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Seed-Transfer Guidelines for Important Tree Species in the Eastern United States

Editors

Carolyn C. Pike

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Dedication

To all forest geneticists—
past and present, near and far—
who had the foresight to
plant common gardens
to help solve
tomorrow's problems.

Preface

Decades of common garden and genetics studies have led to several basic understandings about the biology of forest trees. Trees are masters at migration through pollen and, to a lesser degree, through seed. Trees tend to grow best in their local, or slightly warmer, climate. The consequences of moving tree seed over excessively long distances to sites with profoundly different climates may be realized immediately, through frost or heat damage, or decades later as seed sources fail to meet projected growth targets. Mismatches are often observed during the shoulder seasons (spring, fall): plants may leaf out prematurely in the spring or fail to initiate dormancy in time for the incoming winter season.

This guidebook was created to provide science-based seed-transfer information for important tree species in the Eastern United States in an accessible, easy-to-reference format. The intended audience is nursery managers, land managers, and anyone tasked with making decisions about appropriate seed sources. This guidebook was prompted by increasing demands for seed- transfer information pertaining to assisted migration, or the intentional movement of seed sources from warmer to cooler climates to account for changing climate. This guidebook includes southern pines but is intended for populations occurring along the northern range edges where southern pines are currently scarce or may not occur yet.

The guidebook includes a table for each species placed at the end of each chapter that summarizes the following information: genetics, cone and seed traits, insects and disease, known palatability to browse (white-tailed deer), recommended transfer distances, and range expansion potential. Genetics information includes underlying variation (reflecting prior bottlenecks) and potential for introgression with other species. Transfer distances were derived from the literature—no attempt was made to undertake new analyses of existing datasets. Most provenance trials in the Northeastern United States had sparse coverage of the species ranges, so quantitative transfer functions are coarse and may fail to capture subtle differences among populations. In addition, common gardens were generally placed within the range centers, so range edges are rarely tested. The authors hope that a new generation of scientists will develop new genecology trials and make use of newer genomics tools to develop more refined recommendations for guiding seed-transfer in the future.

Many of the articles in this publication have been previously published in Tree Planters' Notes, a biannual publication of the U.S. Department of Agriculture, Forest Service. This is noted at the end of each article; tables have been updated with transfer distance information and other corrections for typos and style have been made for articles republished in this guidebook.

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About the Authors

Paul Bloese has served as the tree improvement supervisor of Michigan State University (MSU) Department of Forestry's tree improvement program since 1984. Bloese's responsibilities include coordinating seedling production, plantation design and planting, maintenance, data collection and analysis, and maintaining accession and plantation databases. He also oversees the management of the greenhouses at MSU's Tree Research Center. He has a bachelor's degree in American literature from Bennington College, VT, and a master's in forest genetics from Colorado State University.

Dr. Andrew David is a researcher and educator in applied forest genetics at the University of Minnesota. He has led cooperative breeding programs, modeled rogueing schemes for seed orchards and genetic trials to optimize growth and genetic diversity, designed seed collection strategies for imperiled tree species, and researched the potential for establishing endangered tree species in the State.

Katie Frerker is a U.S. Department of Agriculture (USDA), Forest Service climate adaptation specialist with the Northern Institute of Applied Climate Science. She holds degrees in forestry and botany and began her Forest Service career at the International Institute of Tropical Forestry in San Juan, Puerto Rico. She later spent 9 years working as the ecologist and climate change coordinator on the Superior National Forest in northeast Minnesota. Her favorite pastimes include cross country skiing, thimbleberry picking, and romping through the forests of Duluth, MN, with her two small children.

Christel Kern, Ph.D., is a research forester for the USDA Forest Service Northern Research Station. She specializes in forest ecology and management research of northern forests. She also manages five experimental forests, co-leads the research natural areas program, and coordinates numerous research-manager collaborations.

Dr. Stephen R. Keller is an associate professor in the Department of Plant Biology at the University of Vermont. He specializes in genetic and genomic approaches to the study of forest tree diversity, investigating questions of population genetic diversity and structure, range expansion history, disease resistance, and climate adaptation. He is especially interested in using genomics to help estimate potential maladaptation of forest trees in response to climate change, and how we can use these predictions to help guide seed sourcing for restoration, assisted migration, and ex-situ gene conservation.

Nicholas LaBonte, Ph.D., is a regional geneticist with the USDA Forest Service in the Eastern Region. He provides guidance to national forest resource managers on genetics aspects of reforestation and species conservation, as well as ensuring the appropriate genetic makeup of seed provided to national forests from the Oconto River Seed Orchard. Labonte earned a bachelor's degree in forest ecology and management from the University of Wisconsin-Madison and master's and doctoral degrees in forestry and genetics from Purdue University.

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Philip O’Connor is the tree improvement specialist for Indiana’s Division of Forestry. He is the Tree Improvement Committee Chair for the Walnut Council as well as a board member of the Indiana State Chapter. O’Connor identifies and propagates superior selections of 15 hardwood tree species. He works to select the trees for improved phenotypic characteristics like growth rate, form, and disease resistance as well as to improve the productivity and management efficiency of the State’s seed orchards. One of O’Connor’s early professional forays into tree genetics was developing apple cultivars resistant to multiple diseases. Several have subsequently been commercialized.

Carolyn “Carrie” Pike, Ph.D., is a forest regeneration specialist for the USDA Forest Service’s State, Private, and Tribal Forestry Deputy Area in the Eastern Region. She is based in West Lafayette, IN, at Purdue University, co-housed with the Hardwood Tree Improvement and Regeneration Center. Prior to her position with the Forest Service she coordinated the daily work of the Minnesota Tree Improvement Cooperative for 17 years and served as director of operations at the Cloquet Forestry Center in northern Minnesota. She earned her master’s degree in forestry at the State University of New York’s College of Environmental Science in 1998 and her doctoral degree in natural resource science and management at the University of Minnesota in 2013.

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Keith Woeste, Ph.D., worked as a research geneticist with the USDA Forest Service at the Northern Research Station in West Lafayette, IN, from 1999 through 2020. His research focused on tree improvement of hardwoods, especially black walnut. Since then, he has served as project leader of the station’s Hardwood Tree Improvement and Regeneration Center (NRS-14) and in 2023 he became the national program leader for genetics and biodiversity conservation for the Forest Service’s Research and Development Deputy Area.

Introduction

By Katie Frerker

As land managers and stewards, we are motivated by the notion of sustaining forested lands so they can be enjoyed by future generations. The challenge we face is that the conditions our forests will experience in the future are changing, perhaps at a rate so fast that today's forests will not be able to maintain their current species composition. Climate variability and change are threatening the health, diversity, and productivity of forests to the point where tree populations must either adapt, migrate, or face possible extinction (Aitken and Whitlock 2013). However, the predicted changes in climate exceed natural migration and adaptation abilities of many forest trees.

It is apparent that current reforestation strategies, including natural regeneration, may no longer be adequate to meet forest management objectives and this unprecedented change demands a timely response and novel management actions. Enter forest assisted migration, which can be defined as the human-assisted movement of species, populations, or genotypes to areas outside of their historical distributions to maintain biological diversity or ecosystem function in response to climate change (Richardson et al. 2009; Schwartz et al. 2012). Assisted migration can be used to increase the likelihood of maintaining healthy and resilient forests on the landscape by moving seed and plant materials within current species ranges and expanding others to newly suitable habitats in an attempt to "fast track" migration of those species to keep pace with the changing climate.

Despite its many benefits, there are risks associated with assisted migration such as outbreeding depression and phenology mismatches that require the user to approach this tactic with caution and the proper scientific research at hand. The pages in this manual represent a robust review of the current literature that can allow managers to approach assisted migration with confidence and to ensure this climate adaptation action is implemented in an informed and thoughtful manner. Not only are seed-transfer distance recommendations provided, but important factors like insects and disease and palatability to browse are addressed, helping the user ensure the proper site conditions are taken into consideration when planting seed-transferred from outside your seed collection zone.

Ultimately, the projected changes in climate will exceed the natural migration, dispersal, and adaptation abilities of many tree species that are now common in our forests and could lead to increased mortality and decreased ecosystem productivity and carbon sequestration. The old way of approaching seed zone and seed movement is no longer sufficient to maintain the health of our forests. It is crucial that climate change considerations be incorporated into tree planting practices and that these practices are guided by science that helps to determine the "right tree for the right place." The information presented here is meant to be that guide.

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Sugar maple tree. Photo by C. Pike, 2021.

Acer saccharum
Sugar Maple

Carolyn C. Pike and Paul Bloese

Introduction

Sugar maple (*Acer saccharum* Marsh.) is a late-successional, shade-tolerant (Canham 1988), broad-leaved tree species, native to the United States and Canada. The bark is dark grey and exhibits different morphotypes ranging from flat plates, to raised shells, to elongated protrusions (Sajdak 1968). The species is notorious for its colorful fall foliage that can vary from yellow to red (figure 1). Sugar maple occurs across eastern North America with disjunct populations in the tropics, occurring at high elevations as far south as Guatemala (Vargas-Rodriguez et al. 2015). Sugar maple is believed to have had one southern glacial refugium that spread north and westward at the end of the last ice age (Miller and Parker 2009). A study that incorporated disjunct populations, however, found that multiple glacial refugia may better explain the species' current geographic range in temperate and tropical forests (Vargas-Rodriguez et al. 2015).

Sugar maple has a broad ecological amplitude and can grow in northern hardwood (figure 2) and southern boreal forests on a variety of soil types and substrates (Barras and Kellman 1998) but grows best on well-drained loams (Godman et al. 1990). The species has high shade tolerance and is sympatric with basswood (*Tilia americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and black cherry (*Prunus serotina* Ehrh.). In addition, its roots exude a leachate that has some allelopathic properties that may enhance its competitive ability in northern hardwood forests (Tubbs 1973). Sugar maple regeneration is most common from seed, which can successfully establish on a wide range of substrates, such as rotten wood, bare soil, and leaf

Figure 1. Maple leaves vary in color from yellow to orange in the fall, creating a patchwork of colors. Photos by C. Pike, USDA Forest Service, 2021.

Figure 2. This mature stand of sugar maple in Wisconsin was recently thinned to allow light to reach the surface of the forest. Photo by C. Kern, USDA Forest Service, 2021.

litter (Caspersen and Saprunoff 2005). Artificial regeneration is relatively uncommon because of the species' propensity to regenerate naturally in the understory (figure 3).

Sugar maple is projected to adapt well to climate change because of its shade tolerance, ability to shift northward, plasticity (Peters et al. 2020, Prasad et al. 2020), and capacity to inhabit a wider climatic range than it currently occupies (Putnam and Reich 2017). Populations within the current southern range of sugar maple have not yet shown evidence of a range contraction (Hart et al. 2014). Optimum temperatures for sugar maple germination may be higher than current norms, so the species should not be limited by germination temperature in the future (McCarragher et al. 2011). Wide-ranging dendrochronological studies failed to correlate radial growth with any single climate factor and concluded that the species is highly plastic, which bodes well for its ability to adapt to novel climates (Copenheaver et al. 2020).

Sugar production from sugar maple trees (figure 4) is, and has always been, a major food source for Tribes (Chamberlain 1891) and an important commodity to rural economies across the species' range. Sugar production is likely to be impacted by climate change, leading to concerns about the sustainability of this resource (Oswald et al. 2018, Rapp et al. 2020). The zone of optimum production may shift north from the 43rd to the 45th parallel (Rapp et al. 2020) or syrup yield may remain relatively stable across a broad latitudinal and temperature gradient (Houle and Duchesne 2020). Researchers agree that the annual sap collection season will begin and end earlier due to earlier freeze/thaw cycles (Rapp et al. 2020, Skinner et

Figure 3. Sugar maple is highly shade-tolerant and regenerates readily in full and partial shade of the understory. Photo by C. Pike, USDA Forest Service, 2021.

al. 2010). More information on this taxon can be found in Godman et al. (1990) and Nesom and Moore (2006).

Genetics

Sugar maple, a monoecious diploid (Kriebel 1957), is self-compatible, although selfing rarely produces viable seed (Gabriel 1967). Pollen, shed in the spring, is both wind- and insect-dispersed (Gabriel and Garrett 1984) and capable of long-distance dispersal (Khodwekar et al. 2015). The species is also highly dichogamic with male and female organs maturing at different time intervals: on some trees, males mature before females (protandry), while on other trees females mature before males (protogyny) (Gabriel 1968). This flowering asynchrony among trees within a stand may lower local gene flow or genetic diversity since not all combinations of outcrosses are likely (Gabriel 1968). Seeds are medium-sized double samaras, averaging 15,540 per pound (7,030 seeds per kg) and are dispersed in the fall (Zasada and Strong 2008). Usually, only one of the paired samaras contains a viable seed (Godman et al. 1990).

