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

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Abstract

White spruce is a boreal conifer with a transcontinental range and intermediate shade tolerance that thrives in mixed stands. The species has high genetic variation, low population structure, and can tolerate moderate transfer distances with minimal maladaptation effects. White spruce has a tendency to break bud early in the spring and, as such, is susceptible to damage from early spring frosts. Spruce budworm is the most significant pest of white spruce. Seed collection areas should be developed from sources with a range of budbreak times and growth habits to maximize genetic diversity. White spruce is a good candidate for assisted migration because it is expected to experience a range shift, is generally unpalatable to browse from white-tailed deer, and can be transferred long distances with a low probability of maladaptation.

Introduction

White spruce (*Picea glauca* Moench [Voss]) is a transcontinental, long-lived, boreal conifer that grows on a wide variety of sites exclusive of stagnant, wet, or excessively dry sites. Spruce trees provide habitat for small mammals and birds and are generally unpalatable to browse by white-tailed deer (*Odocoileus virginianus* [Zimmerman]). White spruce is valued in commercial forest markets for its use as pulpwood and sawlogs. In the United States, white spruce occurs across the Lake States (Michigan, Minnesota, and Wisconsin), northern portions of New York, Vermont, New Hampshire, and across Maine, but most of its range resides in Canada. White spruce likely had three glacial refugia (two in eastern North America and one in the west) based on evidence of genetic diversity and endemic haplotypes associated with each refugium (de Lafontaine et al. 2010). Two refugia based in eastern North America correspond to areas west and east of the Appalachian Mountains. White spruce from areas west of the Appalachian Mountains migrated northwards towards the Great Lakes, whereas populations east of the Appalachians migrated into New England and northwards into eastern Québec, Labrador, and the Atlantic Provinces (de Lafontaine et al. 2010).

White spruce is generally a minor component of northern forests and has low importance values. It rarely regenerates in an even-aged stand except when such conditions are created artificially through management. White spruce has intermediate shade tolerance and thrives in mixed stands, especially beneath an overstory composed of quaking aspen (*Populus tremuloides* Michx.) and/or paper birch (*Betula papyrifera* Marshall) (Gradowski et al. 2008, Man and Lieffers 1997). The overstory of these northern hardwoods may provide protection from radiational cooling on quiescent seedlings or seedlings that have broken bud in the spring (Groot and Carlson 1996) (figure 1). White spruce requires fewer growing-degree days to leaf out in the spring than other taxa (Lu and Man 2011, O'Reilly and Parker 1982, Rossi and Isabel 2017) rendering it more vulnerable to deleterious effects of early spring frost than trees with buds or flowers that emerge later in the season. In addition, female conelets emerge early in the spring which can increase frost risk to flowers and new shoots that leaf out early (figure 2). White spruce regenerates primarily from seed, but may regenerate by layering, in which lower branches that reach the soil form new roots (Katzman 1971, Stone and McKittrick 1976).

White spruce is intolerant to fire but regenerates well on disturbed sites with mechanically exposed mineral soil (Gärtner et al. 2011) or on sites immediately post-fire (Purdy et al. 2002). Additional details about this

Figure 1. A sapling of white spruce grows vigorously underneath a quaking aspen overstory. (Photo by C. Pike, 2004)

species may be found in the USDA Natural Resources Conservation Service plant guide (Nesom and Guala 2003). The Climate Change Atlas predicts that white spruce habitat will not change greatly, but additional warmth will likely stress the species, especially along its southern range edge (Peters et al. 2020).

