Picea glauca (Moench) Voss White Spruce

Pinaceae Pine family

Hans Nienstaedt and John C. Zasada

White spruce *(Picea glauca),* also known as Canadian spruce, skunk spruce, cat spruce, Black Hills spruce, western white spruce, Alberta white spruce, and Porsild spruce, is adapted to a wide range of edaphic and climatic conditions of the Northern Coniferous Forest. The wood of white spruce is light, straight grained, and resilient. It is used primarily for pulpwood and as lumber for general construction.

Habitat

Native Range

White spruce (fig. 1) has a transcontinental range, from Newfoundland and Labrador west across Canada along the northern limit of trees to Hudson Bay, Northwest Territories, and Yukon. It almost reaches the Arctic Ocean at latitude 69” N. in the District of Mackenzie in the Northwest Territories (149). In Alaska, it reaches the Bering Sea at Norton Bay and the Gulf of Alaska at Cook Inlet. In British Columbia, it comes within 100 km (60 mi) of the Pacific Ocean in the Skeena Valley where it overlaps with Sitka spruce *(Picea sitchensis),* and from there it extends south through British Columbia, and east through Alberta and Manitoba to Lake Winnipeg and south and east through northern Minnesota and Wisconsin, central Michigan, northeastern New York, and Maine. The contiguous distribution shown extending south in the Rocky Mountains into Montana actually may be outliers similar to those found further south in Montana, in the Black Hills in Wyoming and South Dakota (approximately latitude 44” N.), and at Cypress Hills in Saskatchewan *(149).*

White spruce grows from sea level to about 1520 m (5,000 ft) elevation. It is found near 610 m (2,000 ft) on the central tableland of Labrador north of latitude 52” N. *(108),* and in Alaska white spruce forests approach 910 m (3,000 ft) at about latitude 68” N. in the Dietrich River Valley on the south slope of the Brooks Range *(26).* It reaches 1160 m (3,800 ft) in the timberline forest at latitude 61” N. in the Liard Range in the Northwest Territories *(79),* and farther south in the Rocky Mountains it is the dominant species from the edge of the plains at 1220 m (4,000 ft) to about 1520 m (5,000 ft). In interior British Columbia, white spruce grows at elevations as low as 760 m (2,500 ft) in the east Kootenay Valley *(130).*

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Climate

White spruce has been described as a “plastic” species because of its ability to repopulate areas at the end of glaciation. It grows under highly variable conditions, including extreme climates and soils.

In the north, the position of the tree line has been correlated to various factors, including the 10” C (50° F) isotherm for mean July temperature, cumulative summer degree days, position of the Arctic front in July, mean net radiation (especially during the growing season), and low light intensities (see review *39*). None of the variables strictly define the northern limit of spruce, and in northern Alaska the presence of mountainous topography makes it difficult to determine controlling factors *(26).* Other biotic and abiotic variables affecting the northern and altitudinal distribution include lack of soil, low fertility, low soil temperature, fire, insects, disease, human impact, soil stability, and others *(39,158,159).*

The southern limit of the belt in which white spruce forms more than 60 percent of the total stand roughly follows the 18” C (64“ F) July isotherm. The association is particularly close northeast of Lake Superior; in the Prairie Provinces, the species’ limit swings north of the isotherm.

At the northern limit of the species’ range, climatic extremes are significant. For example, –54° C (-65” F) in January and 34” C (94” F) in July were recorded extremes in one study area (102,158). Mean daily temperatures of -29” C (–20° F) for January are recorded throughout the species’ range in Alaska, Yukon, and Northwest Territories, while mean daily July temperatures range from about 21” C (70° F) in the extreme southeastern area of distribution to 13” C (55” F) throughout much of Alaska and Canada. Maximum temperatures as high as 43” C (110° F) have been recorded within the range in Manitoba. Mean annual precipitation ranges from 1270 mm (50 in) in Nova Scotia and Newfoundland to 250 mm (10 in) through the Northwest Territories, Yukon, and parts of Alaska. Conditions are most severe, however, along the southern edge of distribution through Alberta, Saskatchewan, and Manitoba, where a mean annual precipitation of from 380 to 510 mm (15 to 20

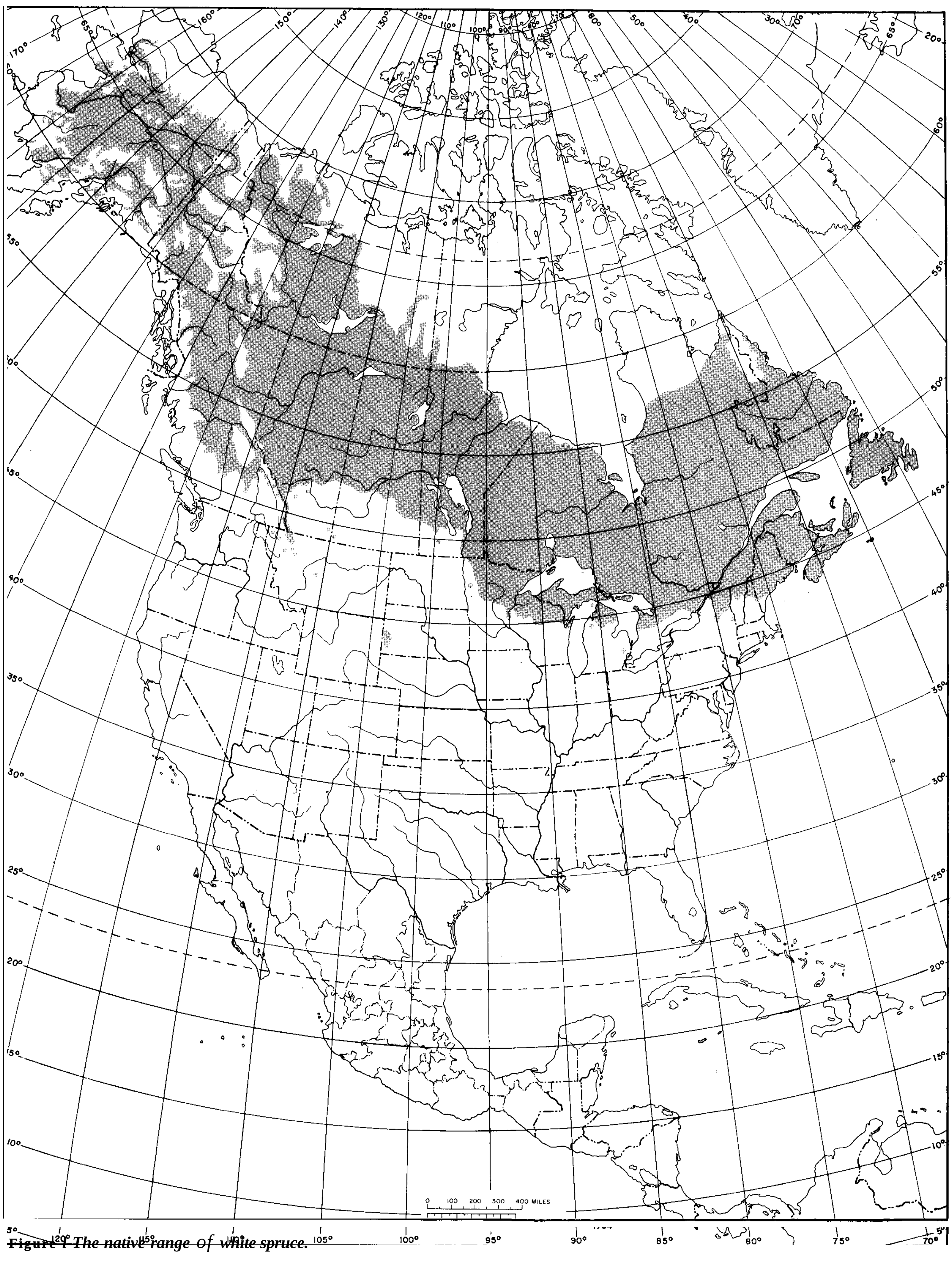

Figure 1-The native range of white spruce.

in) coincides with mean July daily temperature maxima of 24" C (75" F) or more.

The growing season ranges from about 180 days in parts of Maine to about 20 days in parts of Canada. Generally, however, white spruce grows in regions where the growing season exceeds 60 days *(108).*

Photoperiod varies continuously over the range of the species from approximately 17 hours at summer solstice along the southern edge of the species' distribution to 24 hours north of the Arctic Circle in Alaska and parts of northern Canada.

Soils and Topography

White spruce grows on a wide variety of soils of glacial, lacustrine, marine, or alluvial origin. Substrata represent the geological eras from Precambrian to Cenozoic and a great variety of rock formations, including granites, gneisses, sedimentaries, slates, schists, shales, and conglomerates (134,158). Some bedrocks are acidic, such as granites, and others are basic dolomites and limestones.