The taxonomy of sugar maple is not yet settled. Black maple (*Acer nigrum* Michx. f.), the closest relative to sugar maple (Jackson et al. 2020) is sometimes considered a subspecies (*Acer saccharum* ssp. *nigrum*) and may hybridize with sugar maple in the central United States where their ranges overlap (Gabriel 1973, Skepner and Krane 1998). Florida maple (*Acer floridanum* [Chapm.] Pax or *Acer barbatum* Mich.), also known as southern maple, has relatively disjunct populations and is sometimes considered a subspecies (*Acer saccharum* var. *floridanum* [Chapm.] Small & A. Heller). Kriebel (1975) recognized sugar maple as

Figure 4. Maple syrup is a major industry for residents of Northern States and an important food source for Tribes. In this image, a maple tap is testing for sugar content in a sugar maple forest in Michigan. Photo by P. Bloese, Michigan State University, 2014.

a single species with multiple forms—saccharum, nigrum, and floridanum—which correspond to the species *A. saccharum*, *A. nigrum*, and *A. floridanum*. Despite its complicated taxonomy, hybridization of sugar maple with black or Florida maple is not known to widely occur.

The amount of genetic diversity and gene flow varies across the geographic range of sugar maple. Low to moderate genetic diversity is reported in tropical populations where stands are disjunct and isolated (Vargas-Rodriguez et al. 2015). Where sugar maple stands are contiguous, genetic diversity is high and rare alleles are uncommon (Foré et al. 1992, Foré and Hickey 1992, Graignic et al. 2016, Gunter et al. 2000, Khodwekar et al. 2015). Genetic diversity of southern populations in eastern Tennessee may exceed northern populations in Wisconsin (Gunter et al. 2000) due to the presence of rare alleles in the southern populations. Because sugar maple populations along the southern range edge are relatively isolated, rare alleles that evolve are not as readily dispersed to other populations. This low dispersal results in inflated estimates of genetic diversity, which may be an artifact of reduced gene flow or prior hybridization with *A. floridanum* or *A. nigrum*.

Across most of its range, even where populations are relatively continuous, moderate levels of spatial genetic structure have been reported for sugar maple, likely from occasional inbreeding and limited seed dispersal (Geburek 1993; Geburek and Knowles 1992; Perry and Knowles 1988, 1991; Young et al. 1993). Sugar maple's opportunistic nature may also explain this phenomenon. Sugar maple proliferates in the understory of uneven-aged stands resulting in cohorts that are uniquely positioned to take advantage of light gaps or other resource pulses. These cohorts contribute seeds during years when gaps or other favorable conditions are randomly created, resulting in their disproportionate representation. These synchronous cohorts are shaped by a combination of random events and natural selection (Mulcahy 1975).

Seed-Transfer Considerations

Sugar maple growth traits such as height, stem diameter, and leaf tannin content generally exhibit weak clinal (provenance) variation, as observed in both common gardens (Baldwin et al. 1987) and natural stands (Gunter et al. 2000). Conversely, phenological traits often follow predictable geographic patterns. For example, timing of fall coloration exhibited strong latitudinal trends, with sources from northern latitudes (from cooler climates) exhibiting coloration earlier than southern sources (from warmer climates). Similarly, northern sources tend to leaf out earlier in the spring and senesce earlier in the fall than southern sources (Kriebel 1957, Kriebel and Wang 1962, Putnam and Reich 2017, Ren et al. 2020). In common garden studies, sugar maple trees originating from northerly regions (relative to a common garden) are prone to damage from early spring frosts, while trees from southerly sources are more prone to damage from fall frosts (Kriebel 1975). Drought resistance is generally higher in sugar maple trees that originate from dry climates relative to seed sources from cool, moist climates. Sun scorch and leaf injury following extreme summer heat were more severe on northern genotypes than southern genotypes in a common garden trial (Kriebel 1975). Sun scorch also exhibited east-west clines in which sources from Ohio had more leaf damage than sources from Illinois.

Kriebel (1975) defined three ecotypes of sugar maple corresponding to northern, central, and southern populations based on a variety of phenological traits (table 1). For these reasons, Kriebel (1975) defined a local seed source as one that originated within 100 mi (161 km) from the planting site. No other studies have assessed sugar maple seed-transfer distances empirically, so this recommendation may not apply to other parts of its range. Given that sugar maple is likely to expand its range northward with climate change (Caspersen and Saprunoff 2005) and is highly plastic (Guo et al. 2020), it is likely tolerant to seed-transfer distance up to 200 mi (322 km) in the Northern United States. Seed-transfer guidelines are summarized in table 2.

Insects and Diseases

Insects and diseases that impact growth and survival of mature sugar maple have been well-studied, especially across New England. Defoliators are the most common insects that affect sugar maple, including native species such as forest tent caterpillar (*Malacosoma disstria* Hbn.) (Gross 1991), which affects sugar maple in New England and, to a lesser degree, across the Lake States (Minnesota and Wisconsin). The Bruce spanworm (*Operophtora bruceata* Hulst) and saddled prominent (*Heterocampa guttivitta* Walker), both native caterpillars, also feed on sugar maple (Houston et al. 1990). Pear thrips (*Taeniothrips inconsequens* Uzel) (Gardescu 2003) is the most important nonnative defoliator of sugar maple as its feeding can also introduce anthracnose fungi (*Discula campestris* [Pass.] Arx) (Brownbridge et al. 1999, Stanosz 1993). Sugar maple is not considered a primary host for the nonnative spongy moth (formerly gypsy moth) (*Lymantria dispar* L.) (Barbosa and Greenblatt 1979). Seedlings may also be defoliated by caterpillars in the Tortricidae, including black-patched clepsis moth (*Clepsis melaleucana* Walker) (a native generalist caterpillar) and by European slugs (*Arion subfuscus* Draparnaud). Herbivory from a variety of other insects such as leafhoppers (*Typhlocyba* spp.) was reported as well (Gardescu 2003). Sugar maple borer (*Glycobius speciosus* Say) significantly impacts wood quality on mature trees with low vigor, especially after defoliation events (Wink and Allen 2003). Sugar maple is a preferred host of Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), a large beetle native to Asia that travels on firewood and on pallets used for international shipping (USDA APHIS 2022).

Mature trees and seedlings can be impacted by native *Armillaria calvescens* Bérubé & Dessureault (Bauce and Allen 1992), anthracnose (*Glomerella cingulate* [Stoneman] Spauld. & H. Schrenk), and leaf spot fungi such as *Cristulariella depraedans* (Cooke) Hohn (Gardescu 2003). Cankers caused by *Eutypella parasitica* Davidson and Lorenz usually occur on the lower bole (Kessler and Hatfield 1972, Kliejunas and Kuntz 1974). Other factors contributing to decline episodes in sugar maple stands include drought coupled with prior defoliation events (Horsley et al. 2002, Payette et al. 1996), climatic factors (Bauce and Allen 1991), and nutrient stress in New England (Bal et al. 2015) and Pennsylvania (Bailey et al. 2004).

Table 1. A summary of traits for major subgroups of sugar maple, drawn from Kriebel (1957).

Sugar maple population	Drought resistance	Susceptibility to leaf damage during summer	Cold resistance	Apical dominance
Northern	low	high	high	strong
Central	high	moderate	high	strong
Southern	high	high	low	weak

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Summary for *Acer saccharum*

Sugar maple (*Acer saccharum* Marsh.) is a shade-tolerant hardwood tree native to forests across eastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow. Population structure is moderate along range edges where populations are isolated and gene flow may be limited. Sugar maple may hybridize with southern maple (*A. floridanum* [Chapm.] Pax), but hybridization events are considered rare. Common garden studies revealed relatively weak clines for growth traits and strong variation in phenological traits, although few common gardens exist. Seed-transfer distances up to 200 mi (322 km), or roughly 2 degrees latitude northward, are considered a safe recommendation to avoid phenological mismatches. Widespread decline reported in New England and the Lake States has been attributed to insects and diseases on mature trees. Pear thrips, defoliators, *Eutypella*, and *Armillaria* fungi may impact seedlings and mature trees. Sugar maple is likely to expand northward with climate change, but southern populations may be subject to inbreeding from increased isolation among discontinuous stands.

Table 2. Summary of silvics, biology, and transfer considerations for sugar maple.

	Sugar maple (*Acer saccharum*)
Genetics	• Genetic diversity: high • Gene flow (pollen): high • Gene flow (seed): moderate to high
Cone and seed traits	• Medium-sized, winged seeds • 7,070 to 20,110 cleaned seeds per pound (3,200 to 9,100 per kg) (Zasada and Strong 2008)
Insect and disease	• Forest tent caterpillar, pear thrips, sugar maple borer, and Asian longhorned beetle • *Armillaria*, anthracnose, and *Eutypella* canker
Palatability to browse	• Moderately palatable to deer browse
Maximum transfer distances	• Sugar maple is relatively sensitive to seed-transfer; based on available common garden studies, 100 to 200 mi (161 to 322 km) is the longest recommended seed-transfer distance • Note that common garden studies are only available for a limited geographic area
Range-expansion potential	• Northward potential is high • No evidence of southern range-edge contraction • Southern range-edge populations may become more disjunct and isolated

Yellow birch tree. Photo by C. Pike.

Betula alleghaniensis Yellow Birch

Carolyn C. Pike and Christel C. Kern

Introduction

Yellow birch (*Betula alleghaniensis* Britton) is an opportunistic, relatively long-lived mesic hardwood that is readily found in hardwood forests of the northeastern United States and Canada on a variety of soil types. The bark may be golden (figure 1) or brown in color (figure 2) and generally exhibits some peeling characteristics. Yellow birch has intermediate shade tolerance and is less shade-tolerant than its common associates, sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.) (Beaudet and Messier 1998). Like other species in the *Betula* genus, yellow birch thrives on exposed or mixed mineral soil created by major disturbances (Caspersen and Saprunoff 2005, Kern et al. 2019) or on decayed wood debris (Marx and Walters 2008) (figure 3). Yellow birch populations are concentrated across northern portions of New York, New Hampshire, and Vermont and throughout Maine. The species also occurs in lower densities across the western Great Lakes region and at higher elevations along the southern Appalachians as far south as North Carolina. Three glacial lineages exist: a large eastern group (southern Appalachians to New England), a western group in the Great Lakes region, and a small group in Atlantic Canada (Thomson 2013, Thomson et al. 2015a). Introgression among *Betula* species (*B. papyrifera* Marshall, *B. lenta* L., and *B. allegheniensis*) likely occurred during the last glacial maximum (Thomson et al. 2015a), but today the species are largely distinct (Thomson et al. 2015b). Yellow birch has experienced declines attributed to overmaturity (Woods 2000), lack of recruitment (Caspersen and Saprunoff 2005), and/or periodic freeze-thaw events (Bourque et al. 2005). Yellow birch seedlings are also prone to desiccation following lengthy periods of drought.


Figure 1. The bark of this yellow birch can range in colors from bright golden (opening image) to silvery gray. Photo by Rob Routledge, Sault College.

Figure 2. The bark of this yellow birch tree is light brown in color and exhibits patterns of peeling similar to other trees in the genus. Photo by Katie Frerker, USDA Forest Service, 2019.

Yellow birch is not commonly planted because the species regenerates readily from seed. Excessive leaf litter and a lack of bare mineral soil can hamper regeneration success, especially on sites where light is limited (Shields et al. 2007). In managed stands, natural regeneration is promoted with group or patch selection followed by scarification to expose mineral soil (Gauthier et al. 2016, Willis et al. 2015). In addition, one or more seed trees must be retained in or near harvest-created openings (stand basal area >1.3 m^2/ha [5.7 ft^2/ac], <15 m [49 ft] away) (Caspersen and Saprunoff 2005, Willis et al. 2016). Release of advance regeneration through frequent selection cutting can also facilitate attainment of canopy positions for this species (Webster and Lorimer 2005). Seedling survival and growth are best on sites with medium to large light gaps (Gasser et al. 2010, Kern et al. 2012), although excessively large gaps can result in increased competition with shrubs or increased desiccation through temperature extremes (Hatcher 1966, Kern et al. 2013). The species' thin bark renders it highly sensitive to damage from sun scald and fires. Yellow birch root systems are generally shallow and thus sensitive to changes in soil temperature and moisture. White-tailed deer (*Odocoileus virginianus*) and snowshoe hare (*Lepus americanus*) commonly browse yellow birch seedlings. More information about species distribution, growth, and habitat can be found in Neesom and Moore (1998) and Erdmann (1990).

