Section 6.
Black spruce (*Picea mariana*)

1. Taxonomy and use

1.1. Taxonomy

Black spruce [*Picea mariana* (Mill.) B.S.P.], known by many alternate common names including bog spruce, swamp spruce, Canadian spruce, eastern spruce, and shortleaf black spruce (Viereck and Johnston, 1990; Alden, 1997), is one of the most common and important boreal species native to North America, especially in eastern Canada. Black spruce is one of about 40 species in the genus *Picea* of the family Pinaceae, all of which are found in cooler portions of the northern hemisphere (Farrar, 1995). Ten spruce species are native to North America (Weng and Jackson, 2000). There is no consensus among taxonomists regarding subdivision of the genus, but *Picea* is often described as having three sections (*Eupicea*, also known as *Picea* or *Morinda*; *Castica*; and *Omorika*), with black spruce generally placed among the *Eupicea* (Dallimore and Jackson, 1948; Alden, 1987). Mikkola (1969) suggested dividing the genus into only two sections, *Abies* and *Omorika*. Fowler (1983) recommended adopting Mikkola's classification, but splitting the section *Omorika* into two subsections, *Omorikoides* and *Glaucoides*, and placing black spruce into the former subsection based upon species crossability. Other examples of taxonomic classification have also been proposed for the genus (e.g., see Weng and Jackson, 2000).

Black spruce is closely related to red spruce (*P. rubens* Sarg.), a sympatric species with which it is known to naturally hybridise (Perron and Bousquet, 1997). It is also considered to be closely related to the relict European species Serbian spruce (*P. omorika* [Pančić] Purk.) (Fowler, 1980, 1983), but is taxonomically more distant from white spruce (*P. glauca* [Moench] Voss), Engelmann spruce (*P. engelmannii* Parry ex Engelm.), and Sitka spruce (*P. sitchensis* [Bong.] Carrière) (Wright, 1955), species with ranges that partially overlap (or almost overlap, in the case of Sitka spruce in Alaska) with the range of black spruce. A number of different varieties of black spruce are known (Hillier, 1981; den Ouden and Boom, 1982).

1.2. Uses

Black spruce is found on a wide range of habitats throughout its transcontinental range. Structural qualities of the wood including long fibres and comparatively high relative density, plus being relatively unaffected by insects and disease compared to other associates, make black spruce a desired species for reforestation in boreal regions. The wood is sometimes utilised for lumber products, including framing material, millwork, crating, and piano sounding boards (Alden, 1997). However, this species is most notable for the high-quality pulpwood it produces. Black spruce is the most important pulpwood species in Canada, and is also of commercial importance in the Lake States of the United States (Viereck and Johnston, 1990). Specialty products include Christmas trees, spruce gum, and essential oils for aromatherapy (Viereck and Johnston, 1990; Marles *et al.*, 2000).

Marles *et al.* (2000) have described a number of traditional aboriginal uses of black spruce, based on interviews with elders; these are summarised below. Pitch was chewed as a confection, and also to provide endurance while running, or to treat heart problems. Pitch could also be utilised to treat infected wounds. Warm gum or cone decoctions were used for stomachache and mouth infections. Ground wood or charcoal was used as baby powder. Saplings were used in making traps for various animal species. The wood was used in making bark canoes, shelters, snowshoes, dolls, baskets, and used for firewood. Other uses of this species by aboriginal peoples include making fish traps and drying racks (Parish and Thomson, 1994).

2. Natural distribution and migrational history

2.1. Natural distribution

Black spruce is widespread throughout northern North America, with a mainly contiguous range (Figure 1). The natural distribution of this species extends from Newfoundland westward to British Columbia and Alaska. The range extends northward to the treeline above the Arctic Circle at 68°N latitude (Heinselman, 1957), where growth form may be adversely affected (Lavoie and Payette, 1992). The most southerly population is an isolated relict bog at Bear Meadows in central Pennsylvania at a latitude of 40°48’52”N (Abrams *et al.,* 2001). This species grows at elevations ranging from sea level along the Atlantic and Hudson Bay coasts to 1,830 m in the Rocky Mountains (Viereck and Johnston, 1990). While covering a similar natural range to that of white spruce, black spruce may be found on sites that are too extreme for the former to tolerate.

2.2. Evolution and migrational history

Li (1953) suggested that most coniferous genera originated around the periphery of the Pacific basin. Wright (1955) concurred, and proposed that *Picea* most likely originated in northeastern Asia. Florin (1963) inferred from fossil records that generic divergence within the Pinaceae took place about 135 million years ago. There is lack of agreement on whether *Picea* is more closely related to *Pinus* or to *Pseudotsuga* (e.g., Florin, 1963; Prager *et al.*, 1976; White *et al.,* 1993), but Prager *et al*. (1976) suggested that *Picea* may have been one of the first genera to emerge. However, the genus *Picea* has remained evolutionarily conservative (Wright, 1955; Ogilvie, 1972), with all members having a haploid number of 12 chromosomes and most species of the genus having similar karyotypes (Roche and Fowler, 1975).

Conventional theory holds that the entire genus migrated to North America across the Bering Sea *via* a land bridge connection between Siberia and Alaska (Hills and Ogilvie, 1970; Nienstaedt and Teich, 1971). Wright (1955) proposed that black spruce and red spruce migrated independently to North America in an earlier migration than that which brought the northwestern spruces to North America. Fowler (1980) hypothesised that red spruce might have arrived in eastern North America from Europe prior to continental separation during the Cretaceous or early Tertiary Periods, while black spruce arrived in Alaska from Siberia. He believed that Serbian spruce was ancestral to both black and red spruce. An investigation of ribosomal DNA sequences has lent support to the theory that red and black spruce migrated independently from other North American spruces and are closely related to Serbian spruce (Smith and Klein, 1994). Hills and Ogilvie (1970) described fossilised cones from an ancestral species (*Picea banksii*) found in the Canadian Arctic which they believed to be an evolutionary link between Eurasian and North American species, although this theory has not been universally accepted (Roche and Fowler, 1975). Recent evidence points to the possibility that red spruce was derived from fragmentation of a large black spruce population during the Pleistocene era, with subsequent allopatric speciation resulting from genetic drift (Perron *et al.,* 2000; Jaramillo-Correa and Bousquet, 2003).

Figure 1. Natural distribution of black spruce in North America

Source: US Geological Survey 2002, online at: http://climchange.cr.usgs.gov/data/atlas/little/; after Little, 1971

The earliest spruce pollen fossils, dating back to 70 million years before present (b.p.), have been found in North America and elsewhere, according to Morgenstern and Farrar (1964). They noted that fossils resembling modern spruce species, located in Europe, date back to 13 million b.p. These authors stated that black spruce fossil records date back to 1 million b.p.; evidence suggests that the species has been in eastern North America for at least 100,000 years.

A general period of cooling prior to the onset of the last glacial advance, beginning about 25,000 b.p., caused the southward retreat of coniferous forests. There is evidence to suggest that black spruce was able to tolerate the cooling conditions longer than most other associated species. Pollen records from the US Midwest, where *Picea* and *Pinus* forests had predominated in the region prior to the ice age, showed that *Pinus* was gradually replaced by *Picea*, and black spruce became more common than white spruce, during the cooling period prior to glaciation (Baker *et al.,* 1989). By 22,700 b.p. all spruce pollen percentages began to decline. The last (Wisconsinian) glaciation culminated about 18,000 b.p. (Conkle, 1992), when the Laurentide ice sheet was estimated to extend south of the 40th parallel in eastern North America (Critchfield, 1984; Andrews, 1987), and boreal species from present-day northeastern North America were centred in the southeastern US (Webb *et al.,* 1987). Pollen records indicate that spruce was centred south of the Laurentide ice sheet, below the Great Lakes, with less abundant populations extending eastward below the southern margin of the ice sheet (Jacobson *et al*., 1987). Recent mitochondrial DNA analyses have pointed to three or four refugia for black spruce: one west of the Rocky Mountains, probably south of the Cordilleran ice sheet in Washington or Oregon; one near the Great Lakes, west of the Mississippi Valley; one in the New York / New England / central Appalachian Mountains region; and possibly a fourth refugium in unglaciated regions of Labrador and Newfoundland (Jaramillo-Correa *et al.,* 2004).

Following deglaciation, northward migration of *Picea* from its southerly refugia took place. Fossil records show that spruce-dominant forests were established in Manitoba by 11,600 b.p., and in Alberta by 9,800 b.p. (Ogilvie, 1972). In northern Québec near the Hudson Bay coast, black spruce was the first species to colonise the area immediately after deglaciation around 6,000 b.p. (Desponts and Payette, 1993). At the boreal forest - shrub-tundra transition zone in northwestern Québec, black spruce was the first coniferous coloniser, and upon establishment, has dominated the region since 4,000 b.p. (Gajewski *et al.,* 1993). This concurs with Morgenstern and Farrar (1964), who listed resistance to low temperatures, year-round seed dispersal, and having the ability to reproduce by layering should temporary cooling occur as traits ensuring that black spruce was particularly well adapted for northern migration compared to other associated species. Maps of inferred spruce migration from 18,000 b.p. to present are found in Webb *et al.* (1987).

3. Reproductive biology

3.1. Reproductive bud differentiation

In *Picea*, bud differentiation occurs between mid- to late July, when shoot elongation is almost complete (Owens and Blake, 1985). Reproductive bud development continues until dormancy, and continues again the following spring. Timing of floral receptivity may vary by a few weeks according to spring weather conditions, but commonly occurs around mid-May to early June in the southern portion of the range, and a few weeks later in the north (Vincent, 1965; Viereck and Johnston, 1990). The seed cone, which remains receptive for about 10 days, is well-synchronised with peak pollen shedding (Ho, 1991). Ovuliferous scales funnel pollen to the micropylar arms of the ovule, where a pollination drop carries pollen into the pollen chamber (Ho, 1991). Female gametophyte development proceeds throughout the summer. Cones mature in late August to early September, 3 months after pollination; seed dispersal begins in October (Safford, 1974; Young and Young, 1992).

3.2. Natural seed production and dissemination

Black spruce female ovulate strobili are usually located at the top of the crown near the shoot terminals. Male strobili may be well distributed throughout the crown, but are typically found in the lower $^2/_3$ of the crown (Ho, 1991). Seed cones have been observed on black spruce as young as 6 or 7 years of age (Morgenstern and Fowler, 1969; Caron and Powell, 1992), with seed cones common on 10 to 20-year-old trees (e.g., Heinselman, 1957; Horton and Lees, 1961; Vincent, 1965). Cone production increases with tree age (Skeates and Haavisto, 1987; Caron and Powell, 1989), to an optimal age that ranges from 50 to 150 years (Heinselman, 1957). Black spruce is one of the least periodic of spruces, and may produce successive seed crops for many consecutive years (Park *et al.,* 1998), with heavy crops occurring at about 2 to 6-year intervals (Vincent, 1965; Safford, 1974;

Caron and Powell, 1992). Initial pollen cone production may lag behind that of seed cones by several years (Simpson and Powell, 1981; Caron and Powell, 1989).