Mature northern white spruce stands have well-developed moss layers that significantly affect the mineral soil. The layer is most highly developed in regions with adequate moisture conditions and is dominated by feather mosses (e.g., ***Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis,*** and ***Dicranum*** spp.) rather than ***Sphagnum*** species *(92,159).* In the far north, total depth of the live moss-organic mat frequently is from 25 to 46 cm (10 to 18 in) or more. Development is, in part, regulated by flooding and stand composition. Stands in which hardwoods are mixed with white spruce tend to have shallower, discontinuous moss layers. The layer is a strong competitor for nutrients and an effective insulator that reduces temperature in the rooting zone. The temperature reduction varies with latitude and climatic regime. In Alaska, Yukon, and the Northwest Territories, soil temperatures can reach the point at which permafrost is developed and maintained *(53,158,161).*

Podzolic soils predominate over the range of the species, but white spruce also grows on brunisolic, luvisolic, gleysolic, and regosolic soils. On sandy podzols, it is usually a minor species, although white spruce is common on sand flats and other coarse-textured soils in the Georgian Bay area. It grows on shallow mesic organic soils in Saskatchewan, and in central Yukon on organic soils with black spruce *(85,134,149).*

White spruce is able to grow on extremely diverse sites, but to achieve the best development it is generally more demanding than associated conifers. The range of sites supporting the species becomes more limited northward with increasing climate severity *(149).*

In the Algoma District of Ontario, the species is a major component of the stands on calcareous podzol loams and clays and shows exceptionally good development on melanized loams and clays. In Saskatchewan, it does best on moderately well-drained clay loams (84); in Alberta Mixedwoods, the best development is on well-drained lacustrine soils *(60).* Further north in Canada and Alaska, particularly productive stands are found on moist alluvial soils along rivers *(78,79,90,162)* and on south-facing upland sites *(41,158).*

White spruce grows on both acid and alkaline soils and acidity (pH) values from 4.7 to 7.0 and perhaps higher are probably optimum *(10,141,149,176).* On the floodplains of the northern rivers, pH may vary from 5.0 to 8.2 *(194).* In the Northwest Territories, the species grows in the alpine fir forest on strongly acid soils with a surface pH of from 4.0 to 4.5, increasing with depth to pH 5.5 at 15 cm (6 in); but at somewhat lower elevations, the mixed coniferous forest soils have a pH of 4.0 at the surface with pH 8.0 at 38 cm (15 in) depth. Good growth of white spruce on alkaline soils has also been reported in Mixedwoods in the Prairie Provinces *(141).* In New York, one factor common to most white spruce locations is an abundant calcium supply. Of the wide range of sites and soils on which white spruce grows, soils in the orders Alfisols and Inceptisols are most common.

The species also tolerates a range of fertility levels. On the alluvial soils along northern rivers, nitrogen may vary from 0.2 to 0.01 percent and phosphorus from 10 to 2 p/m. On adjacent upland soils derived from loess parent material, nitrogen may vary from 0.1 to 0.4 percent and phosphorus from 10 to 3 p/m *(194).*

Good growth requires a dependable supply of well-aerated water, yet the species will tolerate a wide range of moisture conditions. It will not tolerate stagnant water that reduces the rooting volume. On the other hand, white spruce will grow on dry sites if they are fertile.

Soil fertility, soil moisture, and physical properties are interrelated. Moisture alone will not improve yields unless it is associated with increased fertility *(149).* Nor will increased moisture be beneficial if soil structure is less than optimum. In Riding Mountain, Manitoba, for example, lower yields on the moist sites have been attributed to the higher clay content and massive structure when wet and columnar structure in dry conditions (73).

Table l-Minimum soil fertility standards for planting Wisconsin native conifers *(146)*[1]

Item	Jack pine	Red pine	White pine	White spruce
Approx. site index,[2] m	16	17	18	16
ft	53	57	60	52
Approx. optimum range of pH[3]	5.0 to 7.0	5.2 to 6.5	4.7 to 7.3	4.7 to 6.5
Silt and clay, pct	7.0	9.0	15.0	35.0
Organic matter, pct	1.0	1.3	2.5	3.5
Exchange capacity, meq/100g	2.5	3.5	5.7	12.0
Total N, pct	0.04	0.05	0.10	0.12
Available P, kg/ha	13.4	28.0	33.6	44.8
lb/acre	12	25	30	40
Available K, kg/ha	56.0	78.5	112.1	145.7
lb/acre	50	70	100	130
Exchangeable Ca, meq/100g	0.50	0.80	1.50	3.00
Exchangeable Mg, meq/100g	0.15	0.20	0.50	0.70

'Minimum is an amount sufficient to produce 126 to 157 m^3/ha (20 to 25 cords/acre) at 40 years. All nutrients are given in terms of elements, not oxides.
[2]Base age 50 years.
[3]Data for values above pH 6.5 are insufficient; the range is strongly influenced by climatic conditions.

Other soil factors that must be carefully considered include the depth to ground water, permeability (especially of surface layers), presence of hardpans or claypans, and the mineralogical composition of the parent material.

Minimum soil-fertility standards for white spruce are higher than for other conifers commonly planted in the Lake States *(176)* (table 1).

Fertility requirements for white spruce based on foliar analyses are in percent of dry matter: nitrogen 1.50 to 2.50; phosphorus 0.18 to 0.32; potassium 0.45 to 0.80; magnesium 0.10 to 0.20; and calcium 0.15 to 0.40. At the lower end of the range, plants will respond to fertilizer. These data are from sand-culture experiments and are definitely provisional *(152);* however, except for calcium, they are in line with values published for 3-year-old seedlings in the nursery *(71).*

Little specific information is available on the effects of fertilizer in natural stands or plantations of white spruce, but growth gains have been reported after treatments to overcome nutrient deficiencies (141). Response of established older stands and new plantations to fertilization can occur within a year of treatment (9,156). Observations in progeny test plots in northern Wisconsin suggest that a hand application of 10-10-10 fertilizer may shorten the period of planting shock. In a nursery in which prolonged use may have depleted exchangeable bases and probably micronutrients, an application of micronutrient and major nutrient fertilizers resulted in a greatly increased volume of root systems and their absorbing capacity, and in a decreased top-root ratio. But indiscriminate use of micronutrient fertilizers together with nitrogen fertilizers may reduce seedling quality, making plants succulent, with a high top-root ratio *(71).*

White spruce stand development can significantly affect forest floor composition and biomass and mineral soil physical and chemical properties. The magnitude of these effects will vary with site conditions and disturbance history of the site. On sites in Alaska, organic layers accumulate to greater depths in mature spruce stands than in hardwood stands growing on similar sites. As a result, soil temperatures decrease and, in extreme cases, permafrost develops ***(161,163).*** Acidity of the mineral soil in spruce plantations established on abandoned farmland in Ontario decreased by 1.2 pH units over a 46-year period *(10).* Soil conditions under 40-year-old white spruce differed significantly in some respects from that under aspen, red pine, and jack pine growing on the same soil type; relative differences among species varied with specific nutrients (2).

Associated Forest Cover

Eastern Forest-The forest cover type White Spruce (Society of American Foresters Type 107) *(40)* is found in either pure stands or mixed stands in which white spruce is the major component. Associated species include black spruce, paper birch ***(Betula papyrifera),*** quaking aspen ***(Populus tremuloides),*** red spruce *(Picea rubens),* and balsam fir *(Abies balsamea).* Yellow birch *(B. alleghaniensis)* and sugar maple *(Acer saccharum)* are sometimes included in the community mix.

The type is minor and confined to abandoned fields in New England and the Maritime Provinces, and within the fog belt farther north in Quebec and Labrador. It is more widespread elsewhere in eastern Canada and as far north as the tree line in Ungava and along Hudson Bay.

In northern Quebec, the lichen *(Cladonia)* woodland, the feathermoss forest, and the shrub forest with bog birch *(B. nana)* and heath species are common white spruce communities.

White spruce is an associated species in the following Eastern Forest cover types:

Boreal Forest Region

1 Jack Pine
5 Balsam Fir
12 Black Spruce
16 Aspen

Figure 2—*White spruce stand on the Yukon-Tanana Upland in interior Alaska, regenerated by the shelterwood system.*

18 Paper Birch
38 Tamarack

Northern Forest Region

15 Red Pine
21 Eastern White Pine
24 Hemlock-Yellow Birch
25 Sugar Maple-Beech-Yellow Birch
27 Sugar Maple
30 Red Spruce-Yellow Birch
32 Red Spruce
33 Red Spruce-Balsam Fir
37 Northern White-Cedar
39 Black Ash-American Elm-Red Maple

In three of these types, Aspen (Type 16), Paper Birch (Type 18), and Red Pine (Type 15), white spruce attains increasing importance in the stand composition as the succession progresses and more tolerant species take over.

Western Forest-White Spruce (Type 201) is the pure white spruce forest in the West. In Alaska and the Northwest Territories, the type is largely confined to stream bottoms, river floodplains and terraces, and warm, south-facing upland sites (fig. 2). Farther south in British Columbia and Alberta, it has broader distribution from as low as 760 m (2,500 ft) to 1520 m (5,000 ft).

Associated tree species in Alaska include paper birch, quaking aspen, black spruce, and balsam poplar ***(Populus balsamifera).*** In Western Canada, subalpine fir ***(Abies Zasiocarpa),*** balsam fir, Douglas-fir ***(Pseudotsuga menziesii),*** jack pine *(Pinus* ***banksiana),*** and lodgepole pine *(P.* ***contorta)*** are important associates.