Genetics

Yellow birch is monoecious and can produce male and female flowers on the same or different branches. Pollen

Figure 3. Yellow birches grow best on bare mineral soil or any exposed surface such as the rock in this photo. Photo by Matt Pickar, USDA Forest Service, 2021.

is shed in the spring, and seeds are wind dispersed from August through September (Clausen 1973). The seeds are relatively small, with approximately 450,000 per pound (1,000 per gram) (Karrfalt and Olson 2008). The period of seed dispersal in yellow birch is more extended than other taxa with which it coexists (maple [*Acer* sp.] and beech [*Fagus* sp.]), resulting in a more persistent seed bank (Houle 1994) (figure 4). Production of male and female flowers may commence early in a tree's lifespan, sometimes before age 10 (Clausen 1980) but is generally much later (40 years and older) across most of its range (Erdmann 1990). Seed production increases with the age and abundance of yellow birch in the canopy (Drobyshev et al. 2014). Gene flow, measured with F_{ST} values (a ratio of genetic variation between subpopulations and the total population), has not been reported, but genetic and phenotypic variation is considered high due to effective dispersal of pollen and seed from both young and mature trees over their lifespan.

The *Betula* genus has a transcontinental range across the northern hemisphere and a complicated phylogeny (Wang et al. 2016). Yellow birch is hexaploid (Clausen 1973, Wang et al. 2016) and can hybridize with paper birch (*Betula papyrifera* Marshall, also a hexaploid), most commonly where the species ranges overlap (Barnes et al. 1974; Sharik and Barnes 1971; Thomson 2013; Thomson et al. 2015a, 2015b). Genetics studies of yellow birch have focused on the effects of introgression with other *Betula* spp., most commonly with *B. papyrifera* and less often with *B. lenta* (sweet, or black, birch). These natural hybridization events are most common in the lower Great Lake States where paper birch and yellow birch are sympatric, although the species are genetically distinct despite occurrence of hybridization events (Thomson 2013, Thomson et al. 2015b). Genetic diversity is highest for yellow birch in the central-western Great Lakes region where introgression with paper birch occurred historically (Thomson et al. 2015a, 2015b).

Figure 4. Yellow birch regenerates well on its own, but seeds are also collected and planted to supplement natural regeneration. Photo by Richard Kujawa, USDA Forest Service, 2021.

Seed-Transfer Considerations

Common garden studies found weak clines (latitudinal or longitudinal) for growth traits in both seedlings and 5-year-old saplings (Clausen 1975, Leites et al. 2019). Growth rings, studied in stands of natural origin, were relatively insensitive to variations in climate as well (Drobyshev et al. 2014). Clinal variations along a latitudinal (north-south) gradient are more pronounced for phenological traits associated with cold tolerance than height growth, especially for young seedlings. For example, timing of growth initiation was consistently earlier for northern- than southern-origin sources while southern-origin sources extended growth longer into the late-summer months or early fall (Clausen 1968a, Clausen and Garrett 1969). This extension of the growing season into the fall may increase susceptibility to damage from fall frosts. Traits with uncertain adaptive value, such as catkin, bract, and fruit characteristics, do not follow clear geographic patterns (Clausen 1968b), implying that genetic variation is well-dispersed among stands (Clausen 1980).

A recent analysis derived critical (not to exceed) transfer distance for yellow birch and other taxa (Pedlar et al. 2021) from provenance trials by comparing mean annual temperature (MAT) of each seed source's origin to the MAT of each planting site. Tree height in yellow birch remained above the 10 percent threshold until transfer distances exceeded 7.8 °C (13 °F) to a cooler environment or 70-day shorter growing season (Pedlar et al. 2021). This critical transfer distance, based on tree height alone at a relatively small number of common gardens, may, however, overlook phenology differences that impact survival. Transfer distances of up to 200 mi (approximately 3° latitude northward) is conservative but would likely avert phenological mismatches from excessively long-distance movement of seed. The 200-mi distance is a general recommendation for white spruce (*Picea glauca* [Moench] Voss) (Thomson et al. 2010), which has undergone more extensive provenance testing and may be comparable to yellow birch because of its high genetic diversity and low clinal variation for growth traits. If yellow birch seed orchards are established, a variety of phenotypes from local areas and southerly sites should be incorporated to maximize genetic diversity. In the absence of artificial regeneration, silvicultural prescriptions that incorporate mature seed trees near exposed mineral substrates and canopy openings will improve natural regeneration of the species. As the climate changes, natural hybridization with paper birch may be exacerbated or deterred based on local weather cycles, but these events will likely be impossible to predict or avoid.

The geographic range that yellow birch occupies is not expected to change dramatically with climate change, but the quality and quantity of the habitats within its range may decline (Peters et al. 2020). Its high seed and pollen dispersal is favorable for the species to endure across a dynamic landscape in a changing climate, but fire and pests may negatively affect its habitat (Prasad et al. 2020). Yellow birch is also sensitive to summer droughts and freeze/thaws in the spring and fall when trees are incompletely dormant (Cox and Zhu 2003), which may affect its survival if these conditions become more commonplace in the future. Yellow birch populations residing in its northern range edge were limited by substrate and seed availability but were otherwise relatively neutral to temperature extremes (Drobyshev et al. 2014), suggesting few barriers for its northward expansion. Genetics and seed-transfer considerations for yellow birch are summarized in table 1.

Insects and Diseases

Few major insects and diseases impact the growth and survival of yellow birch. Bronze birch borer (*Agrilus anxius* Gory) and birch skeletonizer (*Bucculatrix canadensisella* Chambers) can lead to mortality of mature trees. Birch leaves (figure 5) are also susceptible to feeding from the introduced gypsy moth (*Lymantria dispar dispar*) and the native forest tent caterpillar (*Malacosoma disstria* Hübner), which may contribute to yellow birch decline, especially in mature forests where trees experience other health issues.

No primary pathogens currently afflict yellow birch, but several decay fungi, such as cinder conk (*Inonotus obliquus* [Ach. ex Pers.] Pilát), are often found on mature or decadent trees (Brydon-Williams et al. 2021). Nectria canker (*Neonectria ditissima*) is damaging to yellow birch but is generally not destructive on a stand level (Ward et al. 2010); trees can live for many years with rather large cankers. Episodes of crown decline may occur with no clear cause, resulting in dead branches in the top of the tree and occasionally substantial crown dieback. Crown dieback may also be triggered by unusual weather events (Bourque et al. 2005) or site disturbance.

Figure 5. Yellow birch leaves are ovoid and serrated and sometimes difficult to distinguish from paper birch. Photo by Jack Greenlee, USDA Forest Service, 2003

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Summary for *Betula alleghaniensis*

Yellow birch (*Betula alleghaniensis* Britton) is a small-seeded hardwood tree native to forests across northeastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow, though few parameters that describe gene flow have been reported. Yellow birch is capable of hybridizing with other *Betula* species. Common garden studies revealed relatively weak clines for growth traits but strong variation in phenological traits, indicating that seed-transfer may be deleterious if seed is moved long distances. No empirical transfer distances have been suggested, but distances of 200 mi (320 km), or roughly 3 degrees latitude northward, is a safe recommendation to avoid phenological mismatches. Widespread yellow birch decline has been described in Canada and attributed to climatic perturbations. Few major pests impact yellow birch except for decay fungi in decadent (overmature) stands. Yellow birch is likely to persist with climate change in its current range because of its high genetic diversity and gene flow.

Table 1. Summary of silvics, biology, and transfer considerations for yellow birch.

Yellow birch (*Betula alleghaniensis*)	
Genetics	• Hexaploid (6 sets of chromosomes) • Gene flow (pollen): high • Gene flow (seed): high
Cone and seed traits	• Small, winged seeds • 450,000 cleaned seeds per pound (992,250 seeds per kilogram) (Karrfalt and Olson 2012) • Seeds released in September
Insect and disease	• Bronze birchborer, nectria canker, cider conk, and skeletonizer • Decadent stands may exhibit crown dieback and decline
Palatability to browse	• High risk of herbivory from white-tailed deer and snowshoe hare
Maximum transfer distances	• Seed-transfer distances for yellow birch are intermediate: transfer distance of 200–300 mi (322–483 km) should be well tolerated • Few common gardens have been established and these recommendations may change with future research. • Potential to hybridize with paper birch or sweet birch where ranges overlap
Range-expansion potential	• Likely to expand range but requires suitable substrate (e.g., exposed mineral soil) and sufficient light to survive (e.g., canopy gaps)

Black walnut tree. Photo by Jim Warren, 2023.

Juglans nigra
Black Walnut

Carolyn C. Pike and Keith Woeste

Introduction

Black walnut (*Juglans nigra* L.) is a highly valued, long-lived, early-successional hardwood tree species that grows in riparian areas (bottomlands) across much of the Central and Southern United States into upstate New York and New England, spanning plant hardiness zones 3 through 9 (USDA ARS 2012). While it is classified as a shade-intolerant species, saplings can survive under light to medium shade, although growth under these conditions is not suited for commercial production (Carpenter 1974). Black walnut grows best on well-draining sandy or silt loams (Losche 1973) and may also grow on mineland soils or spoils if nutrition and drainage are adequate (Ashby 1996). On optimal sites, black walnut exhibits rapid growth, but is notoriously sensitive to site and soil conditions; on subpar sites, its growth is slow and mortality is high. Natural regeneration is severely impacted by heavy competition with grass, especially fescue (*Festuca* spp.) (Krajicek 1975). Therefore, both careful site selection and control of competing grass vegetation is critical for black walnut plantings to be successful (Smith 1983), especially for those grown for timber (figure 1).

Figure 1. A plantation of black walnut, managed for future timber, requires intensive care to ensure that it will thrive. Photo by M. Coggeshall, University of Missouri, 2005.

Black walnut's darkly colored bark and deep fissures distinguish it from the lighter gray bark plates of butternut (*Juglans cinerea* L.) (Farlee et al. 2010). In addition, black walnut's fruits are generally round-shaped and hairless (figure 2), in contrast to the oblong, hairy, and sticky fruits of butternut (Farlee et al. 2010). Black walnut is valued for veneer (figure 3), with board-foot values frequently exceeding those for black cherry (*Prunus serotina* Ehr.) and nearly double those for oak (*Quercus* spp.), which, in many years, is the second most valuable hardwood in the central hardwood region (Settle and Gonso 2020). Black walnut is also cultivated for its edible nuts (Coggeshall 2011, Reid et al. 2009) (figure 4).

Black walnut is sympatric with other riparian, mesophytic hardwoods such as yellow poplar (*Liriodendron tulipifera* L.), white ash (*Fraxinus americana* L.), black cherry, basswood (*Tilia americana* L.), beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall), oaks, and hickories (*Carya* spp.) (Williams 1990).

Black walnuts are notable for the production of juglone, a chemical that has allelopathic properties that can inhibit the growth of some neighboring plants, such as crimson clover (*Trifolium incarnatum* L.) and the nonnative amur honeysuckle (*Lonicera maackii* [Rupr.] Herder) (Rietveld 1983). Phytoxicity on native trees is reported for white birch (*Betula papyrifera* Marshall) (Gabriel 1975), and to a lesser extent on eastern white pine (*Pinus strobus* L.), with such

Figure 2. Three walnuts are shown before (a) and after (b) the husk is removed. Photos by A. Ebrahimi, Purdue University, 2021.

Figure 3. This veneer of black walnut is a good representation of a highly valued timber product from this species. Photo by M. Coggeshall, University of Missouri, 2009.

effects amplified on sites with poor drainage and lower plant vigor (Rietveld 1983). Juglone can inhibit growth of conifer seedlings, but in small quantities it can stimulate their growth (Funk et al. 1979).

The phylogeny of the genus *Juglans*, which includes both butternuts and walnuts, is complex because it traverses multiple continents and is divided into three sections based on origin, but not present locality. For example, black walnut occurs in the *Rhysocaryon* section, which includes all New World walnuts, while butternut is part of the *Cardiocaryon* section, which is otherwise entirely Asian (Aradhya et al. 2006a, b; Aradhya et al. 2007). Although they co-occur, butternut and black walnut cannot hybridize because of their distinct phylogeny. One

Figure 4. This large bag of walnuts was collected from a seed orchard. Black walnuts are best picked from the ground, not directly from the tree. Photo by M. Coggeshall, University of Missouri, 2004

glacial refugium, in the lower Mississippi Valley, is supported by the genetics of extant trees, with no evidence of postglacial bottlenecks (Victory et al. 2006). Black walnut is likely to persist in its present range owing to its high genetic variation and ability to produce and disperse seeds. However, its shade and drought intolerance may limit its growth or survival on sites where such conditions predominate (Morin et al. 2007).