Black spruce cones are persistent and semi-serotinous. Cones can persist on the tree for more than 20 years (Horton and Lees, 1961; Atkinson and Haavisto, 1992), and viable seed within cones has been found after 25 years (Safford, 1974; Viereck and Johnston, 1990). However, viability of seed within cones begins to drop after 3 to 4 years (Haavisto, 1975), decreasing to very low levels after 15 to 20 years (Chai and Hansen, 1952; Waldron, 1957 as cited by Horton and Lees, 1961; Haavisto, 1975). In the absence of fire, the cones open slowly and may disperse seed for several years after ripening (Chai and Hansen, 1952; Johnston, 1977). Seed dispersal can occur throughout the year (Heinselman, 1957; Vincent, 1965), with peak dispersal reported from July to August in Newfoundland (Howard, 1962, as cited in Vincent, 1965), during July in Alaska (Zasada *et al*., 1979), and March to April in Ontario (Haavisto, 1978). Seed may remain viable in the seedbed for one to two years after dispersal (MacGillivray, 1955; Fraser, 1976; Thomas and Wein, 1985). Forest fires may open closed cones on standing trees, significantly increasing seed dispersal in subsequent months or years (Wilton, 1963; Zasada *et al*., 1979). Because of their semi-serotinous characteristic, even scorched cones of fire-killed trees may retain viable seed (Horton and Lees, 1961). Germinative capacity, however, of both dispersed seed and seed remaining in cones can be reduced by fires of sufficiently high intensity (Zasada *et al.,* 1979). Simpson *et al*. (2004) described high germinability (above 80%) of black spruce seed stored for 30 years under ideal conditions (-20˚C and moisture content between 5 and 8%), which they attributed to the semi-serotinous nature of the cones. These authors inferred that seed of this species kept under ideal conditions in undisturbed sealed containers could have a potential storage longevity of up to 100 years.

3.3. Natural regeneration

3.3.1. Seedling regeneration

Despite its very small seed, black spruce exhibits good germination and establishment on many sites. Sphagnum mosses may provide ideal seedbeds, as they retain moisture and provide aeration (Place, 1955). However, if the sphagnum grows too rapidly, it may engulf the black spruce germinant, preventing establishment (LeBarron, 1948; Roe, 1949). Feathermosses provide an adequate seedbed during wet years if not too dense, but may dry out prior to seedling root penetration (Viereck and Johnston, 1990). Litter seedbeds may also prevent root penetration; Place (1955) suggested that the best litter seedbeds are composed of a variety of materials. Moist decayed wood is a favourable substrate (Vincent, 1965). Upland exposed mineral soils, particularly sandy loams, may be suitable, although they are sometimes prone to waterlogging, frost heaving, or drying (Place, 1955; Vincent, 1965). Light burns may favour regeneration of competing species, but severe burns, in which the subsequent organic matter layer is thin or absent, favour black spruce establishment (Vincent, 1965). However, after fire, the burned surfaces may be too hot to allow establishment (LeBarron, 1944; Place, 1955). Manganese in the humus of drier soils is toxic to black spruce seedlings (Duchaufour and Rousseau, 1959).

Germination is epigeal (Safford, 1974). Cotyledon number varies, with 4 commonly being observed (Place, 1955). Survival is highest when germination takes place in June (Heinselman, 1957). Following a winter harvest and prescribed burn in Alberta, seventy percent of germination occurred in June; overwinter survival of June germinants was greater than that of July or August germinants (Berger and Gilmore, 2003). In the first year, early summer rainfall is required. Although initial establishment may be better under light cover than in the open, subsequent survival and growth are better on open sites (LeBarron, 1944; Place, 1955); as black spruce flushes so late, risk of frost damage is minimal. Upon germinating, roots penetrate the soil to about 1 cm (Heinselman, 1957). On upland soils, roots may penetrate to 5 cm after the first growing season, but on moss seedbeds, roots may only extend 3.5 cm after 2 years (Fowells, 1965; Viereck and Johnson, 1990). On some sphagnum bogs where growing moss buries seedling roots and the groundwater is rising, black spruce seedlings may respond by producing advantitious roots from stems (Fowells, 1965). Mycorrhizae are abundant on most sites except those with sphagnum (Place, 1955).

During the first year, seedlings grow only a few cm tall in open sites, less in the understory (LeBarron, 1944). Early growth is often slower on mineral soil than on duff. After 3 years, height ranges from 7 cm to 45 cm on the best sites (Heinselman, 1957). Beyond the first 3 or 4 years, juvenile growth patterns begin to exhibit wide variations associated with habitat; in open, productive upland sites, seedlings may grow 15 to 25 cm a year; on poor muskegs, annual growth may only be 2.5 cm (Heinselman, 1957).

3.2.2. Vegetative propagation

Black spruce may reproduce vegetatively through layering, a process by which live branches at the base of the stem become embedded in suitable rooting medium, such as moss or a thick organic layer, forming adventitious roots and eventually an independent stem (Stanek, 1961). Layering occurs across the range of the species (Stanek, 1975). It may be an important form of regeneration in areas where conditions are not favourable to regeneration by seed (Stanek, 1961; Legere and Payette, 1981) and where fire is less frequent or intense (Richardson, 1981). However, well-stocked even-aged stands having a dense canopy may not produce many layers, as the stems self-prune and do not maintain live branches to the ground (Johnson, 1956; Stanek, 1961).

Stems of layer origin respond favourably to release by cutting, and may be an important source of advanced growth and regeneration (Paquin and Doucet, 1992; Sims and Walsh, 1995). Black spruce of layer origin may grow as well or better than those of seedling origin (Stanek, 1961; Vincent, 1965), though layers, particularly younger stems, may initially have poorer, curved stem form (Stanek, 1968; Foster, 1985). Paquin *et al.* (1999) found that natural seedlings had a greater annual height growth than layers for the first 8 years after release, but equivalent growth rates in years 11 to 15, suggesting a period of acclimation was required by the layers. Nevertheless, layering can produce trees of merchantable size (LeBarron, 1948; Stanek, 1961, 1968). Trees of layer origin may have height, diameter and merchantable volume comparable to those of seedling origin (Lussier *et al*., 1992; Morin and Gagnon, 1992).

3.4. Mating system and gene flow

Black spruce is monoeceous, with a mixed mating system. While mainly outcrossing, self-pollination also occurs. Numerous studies from throughout the species range, investigating variation among populations in allozymes, random amplified polymorphic DNA (RAPD), or sequence-tagged-site (STS) markers from populations separated by between 2 km to sampling the entire range, have found that most of the total genetic variation available resides within populations. Similar estimates of 1% of the total genetic variation attributed to among-population differences were reported for New Brunswick (Boyle and Morgenstern, 1987), Québec (Isabel *et al.,* 1995; Perry and Bousquet, 2001), Ontario (Boyle *et al.,* 1990), and Alberta (Wang and MacDonald, 1992). Perry and Bousquet (2001) found complete outcrossing in both seed-origin and asexual layering-origin stands. Slightly higher estimates of 6% among-population variation were estimated for Newfoundland (Yeh *et al.,* 1986), for isolated stands near the northern species limit in subarctic Québec (Desponts and Simon, 1987), and in northern Ontario (O'Reilly *et al.,* 1985). While some of the above studies were based on low numbers of sampled populations or loci assessed, they do point to widespread outcrossing in black spruce.

Other studies have shown evidence of somewhat higher rates of self-fertilisation in black spruce. Average isozyme multilocus outcrossing rates of 0.924 in New Brunswick (Boyle and Morgenstern, 1986), 0.621 in Alberta (Sproule and Dancik, 1996), and 0.837 for a clonal seed orchard in Ontario (Barrett *et al.,* 1987) were obtained. Park and Fowler (1984), in a study of controlled pollinations in a natural black spruce stand, found a self-fertility rate of 47.2%. Morgenstern (1972) sampled 3 populations each from southern and northern Ontario, and found average inbreeding coefficients of 0.08 for southern populations and 0.03 in the north.

Population substructuring in black spruce appears minimal to nonexistent (Boyle and Morgenstern, 1986, 1987; Knowles, 1991; Perry and Bousquet, 2001). Clustering of similar genotypes was observed in one lowland stand, but mature trees in that stand were not inbred, although trees from an upland stand did exhibit some inbreeding (Boyle *et al.,* 1990). Factors which may prevent significant neighbourhood structure include simultaneous receptivity (O'Reilly *et al.,* 1982), effective gene migration, and absence of diversifying selection intensities over homogeneous environments (Boyle and Morgenstern, 1984).

Sampled Québec populations were in Hardy-Weinberg equilibrium (Isabel *et al.,* 1995). However, investigations of black spruce seed orchard crops, plantations, and natural stands have determined that mating is oftentimes not random, and frequently there are unequal parental contributions to the seed crop (O'Reilly *et al.,* 1982; Knowles, 1985; Barrett *et al.,* 1987; Caron and Powell, 1989; Rogers and Boyle, 1991; Perry and Bousquet, 2001). Particularly in young orchards that are just reaching sexual maturity, a few parents may be the major contributors to the gene pool. Flowering phenology does not appear problematic (O'Reilly *et al.,* 1982), as the typical black spruce habitat experiences a relatively short spring warmup period and short pollination periods, and hence flowering is largely synchronous within a region. Rogers and Boyle (1991) found differences in male reproductive success that could not be attributed to pollen viability. They postulated a number of potential causes: male competition, such as in rate of pollen tube growth; female selection; or post-fertilisation embryo abortion.

Black spruce pollen and seed are both windborne. Typical seed and pollen dispersal for wind-pollinated species generally shows strongly leptokurtotic, skewed distributions (Ellstrand, 1992), with the majority of both pollen and seed remaining close to the parent. However, the accumulated effect of small amounts of pollen from many parents dispersing over long distances can be considerable (Adams, 1992). While seed appears to travel approximately the same distance (Adams, 1992) or slightly less far than pollen (Ellstrand, 1992) for those anemophilous species investigated, because seed is diploid, it has twice the influence on effective population size than the equivalent pollen dispersal (Adams, 1992). Seed is also a better indicator of gene flow than pollen, as it is more likely to produce progeny. As well as seed and pollen dispersal, gene flow depends upon pollen viability, flowering synchrony, successful fertilisation, cone abortion rates, seed viability, seed germination, and seedling establishment. Wind patterns and precipitation during pollen flight may affect pollen dispersal distances, while additional factors influencing seed dispersal include air currents, stand structure and forest fragmentation, and availability of suitable habitat for germination.