The type varies little and generally comprises closed stands. White spruce plant communities in interior Alaska include white spruce/feather-moss; white spruce/dwarf birch/feathermoss; white spruce/avens *(Dryas)*/moss; and white spruce/alder *(Alnus* spp.)/blue-joint ***(Calamagrostis canadensis) (32,43,*** 61). Two communities are common in northwestern Canada and in Alaska: (1) white spruce/willow *(Salix* spp.)/buffaloberry ***(Shepherdia*** spp.)/northern goldenrod ***(Solidago*** *multiradiata)*/ crowberry ***(Empetrum*** spp.) and (2) white spruce/willow/buffaloberry/huckleberry ***(Gaylussacia*** spp.)/dewberry ***(Rubus*** spp.)/peavine *(Lathyrus* spp.).

In White Spruce-Aspen (Type 251), either species may be dominant, but each species must make up at least 20 percent of the total basal area. Paper birch and black spruce may also be represented in Alaskan stands along with balsam fir and lodgepole pine in Canadian stands. The type is common throughout western Canada at lower elevations and in all of interior Alaska. Associated shrubs in Alaska are American green alder ***(Alnus crispa)***, willows, common bearberry ***(Arctostaphylos uva-ursi),*** soapberry, highbush cranberry ***(Viburnum*** *edule)*, and mountain cranberry *(Vaccinium* ***vitis-idaea).*** Associated shrubs in the Prairie Provinces are common snowberry ***(Symphoricarpos*** *albus)*, red-osier dogwood *(Cornus* ***stolonifera),*** western serviceberry ***(Amelanchier*** *al*-***nifolia),*** and western chokecherry ***(Prunus virginiana*** var. ***demissa).***

White Spruce-Paper Birch (Type 202) is defined similarly to White Spruce-Aspen in that either spruce or birch may be dominant as long as each species makes up at least 20 percent of the basal area. Aspen, lodgepole pine, subalpine fir, and black spruce are associated species. The type is common in Western Canada and in Alaska from the Arctic Circle to the Kenai Peninsula. Undergrowth species include willow, American green alder, highbush cranberry, prickly rose ***(Rosa*** *acicularis)*, mountain cranberry, bunchberry *(Cornus* ***canadensis),*** and Labrador-tea ***(Ledum groenlandicum).***

Whereas White Spruce-Aspen and White Spruce–Paper Birch are successional stages leading to the pure White Spruce type, Black Spruce-White Spruce (Type 253) may be a climax near the altitudinal and northern treeline. But black spruce may be replacing white spruce on some intermediate sites on older river terraces *(160).* Black Spruce-White Spruce is the lichen-woodland type from Hudson Bay to northwestern Alaska along the treeline as well as in open stands at alpine treeline sites in interior Alaska and northwestern Canada. It is also found on sites intermediate to the two species, such as older terraces above the floodplain. Paper birch, tamarack *(Larix laricina)*, balsam poplar, aspen, and balsam fir may be found within the stands, In open stands near the treeline, resin birch *(Betula* ***glandulosa),*** alder, and willows may form a continuous shrub cover that on drier sites may be replaced by mats of feathermosses and ***Cladonia*** lichens. Labrador-tea, bog blueberry *(Vaccinium* ***uliginosum),*** mountain cranberry, and black crowberry ***(Empetrum nigrum)*** are other common shrubs within the type.

In addition to these three tree cover types in which white spruce is a major component, the species is an associate in the following Western Forest cover types:

203 Balsam Poplar
204 Black Spruce
206 Engelmann Spruce-Subalpine Fir
217 Aspen
218 Lodgepole Pine
237 Interior Ponderosa Pine
252 Paper Birch
254 Black Spruce-Paper Birch

Several of these types are intermediate in the succession. Paper Birch may advance through White Spruce-Paper Birch to pure White Spruce. Balsam Poplar (Type 203) is eventually overtopped and replaced by white spruce; on some sites the process is very slow. Aspen often precedes the more tolerant spruce and fir forests, and lodgepole pine may be replaced by white spruce in northern latitudes.

In the Canadian boreal spruce-fir forest, American green alder is the most widespread tall shrub, with littletree willow *(Salix* ***arbusculoides),*** gray willow ***(S. glauca),*** and Bebb willow ***(S. bebbiana)*** important in the western range. Mountain maple ***(Acer spicatum),*** showy mountain-ash *(Sorbus decora)*, and American mountain-ash ***(S. americana)*** are important in the East. Highbush cranberry, red currant ***(Ribes triste),*** prickly rose, and raspberry ***(Rubus idaeus)*** are the most common medium to low shrubs. The most wide-ranging members of the herb-dwarf shrub stratum are fireweed ***(Epilobium angustifolium),*** one-sided winter-green ***(Pyrola secunda),*** one-flowered winter-green ***(Moneses*** *uniflora),* northern twinflower ***(Linnaea borealis),*** naked bishops-cap *(Mitella nuda)*, bunchberry, dwarf rattlesnake-plantain ***(Goodyera*** *repens)*, stiff clubmoss ***(Lycopodium annotinum),*** and horsetail ***(Equisetum*** spp.) ***(91).***

An average of 24 bryophytes (17 mosses and 7 liverworts) occur in Canadian white spruce-fir stands (92). The most common mosses are ***Pleurozium schreberi, Hylocomium splendens, Ptilium cristacastrensis, Dicranum*** *fuscescens,* and ***Drepanocladus uncinatus.*** The most common liverworts are ***Ptilidium pulcherrimum,*** *P. ciliare,* ***Lophozia*** spp., and ***Blepharostoma trichophyllum.*** Some common lichens are ***Peltigera apthosa,*** *P. canina,* ***Cladonia rangiferina, C. sylvatica, C. alpestris, C. gracilis,*** and ***Cetraria islandica.***

Life History

Reproduction and Early Growth

Flowering and Fruiting-White spruce is monoecious. Reproductive buds are differentiated at the time shoot growth ceases, the year before flowering and seed dispersal ***(35,118).*** The process lasts about a week. In British Columbia, it occurs during the last 2 weeks of July over a wide range of sites; this suggests that it may occur at about the same time throughout much of the species' range. Development of reproductive buds continues for 2 to 2.5 months and coincides with shoot maturation. The male buds become dormant first (about October 1 at Prince George, BC) followed by the vegetative and female buds about 2 weeks later ***(118).***

Cone-crop potential can be predicted in several ways. An early indication of a potential crop can be abnormally hot, dry weather at the time of bud differentiation, particularly if the current and preceding cone crops have been poor. Estimates of cone crop potential can be made by counting female reproductive buds in fall or winter. Differentiating male and female buds from vegetative buds is difficult, but the external morphology of the buds, and their distribution within the crown, enables the practiced observer to make the distinction (35). Female buds are concentrated in the top whorls. On 17-year-old grafts, the most productive was the 4th whorl from the top, and the productive zone averaged 6.4 whorls ***(112).*** In light crop years, the highest cone concentration is closer to the top than in intermediate or heavy crop years. Male buds generally are located in the middle to lower crown (38).

In the spring, renewed cell division and growth begin before the first evidence of bud elongation. In British Columbia, this is 6 weeks before pollination at low elevations and 8 weeks before pollination at high elevations *(119).* Meiosis takes place during this period about 3 weeks before maximum pollen shedding. Female receptivity coincides with pollen shedding and usually lasts from 3 to 5 days in May, June, or July depending on geographic location and climate. The southern areas definitely have earlier dispersal than northern areas; however, peak dispersal at latitude 48-50" and 65" N. can occur on the same calendar date *(106,108,149,193)*. Pollination is delayed up to 5 weeks at higher elevations *(119,193)*. The latest pollen dispersal occurs near elevational and latitudinal treeline.

The time of pollen shedding and female receptivity is undoubtedly temperature dependent and may vary as much as 4 weeks from year to year (44). Pollen dispersal shows a marked diurnal pattern dependent on temperature, humidity, and wind *(193)*.

The period of peak pollination and female receptivity is a critical stage in seed production and is easily disrupted by adverse weather such as rain and frost *(102,106,181)*. Such events can seriously reduce a promising seed crop.

Before pollen dispersal, male flowers are red and succulent; water can be squeezed from the conelet in a substantial drop. Moisture content (percentage of dry weight) was 500 to 600 percent greater than dry weight before pollen dispersal began and dropped precipitously as the male flower dried and pollen was dispersed. Just before shedding, the males are approximately 10 to 12 mm (0.4 to 0.5 in) long. Then the color changes from red to yellow and the conelet is almost dry when squeezed. This is the ideal time for collecting pollen. After the pollen is shed, the structure turns brown and soon falls.

At maximum receptivity, females are erect, *20* to 25 mm (0.8 to 1.0 in) long, and vary in color from green to deep red. Within an individual tree, the color is uniform. When receptive, the scales are widely separated, but they close shortly after pollination and the cones begin to turn down and gradually dull in color. Turning down takes from 2 to 4 weeks and occurs when the cone is growing most rapidly.

Fertilization occurs from 3 to 4 weeks after pollination *(103,119,128)*. Full size and maximum cone water content and fresh weight are attained in late June or early July. The final cone size may vary considerably from year to year *(193)*; it is determined by the weather the previous season, weather during cone expansion, and heredity.

The primary period of embryo growth occurs after cones attain maximum size. Cotyledons appear in middle to late July and embryo development is completed in early to late August *(103,119,128,188)*. Seed development can vary as much as 3 weeks from year to year *(33)*, and cotyledon initiation may differ from 1 to 3 weeks between high and low sites. Embryos have matured on the same date at both high and low elevations *(119)*; however, there can be large differences among elevations in time of seed maturation *(188)*.