Figure 5. The immature catkins (male flowers) of black walnut will dry prior to opening and releasing pollen. Photo by M. Coggeshall, University of Missouri, 2003.

Genetics

Black walnut is a monoecious diploid, with outcrossing enforced by pronounced dichogamy (i.e., female and male flowers are produced at different times on a tree). Cultivars and clones may be distinguished by their consistent timing of peak male (figure 5) and female bloom (figure 6) (Ebrahimi et al. 2018, Pang et al. 2021), which has implications for breeders and may lead to Wahlund effects, or nonrandom breeding within stands or orchards (Robichaud et al. 2006). Black walnut is characterized by especially high genetic variation and low population structure based on nuclear microsatellites, with F_{ST} values (a ratio of genetic variation between subpopulations and the total population) near 0.017 (Victory et al. 2006). Despite the fruit's large size (figure 7), seeds and pollen are readily dispersed. Few detectable differences in fruit size occur among populations. One study showed that nuts from northern provenances had lower fresh weight than nuts from southern provenances, but no association was found between nut size and fresh weight or seedling vigor (Funk and Polak 1978).

The success of black walnut seed and pollen dispersal may be attributed to several factors, including small mammals (mainly squirrels), hydrochory (i.e., nuts can float and move long distances on rivers), and high levels of wind-dispersed pollen movement. Genetic diversity of neutral alleles is lower in northern populations compared with southern populations, but these latitudinal-based differences account for less than 10 percent of genetic variation (Victory et al. 2006).

Black walnut's high commercial value has led to decades of research on genetics and genetic improvement for artificial reforestation with this species (Beineke and Masters 1973, Mckenna and Coggeshall 2018, Mckenna and O'Connor 2014, Michler et al. 2004). Beineke (1972) speculated that inbreeding from high-grading could be a cause for concern, but merchantable value was not associated with rare alleles that would be lost by thin-from-above practices (Robichaud et al. 2010). Efforts to improve stem form (straightness for log quality), heartwood color, and growth continue today at the Hardwood Tree Improvement and Regeneration Center at Purdue University (West Lafayette, IN).

Figure 6. The female flowers of black walnut, after fertilization, will develop into a nut inside an outer husk. Photo by K. Pang, Purdue University, 2011.

Seed-Transfer Considerations

A series of provenance trials highlighted clinal variation in black walnut, especially between extreme sites (Bey 1976). Cold tolerance, which is a limiting factor for seed-transfer, also varies clinally and latitudinally, with 40 percent of height growth attributed to latitude alone (Williams et al. 1974). Cessation of late-season growth is more differentiated than budbreak timing in the spring. Bey et al. (1971) found that southern sources started growing 3 days earlier and continued for 2 weeks longer than northern sources. Leaf fall is also strongly associated with latitude.

Optimal seed-transfer distances depend, in part, on the location of the planting site relative to the range edge. Populations along the southern range edge may experience insufficient chilling hours to break bud dormancy (Morin et al. 2007), especially if northern sources are moved south two hardiness zones or more (e.g., from zone 5 to zone 7) (USDA ARS 2012). Published seed-transfer zones for black walnut have not been widely implemented (Deneke et al. 1980), but sources from up to 200 mi (322 km) south of the planting site are recommended for production forestry, except in extreme northern sites, where local sources are best (Bey et al. 1971, Bey 1980, Bresnan et al. 1994, Clausen 1983, Rink and Van Sambeek 1988, Wendel and Dorn 1985). The improvement in growth attained by planting southerly sources may be due to an extended growing season because such southern sources flush earlier and drop leaves later than northern (or local) sources when moved northward (Bey et al. 1971). For restoration, managers may consider combining local sources with sources from as far as 200 mi (322 km) south of the planting site to ensure that seedlings have sufficient cold tolerance to survive

Figure 7. This abundant fruit crop is maturing on a grafted tree in a seed orchard. Photo by M. Coggeshall, University of Missouri, 2003.

and thrive on the site. See table 1 for a summary of seed-transfer considerations.

Black walnut exhibits sensitivity to local climate. Average July temperature and length of growing season were strongly correlated with height growth of 15-year-old trees, compared with other factors such as January temperature and annual precipitation (Smith 1983). Cold temperatures during the active growing season are more important than nadir winter temperatures, because fully dormant tissues across provenances are cold hardy to extreme temperatures (George et al. 1977). Rainfall is an important determinant of height growth during periods of active growth (Bey et al. 1971), whereas temperatures of air and soil are more important for determining diameter growth (Bey et al. 1971). In provenance trials, mean annual temperature of the seed source also explained strong clines in tree heights (Leites et al. 2019).

Insects and Diseases

Black walnut has many minor pests and pathogens that feed on foliage, roots, fruit, and stems. These pests can reduce commercial value, but few currently pose major health risks. Several summaries of insect and disease pests have been published and are recommended for more detailed information (Katovich 2004, Mielke and Ostry 2004, Miller 1973).

Insect pests include shoot borers such as *Acrobasis demotella* Grote, which can reduce the dominance of the apical stem and degrade commercial value, but generally do not threaten survival (Katovich 2004). Other shoot borers (e.g., *A. caryivorella* Ragonot and *A. juglandis* LeBaron) feed on black walnut buds, emerging shoots, and leaves, but are usually less common than *A. demotella* (Miller 1973). Ambrosia beetles (*Xylosandrus germanus* Blandford) can attack healthy or declining trees, causing dieback and sprouting from the tree's base (Katovich 2004). The shoot moth (*Gwendolina concitatricana* Heinrich) can injure or kill terminal buds, reducing commercial value. Walnuts are a favored food source for numerous other insects such as curculios and weevils (e.g., *Conotrachelus retentus* Say), and husk flies (*Rhagoletis suavis* Loew) (Miller 1973), which can become problematic in seed orchards. Lepidopterans may be commonly found on walnuts (Nixon and McPherson 1977), but usually pose few threats to tree health except for walnut caterpillar (*Datana integerrima* Grote & Robinson), which can become locally abundant, in certain years, degrading tree vigor (Farris et al. 1982).

Anthracnose (*Gnomonia leptostyla* [Fr.] Ces. & De Not.), the most important foliar disease of black walnut, causes leaves to drop prematurely on susceptible trees, but its association with reduced growth is still not solidly established. Walnut bunch disease, or walnut witches'-broom, believed to be incited by a mycoplasma like organism (Chen et al. 1992), is less common than anthracnose but can lead to stunted crowns and mortality (Berry 1973). *Phytophthera citricola* Sawada, *Cyclindrocladium* species, *Pythium* species, and *Fusarium episphaeria* (Tode) W.C. Snyder & H.N. Hansen, are root pathogens generally associated with mortality of black walnut seedlings growing in nurseries. These root pathogens can be difficult to control even with fumigation (Berry 1973). Thousand cankers disease (*Geosmithia morbida* M.Kolařík, E.Freeland, C.Utley, & Tisserat), vectored by walnut twig beetle (*Pityophthorus juglandis* Blackman) (Grant et al. 2011, Sitz et al. 2021), may pose a threat in the future in areas that experience persistent drought, such as parts of the Western United States where black walnut is not native (Tisserat et al. 2011).

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Summary for *Juglans nigra*

Black walnut (*Juglans nigra* L.) is a shade-intolerant hardwood tree common in riparian forests across the Central United States. Commercial values for top-quality black walnut logs are the highest for any tree in North America. Production of juglone from walnuts may have phytotoxic effects on neighboring plant communities. Genetic diversity of this species is high, due to seed dispersal and pollen flow characteristics, and population structure is low. Common garden studies revealed relatively weak clines for growth traits, but strong latitudinal gradients for cold tolerance. Seed-transfer distances of 200 mi (322 km) from south to north is considered a safe recommendation to maintain growth. At the northern edge of the species' range, such as Minnesota, local sources are best. Leaf anthracnose is an important pest, and thousand cankers disease can be a concern, especially in drought-prone areas. Black walnut is likely to expand northward with climate change, but its migration may require human assistance, and such expansion may be limited by soil conditions, site availability, deer browse, or drought.

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

Black walnut (*Juglans nigra*)	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Large, hard, recalcitrant seeds can be freezer stored for 2 to 3 years; seeds can be sown with husk intact (Rink 1988) • 11 to 100 cleaned seeds per pound (25 to 220 per kg) (Bonner 2008)
Insect and disease	• Anthracnose (leaf disease) • Thousand cankers disease (vectored by walnut twig beetle) may become problematic with increasing drought • Shoot borers and ambrosia beetles can cause dieback and degrade form, especially in stressed trees
Maximum transfer distances	• Sensitive to seed transfer; distances that exceed 200 mi (322 km) south to north are not recommended • Local sources are recommended for reforesting along the northern range edge
Palatability to browse	• Browse and antler rub slow growth and degrade value where white-tailed deer pressure is high
Range-expansion potential	• Likely to migrate northward, but may be limited by soil and moisture conditions • Phytotoxicity of juglone may affect understory or adjacent plant communities

White spruce tree. Photo by Andy David, University of Minnesota, 2022.

Picea glauca
White Spruce

Carolyn C. Pike

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* Zimmermann). 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

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

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 after a fire (Purdy et al. 2002). Additional details about this 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 2 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 subpopulations 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) 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

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, USDA Forest Service, 2009.

Figure 3. Immature cones ripening on a tree at a seed orchard. Unlike cones of the *Pinus* genus, spruce cones only require 1 year to develop. A cut-test of the cone is required to test for ripeness. Once the cone dries, the seed is released in late summer. Photo by C. Pike, USDA Forest Service, 2006.

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 (Nienstaedt 1966, Lu and Man 2011). 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 with no significant genotype-by-site interactions (Lesser and Parker 2004, Lu and Man 2011). For example, genotypes with a tendency to breakbud early were not associated with any single provenance and budbreak was consistent for families across multiple sites. 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 day length 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 have a strong influence on 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 six 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).

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). Budworms serve an important successional role by accelerating the demise of decadent stands of spruce and fir (*Abies* spp.) 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. Over long timespans, 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 subpar 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 yellowheaded 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) are minor pests and associated with open grown trees in largely urban settings. Pathogens affecting weakened white spruce hosts include needle cast caused by *Rhizosphaera kalkhoffii* and *Stigmina lautii* (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 in plantations and along the southern edge of white spruce's range.

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.

Figure 5. The yellowheaded spruce sawfly is an occasional pest on white spruce foliage. Photo by J. Warren, USDA Forest Service, 2011.

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Summary for *Picea glauca*

White spruce (*Picea glauca* [Moench] Voss) 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 migrate northward, is generally unpalatable to browse from white-tailed deer, and can be transferred long distances with a low probability of maladaptation.

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

White spruce (*Picea glauca*)	
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) • Needle casts can afflict spruce
Palatability to browse	• Low risk of herbivory from white-tailed deer
Maximum transfer distances	• White spruce is relatively tolerant of long-distance transfers. • Transfer distances of at least 200 miles (322 km) are acceptable and distances of 300 or more miles (438 km) may be tolerated in some cases. • Sources from 1.0° to 1.5° latitude south (70–100 mi [113–160 km]) 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

Black spruce trees. Photo by Steve Katovich.

Picea mariana
Black Spruce

Carolyn C. Pike and Marcella Windmuller-Campione

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 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 dispersal (Johnstone et al. 2009) (figure 2). In addition, black spruce can regenerate from cones in the soil, although viability of seeds starts declining after 1 year (Fraser 1976). Natural regeneration by seed is common after a 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

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.

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] Voss) 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).

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

Figure 3. Black spruce often grows sympatrically with tamarack (*Larix laricina* [Du Roi] K. Koch) as seen in this northern Minnesota forest. Photo by C. Pike, 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 in boreal or subboreal 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, are evident in maternally inherited mitochondrial DNA but only in subarctic 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 subpopulations 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

Figure 4. This black spruce stand in northern Minnesota is one of a group of North American range-wide provenance trials. 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 C. Pike, USDA Forest Service, 2004.

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 the Maritime Provinces 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 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 (-76 °F [-60 °C]) 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 et al. (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° latitude 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 °F (2.2 °C) warmer mean annual temperature (MAT) (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 43 °F [6.1 °C] less MAT) 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).