Gene flow is thought to be relatively high for most conifer species, including black spruce, at least throughout most of its range. Black spruce pollen dispersal is aided by sacci wings (Owens and Blake, 1985). Black spruce bears the smallest seed of any North American *Picea*, with about 890,000 seeds per kg (Viereck and Johnston, 1990). Thus both seed and pollen are capable of travelling long distances. The longevity, large population size, continuous geographic distribution, high rate of outcrossing, and minimal barriers to gene flow all contribute to effective gene flow in this species. Govindaraju (1988) assessed gene flow based on numbers of migrants per generation, and rated black spruce as having high gene flow. In examining the genetic structure of five isolated black spruce stands located on a chain of small islands in subarctic Québec, Desponts and Simon (1987) suggested that gene flow between the populations was sufficiently high enough to override the effect of geographic isolation. Populations near the northern treeline in Québec exhibited high levels of diversity in nuclear DNA, but not in maternally-inherited mitochondrial DNA, suggesting slower seed dispersal compared to pollen dispersal (Gamache *et al.,* 2003). These authors speculated that vegetative layering in populations near the northern extreme of the species range may actually help to maintain long-term genetic diversity during periods when climatic conditions were less favourable for seed production in these regions.

Viereck and Johnston (1990) stated that black spruce seed dispersal is effective up to 79 m from the windward edge of a stand. Because seed can be released at any time of year, it has the potential to travel more than a mile over crusted snow (Heinselman, 1957); postfire opportunities allow for greater gene flow through reduction of mating barriers and release of seed from the opening of semi-serotinous cones. Pollen of this species has been inferred to travel at least 3.5 km downwind. A rogued black spruce seed orchard ($^2/_3$ of trees removed), coupled with a subsequent decrease in orchard pollen relative to contaminant pollen, resulted in 35% more pollen contamination than in an adjacent unrogued orchard, the source of foreign pollen which the author attributed to a stand located 3.5 km upwind of the orchard (Caron, 1994). A recent study found samples of black spruce pollen 300 m above the ground during maximal pollen release (Di-Giovanni *et al.,* 1996). The authors surmised that, based on grain weight, the pollen could potentially drift 47 km from its source given a steady windspeed of 5 m s^{-1}.

Gene flow between red spruce and black spruce was initially described as minimal, with no real directional difference in crossability (Gordon, 1976). Barriers to gene flow between these species would be expected, as hybrids do not appear to be superior to either parental species, with the exception of resistance to winter desiccation. Hybrids were less fit in tolerance to wet sites than black spruce, and less fit in shade tolerance to hardwood competition than red spruce, indicating presence of strong selection pressures against species introgression. However, later studies have found high amounts of gene flow between these two species, with no asymmetric directionality (Perron and Bousquet, 1997).

4. Hybridisation

A number of artificial crosses have been carried out between black spruce and other *Picea* species. Black spruce is most easily crossed with Serbian spruce (Gordon, 1976; Fowler, 1980), which is generally accepted as taxonomically being the most closely related species to black spruce. Artificial crosses have been made with Sitka spruce (Fowler *et al*., 1979; Gordon, 1981; Fowler, 1983), a west coast species that approaches but does not overlap the range of black spruce. A putative natural black × Sitka spruce hybrid was located in Alaska (Gordon, 1985). Crosses have also been made with Engelmann spruce (Fowler *et al*., 1979), whose range slightly overlaps that of black spruce in southern British Columbia. Apparent crosses have also been made with blue spruce (*P. pungens* Engelm.); Norway spruce (*P. abies* [L.] Karst.) of northern Europe; Yeddo spruce (*P. jezoensis* [Sieb. and Zucc.] Carr.), Sakhalin spruce (*P. glehnii* [Fr. Schmidt] Masters.), and Koyama spruce (*P. koyamai* Shiras.) of Japan; Oriental spruce (*P. orientalis* [L.] Link.); Korean spruce (*P. koraiensis* Nakai); Mexico spruce (*P. mexicana* Martinez); dragon spruce (*P. asperata* Mast.); and Himalayan spruce (*P. smithiana* [Wall.] Boiss.) (Wright, 1955; Morgenstern and Fowler, 1969; Fowler *et al.,* 1973; Gordon, 1975, 1976, 1985).

Although their ranges are largely sympatric, white and black spruces do not readily hybridise. Putative natural hybrids between these species based on intermediate morphology have been observed in northern British Columbia (Roche, 1968, 1969), near the treeline in the Northwest Territories (Larsen, 1965), and in eastern Manitoba (Dugle and Bols, 1971). However, in harsh northern environments, it may be very difficult to distinguish the two species from each other, making identification of possible hybrids based on morphology imprecise.

Much attention has been focussed on a single tree from Minnesota which is believed to be a first-generation hybrid of white × black spruce. Named the Rosendahl spruce, this tree, growing in an abandoned pasture, displays intermediary morphological characteristics (Little and Pauley, 1958), leaf oil terpene composition (von Rudloff and Holst, 1968), flavonoid compound content (Riemenschneider and Mohn, 1975), vegetative and sexual bud size (Winton, 1964c), and heat sum requirements for both initiation of meiosis and pollen release (Winton, 1964a) between those of white spruce and black spruce. However, the validity of the Rosendahl spruce as a hybrid was questioned by Gordon (1976). A study using aggregate hybrid indices for numerous cone and twig characters resulted in the Rosendahl spruce being grouped with white spruce (Parker and McLachlan, 1978). A recent investigation using inter-simple sequence repeat (ISSR), RAPD, and cytological markers on open-pollinated seed collected from the Rosendahl spruce confirmed that the putative hybrid is most likely a white spruce genotype (Nkongolo et al., 2005).

Artificial crosses between black spruce and white spruce are difficult to produce (Fowler *et al.*, 1971; Rauter, 1971; Gordon, 1979; Fowler, 1983). Wright (1955) claimed to have produced small quantities of hybrid seed, but the hybridity of the cross was unverified. Fowler *et al.* (1979) were successful at crossing black spruce from New Brunswick with white spruce from British Columbia, suggesting that barriers to crossing are most evident where the ranges of the two species are sympatric.

The low incidence of natural hybrids and lack of ease in artificially crossing white and black spruce led to speculation regarding barriers to crossing. Winton (1964a) postulated that the difference in heat sum requirements, leading to differential timing of pollen release in these species, is probably the primary isolating mechanism. The frequency of hybridisation between sympatric species tends to be highest near the range limits and / or on disturbed sites where plant competition is less.

Hybridisation between red spruce and black spruce has been extensively studied. Artificial crosses have been made in numerous locations. Natural hybrids between these species occur where their ranges coincide. Hybrid swarms are typically found on sites that have been repeatedly or severely disturbed, where competition is lessened and remnant red spruce trees will be flooded by the more abundant black spruce pollen. In these situations, selection against hybrids appears density-dependent (Manley and Ledig, 1979).

Because of the phenotypic similarity of red and black spruce, much emphasis has been placed on developing definitive methods to distinguish these two species. Techniques include morphological trait differences (Jablanczy, 1964; Morgenstern and Farrar, 1964; Manley, 1971; Gordon, 1976; Weng and Jackson, 2000) and isozyme analysis (Eckert, 1989; Hawley and DeHayes, 1994). Pure red spruce and especially black spruce stands both have relatively high levels of variation, causing subjectivity in interpreting the observed variation using hybrid indices based on morphology. The advent of molecular techniques has allowed for more efficient and sensitive estimates of hybridisation and introgression. Molecular approaches have included restriction fragment length polymorphisms (RFLP's) (Bobola *et al.,* 1992), RAPD's (Perron and Bousquet, 1997; Nkongolo *et al*., 2003), nuclear and chloroplast single nucleotide polymorphisms (SNP's) (Germano and Klein, 1999), and single sequence repeats (SSRs) (Campbell *et al*., 2005).

Estimates of the degree of hybridisation and introgression between black and red spruce vary widely. Widespread hybridisation between red and black spruce throughout the sympatric portion of their ranges has been reported (Morgenstern and Farrar, 1964; Manley, 1972; Perron and Bousquet, 1997). Morgenstern and Farrar (1964) and Perron and Bousquet (1997) described the occurrence of introgression between the two species. Morgenstern and Farrar (1964) predicted that hybrids would subsequently backcross with parental types, which are more fertile than the hybrids, rather than crossing amongst themselves. Alternatively, Manley (1972), Gordon (1976), and Hawley and DeHayes (1994) found little evidence for introgression in parental stands.

Berlyn *et al.* (1990) detected hybridisation along elevational gradients between red spruce and relict black spruce that was occupying higher elevations in mountainous regions of New England. They also noted an east-west gradient, with black spruce proportionally more abundant in the eastern portion of the sympatric region. However, Bobola *et al.* (1996) and Hawley *et al.* (2000) did not observe strong elevational clines in these mountain ranges, nor did they observe black spruce to be dominating high-elevation sites. Morgenstern and Farrar (1964) hypothesised that introgression is strongest at the limits of a species' range, where populations are reduced in vigour (in Nova Scotia for introgression of red spruce genes into black spruce, and in Québec at the northwestern limit of the red spruce range for introgression of black spruce genes into red spruce populations). Small amounts of introgression have been identified in allopatric populations of the species (Eckert, 1989; Bobola *et al.*, 1996; Perron and Bousquet, 1997), suggesting the possibility of historical hybridisation.

Timing of flowering is not asynchronous in red and black spruce and thus not a barrier to crossing. Gordon (1976) observed numerous dead hybrid embryos in artificial crosses between the two species, and ascribed his results to embryo inviability. Negative heterosis of photosynthetic rate was apparent in young red × black spruce hybrid seedlings (Manley and Ledig, 1979), but had disappeared by age 22 in these same hybrid families (Johnsen *et al*., 1998). If, as theorised by Morgenstern and Farrar (1964) and Perron and Bousquet (1997), red and black spruce were previously geographically isolated prior to 1 million years b.p., they may have undergone reproductive isolation and divergent evolution, with black spruce evolving in a boreal climate and red spruce evolving under cool temperate conditions. With the glacial retreat, opportunities for secondary contact and subsequent hybridisation occurred during northward migration, preventing further divergent evolution between the two species. RAPD fingerprints have confirmed the close phylogenetic affinity between red spruce and black spruce (Perron *et al.,* 1995).