The maturation process evidently continues after embryos attain physical and anatomical maturity *(33,177,183)*. Cone dry weight generally increases during this period. Weather is critical to the production of high quality seed. In high elevation and high latitude populations, immature seed with poorly developed embryos are produced during cold growing seasons *(183,193)*. In general, seed quality is highest in years of heavy seed production and lowest in years of low seed production. Cones ripen in August or September from 2 to 3 months after pollen shedding *(21,167,177,183)*.

Cone opening coincides with moisture contents of from 45 to 70 percent and specific gravities of from *0.6* to *0.8 (21,177,193)*. Cone firmness, seed coat color, seed brittleness, and various flotation tests are indicators of cone and seed maturity *(141)*. Cone color can also be used; but because female cone color can be red, pink, or green *(153)*, no standardized cone color changes are associated with maturity. Most authorities agree on the importance of observing cones closely during the last stages of maturity so that the optimum collection period is not missed.

White spruce seeds can be collected from 2 to 4 weeks before they ripen and seed quality improved by storing under cool (4° to 10° C (40" to 50" F)), ventilated conditions. Collection date and method of cone handling affect prechilling required for germination and early seedling growth. No specifics have been recommended for the best cone handling procedures *(33,177,183)*.

Seed Production and Dissemination-Cones and seeds have been produced by 4-year-old trees *(149)*. Production "in quantity" on 10- to 15-year-old trees has been reported, but it is usually low in younger trees and depends on site and season. Seed production in quantity begins at age 30 or older for most natural stands *(44,117)*. The interval between good to excellent cone and seed crops varies with site and geographic location. On good sites, good to excellent years can occur at 2- to 6-year intervals but may be as many as 10 to 12 years apart *(88,167,184,192)*. Excellent seed years may be related to hot, dry summers at the time of bud differentiation *(112)*. They are always followed by poor ones; the alternation can result from carbohydrate and nutrient deficiencies or the lack of sites in the crown able to produce reproductive buds *(117)*.

A mixture of gibberellins, GA4/7, has been found to substantially increase female flowering in white spruce *(15,121)*. Treatment of elongating shoots was effective, but application to dormant shoots was not

(16). Fertilization with ammonium nitrate has also been successful in promoting flowering (68).

Both the initiation and pattern of seed dispersal depend on the weather. Cool, wet, or snowy weather delays the onset of dispersal and causes cones to close after dispersal has begun. Cones reopen during dry weather, A small number of seeds are usually dispersed in August, but most of the seeds fall in September *(30,167,186,192,193).* Early- and late-falling seeds have a lower viability than seeds falling during the peak period *(167).* Cones can remain on the tree from 1 to 2 years after the majority of seeds are dispersed. Cone opening and seed dispersal pattern can vary among trees in the same stand *(186).*

Average weight per seed varies from 1.1 to 3.2 mg (0.02 to 0.05 grains) *(64,193),* and there are approximately 500,000 seeds per kilogram (226,000/lb) *(155).* From 8,000 to 12,000 cones may be produced by individual trees in good years, This corresponds to approximately 35 liters (1 bushel) or about 250,000 seeds (64). Yields in the far north are less (184). Cone production in mature spruce stands occurs primarily in dominant and codominant trees with sporadic and low production in intermediate and suppressed trees *(167).*

The total number of seeds per cone varies significantly among trees and regions-from 32 to 130 have been reported *(87,167,192).* Seeds produced on the apical and basal scales are not viable; therefore, the number of viable seeds per cone is much lower—from 12 to 34 and from 22 to 61 full seeds per cone for open and control pollinations, respectively (87).

Seed dispersal as measured by seed trapping varies with seed year and from day to day. In Manitoba, the maximum annual total seedfall was $1400/m^2$ ($130/ft^2$), and 59 percent were filled. The seed rain exceeded $290/m^2$ ($26.9/ft^2$) in 5 of the 10 years, and 40 to 71 percent of these were filled; for 3 years it was less than $10/m^2$ ($0.9/ft^2$), and of these 2 to 36 percent were filled *(167).* In Alaska, maximum total seed rain in one stand over a 13-year period was 4,000 seeds/m^2 ($371.7/ft^2$). Seed rain exceeded 1,000 seeds/m^2 ($92.9/ft^2$) in 3 years and was between 400 and 500 seeds/m^2 (37.1 and $46.4/ft^2$) in 2 other years. In the remaining years, seed rain was less than $100/m^2$ ($9.3/ft^2$) (184).

White spruce is primarily wind-dispersed, and the time in flight and distance of flight for individual seeds was variable and depended on conditions at the time of dispersal (191). The quantity of seed reaching a given area drops precipitously with distance from the seed source. At 50, 100, 200, and 300 m (162.5, 325.0, 650.0, 975.0 ft), seed rain may be as low as 7, 4, 0.1, and 0.1 percent of that in the stand. The actual percentage of seeds reaching various distances may vary among sites within a local area and among geographical areas (30,186).

White spruce seed collection is expensive, but cost can be reduced by robbing the cone-caches of red squirrels. The viability of seed from cached cones does not vary between the time squirrels begin to cache cones in quantity and the time the last cones are cached *(164).* Viability drops to near zero, however, after 1 to 2 years of storage in a cone cache.

White spruce rapidly regenerates the crown after topping, thereby restoring the seed-bearing capacity. In fact, topping may temporarily increase cone production *(112).* Therefore, it is possible to reduce seed collection costs more than three times by collecting from downed tops *(138).*

Seedling Development-White spruce seed shows conditional dormancy that varies in response to temperature and light conditions and therefore can be modified by stratification or prechilling. Optimum germination temperatures are from 10" to 24" C (50" to 75" F); maximum germination temperature is between 29" and 35" C (84" and 95" F). Minimum constant temperature is 5" C (41" F), but most germination ceases below 10" C (50" F). A diurnal fluctuation in temperature may be favorable *(27,47).*

Prechilling or stratification at 2" to 4" C (36" to 39" F) is recommended for testing seed lots and for improving germination capacity, energy, and survival in the nursery of spring-sown seed. Stratification is not always a prerequisite for complete germination, however *(27,47,171,172,193).* Germination is epigeal *(155).*

The period of germination under field conditions is mid-May through early August. With adequate water, seeds germinate as soon as soil surface temperatures are warm enough. Generally, germination (natural seedfall or artificial seeding in fall) is 75 to 100 percent complete by early July. Some white spruce seeds are able to withstand several wetting and drying cycles without losing their viability *(63,70,168,189).* Germination of spring-sown seeds begins somewhat later than in fall-sown seeds but is complete in 3 to 4 weeks *(24,34).* Adverse conditions offset germination and may delay it to the following year. Germinants developing after the middle of July have a lower survival probability than those originating in early summer *(18,49,62,67,193).*

White spruce is capable of reproducing under mature stands of spruce and early succession tree species; however, the response is highly variable and density and percent stocking are low (89,170). In Saskatchewan, for example, advanced regeneration was not present in 88 percent of the stands studied, and one-half of the remaining stands had less than

1,240 seedlings per hectare (500/acre) (84). On upland sites in interior Alaska, advanced regeneration ranged from 1 to 25 percent stocking and density from 120 to 640 stems per hectare (50 to 260/acre) *(70)*.

Regeneration under established stands, whether spruce or other species, occurs on a variety of seedbeds and commonly on rotted logs *(25,164,168)*. Feathermosses ***(e.g., Hylocomium*** spp., ***Pleurozium*** spp.) and associated organic layers are the most common seedbed surfaces in mature stands (92). Where the L- and F-layers are greater than from 5 to 8 cm (2 to 3 in), they greatly restrict regeneration. This is particularly true in drier western regions. Although this limitation is most often attributed to low water retention, it may be chemical inhibition (allelopathy) caused by some forest floor components, particularly lichens (42). In mature stands, exposed mineral soil after windthrow and floods are the best seedbeds *(29,70,165)*. They can have stocking levels approaching 100 percent.

The average number of seeds required to produce a seedling on recently exposed mineral soil ranges from 5 to 30 *(30,36,50,69,193)*. The seed requirement increases with each year after exposure of the soil because of increasing plant competition and litter accumulation (95). Receptivity of organic seedbeds is generally believed to be extremely low; seed-per-seedling ratios of 500 to 1,000 seeds or more are commonly reported in harvested areas *(36,70)*. These surfaces vary considerably, however, and their receptivity for germination and seedling establishment depend on the amount of solar radiation at the surface, type of organic substrate, degree of disturbance to the organic layers, weather conditions at the time of germination, amount of seed rain, and other biotic and abiotic factors. In undisturbed stands, seedlings are frequently found on organic matter, particularly rotted wood *(32,170,187)*. Germination and seedling establishment, although not as efficient as on mineral soil in terms of seed-to-seedling ratios, are common on organic substrates after harvest in both clearcuts and shelter-woods *(124,178)*.

A key for identifying the seedlings of North American spruce species is available (95).