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

Figure 5. Eastern dwarff 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 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). Yellowheaded 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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Summary for *Picea mariana*

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 that are 1.5 to 2.0 °C mean annual temperature (MAT) 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 200 mi (320 km).

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

Black spruce (*Picea mariana*)	
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
Maximum transfer distances	• Black spruce has intermediate tolerance to seed-transfer distances: 200–300 mi (322–483 km) are well tolerated in most cases • Southern range-edge populations should be prioritized for conservation and moved northward
Range-expansion potential	• Likely to expand northward • May lose habitat from excess fires and loss of soil organic matter

Red spruce tree. USDA Forest Service photo.

Picea rubens
Red Spruce

Stephen Keller

Introduction

Red spruce (*Picea rubens* Sarg.) is a shade-tolerant, coniferous tree that prefers cool, moist sites throughout mid to high elevations in the Appalachian Mountains and along coastal areas of Maine and the Canadian Maritime Provinces. Its geographic distribution shows a strong inverse latitude-elevation relationship, with red spruce occurring at its highest elevations in the Central and Southern Appalachians of West Virginia, Virginia, North Carolina, and Tennessee (most common above 3,300 ft [1,000 m]), more moderate elevations in the Adirondacks and Northern Appalachians of New York and New England (most common between 2,500 to 4,000 ft [750 to 1,200 m]), and near sea level in the northern Maritime forests (Cogbill and White 1991).

Red spruce is associated with a variety of forest types but is probably best known as a codominant member of high-elevation spruce/fir forests where it occurs with balsam fir (*Abies balsamea* [L.] Mill.) or Fraser fir (*A. fraseri* [Pursh] Poir.) in the northern or southern part of its range, respectively (figure 1). At lower mountain elevations, red spruce is a common component of mixed conifer-northern hardwood forests, where it commonly occurs with sugar maple (*Acer saccharum* Marshall), eastern hemlock (*Tsuga canadensis* [L.] Carrière), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.) (Verrico et al. 2020).

Figure 1. This montane red spruce forest in northern Vermont is typical of forest types between 2,500 and 3,500 ft (762 and 1,067 m) in elevation. Photo by Stephen R. Keller, 2019.

In high-latitude coastal areas of its range in Maine and Maritime Canada, red spruce is a dominant member of a cool, maritime-influenced conifer forest community. Elsewhere in the interior of its range, red spruce sometimes occurs in "frost pocket" wetland or bog sites in association with red maple (*Acer rubrum* L.), tamarack (*Larix laricina* [Du Roi] K. Koch), eastern hemlock, and with its closely related black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg). In the Central and Southern Appalachian regions, red spruce is a foundational species that provides critical high-elevation, cool, shady habitat for a variety of regionally rare or endemic wildlife species (Byers et al. 2010) (figure 2).

Historically, red spruce was probably more widespread throughout both the northern and southern extents of its range and occupied additional areas with warmer climates than its current distribution (Cogbill 2000, Van Gundy et al. 2012). Logging, fire, and atmospheric pollution (acid rain) have severely impacted red spruce and reduced its distribution and abundance, particular in lower elevation northern hardwood forests (Foster and D'Amato 2015, Koo et al. 2015, Siccama et al. 1982). In recent years, red spruce has been rebounding in growth and seedling recruitment at lower elevations, including recolonizing downslope in montane forests, suggesting a slow recovery from the legacies of land use and pollution (Foster and D'Amato 2015, Kosiba et al. 2018, Verrico et al. 2020, Wason et al. 2017).

Although associated with high-elevation or high-latitude areas in the Appalachian Mountains, red spruce is not a boreal species but rather a cool-temperate zone species (Dumais and Prévost 2007, White and Cogbill 1992). Red spruce appears to be limited by midsummer (July) temperatures (Cogbill and White 1991, Hamburg and Cogbill 1988), being sensitive to conditions of high temperatures during the growing season when adequate moisture is unavailable through precipitation, humidity, or cloud immersion (Day 2000, Hamburg and Cogbill 1988, Keller et al. in press, Lachmuth et al. 2023). Red spruce is also sensitive to cold temperatures during the fall and spring transition seasons (Yetter et al. 2021) and achieves only moderate cold tolerance in midwinter, incurring damage by temperatures below

Figure 2. This red spruce forest in Spruce Knob, WV, shows structural diversity and recruitment from the understory. Cool, moist conditions at higher elevations (>4,000 ft [1,219 m]) in the Central Appalachians support the development of mature red spruce communities. Photo by Stephen R. Keller, 2013.

-40 °F (-40 °C) unlike true boreal spruce species in the northeast such as white spruce (*Picea glauca* Moench) and black spruce (Strimbeck et al. 2007, DeHayes et al. 2001). Winter injury to red spruce can also occur at less extreme temperatures when a midwinter warm period is followed by an abrupt return to cold. During these times, red spruce will temporarily deharden and resume photosynthesis, resulting in susceptibility of current-year foliage to rapid transitions back to subfreezing temperatures (Schaberg 2000).

Red spruce seedling recruitment is best under partial shade. Photoinhibition damages seedlings exposed to full sunlight (Dumais and Prévost 2007, 2016). Due to its shade tolerance and slow growth habit, red spruce can persist in the understory for decades but requires canopy release to achieve its full growth potential (Rentch et al. 2016). Dominant canopy trees can persist for centuries as a late-successional species in the forest community. Red spruce can grow on a variety of substrates, from poorly drained bogs to exposed upland sites with shallow soils, but it commonly occurs on moist, slightly acidic soils with a well-developed humus layer (Spodosols).

During the last ice age, red spruce retreated to a southern refugium located in the unglaciated areas of the Carolinas and stretching westward toward the Mississippi River Valley, from which it recolonized northward after the glaciers retreated (Keller et al. in press, Lachmuth et al. 2023, Lindbladh et al. 2003, Watts 1979). After glaciation, red spruce may have retreated to a northern coastal refugium near the Canadian Maritimes during the mid-Holocene warm period, approximately 5,000 to 8,000 years ago, after which it is thought to have recolonized inland (Schauffler and Jacobson 2002).

Red spruce is most closely related to black spruce, from which it speciated during the Pleistocene glacial period, and with which it still overlaps geographically in areas from Pennsylvania northward (Jaramillo-Correa and Bousquet 2003). Red spruce and black spruce are known to hybridize naturally throughout their areas of sympatry (Capblancq et al. 2020, de Lafontaine et al. 2015, Jaramillo-Correa and Bousquet 2003, Perron and Bousquet 1997), and artificial hybrids are also possible through controlled crosses (Major et al. 2003, 2005). Despite overlapping ranges in the north, neither red spruce nor black spruce are closely related to white spruce, the latter of which shows closer phylogenetic relationships to western spruces (e.g., *Picea engelmanii* Parry ex Engelm. and *P. sitchensis* [Bong.] Carr.) (Feng et al. 2019, Lockwood et al. 2013).

Genetics

Red spruce is a diploid species (2n=24) with a very large genome (genome size of the closely related black spruce is ca. 18.3 Gbp [Lo et al. 2023]). Red spruce is also monoecious, producing separate male and female cones (figure 3) and has a wind-pollinated, outcrossing mating system. Based on the mating system and compared with other similar conifers (including black spruce), red spruce would be expected to have high genetic diversity and low population structure, but it does not meet these classic expectations (table 1). On the contrary, multiple genetic studies using a variety of marker types have shown red spruce to have quite low levels of genetic diversity compared with similar conifer tree species (Capblancq et al. 2020, Hawley and DeHayes 1994, Keller and Trott 2017, Perron et al. 2000). Low levels of diversity correspond to a bottlenecked effective population size (N_e) in red spruce that shows evidence of long-term decline over thousands of years, pre-dating more recent anthropogenic impacts (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017).

Some of this initial reduction in N_e is attributable to the speciation event with black spruce, in which red spruce is thought to have diverged as a small, isolated subpopulation of black spruce during the Pleistocene glacial period and captured just a subset of its progenitor's genetic diversity (Jaramillo-Correa and Bousquet 2003, Perron et al. 2000). The trend toward declining N_e in red spruce has continued after its divergence with black spruce, with more recent bottlenecks dated to the mid to late Holocene (Capblancq et al. 2020, Jaramillo-Correa et al. 2015, Keller and Trott 2017). Low genetic diversity in red spruce has been associated with reduced seedling vigor under greenhouse conditions, particularly for seedlings originating from the southern part of its range (Capblancq et al. 2021).

At a landscape scale, red spruce shows genetic population structure between three geographically separated ancestry groups: the northern core of the range

Figure 3. Reproductive structures in red spruce include (a) male and (b) female strobili. Photos by Brittany M. Verrico, 2017.

(New York, New England, and Canada), the southern fragmented range edge (Maryland south to North Carolina and Tennessee), and the margin or transition zone between the core and edge (bog sites in central and northern Pennsylvania) (figure 4). These three ancestry groups diverged ca. 8,000 years ago after glacial retreat and, while genetically distinct, there are only modest levels of divergence at nuclear loci, with F_{ST} values (the proportion of genetic variance contained in a subpopulation relative to the total) of 0.02 to 0.03 (Bashalkhanov et al. 2013, Capblancq et al. 2020). Gene flow still occurs between regions but at a very low rate of 1 migrant exchanged every 4 to 20 generations, equating to an approximate maximum migration frequency between regions of 1 individual per 100 years (Capblancq et al. 2020).

At a more local scale within regions, population differentiation in the nuclear genome among populations is typically quite low ($F_{ST} < 0.01$) consistent with its wind-pollinated mating system (Keller and Trott 2017, Verrico 2021). Cytoplasmic genomes (mitochondria and chloroplast) show limited haplotype variability in red spruce relative to black spruce, and a trend for greater population structure in mitochondrial DNA (dispersed through seed) than chloroplast DNA (dispersed through pollen), consistent with higher levels of gene flow through pollen (Gérardi et al. 2010, Jaramillo-Correa and Bousquet 2003).

Red spruce exhibits patterns of local adaptation to climate at both local and regional scales. At the trait level, common garden estimates of genetic variation in budbreak and budset shows clinal patterns of trait variation along climatic gradients of elevation and latitude (Butnor et al. 2019, Prakash et al. 2022, Verrico 2021). Evidence also indicates that plasticity in budbreak timing shows locally adapted genetic variation in response to gradients in climate seasonality (Prakash et al. 2022). At the molecular level, clinal adaptation in stress response genes is evident along seasonal gradients of temperature and precipitation, as well as historic air pollution (Bashalkhanov et al. 2013, Capblancq et al. 2023).

As noted previously, red spruce and black spruce are capable of hybridization. Naturally occurring hybrid genotypes occur in the northern part of the red spruce range (Perron and Bousquet 1997, de Lafontaine et al. 2015, Capblancq et al. 2020). Areas of advanced introgression between red spruce and black spruce can also be found in wetlands and bogs of Pennyslvania. Natural hybrid genotypes with a mix of red spruce and black spruce genetic ancestry show positive heterosis for growth in common garden experiments (Prakash et al. 2022). In contrast, controlled crosses between red spruce and black spruce suggest reduced seed viability and slightly negative heterosis for growth among surviving first-generation hybrids (Major et al. 2003, 2005). The reduced seed set along with the ecological (habitat) separation is probably sufficient to keep the two species distinct, even in the face of occasional hybridization.