Within black spruce, interprovenance hybrid vigour was apparent in 10-month-old seedling growth, at least for crosses made between black spruce populations from eastern Canada, but hybrid superiority was less evident by age 5 (Morgenstern, 1974b, 1975a). However, no evidence for, or slightly negative, heterosis was inferred for ability to withstand winter desiccation in the same test populations.

Major *et al.* (2003) observed negative heterosis in height growth of mature hybrid red × black spruce trees, but not in hybrid seedlings. Major *et al.* (2005) proposed that ecophysiological and crossability barriers (e.g., low proportion of filled seeds of hybrids) may be more important than severe negative heterosis for maintaining species integrity.

5. Genetics

5.1. Cytology

In black spruce, as with all members of the genus *Picea*, the diploid ($2n$) number is 24, and karyotypes are similar to others in the genus (Morgenstern, 1962; Roche and Fowler, 1975). The karyotype is asymmetrical, and considered semi-advanced. Of the 12 chromosome pairs, 3 have submedian centromeres, one is median-submedian, six are median, and two are metacentric; five of the chromosome pairs have a distinctive secondary constriction on one of their arms (Nkongolo and Klimaszewska, 1993). Although black spruce chromosomes are visually similar to those of red spruce, the latter species has been found to contain about twice as much nuclear DNA as black spruce, which averaged only 24 picograms (Berlyn *et al.,* 1990). As with many other gymnosperms, the chloroplast of black spruce appears to be paternally inherited, while the mitochondria are maternally inherited (Bobola *et al.,* 1996).

Winton (1964b) observed that about 1 in 23,000 black spruce seedlings were tetraploid ($4n$), apparently from chromosome doubling in proembryo initials. Such polyploid seedlings were stunted, with short, thick needles, and would probably not survive unless protected from plant competition. Sectional chimeras containing both 2*n* and 4*n* tissue on the same plant have also been found (Winton, 1964b).

5.2. Inbreeding depression

The estimated number of embryonic lethal genes in black spruce is 5 to 7, which is lower than for some other conifers (Park and Fowler, 1984). While these authors found the effect of the genetic load on germination rates to be relatively low in their study, survival of 2-year-old selfed seedlings was only 75% that of progeny arising from a polymix. Others have also found evidence of inbreeding depression. Morgenstern (1972) found lower percentage filled seed and germination plus higher percentage chlorophyll-deficient seedlings in southern compared to northern Ontario populations. He hypothesised that inbreeding in southern populations was a result of those populations being more isolated and smaller in number than the northern ones sampled.

In a study involving a complete 7x7 diallel, Morgenstern (1974a) observed inbreeding depression in germination, survival, and height to age 2; severe inbreeding depression in the form of much reduced growth was still evident in these selfed trees at age 14 (Boyle, 1987). Sampling the same diallel material in a later study, Johnsen *et al*. (1999) found that inbreeding greatly depressed growth, but not carbon isotope discrimination, and stated that selfing did not disrupt photosynthetic potential, but did appear to disrupt subsequent physiological processes that contributed to growth. Further investigation of this study material by Johnsen *et al.* (2003) led to the finding that while carbon fixation did not differ between selfed and outcrossed progeny, utilisation of fixed carbon is apparently modified in the surviving selfed progeny.

Sproule and Dancik (1996) discovered that multilocus outcrossing rates of seeds from cones that had been retained for many years on the tree were significantly higher than the rates for the youngest cones. Their results suggest pregerminative selection against selfed seeds. Whereas Morgenstern (1974a) stressed the importance of high levels of heterozygosity for pioneer species such as black spruce which tolerate suboptimal environments, Sproule and Dancik (1996) pointed out that self-compatibility may be desirable for colonising new habitats.

5.3. Genetic variation

5.3.1. Population-level variation

Range-wide black spruce provenance studies have indicated that clinal variation is the predominant pattern of variation to emerge, particularly in growth and survival at an early age (Morgenstern and Mullin, 1990). The main processes shaping north-south gradients are photoperiod and temperature-based (e.g., growing degree-days, length of growing season). Traits showing clinal variation include germination, growth, juvenile indeterminate shoot expansion, phenology, drought resistance, hardiness, survival, and wood density (Pollard and Logan, 1974; Khalil and Douglas, 1979; Segaran, 1979; Fowler and Park, 1982; Bihun and Carter, 1983; Boyle, 1985; Khalil, 1985; Beaulieu *et al.,* 1989; Morgenstern, 1996). Whereas best growth generally occurs in provenances from regions with more degree-days, best survival occurs with fewer degree-days; thus height and survival trends in relation to growing degree-days are negatively correlated, and fastest-growing provenances often do not have best survival rates (Boyle, 1985; Morgenstern and Mullin, 1990). Clinal variation lessened as seedlings aged in both Ontario and Québec (Boyle, 1985; Beaulieu *et al.,* 1989), but clinal patterns had not diminished up to age 15 in Newfoundland (Hall, 1986). In north-central Alberta, where the Rocky Mountain range has a major impact on the geographic landscape, growth varies clinally with elevation and precipitation (Wei *et al.,* 2004).

One exception to the general clinal pattern of variation occurs on the island of Newfoundland. At age 4, variation appeared ecotypic (Khalil, 1975). While weak north-south trends were noted in central Newfoundland at ages 10 (Khalil, 1986) and 15 (Hall, 1986), growth at age 15 remained ecotypic in the northwestern and southeastern peninsulas of the island, although no trends were noted for survival (Hall, 1986). Complex climatic patterns occur in Newfoundland due to maritime influences, including the cold Labrador current bringing Arctic sea ice and delaying air temperature warming in spring, and summertime southwest winds which cause summer temperatures to be cooler in the south than in the north (Khalil and Douglas, 1979). It has been suggested (Boyle, 1985) that glacial refugia for black spruce may have occurred in Newfoundland, with subsequent random drift and selection processes resulting in genetic differentiation from mainland populations.

Monoterpene composition also does not conform to clinal patterns of variation. Chang and Hanover (1991) separated range-wide populations into 2 east-west clusters, with the dividing line east of the Ontario-Manitoba border. The authors suggested that the clusters represented a branching of populations during the last glaciation.

Numerous investigations exploring potential differences between upland and lowland stand types have been carried out; most found minor or no evidence of edaphic ecotypes (e.g., Morgenstern, 1973, 1996; Fowler and Mullin, 1977; Boyle *et al.,* 1990; Thomson *et al.,* 1990; Wang and MacDonald, 1992, 1993; Zine El Abidine *et al.,* 1994a, 1994b, 1995), although O'Reilly *et al.* (1985) did note greater isozyme differentiation in upland compared to lowland sites. Gene frequency differences would not be expected because of high migration between stands, and low likelihood of black spruce regeneration on upland sites in the absence of disturbance. It is therefore unlikely that adaptation to upland sites would have evolved (Fowler and Park, 1982).

Black spruce generally has high levels of genetic variation for many traits, not unexpected for a hardy species with a widespread, continuous range and adequate gene flow that is adapted to numerous site types. Range-wide provenance studies revealed that best growth occurs at locations around the Great Lakes, with poorest growth at northern sites such as those in northern Québec having cold, nutrient-poor soils and short growing seasons (Morgenstern and Mullin, 1990). Survival was lowest in harsh northern Ontario sites, and highest at the Newfoundland and Prince Edward Island tests.

Typically, better growth at a location occurred with southerly provenances transferred northward, while in boreal regions, southward transfer increased survival (Morgenstern and Mullin, 1990). Local provenances did not always perform the best at a site (Fowler and Park, 1982; Hall, 1986). Poorest performance tended to be with sources from the range extremes (Bihun and Carter, 1983; Boyle, 1985). While provenance × environment interactions occurred at most locations, they were not evident in the Maritimes (Fowler and Park, 1982) or in 15-year survival in Ontario (Boyle, 1985). Observed provenance rank changes and poor age-age correlations in Newfoundland, the Maritimes, the Lake States, Québec, and Ontario led investigators to recommend not practicing early selection in this species based on young seedling measurements (Nienstaedt, 1984; Boyle, 1985; Hall, 1986; Park and Fowler, 1988; Beaulieu *et al.,* 1989). One explanation may be that taller seedlings undergo more planting shock, leading to rank switches (Beaulieu *et al.,* 1989). Juvenile-mature phenotypic correlations of wood ring width at dbh are unreliable until around age 20 (Koubaa *et al.,* 2000).

5.3.2. Within-population variation

High levels of genetic variation in growth and survival of black spruce have been documented in numerous studies. Table 1 lists a sampling of individual and family heritabilities reported for height growth of black spruce across a number of test sites.

Slow-growing black spruce families, including selfed families, appear to have lower endogenous concentrations of growth-promoting gibberellins (Pharis *et al.,* 1991). While predetermined shoot expansion of young black spruce seedlings varies little, genotypes with more indeterminate growth prior to the time when all growth becomes virtually predetermined (between age 5 to 10) has been suggested as a mechanism conferring an early growth advantage that may persist beyond this period (Pollard and Logan, 1974). Mullin *et al.* (1995) suggested that by using short-term testing with extended growth cycles which maximise the opportunity for free growth, culling decisions on a family basis may be made after 4 growth cycles. Trees that flush earlier, with a lower accumulated heat sum threshold, have more leader extension (O'Reilly and Parker, 1982).

Table 1. Examples of reported black spruce individual (h^2_i) and half-sib family (h^2_f) heritabilities for height across multiple locations

Reference	location	$^{\#}$ families	$^{\#}$ sites	age	h^2_i	h^2_f
Mullin *et al*., 1995	N.B. (1979 series)	30	6	5	0.2	0.8
″	″	″	″	10	0.3	0.9
″	″	″	″	15	0.3	0.9
″	N.B. (1980 series)	45	6	5	0.1	0.8
″	″	″	″	10	0.1	0.8
Mullin and Park, 1994	N.S.	10	3	5	0.08	0.84
″	″	″	″	10	0.05	0.7
Nelson and Mohn, 1991	Minnesota	190	3	2 (nursery)	0.43	0.52
″	″	″	″	3 (nursery)	0.53	0.63
″	″	″	″	7	0.1	0.35
″	″	″	″	10	0.11	0.34
″	″	″	″	12	0.11	0.36
Boyle, 1986	Ontario	349	19	10	0.12	0.88

N.B. = New Brunswick, N.S. = Nova Scotia

As in the case of population-level studies, family and individual clone rankings are not stable when comparing early growth (seedlings younger than about age 5) to field performance at age 10 or older (Sulzer *et al.,* 1993; Mullin and Park, 1994). The proportion of additive to nonadditive genetic variance (the latter comprised of mainly epistatic rather than dominance variance) for traits such as growth is initially high, but decreases over time (Boyle, 1987; Mullin and Park, 1994). Best correlations between 25-week greenhouse heights and 10-year field heights occur with half-sib families, followed by full-sib families, with clonal rankings showing the weakest relationship (Mullin and Park, 1994). Evidence presented by these authors suggests that culling the very poorest families might be feasible based on early performance, but early individual-level selections would not be reliable.