Optimum conditions for seedling growth have been delineated for container production of planting stock in greenhouses. The most suitable temperature conditions are alternating day/night levels as opposed to a constant temperature regime. At 400 lumens/m^2 (37.2 lumens/ft^2, or footcandles) light intensity, a 25°/20° C (77°/68° F) day/night regime is recommended for white spruce *(13,122,154)*. Temperature and light intensity effects interact: at low intensities, about 40 lumens/m^2 (3.7 lumens/ft^2), a 28°/13° C (82°/55° F) day/night regime is favorable *(11)*. A short photoperiod (14 hours or less) causes growth cessation, while a photoperiod extended with low light intensities to 16 hours or more brings about continuous (free) growth. Little is gained by using more than 16 hours low light intensity supplement once the seedlings are in the free growth mode. Long photoperiods using high light intensities of from 10,000 to 20,000 lumens/m^2 (930 to 1,860 lumens/ft^2) increase dry matter production. Increasing the light period from 15 to 24 hours may double the dry matter growth *(13,122)*.

Seedling growth can be closely controlled by manipulating the environment. Short photoperiods induce dormancy and permit the formation of needle primordia. Primordia formation requires from 8 to 10 weeks and must be followed by 6 weeks of chilling at 2" C (36° F) *(100,109,123)*. Prompt bud breaking occurs if the seedlings then are exposed to 16-hour photoperiods at the 25°/20° C (77°/68° F) temperature regime. Freedom from environmental stress (for example, lack of moisture) is essential for maintaining free growth (99,100). It must be kept in mind that free growth is a juvenile characteristic. According to Logan *(99)*, it is lost when seedlings are 5 to 10 years old, but our observations suggest that it would be extremely rare in seedlings older than 5 years.

At the end of the first growing season, natural regeneration may be from 10 to 20 mm (0.4 to 0.8 in) tall. Root length is from 20 to 100 mm (0.8 to 4.0 in), depending on site and seedbed type. The stem is unbranched; the taproot normally develops lateral roots that may be from 30 to 50 mm (1 to 2 in) long *(34,62,72,89,193)*.

Natural regeneration usually does not exceed from 30 to 50 cm (12 to 20 in) in average height after 4 to 6 years. The number of branches increases significantly during this period. Lateral root length may be as much as 100 cm (39 in), but rooting depth may not increase significantly. Shoot dry weight (including foliage) increases from 0.2 to 5 g (3.09 to 77.16 grains) and root dry weight from 0.06 to 1 g (0.92 to 15.43 grains) between ages 2 and 6 *(37,70,72,89,165,168,190)*. The length of time required to reach breast height under open conditions ranges from 10 to 20 years depending on site; under stand conditions, growth to this height may take 40 or more years (61).

Growth is greatest at full light intensity *(9,98)*. Reducing light intensity to 50 percent of full light reduced height growth by 25 percent, shoot weight by 50 percent, and rooting depth by 40 percent in lo-year-old seedlings; at 15 percent of full light, no spruce survived (37). Control of competing herbaceous vegetation has resulted in 38 and 92 percent increases in growth 3 years after planting *(150).*

White spruce is sensitive to transplanting shock. Check-the prolonged period of minimal growth-is considered by some forest managers to be a problem serious enough to disqualify white spruce as a plantation species. The cause of check, though not fully understood, is thought to be nutrient stress resulting from the root's inability to develop in the planting zone. Check is difficult to predict and prevent *(141,147)*, but seedling quality is a factor, and any treatment that will improve early root growth is undoubtedly beneficial *(7,9).*

Vegetative Reproduction-Vegetative reproduction from layering is common at some latitudinal treeline sites in Canada and Alaska *(26,39).* Layering probably is an important means of maintaining the stand when sexual reproduction is limited or nonexistent because of climatic limitations.

In the far north, the density of trees originating from layering may reach 1830/ha (740/acre) and generally is inversely related to site quality. Layering is most common in stands in which trees are open grown and the lower branches touch the ground. The branch roots when it is covered by moss, litter, or soil and organic material. The time required for an individual to become independent of the ortet (parent) is not known, but 30- to 50-year-old ramets are no longer connected with the ortet (26).

Air layering on a 6-year-old tree has been successful; early May is the best time for preparing the air layers. Juvenile white spruce can be readily propagated by rooted cuttings *(54,55).* Rooting ability varies greatly from tree to tree, but it is too low for practical use by the time most trees are 10 to 15 years old. Older trees can be grafted. Results are best in the winter (February, March) in the greenhouse, with forced rootstock in pots and dormant scions, but fall grafting is possible. Late winter-early spring grafting in the field also is possible but should be done before bud swelling becomes pronounced (107).

Sapling and Pole Stages to Maturity

Growth and Yield-In white spruce, strong apical dominance of the terminal shoot leads to the excurrent growth form. Crown form may deviate substantially from the idealized conical shape because of variation in the growth of lateral branches as a result of tree and branch age, damage, or growing conditions. The most significant deviations occur near the treeline where marginal growing conditions can result in shrub-like trees. During the juvenile phase, trees can be kept growing continuously if all growth factors are within the optimum range. This is called "free growth." In older trees shoot growth is determinate; that is, the annual complement of needles is preformed in the overwintering bud.

The formation of the following year's buds in British Columbia (lat. 54" to 55" N.) begins in late April or early May with the initiation of the first bud scales. Needles for the next growing season are initiated in August and September after the period of shoot elongation. On productive forest sites, visible signs of shoot growth (flushing) are first observed in early May or early June *(108)*, 6 to 7.5 weeks after the first cell divisions signal the end of dormancy. Up to 6 weeks delay in flushing may result from a 500-m (1,640-ft) increase in elevation *(120).* Growth of the leader and upper branches occurs over a slightly longer period than growth of lower branches (46).

The time of flushing is primarily temperature dependent and therefore varies with the weather. The number of degree days accumulated at the time of flushing may vary from year to year, however, indicating that more than air temperature controls the initiation of the annual shoot-growth cycle (8). Within a stand, there can also be as much as a 3-week difference among individual trees (111,116). The period of shoot elongation is short. In northern Wisconsin, the period from flushing until the terminal leader had completed 95 percent of total elongation ranged from 26 to 41 days among individual trees. This is much shorter than the 6- to 11-week period reported by others (108,149) but agrees closely with data from central British Columbia *(120).* In interior Alaska (lat. 64° N.), 85 to 90 percent of terminal shoot growth was completed by June 14 and 100 percent by June 28 *(70).* The cessation of shoot growth is more dependent on photoperiod than on temperature *(120).*

Cambial activity in Alaska (lat. 64" N.) and Massachusetts (lat. 42" N.) has been compared. The period of cambial activity is about half as long and the rate of cell division twice as great in Alaska as in Massachusetts (56). Wood production (mitotic activity) was observed to begin after 11 degree days (6° C (43" F) threshold) in Alaska (early May) and Massachusetts (late April). Eighty percent of the tracheids were produced in 45 and 95 days in Alaska and Massachusetts, respectively. Variation of the same magnitude depending on site and year has been reported within a small region in Ontario (46).

Culture affects growth; thinned, fertilized stands begin growing about 2 weeks earlier (late May versus early June) and have greater growth during the grand period. Termination of growth is not influenced by thinning *(157).*

Individual white spruce trees more than 30 m (100 ft) tall and from 60 to 90 cm (24 to 36 in) d.b.h. are found on good sites throughout the range. The tallest trees reported are more than 55 m (180 ft) and from 90 to 120 cm (36 to 48 in) d.b.h. (106,149).

Maximum individual tree age appears to occur on stress sites at latitudinal or elevational treeline rather than on good sites where trees attain maximum size. A partially rotted 16.5 cm (6.5 in) tree growing on the Mackenzie River Delta (above lat. 67" N.) had a 589-year ring sequence, and trees nearly 1,000 years old occur above the Arctic Circle *(51).* On good sites, trees 100 to 250 years old are common, and the oldest trees (250 to 300 years) are frequently found in areas protected from fire, such as islands, and in relatively wet upland situations *(83,185).*

Normal yield tables and harmonized site-index (base 100 years) curves provide estimates of growth and productivity for unmanaged stands in Alaska and western Canada. In Alaska, Farr *(41)* reported site indices at age 100 years from 15.2 m (50 ft) to 32.3 m (106 ft). Growth, yield, and selected stand characteristics for well-stocked white spruce stands in Alaska are summarized in table 2.

The lowest recorded mean annual increment (0.5 m^3/ha or 7 ft^3/acre) comes from the Mackenzie River Delta-the northernmost area of white spruce in North America.

Site indices ranging from 15.2 to 27.4 m (50 to 90 ft) (base 70-year stump age) have been reported for the Mixedwood region of Alberta *(82)*, and in the Mixedwood section of Saskatchewan, growth and yield were reported for poor (site index 17.1 m or 56 ft), average (site index 21.9 m or 72 ft), and good (site index 26.8 m or 88 ft) sites (84). The Saskatchewan data are summarized in table 3.

Mean annual increments of 6.3 to 7.0 m^3/ha (90 to 100 ft^3/acre) have been attained on the best loam soils, and the highest site index 36.6 m (120 ft) is for British Columbia white spruce *(61)*. Site indices for the Lake States *(14)* are somewhat higher than the best in Saskatchewan *(84)*, but below the best sites in British Columbia.