Molecular studies shed further light by showing that the barriers to hybridization vary considerably across the genome with some gene loci forming strong isolating barriers, while other loci are highly permeable to introgression (de Lafontaine et al. 2015). Further, genomic studies show that backcrossing of hybrids

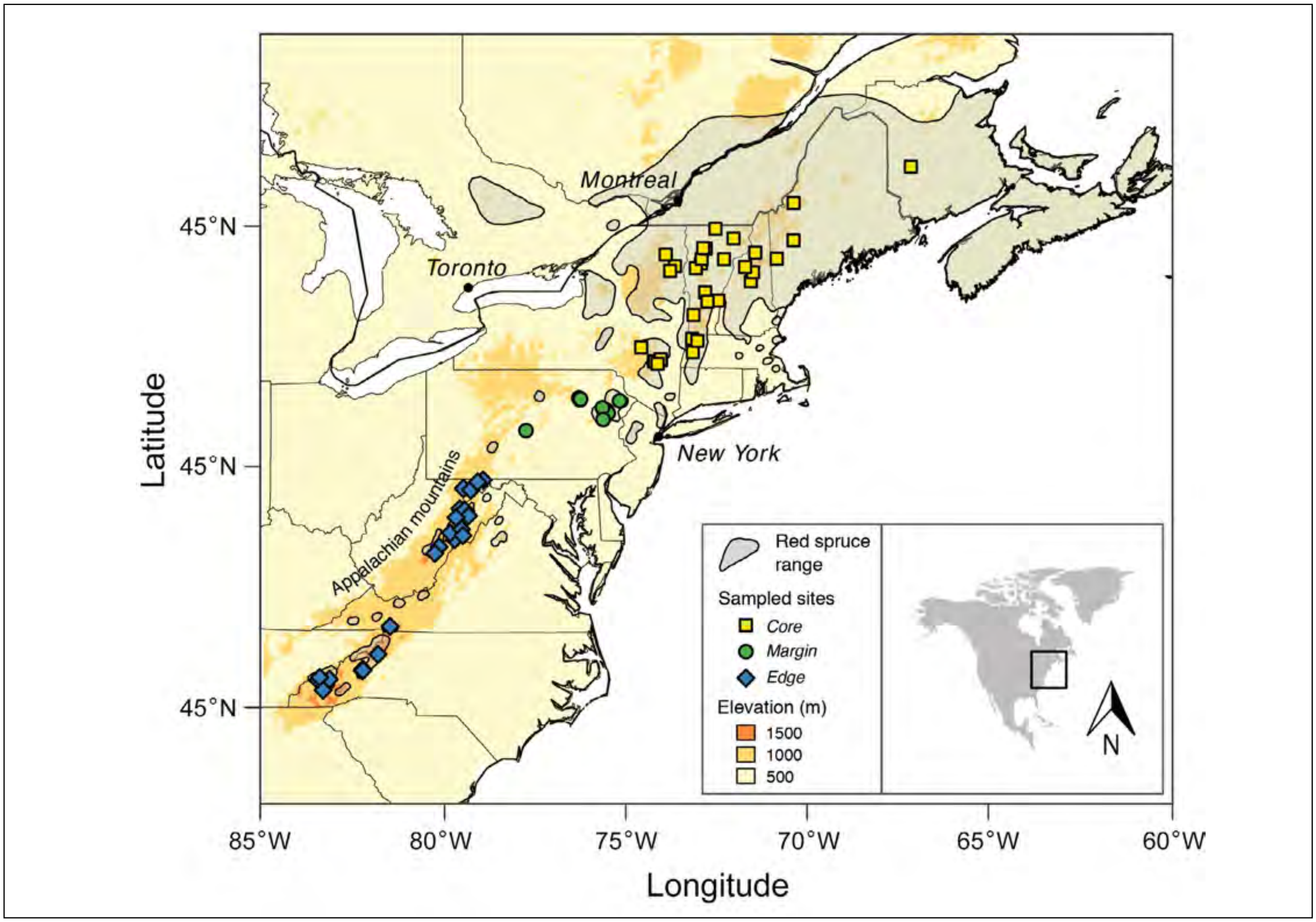

Figure 4. Range-wide structure of genetic ancestry in red spruce. Symbols denote the 65 populations (N=340 individuals total) sampled for exome-capture genomic sequencing by Capblancq et al. (2020). Colors denote genetic ancestry clusters based on principal component analysis of single-nucleotide polymorphisms (SNPs), which separated samples genetically into three regional clusters: a southern range edge (blue), a mid-latitude margin (green), and a northern range core (yellow).

with red spruce occurs more frequently than backcrossing to black spruce, suggesting introgression is directional and occurs more easily toward red spruce (de Lafontaine and Bousquet 2017). Ongoing studies of natural advanced generation backcrosses suggest that introgression introduces adaptive variation into red spruce (which is otherwise low in genetic diversity), which may facilitate its adaptation along climatic gradients (Prakash and Keller, unpublished data). Synthesizing across these studies indicates that hybridization between red spruce and black spruce (1) is relatively common in the north, (2) is likely selected against in the first generation as a result of reduced seed viability, (3) backcrosses preferentially with red spruce where hybrids survive to maturity, and (4) may increase genetic diversity and adaptive potential in red spruce with advanced-generation backcrosses.

Seed-Transfer Considerations

While not grown commercially, red spruce is the focus of active restoration and reforestation efforts for conservation of biodiversity, especially in the southern portions of the range where logging and fire have severely reduced its former range (Adams and Stephenson 1989). Consideration of seed sourcing and transfer guidance for red spruce comes from a variety of sources, including climate models, provenance trials, progeny tests, and genomic analyses. Climate-based species distribution models generally predict a severe contraction of red spruce's range by the end of this century (Beane and Rentch 2015, Koo et al. 2014, Lachmuth et al. 2023) with overall decreases in importance values over much of its existing range (Peters et al. 2020). These forecasts raise awareness that seed sourcing for reforestation and restoration should take into consideration both current and future climates (Walter et al. 2017).

Several provenance trials exist for red spruce (Morgenstern et al. 1981, Wilkinson 1990) that offer insight into the response of red spruce growth to climate transfer distance (TD = test site climate – seed source climate). A recent study of trials in Maritime Canada showed that growth (height and diameter at breast height [DBH]) measured on adult trees responded most to TD based on temperature variables and less so to precipitation (Li et al. 2020). In these trials, growth response of warm-climate provenances was negatively affected by seed-transfer into colder test sites (negative TD); conversely, cold provenances benefited slightly from transfer into warmer test sites, up to 5.4 °F (3.0 °C) warmer than the source climate. These responses were strongest for climate variables associated with growing season length (frost-free period and growing degree days), pointing to risk of cold damage and thus impeded growth upon transfer to colder climates. It is important to note that all the test sites and most of the source provenances in Li et al. (2020) were northerly (eastern Canada), so the data do not necessarily capture the response of midlatitude and southern provenances to warming above their baseline.

A recent test evaluated red spruce progeny from 340 mothers sampled from 65 provenances across the range and grown in raised beds at 3 test sites stratified by latitude (Vermont, Maryland, and North Carolina) (Prakash et al. 2022). The three test sites were generally warmer than the climate at the seed sources (Prakash et al. 2022), producing a range of TD values (based on mean annual temperature) from 7.2° F (4 °C) colder to 22 °F (12 °C) warmer than the source climate. Seedlings showed a decrease in first year height increment growth with increasingly warmer TDs (figure 5). In their second year, growth declined under both the coolest and warmest TDs, but was resilient to, or even slightly benefited from, moderate warming (5.4 to 9 °F [3 to 5 °C]). A related analysis that considered the influence of a broader set of 11 climate variables,

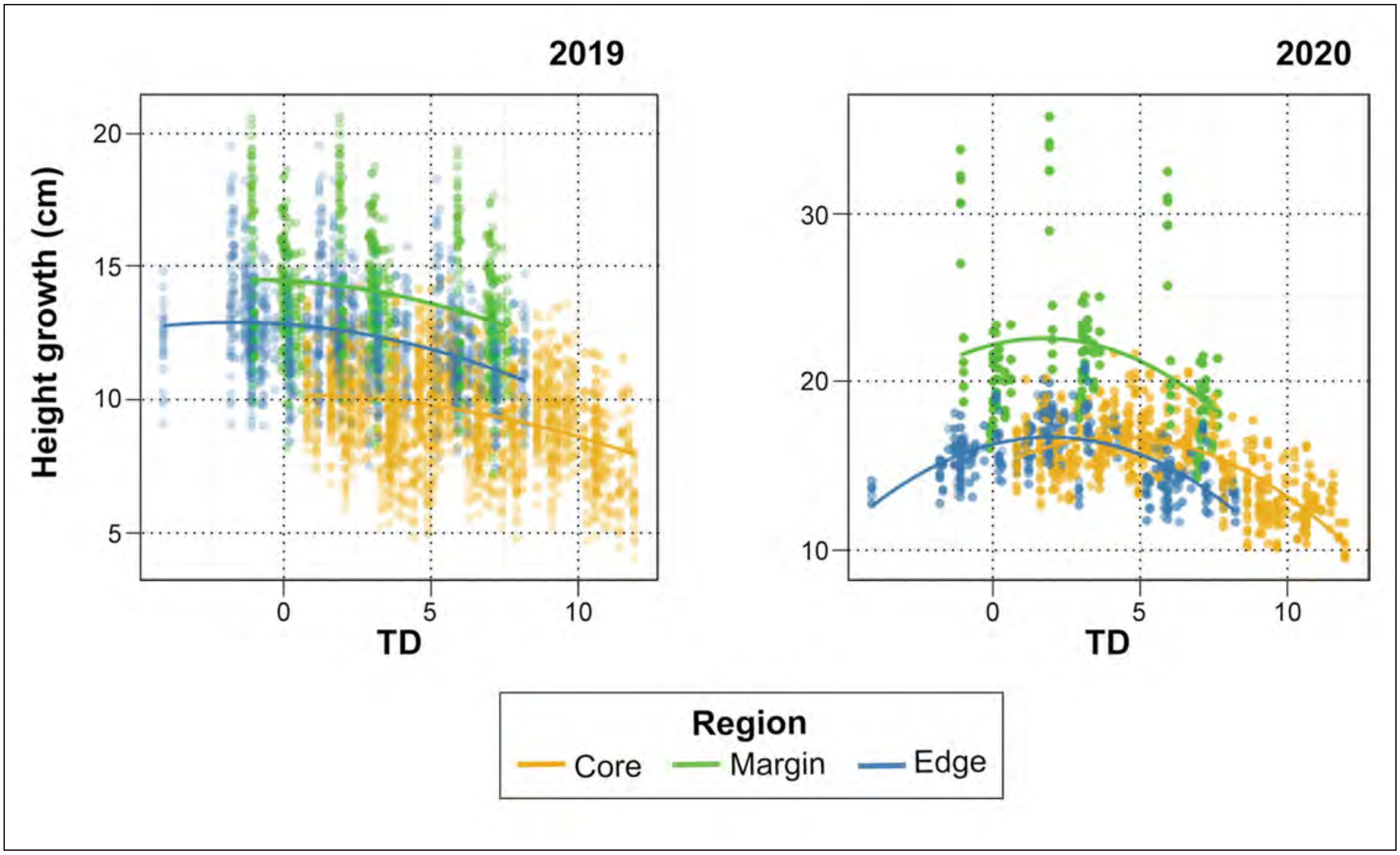

Figure 5. Red spruce seedling height growth after 1 year (2019) and 2 years (2020) post-planting into outdoor raised bed common gardens varied by climate transfer distance (TD = test site – source) based on mean annual temperature (˚C) and regional genetic ancestry groups (core, margin, and edge) assigned based on genomic data (see also figure 4). Height growth data were reanalyzed from Prakash et al. (2022).

including different aspects of seasonal temperature as well as precipitation and humidity-related variables, found a consistent reduction in seedling height growth with increasing transfer distance away from the source climate (Capblancq et al. 2023, Lachmuth et al. 2023).

The entire set of findings on red spruce transfer indicate that red spruce has a negative growth response to seed-transfer toward sites that are both warmer and drier (e.g., higher evaporative demand) than its source climate, and that simple proxies of temperature or geographic distance alone are likely insufficient to properly evaluate the transfer impact. If based solely on mean annual temperature, it appears that red spruce can tolerate, or even benefit from, moderate warming (figure 5) likely reflecting its sensitivity to frost damage (Li et al. 2020). Best practice would thus be seed-transfers into areas where current and future climate will most closely match the historic source climate, considering the combined effects of both growing season temperature and precipitation/humidity, while also being mindful to avoid risk of frost damage under colder transfers. This practice meshes well with dendrochronology studies in red spruce, which show an overall growth benefit from warmer winters (i.e., less cold damage) alongside negative growth impacts of warmer and drier conditions during the growing season (Kosiba et al. 2018, 2013; Yetter, et al. 2021). Ongoing work is aimed at integrating knowledge of local adaptation from quantitative genetics (St. Clair et al. 2022) and population genomics (Lachmuth et al. 2023a, Lachmuth et al. 2023b) into multivariate climate transfer models to help predict optimal seed sources and recipient sites for planting under current and future climate. These genetically informed approaches are under continued development and are available as online tools to provide an additional resource for making seed-transfer decisions (https://fitzlab.shinyapps.io/spruceApp/ and https://seedlotselectiontool.org/sst/).