Numerous other traits of black spruce display high levels of genetic variation. Differences have been described in cone size, seed production, seed size, germination, phenology, seedling biomass, seedling heat tolerance, and morphology (Morgenstern, 1969a, 1969b; Khalil, 1984b; Stoehr and Farmer, 1986; Colombo *et al.,* 1992). Maternal effects are apparent in traits correlated with seed weight and in germination and early growth (Mullin, 1985). Seedling variability in response to soil fertility and nitrogen fertilisation occurs (Maliondo and Krause, 1985; Mullin, 1985). The period of time that a ramet of black spruce is able to produce rootable cuttings is clone-specific, but until recently not successful beyond 5 to 6 years (Cheliak and Rogers, 1990). Rooting success of 10-year-old ramets similar to that of seedlings of the same age has recently been obtained in Québec (Michel Rioux, Ministère des Ressources Naturelles du Québec, pers. comm. 2005).

Wood characteristics of this species are under strong genetic control, including fibre dimensions (length, diameter, and thickness), wood density (of both juvenile and mature trees), and solubility (Khalil, 1985). The mode of inheritance for specific gravity appears to be mainly additive (Boyle *et al.,* 1988). Wood density is negatively correlated with height, diameter, and stem volume (Zhang and Morgenstern, 1995), although a few families do not exhibit this trend (Zhang *et al.,* 1996). The negative relationship between growth and wood density appears to be weaker in more favourable environments (Zhang *et al.,* 1996) and it also appears to weaken with age (Koubaa *et al.,* 2000). Villeneuve *et al.* (1987) estimated that wood density classification of families could be carried out between age 12 and 15.

Northern sources appear to have higher net photosynthesis rates in early spring, and earlier decline in net photosynthetic rates during autumn, than southern sources (Johnsen *et al.,* 1996). Leaf carbon isotope discrimination has a strong negative genetic correlation with growth, displays a lack of inbreeding depression, and appears to be controlled mainly by additive gene action (Johnsen *et al.,* 1999). However, no genetic differences in foliar nitrogen concentration were observed (Johnsen *et al.,* 1999), and different genotypes seem to have a similar response to elevated atmospheric carbon dioxide (Johnsen and Major, 1998). Faster-growing sources showed evidence for an ability to tolerate dehydration, being capable of sustaining growth under drought conditions, compared to slower-growing sources that accumulated more abscisic acid and closed their stomata more rapidly under drought stress (Tan and Blake, 1993, 1997).

Isozyme variation in black spruce has been well documented (Boyle and Morgenstern, 1985; Knowles, 1985; Pitel *et al.,* 1987). Somatic embryogenesis research has revealed that family variation occurs in the proportion of genotypes that give rise to phenotypically normal mature somatic embryos (Cheliak and Klimaszewska, 1991). A number of different variant phenotypes resulting from somaclonal variation have been identified over 5 years of testing somatic embryo-derived plants (*e.g.* morphological abnormalities including dwarfism, plagiotropism, and bushiness, and needle abnormalities including variegation and fasciation), with clonal trends noted in variant type (Tremblay *et al.,* 1999). STS markers have revealed polymorphisms (Perry and Bousquet, 1998), but at low levels compared to microsatellite (SSR) markers (Hodgetts *et al.,* 2001).

5.3.3. Resistance to pests

In comparison to associated species, black spruce is relatively pest resistant. Black spruce is less susceptible to spruce budworm (*Choristoneura fumiferana* [Clem.]) than white spruce and balsam fir, possibly due to its late bud flush (Blais, 1957), but is also less susceptible to spruce budworm than red spruce, another species exhibiting a late bud flush (Manley and Fowler, 1969; Osawa, 1989). Whereas spruce budworm feeds on both foliage and cones of white spruce, when on black spruce, it prefers the cones (Prévost, 1990). Manley and Fowler (1969) speculated that resistance to spruce budworm is polygenic, as segregation was not apparent in red × black spruce hybrids.

White pine weevil (*Pissodes strobi* [Peck]) damage is positively correlated to height (Bihun and Carter, 1983). Black spruce was slower-growing and more resistant to weevil damage than the faster-growing Sitka spruce and Norway spruce when tested together in the Pacific Northwest for 26 years (Mitchell *et al.,* 1974, 1990). High variation in frequency of weevil attack occurred in a black spruce provenance test in Maine, where western sources showed less damage than Great Lakes and Maritimes sources (Bihun and Carter, 1983). No seed orchard clonal differences in resistance were observed for spruce cone maggot, spruce seed moth, or *Lepidoptera* spp. during a good cone crop year when overall damage rates were low (Turgeon, 1990).

Slower-growing northern black spruce provenances grown at the Petawawa Forest Experiment Station were more prone to infection by *Armillaria mellea* shoestring root rot than southern populations (Morgenstern, 1975b). Possible causes may have been root growth that was out of phase with the test environment.

6. Tree growth and phenology

Growth rates of black spruce across its geographic range are very diverse. Regional differences are related to climate, while within a region, soil moisture and nutrient levels are influential (Vincent, 1965). Trees in uneven-aged stands tend to grow more slowly than those in even-aged stands. In fire-origin mixed stands of northeastern Ontario, black spruce takes an average of 18 years to reach breast height, compared to 7 or 8 years for trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and jack pine (*Pinus banksiana* Lamb.) (Vasiliauskas and Chen, 2002). The growth rate of black spruce increases until about age 7 to 9, then decreases (Yang and Hazenberg, 1994). Stands at higher density exhibit slower growth patterns. The transition from juvenile to mature wood occurs at approximately age 15, regardless of stand density (Yang and Hazenberg, 1994).

While generally slow-growing, on upland sites, black spruce growth rates may approach those of white spruce. Best growth is achieved throughout a broad region from southern Québec to Saskatchewan. On good unmanaged sites, trees may reach 12 to 20 m in height and 23 cm dbh, but on poor sites, trees may only attain 8 to 12 m in height and 13 cm dbh (Viereck and Johnston, 1990). Heights of 27 m with dbh of 46 cm have been observed in the Ontario clay belt in stands over 140 years old (Heinselman, 1957).

By contrast, on extreme sites such as the northern taiga region or poor muskegs, growth may be minimal; trees may be shrubby, only 3 to 6 m tall with dbh of 3 to 5 cm, even after 100 years (Heinselman, 1957; Vincent, 1965). At the northern limits of its range, black spruce exhibits a range of growth forms that develop in response to gradients in temperature, snow depth, and wind associated with the winter environment (Lavoie and Payette, 1992; Boivin and Bégin, 1997). The forms range from regular symmetric trees to prostrated, matted growth less than 30 cm in height, with various intermediate forms of shrub, reiterated branch, and bare stem complexes (Payette, 1974 as cited in Lavoie and Payette, 1992).

Black spruce is longlived for a boreal species, commonly reaching 200 to 250 years. Generally, this species survives longer in swampy sites than on upland sites, as on the latter butt rot may occur between ages 70 to 100, causing trees to be subject to windthrow (Heinselman, 1957). Deterioration on lowland sites generally occurs after 130 to 180 years. It is common to obtain total volumes on good sites of 196 m^3 / ha by age 80 to 100, with one report of a volume of 492 m^3 / ha at age 100 (Vincent, 1965).

Phenology varies widely across the range of black spruce. Mitotic activity and swelling of vegetative buds begin prior to budburst; the length of this period is dependent upon spring weather conditions. Budburst takes place when soils are not much warmer than freezing, and occurs on average about 7 to 10 days after white spruce has flushed (Vincent, 1965). Budswell is noticable between mid-April and mid-May in the Lake States (Heinselman, 1957). In this region, budburst occurs between the beginning and middle of June, and budset has occurred by August 1 to 10 (Vincent, 1965). In Maine, budburst has been observed between May 17 and June 17, with budset between mid- to late August (Heinselman, 1957). In northern Ontario, budburst occurs between early and mid-June; in the Alberta foothills, vegetative growth typically commences around June 1, and ends around August 2 (Vincent, 1965).

Radial growth in the Lake States takes place between about mid-May to August (Heinselman, 1957). In northern Ontario, radial growth occurs between June 1 and September 30 (Heinselman, 1957). At Chalk River, Ontario, radial growth begins between May 10 and May 25, ending between July 30 to August 10, a period averaging 78 days (Vincent, 1965).

7. Ecology

7.1. Habitat

7.1.1. Climate

Black spruce occupies cold boreal habitats, with moisture regimes ranging from humid to dry subhumid. Viereck and Johnston (1990) list the following temperature and precipitation ranges for the species: mean annual temperature ranging from 7°C to -11°C near the treeline; average January temperatures between -30°C in the northwest to -6°C in the southeast; extreme recorded low of -62°C; extreme recorded high of 41°C; mean annual precipitation decreasing from east to west, from 1,520 mm in the Maritimes to 150 mm in Alaska; snowfall from 500 cm in eastern Canada to 100 cm in western Canada and Alaska; and mean snowdepth of 50–75 cm, but over 100 cm in parts of Québec and Labrador. Snow may last until late May or early June in some areas.

The frost-free period ranges from 130–140 days in the southeast part of the range to less than 60 days in the north, and permafrost is found north of 62°N latitude (Heinselman, 1957). The longest daylength at summer solstice varies from 24 hours above the Arctic Circle to 16 hours near the southern limit (Viereck and Johnston, 1990). Growing degree-day estimates (5°C base) vary from 100 to 2,700, with 80% of the species found between 500 and 1,500 growing degree-days (Thompson *et al.,* 1999).

