeft een grote verscheidenheid in topografie en klimaat. Het bruikbare en productive deel van het bosareaal is 43 milioen ha. Ongeveer 1% hiervan wordt jaarlijks geoogst. Bijna het gehele bosareaal is staats eigendom. De Forest Service regelt het bosbeheer via zes districten in B.C. en een aantal afdelingen in Victoria. "Biogeoclimatic zones" worden gebruikt voor herbebossingsbeslissingen. Er zijn 16 commerciële boomsoorten en minstens evenveel niet commerciële. De belangrijkste uitvoer markten voor B.C. zijn de Verenigde Staten, Japan en de Europese Unie. In 1995 was de waarde van alle uitvoer (zaaghout, voeghout, pulp en papier) $ 11 miljard (Canadese dollars). Een blijvende opbrengst wordt verzekerd door de jaarlijks toelaatbare kap, gebaseerd op beschikbare volumes in volwassen en jong bos, te verwachten groei en verliezen gedurende de omloop. Natuurlijke regeneratie zorgde voor herbebossing tot de dertiger jaren aan de kust en de zestiger jaren in het binnenland, toen het herplanten een aanvang nam. De verantwoordelijkheid voor herbebossing werd in 1987 overgeheveld van de "Forest Service" naar de houtmaatschappijen. In 1995 waren er 3 kwekerijen van de "Forest Service", 5 van houtmaatschappijen en ongeveer 45 privé met een gezamelijke productie capaciteit van meer dan 250 miljoen zaailingen per jaar. Alle houtoogst moet van te voren goedgekeurd worden op basis van oogst - en herbebossingsplannen. In 1956 begon zaad registratie en in 1971 werden zaad gebruik gebieden in kaart gebracht. In de zestiger jaren werd herkomstonderzoek begonnen voor "interior spruce", "interior Douglas fir" en "lodgepole pine". Selectie van ouderbomen werd gedaan gedurende 1968 - 1992 voor "interior spruce", "lodgepole pine", "western white pine", "interior Douglas fir" and "western larch". In totaal werden ongeveer 8500 bomen geselecteerd. Aanleg van zaadtuinen begon in 1974 en is nog steeds gaande. In 1995 waren er 8 zaadtuincomplexen en 42 zaadtuinen aangelegd en 5 in voorbereiding in de "interior". Volledige productie van alle zaadtuinen zal voldoende zaad leveren voor circa 144 miljoen zaailingen.

Het effect van droogte op bloei werd bestudeerd in de "Central Plateau low elevation interior spruce" zaadtuin in 1985 - 1987. Droogte, toegepast vanaf het begin van het groeiseizoen totdat 50% van de nieuwe scheuten de groei beëindigd hadden, verhoogde het aantal vrouwelijke, maar niet mannelijke, bloemen in het jaar na de behandeling. Een langer aangehouden droogte resulteerde in een lagere vermeerdering van het aantal bloemen. Droogte werkte ook in klonen zonder een duidelijke bloei aanleg.

Het effect van combinaties van droogte en N bemesting op bloei en hoogtegroei werd bestudeerd in de "Shuswap Adams low elevation interior spruce" zaadtuin in 1988 - 1990. Droogte, toegepast vanaf het begin van het groeiseizoen totdat alle nieuwe scheuten de groei beëindigd hadden, verhoogde het aantal vrouwelijke bloemen in het jaar na de behandeling en verminderde de hoogtegroei in het jaar van de behandeling. Dit effect was groter in het warme en droge klimaat van Kalamalka dan in het relatief vochtige en koele klimaat van Skimikin. Verminderde N bemesting op zichzelf had geen effect op de bloei of hoogtegroei, maar versterkte het effect van droogte.

Het effect van het toedienen van bloei hormonen op de bloei werd bestudeerd in de "Willow Bowron lodgepole pine" zaadtuin in 1991 - 1993. $GA_{4/7}$, toegediend via injectie in de stam, verhoogde vrouwelijke maar niet mannelijke bloei in het jaar na de behandeling. De dosering moet lager zijn dan wat voor "interior spruce" gebruikt wordt omdat "lodgepole pine" gevoeliger is voor schadelijke effecten. De beste tijd voor de behandeling is later in het groeiseizoen dan voor "interior spruce". De toediening in half Juli gaf de beste resultaten voor vrouwelijke bloei. Voor mannelijke bloei is half Juni waarschijnlijk de beste tijd.