Insects and Diseases

Red spruce is the target of a few pests but none that have achieved high levels of impact across broad landscapes. Perhaps the most damaging insect pest is the spruce budworm (*Choristoneura fumiferana* Clemens), a native insect that damages buds and current-year shoots of red spruce, especially when growing sympatrically with balsam fir. An important seed pest in some areas is the spruce coneworm (*Dioryctria reniculelloides* Mutuura & Munroe), whose larvae tunnel into developing seed cones and consume the seeds; this can sometimes have considerable local impact on the seed crop (figure 6). In some areas, yellow-headed spruce sawfly (*Pikonema alaskensis* Rohwer) larvae will feed on new needle growth and cause high impacts locally. The eastern spruce gall adelgid (*Adelges abietis* L.) is an introduced pest from Europe that primarily attacks Norway spruce but is occasional on red spruce, with its nymphs feeding at the base of current-year twigs and creating pineapple-shaped galls. The parasitic plant eastern dwarf mistletoe (*Arceuthobium pusillum* Peck) primarily infects black spruce but can also be common on white spruce and red spruce (in its northern range), producing the characteristic "witches' broom" growth form, reducing growth, increasing susceptibility to other stressors, and in some cases causing mortality (Baker et al. 2006).

Figure 6. These red spruce cones in northern Vermont show damage incurred by spruce cone worm *(Dioryctria reniculelloides*). Note the small entrance holes visible on the cones and the brown discoloration indicating seed predation. Photo by Stephen R. Keller, 2017.

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Summary for *Picea rubens*

Red spruce (*Picea rubens* Sarg.) is a cool, temperate zone conifer that is widespread in the Northeastern United States and Canada and associated with fragmented, high-elevation mountainous areas of the Central and Southern Appalachians. The species prefers cool, moist climates with moderate summer temperatures and low exposure to drought stress. Red spruce is sensitive to cold stress, especially during midwinter thaws followed by abrupt return to subfreezing conditions. The species has low genetic diversity for an outcrossing, wind-pollinated conifer. Genetic data show an ongoing decline in effective population size exacerbated by more recent impacts of logging, fire, and acid rain. Red spruce naturally hybridizes with black spruce (*P. mariana* [Mill.] Britton, Sterns, & Poggenburg), which may provide a source of adaptive variation when reproductive barriers are overcome. Ongoing research suggests red spruce is vulnerable to climate change, especially where habitat fragmentation constrains natural opportunities for dispersal. Trait and genomic-based analyses of climate adaptation offer guidance for seed-transfer and potential assisted migration within the species' range. Damage from insects and other pests is not widespread, but local outbreaks can cause damage to current-year growth and cone crops.

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

Red spruce (*Picea rubens*)	
Genetics	• Genetic diversity: low compared to other outcrossing conifers; long-term history of diversity decline • Genetic structure: three geographically distinct regions of genetic ancestry are the northern, midlatitude, and southern parts of the range; F_{ST} between regions = 0.02–0.03 • Gene flow: historically high within regions, though may be reduced due to habitat fragmentation and land use; gene flow between regions appears limited
Cone and seed traits	• Abundant cone crops every 3 to 8 years • Non-serotinous cones averaging 150,000 cleaned seeds/pound (330,000 seeds/kg) • Seeds disperse in late summer/early fall from cones produced that year • Seeds possess no physiological dormancy
Insect and disease	• Impacts on red spruce from insect pests and other diseases are generally low • Reductions in growth and vitality can arise during local outbreaks of spruce budworm, spruce coneworm, yellowheaded spruce sawfly, and eastern dwarf mistletoe • Eastern spruce gall adelgid is an introduced species that alters growth form of current year shoots
Palatability to browse	• Low; not a preferred browse by deer or moose
Maximum transfer distances	• Intermediate tolerance to seed-transfer (200–300 mi [322–483 km]) • Transfer to colder climates (more than 1.8 °F [2 °C] colder than the source) often results in cold damage and reduced growth • Transfer into warmer climates (5.4 to 9 °F [3 to 5 °C]) warmer than source) may be tolerable but must be evaluated with consideration to temperature seasonality (warmer winters may benefit red spruce while warmer summers do not) and transpirational demand • Southern range-edge populations may be at risk for extirpation due to climate conditions near current thresholds, low genetic diversity, and habitat fragmentation
Range-expansion potential	• Regional stands in New England, northern New York, and eastern Canada are likely to expand northward, but will still be constrained by long-range dispersal capacity • Opportunity for infilling in areas of former range where land-use change and other anthropogenic disturbances eliminated spruce during the last two centuries, especially at lower elevations • Regional populations in the mid-Atlantic and Central and Southern Appalachians have limited range-expansion potential due to fragmentation and lack of continuous suitable climate habitats

Jack pine tree. Photo by C. Pike, 2023.

Pinus banksiana
Jack Pine

Carolyn C. Pike

Introduction

Jack pine (*Pinus banksiana* Lamb.) grows across North America and is the most northerly occurring species of its genus, occurring predominantly in Canada. Its southern range edge dips into the Lake States (Michigan, Minnesota, and Wisconsin) with disjunct populations in parts of upstate New York, New Hampshire, and Maine. Modern jack pine populations in the Eastern United States are likely derived from at least three glacial refugia: one in the Appalachian Highlands (Yeatman 1967), a second in the Southeastern United States (Critchfield 1985), and a third along the Atlantic coast (Godbout et al. 2010).

Jack pine is shade intolerant (requires full sunlight), indeterminate (capable of producing additional flushes of vertical growth after budset if weather conditions permit), and regenerates best on bare mineral soil in pure or mixed stands. Young, dense stands are critical habitats for the Kirtland's warbler (*Setophaga kirtlandii* Baird), a rare bird that was recently removed from the endangered species list (Parham and Golder 2019). Jack pine is highly drought tolerant and can survive on sandy, nutrient-poor soils along the prairie edge (figure 1) and across boreal forests (figure 2). This resilience to xeric conditions may allow populations of this species in its southern range edge to persist as the climate warms (Prasad et al. 2020), but provenance (geographic origin) trials have revealed that optimal temperature regimes for its growth may shift northward as the climate warms (Thomson and Parker 2008).

Commercial products derived from jack pine include pulp, boards, shipping crates, and posts (Rudolf 1985). Jack pine is usually associated with even-aged stands but also occurs in stands with more age complexity along the southern range edge in Minnesota where cones are largely non-serotinous (Gill et al. 2015). Cones are generally closed (serotinous) across most of its range, but non-serotinous (open) cones are common along the southern range edge in Minnesota (Schoenike 1976). Jack pine is moderately palatable to browse by white-tailed deer (*Odocoileus virginianus* Zimmermann) and often requires protection during the winter months. Additional details about this species can be found online in the USDA Natural Resources Conservation Service plant guide (Moore and Walker Wilson 2006) and at the Climate Change Atlas (Peters et al. 2020). The Climate Change Atlas predicts a small decrease in the habitat suitability, but the species will likely be buffered by its abundance and inherent drought tolerance.

Genetics

Jack pine has high genetic diversity that is typical of other conifers but exhibits more population structure, phenotypically and genetically, than would be expected of a wind-pollinated tree (Cheliak et al. 1984, Godbout et al. 2010, Naydenov et al. 2005). Phenotypic differences among populations are manifest in traits such as cone serotiny and bark thickness and, to a lesser degree, in needle morphology and cone curvature (Schoenike 1976). Foliage of northern seed sources tends to turn purple or bronze during the winter months, whereas southerly sources remain predominantly green, a finding confirmed to have a genetic basis in common garden studies (Sprackling and Read 1974, Stoeckeler and Rudolf 1956, van Niejenhuis and Parker 1996). The adaptive value of winter foliage color is not known, but the visibility of this trait may serve as a physical indicator of seed origin for seedlings growing in nurseries (Stoeckeler and Rudolf 1956). Jack pine is capable of hybridizing with lodgepole pine; introgressed populations are widespread in Alberta and Northwest Territories in Canada (Wheeler and Guries 1987).

Genetic diversity in jack pine varies clinally across its range, but population substructure is evident from studies of neutral DNA (genes that are not associated with physical traits). In pines, chloroplasts are paternally

Figure 1. These young jack pine trees are growing on a xeric site in northwest Minnesota, the southwestern edge of jack pine's range. Photo by C. Pike, USDA Forest Service, 2008.

Figure 2. Jack pine is common in boreal forests where tree form is often tall and straight, as exhibited by this tree. Photo by C. Pike, USDA Forest Service, 2008.

inherited (via pollen). Chloroplast DNA and allozymes (proteins with enough natural variation that they can be used as genetic markers) revealed moderate levels of gene flow among jack pine populations in southern Ontario, Québec, and the Lake States (Godbout et al. 2010, Naydenov et al. 2005, Saenz-Romero et al. 2001, Xie and Knowles 1991). These results imply that pollen flows relatively unobstructed across populations. In contrast, mitochondrial DNA, which is maternally inherited, revealed pronounced separations among populations (Godbout et al. 2005, Godbout et al. 2010) implying that gene flow via seed is more restricted than that of pollen. The discrepancy in gene flow among populations between maternal and paternal sources of variation may be attributed, in part, to a lag time in seed dispersed from serotinous cones (Godbout et al. 2010, Ross and Hawkins 1986).

Fire has strongly influenced phenotypic and genetic variation of jack pine. This influence is especially evident in cone traits. Across its range, jack pine trees with serotinous cones are the predominant type, requiring high heat to open and release seeds (figure 3). Jack pine with non-serotinous cones that open and release seeds under ambient conditions are generally associated with southern range-edge populations in the Lake States and New England (Hyun 1977, Rudolf et al. 1959, Schoenike 1976). Tree crowns may bear cones of one type (all serotinous or all non-serotinous) or contain a mix of both types (Gauthier et al. 1992, Rudolf et al. 1959) (figure 4). Serotiny appears to be under strong genetic control, with relatively simple inheritance (Rudolf et al.1959), so this trait is likely to evolve rapidly to environmental change. The presence of non-serotinous cones in the south may be favored by natural selection in areas where fire is absent (Gauthier et al. 1996). Bark thickness, a trait that influences tolerance to ground-level fires, also tends to be thicker for jack pine growing in warmer, drier climates where fires are more commonplace than in mesic regions such as the Maritimes (Schoenike 1976). Phenotypic traits associated with needle, bark, branch angle, and cone traits vary clinally across the range suggesting that gene flow, for the most part, is high in jack pine (Schoenike 1976). In Minnesota, natural stands of jack pine exhibit a sharp cline with distinct boundaries approximately 65 mi (100 km) wide (Critchfield, 1985, Schoenike 1976) that do not coincide with other environmental gradients. Trees north of this line tend to have straight, closed cones while trees south of this line tend to exhibit curved cones that readily open and disperse seeds. This enigmatic population substructure has been attributed to different glacial refugia (Critchfield 1985), but underlying causes remain unresolved.

Figure 3. Serotinous (closed) cones, exhibited on this branch, are the most common type across most of jack pine's range. In addition, the cones are curled, as opposed to straight, a trait that also varies geographically but the adaptive value is unknown. Photo by C. Pike, USDA Forest Service, 2010.

Seed-Transfer Considerations

Jack pine has high genetic diversity but is more sensitive to seed-transfer than other conifers in the Eastern United States. In other words, long-distance transfer of jack pine seeds increases the likelihood of maladaptation compared with other conifers, such as white spruce (*Picea glauca* [Moench] Voss), where gene flow from seed and pollen are both relatively unobstructed. This sensitivity to transfer has been observed in common garden studies both in the United States (Lake States) and Canada (western Ontario) but was less obvious in Maine where jack pine sources from the Lake States performed above the mean (Carter and Canavera 1984). This finding, however, does not impose a blanket endorsement for seed-transfer from Lake States to New England; seed sources significantly interacted with sites increasing the risk of failure without a priori testing. Furthermore, evidence suggests that some jack pine populations in the Northeast belong to unique, local genetic lineages (Godbout et al. 2010) that merit preservation. Seed source by site interactions are significant for jack pine across the Lake States, implying the importance of using local, rather than distant, sources (Bloese and Keathley 1998, Jeffers and Jensen 1980, King 1965, Morgenstern and Teich 1969). A summary of considerations for moving jack pine seed is contained in table 1.

Jack pine is relatively sensitive to seed-transfer in the Lake States because of its heightened population structure. Seeds are not dispersed as ubiquitously as for other conifers, leading some populations to differentiate from others. Northern seed sources (relative to a common garden) were generally below the mean for tree height across the Lake States, Nebraska, Ontario, and Maine (Carter and Canavera 1984, Jeffers and Jensen 1980, Savva et al. 2007, Schantz-Hansen and Jensen 1952, Sprackling and Read 1974, Thomson and Parker 2008, van Niejenhuis and Parker 1996). Seed sources originating approximately 100 mi (160 km) to the south are generally the tallest in provenance trials in Ontario and the Lake States (Jeffers and Jensen 1980, Morgenstern and Teich 1969, Thomson and Parker 2008). Studies of diameter growth, as measured by tree rings, recommend similar transfer limits of 100 mi (160 km) (Savva et al. 2007) from southern to northern locales. Long-distance transfers (greater than 250 mi [400 km]) of jack pine seed sources should generally be avoided across the Northern United States.