7.2.2. Soils and site type

Black spruce is most commonly found on wet organic soils, but is also found on other soil types including deep humus, clays, loams, sands, coarse till, boulder pavements, and shallow soils over bedrock (Viereck and Johnston, 1990). Black spruce can tolerate conditions ranging from very wet to dry, and can withstand flooding up to 48 days (Ahlgren and Hansen, 1957). In the southern portion of the range, black spruce is found mainly in peatlands with peat or organic layers greater than 30 cm thick, although it also occurs on upland sites and on transitional sites between peatland and upland (Johnston and Smith, 1983). The most productive sites in the U.S. tend to be transitional sites with shallow organic to wet mineral soils. In New England, black spruce is most often associated with the Adirondack-New England highlands. In the portion of the range adjacent to the Great Lakes, this species commonly inhabits Histosol peat bogs, swamps formed in old glacial beds, muck-filled seepages, stream courses, and lake-swamp-moraine plains; on these sites, peat deposits may be from 0.5 to 6 m deep (Rudolf, 1965; Johnston and Smith, 1983; Viereck and Johnston, 1990). On peatlands of the Great Lakes region, best productivity occurs on dark brown to black peat with high decomposed woody matter containing water-borne nutrients from adjacent mineral soils, while lowest productivity occurs on thick deposits of partially decayed sphagnum (Johnston and Smith, 1983; Viereck and Johnston, 1990).

In the absence of disturbance such as fire, black spruce is usually confined to wet or occasionally very dry sites, but with disturbance, this species is able to inhabit rich upland environments (Fowler and Park, 1982). Productivity is higher on the upland sites than the lowlands. In central and eastern Canada, upland sites include podzolic Spodosols and, on gentle slopes underlain by glacial till-origin clays, gley Inceptisols (Viereck and Johnston, 1990). These clay soils are derived from calcarious material and are thus neutral or slightly alkaline. The most productive soils are on better drained sites such as sandy glacial deposits, river terraces, and Entosol outwash plains in association with hardwoods (Viereck and Johnston, 1990). Black spruce on glacial tills of predominantly sandy loams and loamy sands has been found to have higher productivity than those on very-well drained fluvioglacial or alluvial deposits (Hamel *et al.,* 2004). Total net primary productivity of a closed-canopy site having a feathermoss ground cover over moderately drained soils was significantly greater than that of an open-canopy site of similar age having *Sphagnum* ground cover over poorly drained soils (O'Connell *et al.,* 2003).

At the northern extent of the range, the shallow, poorly developed mineral soils are underlaid by permafrost. Due to its shallow rooting, black spruce is the species best adapted to permafrost conditions (Viereck and Johnston, 1990). Black spruce sites of the taiga in the interior of Alaska are the most fire-prone, most nutrient-limited, and least productive sites of that region (Van Cleve *et al.,* 1982). Such sites are low in nitrogen, have high lignin content, and are very acidic. Wildfire in permafrost regions temporarily increases the thaw depth (Viereck and Johnston, 1990), and for 10 to 20 years following fire, soils will be warmer, and these sites will be more productive (Van Cleve *et al.,* 1982).

7.2. Synecology and associated species

Black spruce is often found in pure stands on organic soils, and is commonly found in mixed stands on mineral soils. At the northern treeline, black spruce may be in pure stands or interspersed with white birch, trembling aspen, white spruce, tamarack (*Larix laricina* [Du Roi] K. Koch), or balsam poplar (*Populus balsamifera* L.). Common associates across most of the species range include white spruce, trembling aspen, balsam fir (*Abies balsamea* [L.] Mill.), white birch, and tamarack (Viereck and Johnston, 1990). Eastern white cedar (*Thuja occidentalis* L.) and red spruce may also be stand components in the southeastern portion of the range. Infrequently in the east, black spruce may be a minor component in moist mixed stands containing black ash (*Fraxinus nigra* Marsh.), American elm (*Ulmus americana* L.), and red maple (*Acer rubrum* L.), or in the understory below red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) (Heinselman, 1957). On dry sands and gravels, black spruce may succeed jack pine, while in the west, black spruce may succeed lodgepole pine (*Pinus contorta* Dougl. ex Loud.) on moist loamy tills and well-drained uplands (Vincent, 1965). In the northwest at higher elevations, black spruce occasionally grows with subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (Heinselman, 1957).

On better sites in the eastern portion of the range, shrubs found in association with black spruce include mountain maple (*Acer spicatum*), beaked hazel (*Corylus cornuta*), speckled alder (*Alnus rugosa*), red-osier dogwood (*Cornus stolonifera*), and red raspberry (*Rubus idaeus*) (Viereck and Johnston, 1990). On eastern sites of lower productivity, shrub associates include dwarf birches (*Betula pumila* and *B. glandulosa*), bog-rosemary (*Andromeda glaucophylla*), Kalmia (*Kalmia angustifolia* and *K. polifolia*), Labrador-tea (*Ledum groenlandicum*), and leatherleaf (*Chamaedaphne calyculata*) (Viereck and Johnston, 1990). In the west, common shrubs include willows (*Salix arbusculoides*, *S.glauca*, and *S. bebbiana*), prickly rose (*Rosa acicularis*), green alder (*Alnus crispa*), and blueberry and cranberry (*Vaccinium* spp.).

Feathermosses and sphagnum mosses provide nearly continuous ground cover in many black spruce stands, but are typically replaced by lichens in open areas in the north (Viereck and Johnston, 1990). Herbaceous species common to much of the black spruce range include panicle bluebell (*Mertensia paniculata*), fireweed (*Epilobium angustifolium*), one-sided pyrola (*Pyrola secunda*), twinflower (*Linnaea borealis*), bunchberry (*Cornus canadensis*), wild sarsaparilla (*Aralia nudicaulis*), false lily-of-the-valley (*Maianthemum canadense*), starflower (*Trientalis borealis*), bluejoint reedgrass (*Calamagrostis canadensis*), and sheathed cottonsedge (*Eriophorum vaginatum*) (Viereck and Johnston, 1990).

7.3. Competition, succession, and stand structure

Black spruce, although shade-tolerant, is unable to compete with faster-growing associates including balsam fir, jack pine, tamarack, white birch, and trembling aspen unless conditions are unsuited to these species. Where they occur together, black spruce may have more rapid juvenile growth than white spruce (Heinselman, 1957). However, black spruce generally requires site disturbance to be able to become established on rich upland sites, and without further disturbance, it is unlikely to regenerate on these sites, being succeeded by balsam fir, white spruce, and white birch. At the edge of bogs in association with advancing sedge mats, black spruce is one of the first pioneer species, preceded by tamarack (Heinselman, 1957).

Black spruce is well adapted to post-fire establishment, chiefly through its abundant production of semi-serotinous cones, which maintain an aerial seed bank that is readily released in the months and years immediately following fire (Viereck, 1983). Seedling establishment may begin in the year following fire, though reported recruitment rates vary. St-Pierre *et al*. (1992), Lavoie and Sirois (1998) and Greene *et al.* (2004) found that most seedlings became established within 3 years of fire. Lieffers (1986), Sirois and Payette (1989), and Landhäusser and Wein (1993) observed peak recruitment 5 to 8 years following fire. Studying post-fire recruitment in the Yukon and Alaska, Johnstone *et al.* (2004) found that on a mixedwood site, black and white spruce did not reach 50% of net establishment until 5 to 10 years after fire; on a dominantly black spruce site, 50% of net establishment occurred within 3 years of fire, with little change after 10 years. In Québec, black spruce mean fecundity (measured as recruits per square metre of parent basal area) increased with increasing fire severity, a result attributed to a reduction in the rodent population and granivory rate (Greene *et al.,* 2004). Though black spruce can reproduce vegetatively by layering, this does not appear to be a significant mechanism of early post-fire re-establishment.

Pattern, intensity and frequency of forest fire influence the nature of regeneration and successional pathways of black spruce types. Seedbed quality and seed germination and survival may be affected by fire intensity (Carleton, 1982; Zasada *et al*., 1983; Zasada *et al.,* 1992 as cited in Berger and Gilmore, 2003; Sirois, 1993), causing long-term impacts on subsequent stand development (Arseneault, 2001). However, Berger and Gilmore (2003) observed no significant difference in the number of spruce germinants, or their winter survival, among three levels of burn intensity following prescribed burns in Alberta. Forest fires of sufficient intensity serve to remove competition, enhance the seedbed, and open cones causing seed dispersal, which combine to promote the establishment of dense even-aged black spruce stands (Johnson, 1956; Black and Bliss, 1978). This is often the case throughout much of the range of black spruce. In some cases, white birch and trembling aspen may initially invade black spruce sites following fire, to be subsequently replaced by spruce (see Viereck, 1983). In maritime Labrador, a relatively long fire cycle allows for the accumulation of a thick organic layer, which results in slow re-establishment of black spruce and an uneven-aged structure (Foster, 1985). In areas supporting both black spruce and jack pine, a short fire interval may favour the more precocious jack pine (Lavoie and Sirois, 1998; Larocque *et al*., 2000; Parisien and Sirois, 2003). Simulation work by Goff and Sirois (2004) showed that a fire interval less than 60 years may lead to the local extinction of black spruce on well-drained but not poorly drained sites in Québec. The more shade-tolerant black spruce, however, can establish in the subcanopy of jack pine dominant stands (Carleton, 1982). In the Abitibi Region of Québec, Harper *et al*. (2002) observed changes in stand-level canopy dominance during the 100 years following fire, with stands initially dominated by deciduous species and jack pine shifting to black spruce composition.

In the absence of fire, black spruce may be succeeded by more shade-tolerant balsam fir and white cedar (Hatcher, 1963; Viereck, 1983), and white spruce and white birch (LeBarron, 1948). In Québec, Cogbill (1985) found that stands over 200 years of age had poor growth and limited reproduction; layers only partially filled gaps created by mortality. Foster (1985) suggested that black spruce layers and balsam fir seedlings effectively replaced senescent trees of a 230-year-old cohort, maintaining a closed, multi-aged canopy. In the absence of disturbance, uneven-aged, self-perpetuating stands appear to develop on nutrient-poor peatland sites in Ontario, as mortality within the initial cohort is replaced by recruitment from layers (Groot and Horton, 1994). In Québec's North Shore region, an area having a long fire cycle, Pham *et al.* (2004) found that older, black spruce dominated stands were self-replacing; gaps caused by successive events of individual tree mortality were regenerated, largely through layering. The importance of gap dynamics in the development of old growth black spruce stands was also noted by Harper *et al*. (2003) in the Clay Belt region of Ontario and Québec.

7.4. Species interactions and dynamics

Due to its shallow rooting habit and vulnerability to root rot, black spruce may be susceptible to wind damage through stem breakage and uprooting, particularly in older stands and along cut edges (LeBarron, 1948; Robinson, 1974; Whitney and Fleming, 1995). Heavy snow load occasionally causes crown breakage (Van Cleve and Zasada, 1970). Although very cold-hardy and at low risk of spring frost damage due to its late flushing habit, black spruce experiences occasional frost damage. Vincent (1965) described black spruce vulnerability to drought, while excessive flooding, particularly in peat bogs, also occurs (Heinselman, 1957). Both crown fires and ground fires can cause black spruce mortality (Heinselman, 1957). Peat bogs are less prone to fires except when conditions are very dry (Johnston, 1977).

