Black Spruce: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) is a dominant boreal tree species that is common across the northern Great Lakes and northern New England. This species competes best on lowland peat bogs and on upland sites. Black spruce regenerates naturally from seed rain from semi-serotinous cones or from seed released from cones in the duff layer. Interspecific crosses between black spruce and red spruce (*Picea rubens* Sarg.) occur commonly in areas where they are sympatric, primarily in Québec. Black spruce has high genetic variation and low population structure, but populations differentiate along latitudinal temperature gradients. Northern populations are likely to benefit from increased warming, while southern populations should be conserved and transferred northward as a strategy to retain favorable growth characteristics. Sources from 1.5 to 2.0° C mean annual temperature warmer than the planting site are considered suitable. In the Eastern United States, this would translate into a transfer distance of up to approximately 3˚ latitude, or 207 mi (333 km).

Introduction

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) is a relatively shade-tolerant tree species native to boreal and subarctic forests across North America. Black spruce can be considered both an early-successional species that regenerates after stand-replacing disturbances, and an important late-successional species that is able to survive as advanced regeneration in the understory. The species has a broad ecological amplitude, occurring both in lowland peat bogs (figure 1) and on upland sites, but charred organic matter is a preferred substrate (Jean et al. 2020). Trees can begin producing

Figure 1. Black spruce grows well in upland and lowland sites, such as this *Sphagnum* bog in northern Minnesota. (Photo by Jim Warren, USDA Forest Service, 2008)

semi-serotinous cones as young as 10 years old (Viereck and Johnston 1990). The semi-serotinous nature of their cones permits natural regeneration from seed rain without fire (Johnstone et al. 2009) (figure 2). In addition, black spruce can regenerate

Figure 2. Black spruce produces semi-serotinous cones which extends the window for seed dispersal. The current-year cones on black spruce (top) in this photo have not fully ripened; ripe cones are typically dark and lignified. (Photo by Carolyn Pike, 2010)

from cones in the soil, although viability of seeds starts declining after 1 year (Fraser 1976). Natural regeneration by seed is common post-fire and may be supplemented through artificial regeneration with mechanical site preparation and subsequent planting (Hébert et al. 2014) or with limited site preparation and aerial seeding (Yuska 2022) (figure 3). Climatic warming, coupled with increased frequency of wildfire, may reduce the thickness of the soil organic layer, leading to black spruce's replacement by other conifer or hardwood tree species and/or increasing dominance of shrub species (Baltzer et al. 2021, Wilson et al. 2021). The Climate Change Atlas predicts that black spruce may lose habitat but will likely remain as a component of boreal forests in the Eastern United States because of its genetic diversity and ecological plasticity (Peters et al. 2020).

Black spruce is the progenitor to the more temperate red spruce (*Picea rubens* Sarg.) (Jaramillo-Correa and Bousquet 2003). Hybridization occurs naturally where red spruce and black spruce grow sympatrically in Québec (Perron and Bousquet 1997). Cytoplasmic gene capture (movement of organelles between species) may also have occurred in this sympatric region, further complicating the genetic history of black spruce and red spruce (Gérardi et al. 2010). Black spruce and white spruce (*Picea glauca* [Moench]) occupy similar transcontinental ranges across boreal forests but are genetically distinct and do not hybridize. Black spruce likely had five putative glacial refugia: two in the Central United States, one in the Pacific Northwest United States, one off the coast of Labrador, and one in Alaska (Gérardi et al. 2010, Jaramillo-Correa et al. 2004).

Genetics

Black spruce is comparable to other conifers in having high genetic variation and low population differentiation due to excessive migration of pollen and seed (to a lesser extent). In addition, black spruce can regenerate asexually through layering, a feature more common in subarctic and montane environments than

Figure 3. Black spruce often grows sympatrically with tamarack (*Larix laricina* [(Du Roi) K. Kochin]) as seen in this northern Minnesota forest (Photo by Carolyn Pike, 2004).

in boreal or sub-boreal forests. In areas where layering is common, genetic diversity remains high, a relic of previous warm climates where sexual reproduction was favored (Gamache et al. 2003).