In een studie over het effect van de afmeting van de kegeloogst op de afmeting van zaden en van de afmeting van zaden op de afmeting van de zaailingen werd in drie van de vijf families gevonden dat klein zaad inderdaad kleine zaailingen produceert. Het effect van de afmeting van het zaad is alleen gedurende de eerste paar jaren duidelijk. Het sorteren van zaad of zaailingen kan daarom een effect hebben op de genetische samenstelling van de resulterende plantage. Bomen met een grote intrinsieke groeikracht kunnen net zo goed voortkomen uit kleine als uit grote zaden.

Boom veredeling programmas moeten beginnen met herkomst onderzoek om vast te stellen in hoeverre verbeterde populaties ook buiten het herkomstgebied gebruikt kunnen worden zodat veredelingszones gedefiniëerd kunnen worden. Phenotypische selektie van ouderbomen in een zone wordt gevolgd door nakomelingschapstoetsen om hun genetische waarde ("general combining ability") vast te stellen. De beste bomen worden vertegenwoordigd in een zaadtuin, waar volledige onderlinge kruising kan worden aangemoedigd door kulturele maatregelen, zodat de optimale genetische verbetering in de produktieplantages gerealiseerd kan worden. Zaadtuinen, die alle phenotypische selekties bevatten, kunnen worden verbeterd door het verwijderen van de minder gewenste klonen op grond van resultaten van nakomelingschapstoetsen. Nakomelingschappen kunnen geproduceerd worden via open bestuiving, gecontroleerde kruising of door een "polycross". Een nakomelingschapstoets volgens de eerst en laatstgenoemde methoden werd in 1990 voor de "Shuswap Adams low and high elevation interior spruce" zaadtuinen op een laag en op een hoog boven zeeniveau gelegen groeiplaats toegepast. Metingen op leeftijden 3, 5 en 10 jaar maakten de volgende conclusies mogelijk. Er was een duidelijke en sterke familie maal groeiplaats interaktie. De beoordeling van ouderbomen op grond van open bestoven zaad en op grond van een polycross gaven niet dezelfde uitkomsten. Overleving en groei waren veel beter op de lage groeiplaats. Erfelijkheidsschattingen waren veel hoger op de lage groeiplaats. Het verbeteren van zaadtuinen moet gebaseerd zijn op de resultaten van de juiste groeiplaats. Nakomelingschappen moeten getoest worden in de omgeving waar het zaad uit de zaadtuin gebruikt zal worden. De schatting van genetische vooruitgang moet gebaseerd zijn op vergelijking met een controle-populatie. De schattingen van genetische vooruitgang, hier genoemd, zijn aan de hoge kant omdat zij veronderstellen dat alle klonen in de zaadtuin op evenredige wijze deelnemen aan de productie van vrouwelijke en mannelijke gameten. De schattingen zijn gebaseerd op individuele boomgroei. Verwezenlijkte vooruitgangstoetsen zijn nodig voor schattingen van het volume per ha. Op de hoge groeiplaats is veel meer tijd is nodig voordat er conclusies getrokken kunnen worden.

Verbeterde herbebossing en plantage beheer, gecombineerd met het gebruik van verbeterde boompopulaties, kunnen de productiviteit verhogen zodat grotere delen van het bosareaal opzij gezet kunnen worden als parken. Investering in boomveredeling zou weggegooid geld zijn zonder zaadtuinen om de genetische vooruitgang af te leveren naar de produktie plantage. Zaadtuin beheer moet gericht zijn op het verbeteren van de volledige en evenredige deelname van alle klonen in de kruisbevruchting en het verhogen van de zaadproduktie. Bruikbare bloeibevorderende methoden zijn onder anderen droogte en hormoon toediening. Tot op heden is men niet in staat geweest een verminderde genetische variatie aan te tonen in plantages die verbeterd materiaal bevatten. Omdat zaad - en zaailingsortering de gene-tische compositie van verbeterde platages kunnen beinvloeden moeten de kwekerij methoden herzien worden. Familie maal groeiplaats interactie kan verwacht worden wanneer twee groeiplaatsen voor nakomelingschap toetsen flink van elkaar verschillen. Het is van belang dat ouderbomen worden getoetst onder dezelfde groeiomstandigheden als waar het zaad uiteindelijk gebruikt zal worden. Boomveredeling voor marginale groeiplaatsen is geen goede investering. Lage erfelijkheid en lage winst schattingen, gecombineerd met langzame groei van de produktie plantages, leiden tot zeer lage winst. Boomveredelings werk moet zich concentreren op de betere groeiplaatsen. De "polycross" is beter dan de open bestoven methode om nakomelingschapppen te vergelijken voor de beoordeling van de ouderbomen omdat alle moederbomen dan het zelfde stuifmeel mengsel ontvangen. De beste manier om een "polycross" uit te voeren voor bestaande zaadtuinen is die waarbij de nakomelingschappen komen uit zaad van open bestuiving in de zaadtuin. Het realiseren van genetische winst door het verkorten van de omlooptijd kan enrstige gevolgen hebben voor de kwaliteit van het hout en van de groeiplaats.