Eastern dwarf mistletoe (*Arceuthobium pusillum* Peck.) is a serious disease of black spruce in the Lake States and eastern Canada, less so in the western part of its range (Heinselman, 1957). Affecting both small seedlings and larger trees (LeBarron, 1948), the disease stunts growth, causes witches'-broom, and often kills trees. In northern Minnesota, Baker and Knowles (2004) suggested that all residual black spruce should be eradicated after harvesting infested stands, to prevent unacceptable losses in the regenerating stands.

Black spruce is susceptible to a number of decay fungi that result in stem and root rots. These include Armillaria root rot (*Armillaria* spp), tomentosus root rot (*Inonotus tomentosus* [Fr.] Teng), velvet top fungus (*Phaeolus schweinitzii* [Fr.:Fr.] Pat.), red ring rot (*Phellinus pini* [Brot.:Fr.] A.Ames), *Coniophora puteana* (Schumach.:Fr., P.Karst.) and *Climacocystis borealis* ([Fr.:Fr.] Kotl. & Pouzar) (Johnston and Smith, 1983; Myren and Cameron, 1995). Rot may cause direct mortality, reduced height and diameter growth, and greater susceptibility to windfall (*e.g*. Livingston, 1990; Whitney, 1994; Whitney and Fleming, 1995). Losses can be significant: Whitney (1989) estimated that 23% of the total merchantable volume was lost due to rot in sampled black spruce stands in Ontario.

Spruce budworm is one of the most important insect pests of black spruce (Johnston and Smith, 1983). The budworm is indigenous to eastern North America, and outbreaks occur in spruce-fir stands in the central and southern Boreal, the northern Great Lakes-St. Lawrence, and Acadian forest regions (Blais, 1983). Black spruce is less susceptible to budworm than balsam fir or white spruce, a response attributed to the later flushing of black spruce relative to the spring emergence of the budworm (Blais, 1957, Nealis and Régnière, 2004). In a boreal mixedwood stand in Ontario, mortality due to budworm was relatively low for black spruce, whereas most of the codominant and intermediate balsam fir had been killed (90% basal area reduction) and white spruce been reduced by half (50% basal area reduction) (Nealis and Régnière, 2004). Nevertheless, where it occurs in mixed stands with these species, black spruce may also be affected. Studying a budworm outbreak in Québec, Bouchard *et al.* (2005) found mortality rates for black spruce of 78.6% in mixed boreal stands and 56.6% in balsam fir dominated stands. In mixed stands, the mortality of balsam fir may leave black spruce susceptible to windfall (Heinselman, 1957). Pure black spruce stands, though less vulnerable, may also be attacked (Raske and Sutton, 1986). Spruce budworm defoliations for several successive years can cause growth reductions and mortality (Elliot, 1960; Krause and Morin, 1999), and may leave black spruce susceptible to damage by secondary agents, such as bark beetle (*Polygraphus rufipennis* [Kirby]) and root rot (*Armillaria* spp.) (Raske and Sutton, 1986). The budworm may cause significant damage to flowers and cone crops (Schooley, 1980; Prévost *et al.,* 1988).

The yellow-headed spruce sawfly (*Pikonema alaskensis* [Roh.]) may severely defoliate young, open-grown black spruce (Martineau, 1984; Syme, 1995); repeated defoliations may result in loss of vigour and mortality (Hopkin *et al.,* 1994b). The green-headed spruce sawfly (*Pikonema dimmockii*) occasionally attacks black spruce (Martineau, 1984; Viereck and Johnston, 1990). In eastern Canada, the European sawfly (*Diprion hercyniae* Htg.) may cause heavy defoliation, growth reduction and mortality (MacAloney, 1936; Reeks and Barter, 1951).

White pine weevil may feed on black spruce (Belyea and Sullivan, 1956), resulting in girdling and death of the top portion of the main stem (Syme, 1995). Hopkin *et al*. (1994a) found that only a small percentage of trees in Ontario plantations were affected, chiefly those 2 to 6 m in height.

The spruce coneworm (*Dioryctria reniculelloides* Mut. and Mun.) feeds on foliage and cones of black spruce (West, 1986; Syme, 1995). It is often found in association with spruce budworm, and may cause relatively more (Spies and Dimond, 1985) or less damage (Ives and Wong, 1988; Prévost *et al.,* 1988). The black spruce cone maggot (*Strobilomyia appalachensis* Michelsen) and the white spruce cone maggot (*Strobilomyia neanthracina* Michelsen) feed internally on seeds within cones and may significantly reduce seed production without adversely affecting vegetative growth (Syme, 1995; Wanner *et al.,* 1995).

Red squirrels (*Tamiasciurus hudsonicus* [Erxleben]) frequently harvest cones of coniferous species, including those of black spruce (West and de Groot, 1990). In Ontario, cone losses of 18 to 28% have been reported (Prévost *et al.,* 1988; Wanner *et al*., 1995). In Newfoundland, West (1989) observed cone losses of 64 to 96% in small crop years, but only 1% in a good crop year. Seed and seedling predation by small rodents (e.g., deer mouse (*Peromyscus maniculatus* Wagner), red-backed vole (*Clethrionomys gapperi* Vigor) and heather vole (*Phenacomys intermedius* Merriam)) can adversely affect post-fire seedling establishment of black spruce (Côté *et al.,* 2003). Côté *et al.* (2005) found that seed predation by invertebrates ranged from 9% to 19%, varying with habitat type; juvenile seedling predation ranged from 2% to 12%. A variety of bird species utilise black spruce for food and cover including spruce grouse, ruby-crowned kinglet, magnolia warbler, Cape May warbler, ovenbird, pine grosbeak, pine siskin, and crossbill (Viereck and Johnson, 1990). Moose (*Alces alces americana*) and white-tailed deer (*Odocoileus virginianus*) may browse on black spruce, but it is not a preferred food source (Heinselman, 1957). Snowshoe hares (*Lepus americanus*) may cause significant damage to young spruce by debarking stems and removing leaders and branches (Heinselman, 1957). Numerous other mammals are associated with black spruce habitat for forage and/or cover, including mouse, vole, chipmunk, muskrat, shrew, mink, porcupine, raccoon, skunk, beaver, and black bear (Viereck and Johnston, 1990; Parish and Thomson, 1994).

In older black spruce stands, small-scale disturbances due to windthrow may be common. Harper *et al.* (2002) found that 16% of the area occupied by 100- to 250-year-old black spruce was affected by windthrow; fine, coarse and thin soil site types were more adversely affected than organic sites.

8. Reforestation practices

8.1. Provenance transfer

Black spruce was reportedly first introduced into Europe in the 18th century (Sargent, 1898 as cited in Morgenstern and Farrar, 1964). Provenance testing of this species has been carried out in Germany, Norway, and several other European countries (Morgenstern, 1969a, 1996; Braekke, 1990).

Provenances performing best in Newfoundland were from Newfoundland, Prince Edward Island, and Nova Scotia (Hall, 1986), although Morgenstern and Mullin (1990) recommended that fast-growing sources from New Brunswick, Ontario, and Québec could also be transferred to Newfoundland. Khalil (1984a) suggested that intensive family selection would be most appropriate for Newfoundland, while Hall (1986) recommended using well-performing sources from within each forest region.

In the Maritimes, Maine, and Minnesota, best-growing sources were from southern Great Lakes sources (Fowler and Park, 1982; Bihun and Carter, 1983; Merrill *et al.,* 1984). In northern and central Maine, source transfer 1 to 2° northward was suggested for best growth, in conjunction with Prince Edward Island and New Brunswick sources, while in southern New Brunswick, local sources plus those from Prince Edward Island were recommended (Fowler and Park, 1982; Park and Fowler, 1988). These authors also advised using local sources plus New Brunswick sources in Prince Edward Island. They recommended use of 3 overlapping breeding zones for the Maritimes. Black spruce populations in Nova Scotia may actually be mainly composed of red × black spruce hybrids; local sources exhibited comparatively poor growth, prompting recommendations of Prince Edward Island and central / southern New Brunswick sources (Fowler and Park, 1982; Park and Fowler, 1988). Poor growth of Cape Breton, Nova Scotia provenances was observed at all Maritimes sites. These sources are from geographically isolated populations that are phenologically out of phase with the rest of the region, and probably inbred (Fowler and Park, 1982). In that region, local sources plus additional sources from Newfoundland and northern New Brunswick have been recommended.

Sources from the southwest portion of the black spruce range grew best in Québec, while poorest growth was from sources from the northeast portion of the range (Beaulieu *et al.,* 1989). Most (50–75%) of the observed variation was within provenances. The authors suggested 5 breeding zones for Québec, and recommended incorporation of well-performing provenances from outside of the province into their black spruce programs. In Ontario, best performance was observed in sources from central and western Ontario and Québec (Boyle, 1985). Local sources were recommended for the Ottawa River vicinity (Morgenstern and Mullin, 1990). Significant genotype by environmental interactions occurred in Ontario provenance tests (Boyle, 1986). Low-intensity, rapid selection was recommended for black spruce in Ontario. In the prairies, best growth was from southern provenances (Morgenstern and Mullin, 1990). Early provenance trial results in Manitoba indicated that seed source selection may be more important on poor, nutrient-deficient sites compared to better sites, where choice of seed source appeared less critical (Segaran *et al.,* 1978). Based on these early results, southern provenances grew best when transferred north (between 2 and 5° latitude), and outperformed local sources, whereas northern provenances grew less when transferred south (Segaran, 1979).

8.2. Breeding programs

Black spruce breeding programs have been established in most jurisdictions where the species occurs naturally, and are of greatest importance in the eastern portion of the range. Selection is primarily based upon stem growth and wood quality traits, as stem and crown form are fairly uniform in this species (Morgenstern and Park, 1991). New Brunswick has one of the most advanced programs, where second generation seed orchards were initiated in 1989 and are now producing enough seed for the province’s reforestation needs. Nova Scotia and Prince Edward Island have also established second generation seed orchards, but are not yet producing significant quantities of seed. Ontario and Québec are in the process of establishing second generation seed orchards. Alberta, Manitoba, and Newfoundland all have first generation seed orchards. In the U.S., first generation seedling seed orchards have been established in Maine, Vermont, and Minnesota (Carter *et al.,* 1988; Nelson and Mohn, 1991). Updates of the Canadian programs are regularly presented in the biannual Canadian Tree Improvement Association proceedings members’ reports.