Biomass production in white spruce is not well documented. In the Yukon Flats Region, AK, a 165-year-old stand with a density of about 975 trees per hectare (394/acre), 63 percent less than 20 cm (8 in) in d.b.h., had a standing crop of 12.61 kg/m^2 (2.58 lb/ft^2). It was 97 percent spruce and 3 percent alder and willow. A 124-year-old stand (maximum tree age) with a density of about 3,460 trees per hectare (1,400/acre), 97 percent less than 10 cm (4 in) in d.b.h., had a standing crop of 4.68 kg/m^2 (0.96 lb/ft^2). It was 91 percent spruce and 9 percent alder and willow. Of a total biomass of 57.13 kg/m^2 (11.70 lb/ft^2), 44 percent was overstory, 34 percent forest floor, and 22 percent roots in a 165-year-old interior Alaska stand *(194).* Within-tree biomass distribution in two approximately 40-year-old trees (total biomass 25 kg or 55 lb) was foliage, 31 percent; branches, 31 percent; and stem, 38 percent. Proportionally, stem biomass was much higher (59 percent) in a 95-year-old tree with a total weight of 454 kg (1,000 lb) above ground; 21 percent was foliage and 18 percent branches *(80)*. Total biomass in an unthinned white spruce plantation in Ontario has been measured at 13.89 kg/m^2 (2.84 lb/ft^2); 19 percent was in roots, 9 percent foliage, and the remaining 72 percent was in the branches and main stem *(142).*

Natural stands of white spruce can respond well to cultural practices. Released 71-year-old trees in Maine had a mean annual increase (lo-year period) in circumference of 1 cm (0.4 in) compared to 0.6 cm (0.2 in) for control trees (45). Basal area increment

Table 2—Growth, yield, and selected stand characteristics for well-stocked white spruce stands in Alaska (adapted from 41)

Site index (base age 100)	Stand density	Basal area	Total volume	Mean annual increment (M.A.I.)[1]	Culmination of M.A.I.
m	*trees/ha*	*m^2/ha*	*m^3/ha*	*m^3/ha*	*yr*
14.9	1,324	22.5	78.1	0.8	150
24.4	1,122	33.1	227.2	2.2	100
30.5	959	40.0	351.3	3.6	80
ft	*trees/acre*	*ft^2/acre*	*ft^3/acre*	*ft^3/acre*	*yr*
49	536	98	1,117	12	150
80	454	144	3,245	31	100
100	388	174	5,018	51	80

'Trees larger than 11 cm (4.5 in) in d.b.h

Table 3—Growth and yield of white spruce in a Mixedwood section of Saskatchewan (adapted from *84*)

Site index (base age 70 at stump)	Stand density	Basal area	Total volume	Mean annual increment (M.A.I.)[1]	Culmination of M.A.I.
m	*trees/ha*	*m^2/ha*	*m^3/ha*	*m^3/ha*	*yr*
17.1	1,063	25.7	179.1	2.0	80
22.9	976	35.8	276.4	3.2	70
26.8	815	45.9	373.8	4.3	70
ft	*trees/acre*	*ft^2/acre*	*ft^3/acre*	*ft^3/acre*	*yr*
56	430	112	2,500	28	80
72	395	156	3,950	45	70
88	330	200	5,340	62	70

'Trees larger than 9 cm (3.6 in) in d.b.h in 70-year-old Alaskan spruce for a 5-year period was increased 330 percent by thinning and fertilization, 220 percent by thinning, and 160 percent by fertilization *(157).* Even old white spruce can respond to release.

The ability to respond is related to type of release and degree of damage sustained during release *(66).* In Manitoba, diameter increment of spruce of all size classes (ages 10 to 60 years) was doubled by removing competing aspen *(138).* Spruce having their crowns in contact or immediately below those of aspen can be expected to double their height growth following release. The combined effect of increased diameter increment and height growth can increase spruce volume production by 60 percent.

In unmanaged plantations, the onset of density-dependent mortality is determined by site quality and initial spacing. Yield tables for unmanaged white spruce plantations in Ontario *(143)* indicate that mortality at age 20 years will have occurred at 6,730 trees per hectare (2,722 trees/acre) at site index 15.2 m (50 ft) (base age 50 years). At site index 24.4 m (80 ft), mortality will have occurred at densities of 2,990 trees per hectare (1,210/acre) or more by age 20. At 1,080 trees per hectare (436/acre), predicted mortality begins between 30 and 35 years for site index 24.4 m (80 ft.) and 40 and 45 years for site index 21.3 m (70 ft). Total volume production in unthinned plantations in Ontario (table 4) is higher than the production in natural stands in Saskatchewan.

White spruce stands should be maintained at basal areas from 23.0 to 32.1 m^2/ha (100 to 140 $ft^2/acre$) to provide maximum volume growth and good individual tree development; below these levels, individual tree increment and resistance to some pests are greatly increased, but total volume production is reduced. For the sites studied, maximum mean annual increment occurred at about age 55 in unmanaged plantations; at this age, 10 percent of total volume is lost from competition *(5,9,140,142).*

Table 4—Volume of white spruce in unthinned plantations in Ontario (adapted from *121*)

Planting density	Plantation age	Site index at base age 50 years: 15.2 m or 50 ft	Site index at base age 50 years: 24.4 m or 80 ft
trees/ha	*yr*	*d/ha*	
6,714	20	43.3	124.8
	50	275.8	513.0
2,197	20	26.8	86.6
	50	212.5	461.7
1,077	20	19.0	66.3
	50	172.8	430.5
trees/acre	*yr*	*ft^3/acre*	
2,717	20	619	1,783
	50	3,940	7,329
889	20	383	1,237
	50	3,036	6,596
436	20	271	947
	50	2,469	6,150

Rooting Habit-White spruce is frequently characterized as shallow rooted. This generalization stems, however, from the species' ability to occupy sites where soil conditions limit rooting depth *(148);* depending on soil conditions, competition, and genetics, different forms of taproots and layered roots do develop *(145,166).* The adventitious multilayered root, systems that develop on floodplains in response to silt deposits are particularly noteworthy. Trees from 2 to 132 years old can grow new roots in this way; the response is probably important for maintaining tree vigor (77,164).

Depth of rooting in white spruce is commonly between 90 and 120 cm (36 and 48 in), but taproots and sinker roots can descend to a depth of 3 m (10 ft). Eighty-five percent of the root mass was in the top 0.3 m (1 ft) on sites in Ontario, but on the most northern sites, large roots are heavily concentrated within 15 cm (6 in) of the organic-mineral soil interface. Lateral spread of the root system was reported to be as much as 18.5 m (61 ft) on sandy soils in Ontario, and lateral root extension was estimated at 0.3 m (1 ft) per year *(141,145,148).*

Fine-root production in a Maine plantation was 6990 kg/ha (6,237 lb/acre); 87 percent of this material was located in the top 15 cm (6 in) of soil *(136).* In an Ontario plantation, fine roots 0.25 cm (0.10 in) in diameter and smaller comprised about 10 percent (2670 kg/ha or 2,382 lb/acre) of the total root biomass *(143).* Sixty-seven percent of the fine-root production in a mixed spruce-fir stand in British Columbia was in the forest floor and A horizon; the average depth of these horizons was 8.3 cm (3.3 in) (86). Mycorrhizae are an important component of the fine roots (143) of most conifer species *(89),* but only a few of the fungi that form mycorrhizae have been found on white spruce.

Root grafting appears to be fairly common in white spruce. In one study, about 27 percent of the trees had root grafts with other trees (140,149).

Reaction to Competition-White spruce is intermediate in tolerance to shade. It is equally or less tolerant to shade than black or red spruce, hemlock (*Tsuga* spp.), balsam and alpine fir, sugar maple, and beech (*Fagus* spp.). It is more tolerant than aspen, paper birch, and lodgepole pine.

Large numbers of white spruce may become established immediately following disturbance and form even-aged stands. Because seedling and juvenile growth of white spruce is slower than its early successional associates, it remains in the understory for *50* to *70* years *(25,104,160,169).* Although white spruce survives this period of suppression, growth will be significantly reduced *(139).* White spruce shows a significant response to release resulting from natural causes or silvicultural treatment; ages of trees exhibiting good growth after release range from very young to 200 or more years *(6,22,45, 139,185).*

White spruce also forms multi-aged pure stands or is a component of multi-aged, late-succession stands mixed with the true firs, maple, beech, and other species. In such stands, age ranges from 200 to 250 years in Alberta (25) and from 300 to 350 years in British Columbia *(104)* and at treeline in northern Alaska (26). Natural stands occurring within relatively small areas can show markedly different age structures depending on age of the site, stand history, soil conditions, and other variables (83). The distribution of ages is not continuous but consists of several groups of ages separated by periods when no white spruce become established.

Damaging Agents-Throughout the range of white spruce, fire has been an important, sometimes dominant factor in forest dynamics *(25,136,162).* Mature forests are easily destroyed because of their high susceptibility to fire. Under certain circumstances, in unmanaged forests white spruce may be eliminated; the probability increases with latitude because seed years are infrequent and seed quality poor in some years in the north *(136,183).* During early- and mid-succession, white spruce is more susceptible to fire than aspen, birch, black spruce, and lodgepole pine *(182).*

Fire frequency, intensity, and severity, and not simply the presence of fire, determine white spruce distribution and growth. Fire frequency may range from 10 years or less to more than 200 years; most commonly, it is from 60 to 200 years. If fires occur at short intervals (less than 40 or 50 years), the source of white spruce seed can be eliminated. The reduction in depth of organic matter depends generally on fire severity and is a critical factor because the organic substrate that remains following fire makes a poor seedbed. In general, even severe fires do not expose mineral soil on more than 40 or 50 percent of a burn, and this area is usually distributed in small patches.