High levels of genetic diversity in black spruce have been confirmed with allozymes (proteins that are phenotypically neutral) (Rajora and Pluhar 2003) and with nuclear and chloroplasts DNA. Chloroplast DNA, which is paternally inherited through pollen, revealed little structure among populations (a signal of high levels of pollen dispersal) (Gérardi et al. 2010) and was similar in magnitude to nuclear markers (Gamache et al. 2003). Lower levels of gene flow, through seeds, is evident in maternally inherited mitochondrial DNA but only in sub-Arctic populations (Gamache et al. 2003). Gamache et al. (2003) also reported finding rare alleles in populations residing along the northern range edges, a finding that was attributed to occasional long-distance dispersal events. Even along range edges in Newfoundland and Manitoba, low F_{ST} values (a ratio of genetic variation between sub-populations and the total population) were reported (0.059, 0.069, and 0.048 for Newfoundland, Manitoba uplands, and Manitoba lowlands, respectively) (O'Reilly et al. 1985, Yeh et al. 1986), indicating high rates of pollen and seed dispersal.

Seed-Transfer Considerations

Black spruce's importance to the pulp and paper industry has led to an extensive network of range-wide provenance tests (figure 4) to aid in tree improvement efforts. In eastern North America, genetic differences are expressed clinally, as opposed to ecotypically, with a pronounced latitudinal (north-south) trend (Morgenstern 1968, 1978; Morgenstern and Mullin 1990; Park and Fowler 1988; Pedlar et al. 2021). The species' excessive gene flow and genetic diversity generally preclude ecotypes from forming because unique gene assemblages are disrupted with nonlocal pollen or seed sources. Clinal variation is generally latitudinal, except in Maritimes where oceanic influences create a distinct east-west gradient. This north-south clinal variation is driven predominantly by adaptations to temperature gradients (Morgenstern 1978, Pedlar et al. 2021, Thomson et al. 2009, Yang et al. 2015). Across all these studies, moisture was a weak predictor of growth among black spruce provenances.

Survival and growth of black spruce is strongly impacted by synchrony of phenological traits, such as budbreak, with local conditions. Populations have adapted to spring temperatures by adjusting their heat requirements to synchronize budbreak with optimal conditions (i.e., northerly sources have a lower

Figure 4. This black spruce stand in northern Minnesota is one of a group of North American range-wide provenance trials planted with a similar set of families in the same year. This group of trials is valuable for measuring the effects of seed transfer and to study the association of genotype and phenotype in black spruce. (Photo by Carolyn Pike, 2004)

heat requirement compared with more southerly sources) (Johnsen et al. 1996, Usmani et al. 2020). As a result, southern sources will break bud earlier than northern sources at a common garden. Black spruce is resilient to freezing temperatures (-60° C [-76° F]) during endodormancy (the deepest form of winter dormancy) (Man et al. 2017). Black spruce is also relatively resilient to freezing temperatures during late winter and early spring, even after budbreak occurs (Man et al. 2021). Budset, which occurs in mid-summer (July) for black spruce, is relatively insensitive to temperature and likely predetermined genetically or affected by photoperiod (Usmani et al. 2020).

Transfer of black spruce seed from southern to northerly locales is recommended to ameliorate predicted adaptation lags when southern range-edge seed sources are growing in a climate that is warmer than optimal for the species (Pedlar et al. 2021, Thomson et al. 2009, Yang et al. 2015). Thomson and Parker (2009) showed that maximum height growth for a majority of provenances tested occurs at planting sites between 45 to 47° and 46 to 48° north latitude for eastern and western Ontario, respectively, north of the southern range edge. This optimal habitat will likely shift 2 to 4° northward with climate change, which is congruent with other predictions that suggest a habitat reduction is likely along southern range edges. Southern sources that are moved northward may experience delayed budbreak and budset (Johnsen et al. 1996). Southern range-edge sources are considered adequate for reforesting in central and northern parts of the range (Thomson et al. 2009), but conservation of these genotypes should be prioritized before they are extirpated. A generalized transfer recommendation of 2° latitude and 656 ft (200 m) in elevation was recommended for Canada to maximize yields (Morgenstern and Fowler 1969) and later refined to sources originating from sites that are 2.7 °F (1.5 °C) (Yang et al. 2015) to 4.0 °F (2.2 °C) warmer mean annual temperature (Pedlar et al. 2021). Black spruce can also tolerate transfers to drier (up to 18 in [455 mm] less mean annual precipitation) or cooler climates (up to 11 °F [6.1 °C] mean annual temperature) than climate origin before a reduction of 10 percent or more in height growth (Pedlar et al. 2020). Northward shifts of black spruce into subarctic zones are already evident through natural regeneration (Truchon-Savard et al. 2018), but artificial regeneration may be needed to bolster its presence on upland soils or on sites where soils have lost organic matter from fires (Baltzer et al. 2021). Seed transfer guidelines are summarized in Table 1.