Genetics

White spruce seeds are lightweight, winged, and rapidly released when cones dehisce, usually in August (figure 3). Cones ripen and mature in one growing season as opposed to cones of *Pinus* species that require two years to mature. Mobile seeds and wind-dispersed pollen contribute to high rates of gene migration (O'Connell et al. 2006), resulting in high genetic diversity across the species' geographic range (Furnier et al. 1991). Genetic variation is low among populations (stands) and reflects high rates of migration: F_{ST} values (a ratio of genetic variation between sub-populations and the total population) range from as low as 0.006 to 0.007 (Cheliak et al. 1988, Namroud et al. 2008) to as high as 0.113 along the northern range edge in Québec (Tremblay and Simon 1989). This high genetic diversity confers a strong capacity to adapt to local conditions. Provenance (geographic origin)

Figure 2. Spruce trees tend to leaf out earlier in the spring than other plants. Early spring frosts can damage female inflorescence (immature cones in photo) or developing shoots. (Photo by C. Pike, 2009)

Figure 3. Immature cones ripening on a tree at a seed orchard. Unlike cones of the *Pinus* genus, spruce cones only require one year to develop. A cut test of the cone is required to determine ripeness. Once the cone dries, the seed is released in late summer. (Photo by C. Pike, 2006)

effects are often insignificant and overshadowed by differences among trees within a provenance (Li et al. 1993). In other words, within any single provenance, trees with a variety of traits and habits can be found. White spruce is not known to hybridize with other *Picea* species in the wild. In summary, white spruce has high gene flow, high genetic variation, and greater differences among trees within a stand than among stands.

Clinal variation across the landscape is generally weak for white spruce, with steepest gradients occurring between eastern and western populations as observed in range-wide provenance trials (Khalil 1985, Sebastian-Azcona et al. 2019, Wilkinson et al. 1971). Sharp differences between eastern and western populations may be attributable to distinct refugia that were isolated during prior glaciation. In the eastern part of the range, differences among populations attributable to latitude of origin are generally weak but may be detected for some traits (Lesser and Parker 2004; Li et al. 1993, 1997; Lu and Man 2011; Lu et al. 2014).

White spruce trees have determinate growth and require a period of deep chilling (cold temperatures below freezing threshold) for shoot growth to resume after buds are set in the summer. Young seedlings may exhibit indeterminate growth, a habit that ceases by the fourth year (Nienstaedt 1966). Phenology traits (time to budbreak and budset) are important predictors for growth. After the chilling requirement has been met, warm temperatures in the spring (tabulated as growing degree days) lead to budbreak after a threshold is met (Lu and Man 2011, Nienstaedt 1966). The calendar date for budbreak timing varies annually by 1 or more months depending on spring temperatures (Pike et al. 2017). The amount of warming needed to induce budbreak is under strong genetic control (Lu and Man 2011, O'Reilly and Parker 1982). Even though budbreak time is highly adaptive, the trait exhibits weak clinal variation and no significant genotype-by-site interactions (Lesser and Parker 2004, Lu and Man 2011). For example, genotypes with a tendency to break bud early were not associated with any single provenance and were consistent for families across multiple sites (Lesser and Parker 2004, Lu and Man 2011). This paradox–an adaptive trait that is not associated with its native location–is best explained by the excessively high gene flow in white spruce that precludes isolation and local adaptation. Changes in daylength are the primary trigger for budset and the onset of winter dormancy in the fall (Hamilton et al. 2016). White spruce is generally not affected by fall frosts because the buds are set by mid-summer.

Seed Transfer Considerations

White spruce is a good candidate for assisted migration because of its extensive genetic variation and its capacity to adapt (Lu et al. 2014). In addition, white spruce is highly tolerant of long-distance seed transfer with large optimal breeding zones of 3° latitude (approximately 200 mi [322 km]) and 10 to 12° longitude (Thomson et al. 2010). Mid- and northern populations grow in suboptimal conditions, and best seed sources generally originate from 1.0 to 1.5° latitude south of a site (Morgenstern et al. 2006, Prud'Homme et al. 2018, Thomson et al. 2010).

Southern sources moved north to a common garden are more likely to experience budbreak delays relative to northern sources because of the extra time required to accumulate degree days (Blum 1988, Lesser and Parker 2004, Prud'Homme et al. 2018). Migration of seed across short distances, however, is unlikely to strongly influence budbreak time (Lu and Man 2011). Seed collection areas should be developed from sources with a range of budbreak times and growth habits to maximize genetic diversity. Considerations for moving white spruce seed are summarized in table 1.