On floodplains in the northwestern part of the range, floods and silt deposits provide a seedbed for germination and seedling establishment. Flooding is detrimental to young seedlings, however, and establishment of spruce stands may be prevented until the flooding frequency declines. Fifty years may be required after initial sandbar formation before sedimentation rate declines enough for white spruce to colonize *(104).* As much as 20 percent of the seedlings may be killed on moist and wet sites that have been scarified by tractor and bulldozer blade (94).

Slow initial root growth makes young seedlings and transplants particularly susceptible to frost heaving. The severity of damage generally is greatest on fine-textured and wet soils where water is adequate for ice crystal formation in the surface soil. Late fall and winter seeding and spring field planting are best in most cases *(141).* White spruce roots respond vigorously to pruning *(146)*; spring planting with root pruning is likely to be of some protective value against frost heaving.

Depending on soil texture and drainage, white spruce may be prone to windthrow. Windthrow is common along stand edges and in heavily thinned stands on shallow or poorly drained soils where root systems are surficial. On soils where a strong taproot, strong descending secondary roots, or multilayered root systems develop, the species is much more windfirm. In mixed stands in which white spruce is overtopped by hardwoods, the leader and upper stem of spruce are frequently damaged by hardwood branches whipping in the wind.

Snow and ice can break up to 70 percent of white spruce in stands and hail can cause defoliation, stem lesions, and leader or terminal bud mortality *(31,52,156).*

White spruce vegetative and reproductive growth are particularly susceptible to frost damage at the time of flushing *(116,181).* The risk of frost damage is less for late flushing genotypes *(110,116).* Damage by fall frost is uncommon but has been observed in l-year-old seedlings, when plantations heavily damaged by spring frost have responded with regrowth in August. Damage from spring frost is less serious after trees reach from 4 to 6 m (13 to 19 ft) in height. Because the species is so susceptible to frost damage, sites exposed to late spring frost should be avoided in all white spruce regeneration efforts.

Young seedlings are damaged by rodents. The snowshoe hare can be a significant pest, but white spruce is not a preferred animal food *(4,12).*

Environmental factors such as frost, mammals, birds, insects, and disease reduce the number of cones and the number of dispersed seeds *(101,181).*

The impact of squirrels can be substantial. In Alaska, they may harvest as much as 90 percent of the cone crop *(144,193).* Small mammals such as deer mice, red-backed and meadow voles, chipmunks, and shrews can be an important cause of failure of natural regeneration and artificial regeneration by direct seeding. Seed consumption by individual animals can be very high-2,000 white spruce seeds per day for caged animals of the species mentioned— and the population density substantial but highly variable. Estimates range from 7 animals per hectare (3/acre) to as high as 44/ha (18/acre). Even at the low density, the impact on regeneration would be unacceptably high (126,141). The impact on seed varies with the time of seeding: 50 percent for spring-sown seeds as compared to 19 percent or less for winter-sown seeds. Coating seeds with repellent is effective and has little influence on seed germination even when coated seeds have been stored for 5.5 years *(125,127).*

The impact of birds feeding on seeds is small compared to that of rodents *(126),* but chickadees, grosbeaks, crossbills, juncos, and sparrows feed on coniferous seeds.

Seed losses from insects can be a serious problem. The spruce cone maggot ***(Hylemya (Lasiomma) anthracina),*** the fir coneworm ***(Dioryctria abietivorella),*** and the spruce seed moth ***(Laspeyresia youngana)*** are most important. ***Hylemya*** leaves the cone in midsummer and, as a result, ***Laspeyresia*** is blamed for the damage it does; however, where the infestation is severe, ***Hylemya*** may destroy 100 percent of the seed *(59).* Damage by ***D. abietivorella*** is particularly severe in years of heavy cone crops and appears to be found when cones develop in clusters. The following insects also attack seeds and cones but do less damage: the spruce cone axis midge ***(Dasineura rachiphaga),*** the spruce seed midge ***(Mayetiola carpophaga),*** the seed chalcids ***(Megastigmus atedius*** and ***M. picea),*** the cone cochylid ***(Henricus fuscodorsana),*** and the cone moth ***(Barbara mappana)*** (59). The only disease associated with cone production is the cone rust ***Chrysomyxa pirolata*** *(151).* Seeds produced from infected cones are about half the weight but the same size as healthy seeds. Seeds are fragile because seed coats are poorly developed, and seed mortality is almost 100 percent in severely affected cones ***(101,151).*** Even if viable seeds are produced, they are not readily dispersed because cone malformation and resinosis prevent efficient opening of the cone scales ***(151).***

White spruce seedlings are affected by disease during the dormant and growing seasons. Snow blight ***(Phacidium infestans)*** causes damage in nurseries and the field. Various species of ***Pythium, Rhizoctonia, Phytophthora,*** and ***Fusarium*** have been shown to be moderately to highly pathogenic to spruce seedlings in both pre- and post-emergent conditions ***(65). Pythium*** and ***Fusarium*** as well as ***Epicoccum*** and ***Phoma*** can also injure seedlings in cold storage; many of these damaged seedlings die when they are field planted (67). Nematodes have been shown to cause winterkill and reduce seedling vigor.

Needle and bud rusts are common throughout the range of white spruce. The most important rust causing premature defoliation in Canada is ***Chrysomyxa ledicola.*** Losses of up to 90 percent of the current year's needles have been observed in Western Canada. Other needle rusts that infect white spruce are ***C. weiri, C. empetri, C. ledi,*** and ***C. chiogenis.*** The witches' broom rust ***(C. arctostaphyli)*** frequently causes dead branches, abnormally proliferating branches, deformed boles, and reduced growth. A bud rust *(C. woroninii)* is more prevelent in far northern areas and infects seedlings and vegetative and female buds of mature trees ***(65,101,195).***

Stem diseases of white spruce are not of major importance. A canker caused by ***Valsa kunzei*** has been reported. One of the most conspicuous and common stem and branch deformities is a tumor-like growth of unknown origin. These tumors occur throughout the range and may reach 0.6 to 0.9 m (2 to 3 ft) in diameter. In a small test of grafts of tumored and tumor-free trees, tumor growth was transmitted to some, but not all, ramets in some clones of tumored trees (44).

Root diseases of white spruce affect both seedlings and mature trees. ***Inonotus tomentosus*** is a major cause of slow decline and death of white spruce in patches of 0.4 ha (1 acre) or more in Saskatchewan. The disease has been called the "stand-opening disease." It develops slowly over a period of 20 to 30 years but the impact can be substantial-37 percent of white spruce in mixed stands either dead or heavily rotted at the butt. Stand openings occur on soils of all textures but rarely on alkaline soils ***(174).*** Trees planted in infected areas are also damaged ***(175).*** Other root-rot fungi associated with white spruce are ***Coniophora puteana, Scytinostroma galactinium, Pholiota alnicola, Polyporus guttulatus, I? sulphureus,*** and ***Phaeolus schweinitzii.***

Trunk rots affecting white spruce include ***Haematostereum sanguinolentum, Peniophora septentrionalis,*** and ***Phellinus pini.*** These species produce rot development beyond the tree base. ***Coniophora puteana, Fomitopsis pinicola,*** and ***Scytinostroma galactinium*** are associated only with butt rot. In general, cull percentage in white spruce caused by rot is low, particularly for trees less than

100 to 120 years old. Most trees older than 200 years have significant amounts of rot, however.

Although most spruce species are seriously injured by the European strain of scleroderris canker (*Gremmeniella abietina*), white spruce suffers only from tip dieback and eventually recovers (137). Dwarf mistletoe (*Arceuthobium pusillum*) is usually associated with black spruce, but it has killed white spruce in Minnesota (3), along the coast of Maine, and in the Maritime Provinces.

White spruce is attacked by a number of bark beetles in the genera *Dendroctonus, Ips, Trypodendron, Dryocoetes, Scolytus, Polygraphus,* and others. Although most of these species attack trees of low vigor, dying trees, windthrows, and slash, the spruce beetle (*Dendroctonus rufipennis*) attacks trees of normal vigor and has killed large areas of white and other spruces. In areas with transition maritime climates, such as western and south-central Alaska, prolonged extreme cold (-40" C or -40" F) kills large numbers of beetles. Where spruce beetle outbreaks are common, resistance of trees is greater in mature stands with stocking levels of $18 m^2/ha$ (80 $ft^2/acre$) or less because of wide tree spacing and rapid growth (58). Dense stocking contributes to cold soils in the spring and thus tree moisture stress, which predisposes the trees to beetle attack (57). Bark beetles bore or mine in the phloem or inner bark and girdle the tree. Symptoms of beetle attack are pitch flow tubes and fine wood particles on the bark or at the base of the tree. The foliage of the attacked tree changes color and dies, but this may not occur until after the beetle has left the tree. The best method of preventing beetle outbreaks is to remove or destroy desirable habitat such as slash and damaged trees; trees weakened by budworms are particularly susceptible.

Wood-boring insects (*Monochamus* spp., *Tetropium* spp., and *Melanophila* spp.) attack weakened or dead white spruce and are particularly attracted to burned areas. They can attack trees almost before the fire cools. The intensity of attack is determined by the condition of the individual tree (173). Lumber recovery from heavily infested trees declines rapidly because of extensive tunneling.