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TREE SPECIES MENTIONED IN THE TEXT

Alaska larch	*Larix laricina* (Du Roi) K. Koch
alder, red	*Alnus rubra* Bong.
alpine larch	*Larix lyallii* Parl.
amabilis fir	*Abies amabilis* (Dougl.) Forbes
arbutus	*Arbutus menziesii* Pursh
Arizona cypress	*Cupressus arizonica* Greene
aspen	*Populus tremuloides* Michx.
balsam	*Abies lasiocarpa* (Hook.) Nutt.
birch	*Betula papyrifera* Marsh.
birch, paper	*Betula papyrifera* Marsh.
black cottonwood	*Populus trichocarpa* Torr. & Gray
black spruce	*Picea mariana* (Mill.) B.S.P.
broadleaf maple	*Acer macrophyllum* Pursh
cedar, western red	*Thuja plicata* Donn.
cedar, yellow	*Chamaecyparis nootkatensis* (D. Don) Spach
Corsican pine	*Pinus nigra* Hort. var corsicana
cottonwood	*Populus trichocarpa* Torr. & Gray
dogwood, western flowering	*Cornus nuttallii* Audubon
Douglas fir	*Pseudotsuga menziezii* (Mirb.) Franco
Douglas maple	*Acer glabrum* Torr.
Eastern white pine	*Pinus strobus* L.
Engelman spruce	*Picea Engelmannii* Parry
European larch	*Larix decidua* Mill.
fir	*Pseudotsuga menziezii* (Mirb.) Franco
Garry oak	*Quercus garryana* Dougl.
grand fir	*Abies grandis* (Dougl.) Lindl.
hemlock, mountain	*Tsuga mertensiana* (Bong) Carr.
hemlock, western	*Tsuga heterophylla* (Raf.) Sarg.
jack pine	*Pinus banksiana* Lamb.
Japanese larch	*Larix leptolepis* (Sieb. & Zucc.) Gordon
larch alpine	*Larix lyallii* Parl.
larch, Alaska	*Larix laricina* (Du Roi) K. Koch
larch, European	*Larix decidua* Mill.
larch, Japanese	*Larix leptolepis* (Sieb. & Zucc.) Gordon
larch, western	*Larix occidentalis* Nutt.
limber pine	*Pinus flexilis* James
loblolly pine	*Pinus taeda* L.
lodgepole pine (interior)	*Pinus contorta* Dougl. var. latifolia
longleaf pine	*Pinus palustris* Mill.
maple, broadleaf	*Acer macrophyllum* Pursh
maple, Douglas	*Acer glabrum* Torr.
metasequoia	*Metasequoia glybtostroboides* Hu et Cheng
mountain hemlock	*Tsuga mertensiana* (Bong) Carr.
Norway spruce	*Picea abies* Karst.
oak, Garry	*Quercus garryana* Dougl.
pacific willow	*Salix lasindra* Benth.
paper birch	*Betula papyrifera* Marsh.
pine, Corsican	*Pinus nigra* Hort. var corsicana
pine, jack	*Pinus banksiana* Lamb.
pine, limber	*Pinus flexilis* James
pine, loblolly	*Pinus taeda* L.