White spruce growth and survival can be correlated with weather conditions that occur during the active growing season. For example, tree growth (height and diameter) was related to maximum temperatures in May, June, and August across 6 sites in western Ontario (Thomson et al. 2010). Other studies determined that temperature and precipitation both contributed to growth (Andalo et al. 2005, Lesser and Parker 2004). White spruce is relatively insensitive to nadir winter temperatures (minimum temperatures in January, for example) (Lu et al. 2014) because it is hardy to -22 °F (-30 °C) by mid-fall and remains dormant until dormancy is released with spring warming (Sebastian-Azcona et al. 2019).

Table 1. Summary of considerations for moving white spruce seed.

White spruce, *Picea glauca* Moench	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Small, winged seeds • 135,000 to 401,000 seeds per pound (297,000 to 882,200 per kg) • Non-serotinous cones • Seeds are released in late summer
Insect and disease	• Spruce budworm (major), sawfly (minor) • Needlecasts can afflict spruce
Palatability to browse	• Low risk of herbivory from white-tailed deer
Maximum transfer distances	• White spruce can handle relatively long transfer distances relative to other taxa: – Up to 200 mi (322 km) south to north – Up to 300 mi (483 km) east to/from west • Sources from 1.0 to 1.5° latitude south are generally superior to local or northern sources
Range-expansion potential	• Spruce is likely to experience a northward range-shift but may persist along its southern range edge because of high genetic variation and low deer palatability

Figure 4. Spruce budworm is the most economically important pest of white spruce across North America. The adult form is shown in this photo, but most damage occurs from feeding by larvae. (Photo by J. Warren, USDA Forest Service, 2011)

Insects and Diseases

Spruce budworm (*Choristoneura fumiferana* [Freeman]) is indigenous to North America and is a highly destructive pest of white spruce across its range (figure 4). Budworm serves an important successional role by accelerating the demise of decadent stands of spruce and fir (*Abies* sp.) in northern forests. Silvicultural practices that create monocultures of white spruce may help sustain populations of budworm and increase the vulnerability of managed forests to mortality (Blais 1983). Seed orchards that are tightly spaced can also be inundated with feeding during budworm outbreaks. Budworm outbreaks occur at approximately 40-year intervals (Blais 1983, Boulanger and Arseneault 2004), although intervals may be shorter if conditions favor the insects' proliferation. The intensity and extent of outbreaks depend on myriad site factors and can devastate timber resources (Gray and MacKinnon 2006).

Spruce budworm adults lay eggs in the summer on host trees, and larvae overwinter as second instars. Upon emergence in the early spring, larvae disperse and feed on shoots, favoring trees with buds that have recently emerged from their sheath. Larvae that emerge from winter hibernation before new shoots are available as a food source must find sustenance on sub-par sources, such as older needles. Thus, synchrony with new shoot growth in host trees is imperative (Blum 1988) to ensure the survival of newly emerged larvae. The movement of seed sources from southern to northern locales will likely interact with the budworm (i.e., if budbreak is delayed, then it may evade infestation barring any other adaptations by the insect).

Other insect pests that affect white spruce include yellow-headed spruce sawfly, (*Pikonema alaskensis* [Rohwer]) (figure 5) which can occasionally produce outbreaks (Katovich et al. 1995). Spruce budmoth (*Zeiraphera canadensis* Mutuura and Freeman) and spruce spider mites (*Oligonychus ununguis* [Jacobi])

Figure 5. Yellow-headed sawfly is an occasional pest on white spruce foliage. (Photo by J. Warren, USDA Forest Service, 2011)

are minor pests and associated with open grown trees in largely urban settings. Pathogens associated with white spruce affecting weakened hosts include *Rhizosphaera kalkhoffii* and *Stigmina lautii* needle cast (Walla and Bergdahl 2016), *Phomopsis* canker (*Phomopsis juniperovora*), and Diplodia tip blight (*Diplodia sapinea*) (Stanosz et al. 1997, Stanosz et al. 2007). *Rhizosphaera* and *Stigmina* are also likely important pathogens, especially in plantations and along the southern edge of white spruce's range.

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