The spruce budworm (*Choristoneura fumiferana*) and the western spruce budworm (*C. occidentalis*) feed and mine in old foliage, in developing reproductive and vegetative buds, and in new foliage of the expanding shoot. True firs are the principal hosts, but spruces are readily attacked and injured. Budworms are the most destructive conifer defoliators; severe defoliation for 2 years reduces growth, and sustained outbreaks have killed all spruce in some stands (48,81). Plantations are not usually subject to serious damage until they are about 6 m (20 ft) tall (141).

The yellowheaded spruce sawfly (*Pikonema alaskensis*), another defoliator, is not important in closed stands but can seriously reduce growth or kill plantation-grown trees if defoliation continues for 2 or more years (141). A number of other sawflies including the European spruce sawfly (*Diprion hercyniae*), also damage the species.

Spruce spider mites (*Oligonychus* spp.) build up in damaging numbers in early spring and summer and sometimes in fall. They are also common on young white spruce plants growing in greenhouses. Their feeding destroys the chlorophyll-bearing cells of the needle surface, causing a bleached look. Continuous attacks weaken and eventually kill the tree (81).

The European spruce needleminer (*Epinotia nanana*) causes unsightly webbing and kills needles on spruces in the Eastern United States. Heavy attacks cause severe defoliation, and weakened trees succumb to secondary pests. Other needleminers of less importance are in the genera *Taniua* and *Pulicalvaria* (122). Other insects damaging spruce needles include needle worms, loopers, tussock moths, the spruce harlequin, and the spruce bud scale.

The gall-forming adelgids (*Adelges* spp.), of which the eastern spruce gall adelgid (*A. abietus*) is the most prevalent, cause cone-shaped galls on the shoots. Other gall-forming insects belong to the *Pineus* and *Mayetiola* genera (122). Although not important for forest trees, these galls can deform and stunt the growth of seedlings, saplings, and ornamental trees (48,81).

Spruce buds are damaged by bud moths, *Zeiraphera* spp., the bud midge (*Rhabdophaga swainei*), and bud and twig miners (*Argyresthia* spp.). None of these insects causes serious damage (122), but killing of the terminal leader by *Rhabdophaga* results in multiple leaders and thus poor tree form.

White spruce is considered lightly susceptible to damage by the white pine weevil (*Pissodes strobi*) and certainly is much less damaged than either black or Norway spruce (*Picea abies*). However, an ecotype of the insect, sometimes called the Engelmann spruce weevil, is an important pest in plantations in interior British Columbia and on natural regeneration in British Columbia and Alberta (141).

Warren's collar weevil (*Hylobius warreni*) does cause appreciable damage on spruce. Small trees may be girdled and killed; on older trees, the wounds are entries for root rots such as *Inonotus tomentosus* (122). In controlled experiments, 4-year-old white spruce has shown high radio-sensitivity when exposed to chronic gamma irradiation. The trees were most sensitive in mid-July when the central mother-cell zone was enlarging.

Special Uses

White spruce trees yield many useful products (105,148). The manufacture of wood fiber and lumber products is well known and white spruce continues to be one of the most important commercial species in the boreal forest. Less well-known uses of white spruce wood are for house logs, musical instruments, paddles, and various boxes and containers.

Historically, white spruce provided shelter and fuel for both Indians and white settlers of the northern forest. White spruce was the most important species utilized by natives of interior Alaska *(105)*. The wood was used for fuel, but other parts of the tree also had a purpose; bark was used to cover summer dwellings, roots for lashing birchbark baskets and canoes, and boughs for bedding. Spruce pitch (resin) and extracts from boiled needles were used for medicinal purposes *(163)*.

White spruce stands are a source of cover and food for some species of game. Moose and hares frequent these forests but seldom eat white spruce, whereas red squirrels and spruce grouse live in these forests and also consume parts of the tree. Prey species (furbearers) such as marten, wolverine, lynx, wolves, and others utilize these forests.

White spruce forests have significant value in maintaining soil stability and watershed values and for recreation. White spruce can be planted as an ornamental and is used in shelterbelts.

Genet ics

Population Differences

White spruce is highly variable over its range; the variation pattern is clinal and generally follows the latitudinal and altitudinal gradients. As an example, southern provenances are the fastest growing and the latest flushing when tested near the southern edge of the range; Alaskan trees are dwarfs and are susceptible to spring frost because they flush early. Soil-related adaptive variation has been demonstrated, and variation in germination temperature requirements have also been described *(117)*. Because the species shows such strong adaptive affinity to local environments, seed collection and seed and seedling distribution must adhere to seed zoning and seed transfer rules.

Variation in monoterpenes, DNA content, and taxonomic characteristics suggest two major populations-one in the East, east of longitude 95" W., and another in the West. Further subdivision of these populations must await new research *(117)*. *Two* high-yielding provenances have been identified. In the East, a source centered around Beachburg and Douglas in the Ottawa River Valley about 97 km (60 mi) northwest of Ottawa has proven superior in the Lake States, New England, and southern portions of the range in eastern Canada (96). In the West, the Birch Island provenance (lat. 51" 37' N., long. 119" 51' W., elev. 425 m (1,400 ft)) has been exceptional. In coastal nurseries, it will grow as fast as Sitka spruce.

Provisional seed zones have been summarized for Canada *(141)* and are being developed for Alaska. In the Lake States, general zones have been developed, and superior and also inferior seed sources identified (113,135). Tentative seed transfer rules have been suggested for British Columbia. They limit altitudinal movement to 150 m (500 ft) and suggest that high-elevation spruce provenances from southern latitudes can be moved 2 to 3 degrees of latitude. They also warn that a transfer north of more than 3 degrees will probably result in a detrimental silvicultural effect in southern provenances from low elevations *(131)*. Analysis of enzyme patterns is providing new information on population structure that can be used for improving and refining seed management practices for reforestation *(2,17,20)*.

Hybrids between provenances have been tested on a small scale with promising preliminary results *(179)*. Constructing seed orchards of mixed provenances or of selected alien trees and selection from the local provenance could be an inexpensive approach to increasing yields.

Individual Tree Differences

Genetic variation at the individual tree or family level has implications of silvicultural importance. Large differences exist among families representing individual trees within a stand. For example, in a study representing six families from each of seven stands located over a 3550 km^2 (1,370 mi^2) area in the Ottawa River Valley, no differences could be demonstrated. The best of all the families was 28 percent taller than the family mean height *(28)*. This indicates that substantial genetic improvement can be achieved through mass selection and low-cost tree improvement programs.

The general feasibility of phenotypic selection in white spruce has been demonstrated (74). Seed trees, therefore, should be selected for rapid growth and other desirable characteristics; in even-aged stands on uniform sites, this approach may lead to limited improvement. Similarly, the slower growing, poorer trees should consistently be removed in thinning.

Juvenile selections made in the nursery based on height growth maintain superior growth until age 22 and their phenotypic growth superiority probably reflects genetic superiority (111). Silvicultural implications are that extra large seedlings should never be culled merely because "they are too large for the planting machine." On the contrary, they should be given extra care to assure survival and immediate resumption of growth without "check." Furthermore, propagules of such juvenile selections used in intensively managed plantations may lead to immediate yield improvement (115).

Selfing results in serious losses in vigor and lowered survival. Height growth reduction as great as 33 percent has been reported ***(180).*** Not much is known about natural selfing in white spruce, but relatedness between individuals within a stand has been demonstrated; it manifests itself in terms of reduced seedset and slower early growth (19). These relations have several implications: (a) culling small plants in the nursery is desirable because it may eliminate genetically inferior inbred seedlings; (b) collecting seed from isolated trees is undesirable because they are likely to produce a high proportion of empty seeds and weak seedlings; and (c) collecting seed in stands likely to represent progeny of one or a few parent trees, as in old field stands, may lead to a degree of inbreeding.

Races and Hybrids

No races of white spruce are recognized, but four varieties have been named: ***Picea glauca, Picea glauca*** var. ***albertiana, Picea glauca*** var. ***densata,*** and ***Picea glauca*** var. ***porsildii.*** It seems unnecessary to distinguish varieties, however *(23,96).*

White and Engelmann spruce are sympatric over large areas in British Columbia, Montana, and Wyoming. White spruce predominates at lower elevations (up to 1520 m or 5,000 ft), and Engelmann spruce predominates at higher elevations (over 1830 m or 6,000 ft). The intervening slopes support a swarm of hybrids between the two species; these hybrids are the type that gave rise to the so-called variety ***albertiana.***

Sitka and white spruce overlap in northwestern British Columbia and areas in Alaska. The hybrid ***Picea*** x *lutzi* Little occurs where the species are sympatric. The population in Skeena Valley has been studied in some detail. It represents a gradual transition from Sitka to white spruce, a hybrid swarm resulting from introgressive hybridization (20,130).

Natural hybrids between black and white spruce are rare along the southern edge of the species' range, undoubtedly because female receptivity of the two species is asynchronous. A single occurrence from Minnesota has been described (97) and its hybrid origin definitely established ***(129).*** To the north, they are more common; intermediate types occur north of latitude 57" N. along the Alaskan highway in British Columbia (130). The hybrids have also been found along the treeline in the forest tundra (93).

Many artificial hybrids have been produced (75,117); a few show some promise, but none has achieved commercial importance.

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