The majority of first-generation programs are based on open-pollinated family selection, with seed orchard roguing typically carried out after progeny tests are measured at around age 10. Second-generation strategies are more diverse, and often include stratification of the breeding population. For instance, New Brunswick is using a complimentary mating design with polycrossing for estimation of breeding values, and sublining with assortative mating for the breeding population (Park *et al.,* 1993). One elite subline consisting of the best material will use a disconnected diallel, while the regular sublines use a weighted assortative mating scheme, with the best material used in more crosses (Park *et al.,* 1998). Ontario has adopted a nucleus breeding system, with the breeding population substructured into elite and infusion populations (Cherry and Joyce, 1998). Amalgamation of black spruce seed zones in northwestern Ontario has recently been carried out using GIS-based Focal Point Seed Zone methodology (Parker, 1992). In Québec, a GIS-based tool is used to guide seed source transfer. This tool was developed with Campbell's relative risk concept, land district maps, and mathematical models to relate variation in adaptive traits to geoclimatic characteristics of seed source (Beaulieu *et al.,* 2004).

The black spruce program in Québec is experimenting with both containerised seed orchards and field-based miniature orchards, both of which are intensively managed (Mercier and Périnet, 1998). These alternative orchard types are both easily manipulated, with the goal of early, abundant seed production. This province is also examining methods to improve pollination efficiency and to partially shelter orchards by using polyhouse tunnel covers or strategic windbreaks (Mercier and Périnet, 1998). Deployment of stock as mosaics of family blocks is being compared to deployment of family mixes in New Brunswick (Adams and Tosh, 1998).

Unequal clonal contributions to seed orchard seed crops have been observed, necessitating intervention to achieve better balance such as adjusting cone harvesting by clone, partial roguing, preferential flower induction, and supplemental mass pollination (Adams and Kunze, 1996). Isozyme studies of black spruce have been proposed as useful in identification of pollen contamination, checking for errors in seed handling, controlled crossing, and clonal propagation (Pitel *et al.,* 1987), and in making inferences regarding nonrandom mating in seed orchards (Knowles, 1985).

8.3. Reproductive propagation

8.3.1. Flower induction

Gibberellin $GA_{4/7}$ has been successfully used to promote female flowering, as a foliar spray (Greenwood *et al.,* 1988) and also *via* stem injection (Mercier and Périnet, 1998). $GA_{4/7}$ is particularly effective in heavy cone crop years (Brockerhoff and Ho, 1997). However, male strobilus production has been very inconsistent in response to $GA_{4/7}$ application (Greenwood *et al.,* 1988). Stem injections are easier to apply than foliar sprays, particularly in taller trees such as those in seed orchards, and are also not affected by precipitation or aerial drift (Brockerhoff and Ho, 1997). Québec and New Brunswick both use stem injections of $GA_{4/7}$ in their breeding programs (Simpson, 1997; Mercier and Périnet, 1998).

Québec researchers have also investigated using red light flashes (interrupting the nightly dark period) during spring as a way to induce flowering without undue stress (Mercier and Périnet, 1998). New Brunswick has refined crown management techniques and used nitrogen fertilisation for promoting flowering, and has used accelerated growth cycles of grafted seed orchard stock prior to outplanting to promote early flowering (Simpson, 1997; Simpson and Tosh, 1997; Adams and Tosh, 1998). Other operational techniques to stimulate flowering include root pruning and water stress.

8.3.2. Vegetative propagation

Black spruce may be vegetatively propagated through rooted cuttings, not unexpected in light of the ability of this species to layer naturally. Black spruce clonal forestry programs have been initiated, although early challenges included inability to maintain juvenility, plagiotropism, poor root development, and high production costs (Cheliak and Rogers, 1990; deWitt, 1990a, 1990b; Kleinschmidt, 1992). The New Brunswick Tree Improvement Council has refined rooted cutting techniques for both dormant (hard) and semi-lignified (soft) cuttings; both are used in reforestation with improved stock (Adams and Tosh, 1998). Black spruce grafts readily, and grafts are utilised in clonal seed orchards and clone banks, although grafting success may be influenced by the very small scions sometimes obtained from mature black spruce (Morgenstern and Park, 1991). Québec is using rooted cuttings instead of grafts for establishing second generation seed orchards (Tousignant *et al.,* 1995; Mercier and Périnet, 1998) and also produces over 2 million rooted cuttings annually for the reforestation program.

Somatic embryogenesis may be used in clonal breeding programs to capture nonadditive gain. This procedure may also be useful in preserving genotypes, which would circumvent the difficulty in attempting to retard aging in black spruce clone banks until field testing has been carried out and rooted cuttings of selected genotypes can be struck. The first report of somatic embryogenesis in black spruce was by Hakman and Fowke (1987), who established embryonic callus using immature zygotic embryos. Since then, somatic embryogenesis culturing techniques of both zygotic and mature embryos have been refined for this species. Tautorus *et al.* (1990) successfully derived embryonic tissue from mature embryos of seed that had been stored for 13 years. Attree *et al.* (1990a) regenerated plantlets from 12-day-old seedlings, and plantlets were successfully transferred to soil (Attree *et al.,* 1990b). Cryopreservation of embryonic black spruce cultures is now possible (Klimaszewska *et al.,* 1992). Encapsulation procedures that allow handling of fragile embryos, and offer the potential for automated planting at operational scales, have been developed (Lulsdorf *et al.,* 1993). Somatic embryogenesis has now been widely implemented in numerous black spruce genotypes (Adams *et al.,* 1994).

Gene transformation has been demonstrated in black spruce using *Agrobacterium*-mediated, microprojectile particle bombardment, and electroporation techniques (Klimaszewska *et al.,* 2003; Tang and Newton, 2003).

8.4. Stock deployment

Artificial regeneration of black spruce may take the form of planting seedlings or rooted cuttings, or aerial seeding. While bareroot seedling production was common in the past, currently most planting material is container stock grown in greenhouses. Emblings resulting from somatic embryogenesis are now available, and may be integrated into planting programs in the near future once operational techniques have been developed.

Planting programs are well-developed in eastern Canada and the northeastern U.S., and black spruce is the most widely planted species in eastern Canada. According to the National Forestry Database Program (Canadian Council of Forest Ministers, 2002), over 307 million spruce seedlings were planted across Canada in 2000, accounting for 50.1% of all planting stock. In Québec, over 80% of the area harvested annually is now being naturally regenerated. In British Columbia, little to none of the spruce planted is black spruce; if this province is eliminated from the total, about 242 million spruce seedlings were planted in the remainder of Canada, the majority of which was black spruce. Species breakdowns were not available for amount of land aerial-seeded and number of rooted cuttings planted.

8.5. Conservation of genetic resources

Black spruce is widespread and abundant, and easily propagated with few barriers to gene flow. While studies have indicated little difference in diversity measures between natural and plantation stands including those originating from clonal seed orchards (Knowles, 1985), and between logged layer-origin stands and fire regenerated seedling-origin stands (Perry and Bousquet, 2001), genetic diversity of the species may be influenced by both domestication and by reduction of the forest landbase. Populations at the extremes of the range, which may be more isolated with more frequent inbreeding and purging of genes, are perhaps most at risk of loss of diversity. Selection against certain genotypes may occur during cone collection, nursery practices, tree improvement programs, precommercial thinning, and harvesting. Reduction of the gene pool and loss of coadapted gene complexes may result in elimination of genes that would be advantageous for future adaptation.

Concerns regarding depletion of the black spruce gene pool as a result of 50 years of extensive harvesting in northern Ontario had been expressed over 2 decades ago, leading to the development of an early program to preserve the gene pool (Brown, 1979). New Brunswick implemented a reserve-stand policy for black spruce as a method of *in situ* conservation (Fowler, 1986). A recent investigation, based on black spruce allozymes of Manitoba populations, claims that the effects of clearcut harvesting on genetic diversity are not significantly different than those due to forest fires (Rajora and Pluhar, 2004).

In situ conservation may be practiced through maintenance of forest reserves and protected areas, and, in regions where population fragmentation occurs, migration corridors. Reserves that are sufficient to allow for natural evolutionary processes such as mutation, gene flow, mating, and selection to occur are preferable. Control over seed transfer and stand management practices aimed at increasing diversity may provide further conservation measures. Populations most at risk of genetic depletion need to be identified, and steps taken to protect them.

Ex situ conservation may be most useful in preserving material from populations facing the greatest risk of gene loss. *Ex situ* conservation includes storage of seed in seed banks, germplasm by cryopreservation, clone banks, seed orchards, field trials, and even plantations. Most provinces operate their own seed storage facilities. Natural Resources Canada also operates a National Forest Genetic Resources Centre (which includes the National Tree Seed Centre) based at the Atlantic Forestry Centre, with the goal of gene conservation of species native to Canada (Simpson and Daigle, 1998). Samples from across the range of a species are being obtained. The multiple population breeding system is designed to manage populations in tree breeding programs in such a way that genetic diversity is maintained or even increased, despite reduction of the population size through ongoing selection (Ericsson *et al.,* 1993). This system thus offers a viable strategy that would be applicable in black spruce tree breeding programs.

9. Summary

Black spruce, one of the most widespread species in North America, is of great economic importance in eastern Canada and northeastern U.S. due to its high pulpwood quality. This boreal species is unique in its ability to be both a pioneer species on disturbed upland habitat, as well as a late-successional species on lowland sites. Black spruce is very resilient, able to survive under extreme environmental conditions, and can occupy sites where other species cannot survive. This species is late-flushing, and normally not as susceptible to spring frosts as is white spruce. It is less affected by insect or disease pests than many associate species.

Black spruce, with its large contiguous range and extensive gene flow, is a predominantly outcrossing, genetically variable species. It is easily regenerated both vegetatively through layering and by seed. The persistent, semi-serotinous cones can remain on the tree for many years with seed remaining viable. Black spruce is adapted to fire ecosystems, and opportunities presented by disturbances such as fire allow the species to readily regenerate.

Although the range of black spruce is very similar to that of white spruce, the two species rarely hybridise, and evidence points to mating barriers such as asynchronous flowering and bud phenology. Black spruce does hybridise with red spruce, which is found in the eastern portion of the black spruce range. Black spruce and red spruce appear more closely related to each other than to other North American members of *Picea*, and seemingly migrated to this continent in a different manner than the other spruces. However, these two species may have undergone divergent evolution as a result of geographic isolation prior to the last glaciation, with further divergent evolution being halted through hybridisation during northward migration with the glacial retreat.

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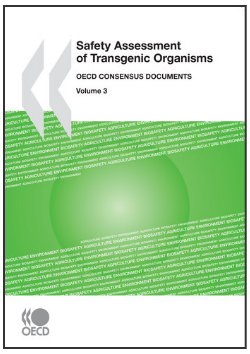

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