Insects and diseases

Eastern dwarf mistletoe (*Arceuthobium pusillum* Peck), a native parasitic plant, is one of the main mortality agents of black spruce in the Lake States (figure 5). The plant's sticky seeds are released by catapulting, thereby facilitating their spread among trees, even trees of small stature (Baker and Knowles 2004). While other dwarf mistletoes only result in decreased growth, eastern dwarf mistletoe kills 75 percent of trees within 15 to 20 years (Baker and French 1980) (figure 6). Because eastern dwarf mistletoe can impact large and small stature trees, it can reduce black spruce regeneration and alter the light environment; species composition may shift to other early successional species, such as paper birch (*Betula papyrifera* Marsh.) and eastern larch (*Larix laricina* [Du Roi] K. Koch), in otherwise spruce-dominated forests (Skay et al. 2021).

Table 1. Summary of silvics, biology, and transfer considerations for black spruce.

Black spruce, *Picea mariana* (Mill.)	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Serotinous to partially serotinous cones, 335,000 to 664,000 seeds per pound (739,000 to 1,464,100 seeds per kg)
Insect and disease	• Budworm, mistletoe
Palatability to browse	• Low; generally not preferred by white-tailed deer
Recommended transfer distances	• Southern range-edge populations should be prioritized for conservation and moved northward • Transfer distances up to 3° northward (70 to 200 mi [113 to 322 km]) are likely safe • Sources with mean annual temperature up to 2.7 to 4.0 °F (1.5 to 2.2 °C) warmer than the designated planting site
Range-expansion potential	• Likely to expand northward • May lose habitat from excess fires and loss of soil organic matter

Figure 5. Dwarf mistletoe, a parasitic plant, can devastate black spruce stands in northern Minnesota. These photos illustrate the growth form on black spruce twigs. (Photos by Ella Gray, University of Minnesota, 2021)

Figure 6. This black spruce stand shows the typical damage incurred by dwarf mistletoe in northern Minnesota including witches' brooms where the mistletoe proliferates, dead crowns, and fallen dead trees. (Photo by Raychel Skay, University of Minnesota, 2021)

Spruce budworm (*Choristoneura fumiferana* [Clem]) is the most important defoliator of spruce species across North America. Spruce budworm is more likely to cause severe defoliation in mixed stands of balsam fir (*Abies balsamea* (L.) Mill) and black spruce compared with pure stands of black spruce because balsam fir is a preferred host (Lavoie et al. 2021). In the Lake States, white spruce is generally favored as a host for spruce budworm because of its early budbreak relative to black spruce (Nealis and Régnière 2004). In New England, spruce budworm prefers red spruce over black spruce as a host (Fraver et al. 2007), especially in introgressed regions of Québec (Manley and Fowler 1969). Yellow-headed spruce sawfly (*Pikonema alaskensis* [Rohwer]) defoliates spruce species when trees are less than 10 to 12 years old, but usually prefers white spruce over black spruce in the Lake States (Katovich et al. 1995). Stigmina needle cast (*Stigmina lautii*) and Rhizosphaera needle cast (*Rhizosphaera kalkhoffii*) can damage black spruce foliage (Juzwik 1993). Black spruce cones may be afflicted with spruce cone rust (*Chrysomyxa pirolata* Wint.) which can reduce seed yields considerably (Singh and Carew 1990). In Alaska, spruce bud rust (*Chrysomyxa woroninii* Tranz.) has been reported on black spruce and white spruce (McBeath 1984), but it is not a common pathogen in the Eastern United States.

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