pine, lodgepole (interior)	*Pinus contorta* Dougl. var. latifolia
pine, longleaf	*Pinus palustris* Mill.
pine, Ponderosa	*Pinus ponderosa* Laws
pine, radiata	*Pinus radiata* D. Don
pine, red	*Pinus resinosa* Ait.
pine, Scots	*Pinus silvestris* L.
pine, shore (coast)	*Pinus contorta* Dougl. var.contorta
pine, shortleaf	*Pinus echinata* Mill.
pine, slash	*Pinus elliottii* Engelm.
pine, sugar	*Pinus lambertiana* Dougl.
pine, Virginia	*Pinus virginiana* Mill.
pine, white eastern	*Pinus strobus* L.
pine, white western	*Pinus monticola* Dougl.
pine, whitebark	*Pinus albicaulis* Engelm.
pine, yellow	*Pinus ponderosa* Laws
Ponderosa pine	*Pinus ponderosa* Laws
radiata pine	*Pinus radiata* D. Don
red alder	*Alnus rubra* Bong.
red pine	*Pinus resinosa* Ait.
Scots pine	*Pinus silvestris* L.
shore pine (coast)	*Pinus contorta* Dougl. var.contorta
shortleaf pine	*Pinus echinata* Mill.
Sitka spruce	*Picea sitchensis* (Bong.) Carr.
slash pine	*Pinus elliottii* Engelm.
spruce, black	*Picea mariana* (Mill.) B.S.P.
spruce, Engelman	*Picea Engelmannii* Parry
spruce, Norway	*Picea abies* Karst.
spruce, Sitka	*Picea sitchensis* (Bong.) Carr.
spruce, white	*Picea glauca* (Moench) Voss
subalpine fir	*Abies lasiocarpa* (Hook.) Nutt.
sugar pine	*Pinus lambertiana* Dougl.
sugi	*Cryptomeria japonica* D. Don
tamarack	*Larix laricina* (Du Roi) K. Koch
trembling aspen	*Populus tremuloides* Michx.
Virginiana pine	*Pinus virginiana* Mill.
western flowering dogwood	*Cornus nuttallii* Audubon
western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
western larch	*Larix occidentalis* Nutt.
western red cedar	*Thuja plicata* Donn.
western white pine	*Pinus monticola* Dougl.
western yew	*Taxus brevifolia* Nutt.
white spruce	*Picea glauca* (Moench) Voss
whitebark pine	*Pinus albicaulis* Engelm.
willow, pacific	*Salix lasindra* Benth.
yellow cedar	*Chamaecyparis nootkatensis* (D. Don) Spach
yellow pine	*Pinus ponderosa* Laws
yew, western	*Taxus brevifolia* Nutt.

GLOSSARY

AAC	Annual allowable cut (not to exceed annual net growth).
bareroot seedling	Tree seedling grown in open field at a nursery; not in a container in agreenhouse.
backward selection	Selection of female parents with high GCA.
BCFS	British Columbia Forest Service.
breed arboretum	Plantation of clones of selected parent trees established to enable breeding.
clear-cut	Removal of all trees in a stand.
clinal	Variation of phenotype or genotype is continuous along a geographical gradient.
clone bank	Plantation of clones of selected parent trees for preservation of their genotypes.
culling	Removal of below standard seedlings in the nursery.
degree days	Sum of mean daily temperatures above 6°C during the growing season.
shoot growth	Early slow: prior to bud burst - mostly cell division. Fast: after bud burst - mostly cell elongation Late slow: towards end of shoot elongation.
ecotypical variation	Discontinuous gradient between races adapted to local conditions.
embling	Tree derived through vegetative propagation of cells taken from an embryo.
fascicle	Bundles of two, three or five needles in pine species; short shoots
forward selection	Selection of the best individuals in the best families in progenies of tested parents.
free to grow	Unencumbered by competing vegetation.
GA	Gibberellic acid - a flower promoting substance.
GCA	General combining ability - the ability of a genotype to produce good performing progenies in crosses with many different genotypes.
general combining ability	Good CGA signifies high performance of its progenies in various crosses.
genetic gain	Increase in growth (or other traits) realized in the progeny of selected trees; i.e. in the commercial plantation.
girdling	Two overlapping partially circumferential sawcuts through the bark.
juvenile wood	Formed within live crown - rapid growth - short, wide, thin-walled tracheids.
Kalamalka	Breed arboretum and seed orchard site near Vernon.
not satisfactorily restocked	Areas with less than 750, well spaced, seedling or juvenile stems per ha.
NSR	Not satisfactorily restocked.
open pollinated progeny test	Test to assess GCA, whereby the seed collected from the female parent has been derived through natural pollination; i.e. in natural stands.
ovulate strobilus	Female flower structure: conelet.
parent tree	Tree phenotypically selected in a natural stand.
PGTIS	Prince George Tree Improvement Station.
phenology	Science of relations between plant development and weather.
PHSP	Pre-harvest silviculture prescription.
plantation	A forest established through artificial regeneration; i.e. planting
polycross progeny test	Test to asses GCA whereby each female parent receives the same pollenmix, obtained from a number of male parents.
provenance	Original location of origin of seed.
PSB	Plug styrofoam block - styrofoam block with cavities for growing of seedlings.
PSB 313B	Same; 160 cavities in block - each 3.0 cm wide and 12.7 cm deep.
PSB 415B	Same; 112 cavities in block - each 3.5 cm wide and 14.9 cm deep.
ramet	A graft when planted in an orchard, clone bank or breed arboretum .
roguing	Removal of less desirable parents on the basis of progeny test results.
rotation age	Age at which mean annual increment reaches its maximum.
scion material	Twigs for grafting.
seed efficiency	Number of seeds per cone compared to potential number of seeds per cone.
seed orchard	Plantation of clones of selected trees for the production of improved seed.
seed production area	Natural stand preserved for the collection of seed.
seed set	Number of seeds formed in one cone; depends on pollen availability.
seedzone	Area defined to restrict the transfer of seed for plantations.
selection harvest	Removal of single trees in a stand; reliance on natural regeneration.

Skimikin	Forest nursery and seed orchard site near Salmon Arm.
staminate strobilus	Male flower structure - pollen production apparatus.
steckling	Rooted cutting.
stock types	Seedlings are described by the way they have been grown in the nursery; e.g. 2-0 describes bareroot seedlings, which have been grown in the seedbeds outside for two years. 1-0 PSB 313B describes seedlings that have been grown in a greenhouse in a styrofoam container, with 160 cavities each 3.0 cm wide and 12.7 cm deep, for one year.
stumpage	A fee based on value and cost of extraction per m^3 of wood.
sustained yield	Situation where harvest does not exceed net growth.
synergism	two treatments combined provide more than the sum of the individual results
transplant beds	Areas where stock, which has been returned by the planters, is outplanted to grow for another season. Transplanting is also used in bareroot nurseries to produce larger stock required for sites with heavy brush competition, e.g. 2-1 stock is grown for two years, lifted and stored and outplanted again the following spring.
trickle irrigation	Slow drip system - requires less water than sprinkler system.
Willow Bowron	Old lodgepole pine seedzone east of Prince George.

ABSTRACT

Albricht, G.M., 2001. The delivery of genetic gain in the interior of Britisch Columbia. Doctoral Thesis. Wageningen, the Netherlands.

The forest industry is important for the province of British Columbia, Canada. Timber harvest is regulated on a sustained yield basis. Productivity can be increased by enhanced reforestation, stand tending and tree improvement thus reducing the area needed to provide the required amount of wood so that more forest land can be preserved. Tree breeding is done by selection and progeny testing. Genetic gain is delivered through seed orchards where panmixia and seed production can be enhanced. Drought stress and hormone application appeared useful flower enhancement techniques. In a spruce progeny test strong family by site interactions were found. The polycross and the open pollinated progeny tests gave different estimates of the general combining abilities of the same parents, indicating the inferiority of open pollinated progeny tests. Genetic gains for marginal growing sites appeared very low as well as growth rates themselves. Tree improvement must concentrate on better growing sites. Utilizing genetic gains through shortening rotations can have serious consequences for wood and growing site quality.

CURRICULUM VITAE

De auteur werd op 2 Maart 1938 geboren in Bilthoven. Na zijn eindexamen aan de HBS te Enschede ging hij studeren aan de Landbouwhogeschool te Wageningen. Tijdens zijn studie vervulde hij de dienstplicht en was officier in de artillerie van het Nederlandse leger. In 1967 behaalde hij het ingenieurs diploma in de bosbouw met als specialisaties houtteelt en planten veredeling. In 1965 heeft hij, in het kader van zijn praktijktijd, gewerkt bij de Inventory Division van de British Columbia Forest Service (BCFS). In 1967 is hij geëmigreerd naar Canada. Van 1967 tot 1975 heeft hij gewerkt voor de Inventory Division van de BCFS. Van 1975 tot 1997 heeft hij gewerkt in het zaadtuin beheer voor de Silviculture Branch van de BCFS. In 1997 ging hij met pensioen.