For Lake States and Ontario seed sources, variability in jack pine provenance trials is more closely associated with temperature and photoperiod than with precipitation at the geographic origin (Matyas and Yeatman 1992). Specifically, jack pine growth is sensitive to mid-summer and winter temperatures (Thomson and Parker 2008, van Niejenhuis and Parker 1996) and, to a lesser degree, precipitation (van Niejenhuis and Parker 1996). Seed sources that are adapted to longer summer seasons may be genetically predisposed to late-season indeterminate growth, in which multiple flushes in a season are possible under the right conditions. Northern sources exhibit more conservative growth patterns than other sources in common garden experiments, presumably because they are genetically adapted to shorter growing seasons and colder mid-winter temperatures (Thomson and Parker 2008). Efforts to conserve southern range-edge populations are warranted as these populations are likely candidates for transfer to more northerly sites as the climate warms.

Insects and Diseases

Jack pine budworm (*Choristoneura pinus* Freeman) is the most important insect on mature stands of jack pine in the Lake States (McCullough et al. 1994, McCullough 2000). Minor pests include white pine weevil (*Pissodes strobi* Peck) and eastern pine shoot

Figure 4. Non-serotinous cones (foreground) and serotinous cones (background) can sometimes occur on a single tree. Photo by C. Pike, USDA Forest Service, 2010.

borer (*Eucosma gloriola* Heinrich), both of which damage or deform young trees, lowering future commercial value. Differences among seed sources for susceptibility to pine shoot borer were not significant in provenance trials (Hodson et al. 1982, King 1971). Pitch nodule maker (*Petrova albicapitana* Busck) is also a minor pest but may become problematic if outbreaks coincide with other pests (King 1971, McLeod and Tostowaryk 1971). Several sawfly species impact jack pine, including redheaded pine sawfly (*Neodiprion lecontei* Fitch) and jack pine sawfly (*Neodiprion Swainei* Midd.) (figure 5). Insects that feed on cones or seed can affect half or more of jack pine cones in a seed orchard (Rauf et al. 1985).

Several diseases affect jack pine across the Lake States. Two types of gall rusts occur in the Lake States and are largely allopatric: western gall rust (*Endocronartium harkensii* [J.P.Moore] Y. Hiratsuka) (Anderson 1970) and eastern gall rust (*Cronartium quercuum* [Berlc.] Miyabe ex Shirai) (Dietrich et al. 1985, Nighswander and Patton 1965) (figure 6). Eastern gall rust is more virulent and problematic on jack pine than western gall rust. The separation between their ranges is parallel to, and approximately 50 mi (80 km) west of, the divide between central and northern floristic regions in Minnesota (Aaseng et al. 2011). The northern edge of eastern gall rust corresponds with the same clinal break in jack pine illustrated in Schoenike (1976) and redrawn in Critchfield (1985). Susceptibility to eastern gall rust is strongly influenced by seed source: sources from northern Minnesota were significantly more susceptible at common gardens in lower Michigan and southern Wisconsin than local sources (King 1971). No other pests or insects studied demonstrated a similar association with latitude. Diplodia tip blight (*Diplodia sapinea* [Fries] Fuckel) has also become a major issue on young

Figure 5. Sawfly larvae can defoliate large swaths of jack pine. Photo by J. Warren, USDA Forest Service, 2011.

Figure 6. Eastern gall rust is a devastating pathogen on jack pine in the Lake States. The globose galls (shown) can lead to windthrow and may dominate the canopy of highly susceptible trees. Photo by C. Pike, USDA Forest Service, 2008.

jack pine seedlings in the Lake States (Nicholls 1990, Stanosz et al. 2007). Needle cast, caused by *Hypodermella ampla* (Davis) Dearn has been reported in provenance trials (King and Nienstaedt 1965), but differences were not attributable to geographic origin of seed sources and this disease has not been problematic in recent years.

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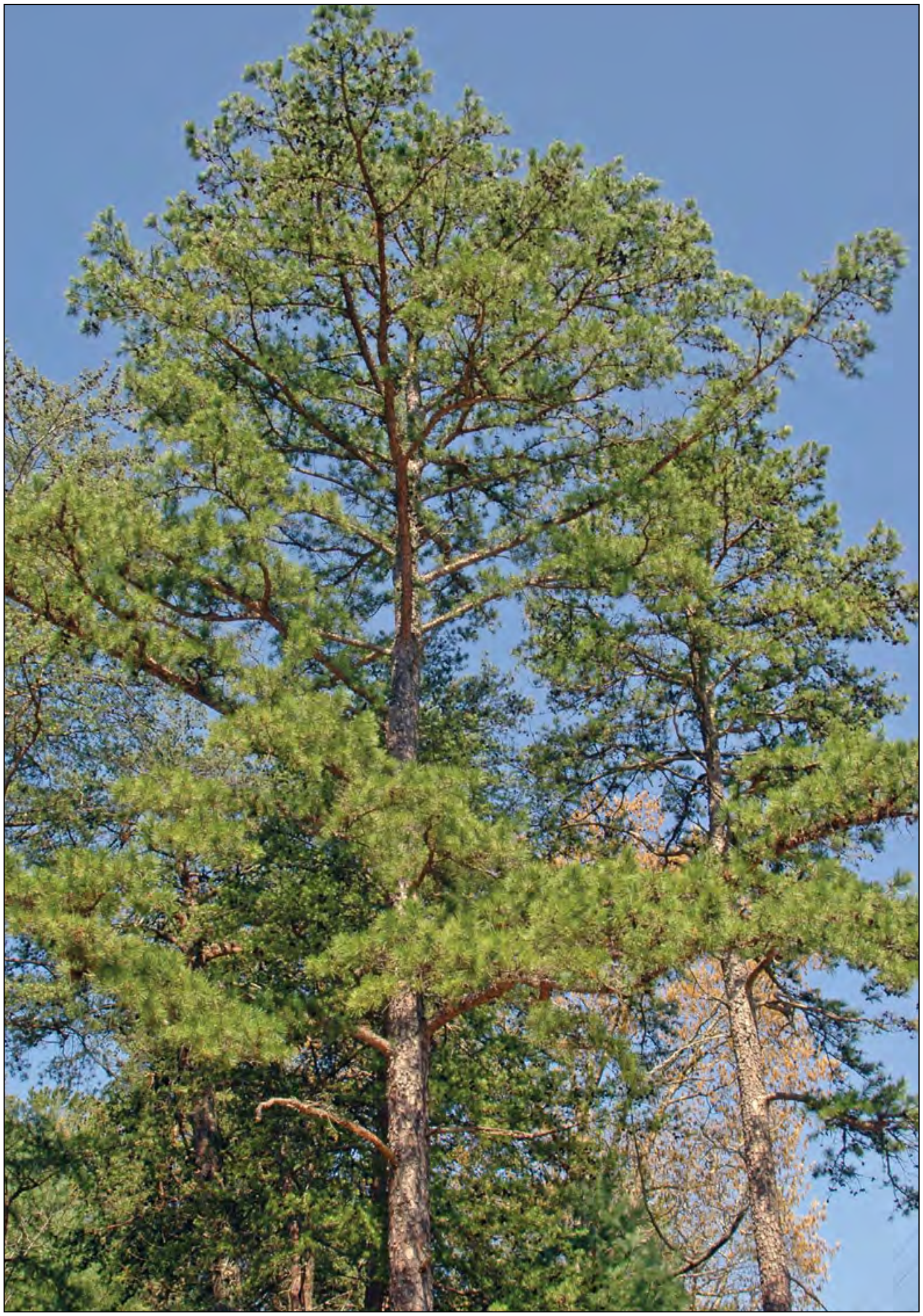
Summary for *Pinus banksiana*

Jack pine (*Pinus banksiana* Lamb.) grows in boreal forests across the North American continent. Genetic diversity of this species is high and clinal, but populations exhibit genetic structure that is higher than other conifers with similar life history traits. Cones are serotinous across most of its range but may be non-serotinous along the southern edge in the Lake States. The serotinous habit may limit seed dispersal and is likely the primary contributor to the genetic structure apparent in studies of mitochondrial DNA. Jack pines originating from southern sources tend to outgrow local or northern sources. Jack pine is likely to persist with climate change in its current range because of its tolerance to xeric conditions. Assisted migration should be well-tolerated by planting seed originating from 100 mi (160 km) to the south, but managers should avoid transferring seed more than 100 miles from origin and be aware of potential pests, including jack pine budworm and eastern gall rust.

Table 1. Summary of considerations for moving jack pine seed.

Jack pine (*Pinus banksiana*)	
Genetics	• Genetic diversity: high • Gene flow: high (pollen); medium (seed)
Cone and seed traits	• Small, winged seeds, 131,000 seeds per pound (288,200 per kg) • Cones may be serotinous or non-serotinous • Seed is released in late summer to early fall
Insect and disease	• Jack pine budworm, sawfly • Eastern gall rust, western gall rust, Diplodia (young seedlings)
Palatability to browse	• Moderate to high browsing from white-tailed deer in the winter months
Maximum transfer distances	• Sensitive to seed-transfer in the Eastern United States • Seed sources originating 70 to 140 miles south of the planting site (112 to 160 km; 1° to 2° latitude) display higher growth rates than local sources but latitudinal distances greater than 200 miles should not be exceeded
Range-expansion potential	• Likely to shift northward into Canada but southern range edge may persist in the United States due to its drought tolerance



Shortleaf pine tree. Photo by Chris Evans, University of Illinois.

Pinus echinata
Shortleaf Pine

Carolyn C. Pike and C. Dana Nelson

Introduction

Shortleaf pine (*Pinus echinata* Mill.) is a long-lived, shade-intolerant conifer that grows on relatively dry, infertile sites across the Southern United States. It has the largest range of any southern pine, growing across 22 States and as far north as New York's Long Island (Lawson 1990). Shortleaf pine may occur as pure stands (figure 1) or as a component of pine/oak and loblolly/shortleaf pine forests (Lawson 1990), driven in large part by past disturbance regimes (Guyette et al. 2007). Sharp declines in abundance over the last 50 years are attributed to a combination of overharvesting, fire suppression, and stand replacement by loblolly pine (*Pinus taeda* L.), which is a preferred commercial species (McWilliams et al. 1986). Shortleaf pine wood is relatively dense and is used for building construction, railroad ties, and plywood (Alden 1997). In pine/oak stands, shortleaf pine is sympatric with black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), and hickory (*Carya* spp.), but it may be out competed in the absence of disturbances that increase available light (Stambaugh et al. 2002) or bare mineral

Figure 1. Shortleaf pine is commonly associated with oaks (*Quercus* spp.), seen in the foreground, since both require high light environments and similar temperature and moisture regimes. Photo by C. Pike, USDA Forest Service, 2019.

soil for natural regeneration (Guyette et al. 2007). Efforts to reduce competition are often required if hardwoods are dominant in the understory (figure 2). Low recruitment, along with the decline in abundance, has led to increased restoration and tree planting efforts (figure 3) such as the Shortleaf Pine Initiative (https://shortleafpine.org). Compared with other southern pines, shortleaf pine is slower growing in its early years, but is relatively cold tolerant and fusiform rust resistant. Cold injury may appear as winter burn on needles and frost heave (Pickens and Crate 2018).

Shortleaf pine is moderately fire tolerant because of its thick, platy bark and its ability to resprout after low- to moderate-intensity fires (figure 4). Mature stands can tolerate exceptionally hot fires if crowns are not burned (figure 5). The presence of a basal crook at the root collar protects dormant buds during fires, allowing the species to resprout (Bradley et al. 2016, Lilly et al. 2012, Little and Somes 1956, Stewart et al. 2015) (figure 6). This characteristic is absent in loblolly pine and loblolly-shortleaf pine hybrids. In addition, shortleaf pine may allocate more resources to coarse roots than stem mass compared with loblolly pine (Bradley and Will 2017), which may enhance its drought tolerance. High drought and fire tolerance contribute to its likely persistence in a drier and warmer future climate (Peters et al. 2020). Warmer temperatures in the winter months, as has been observed in the Ozarks (Stambaugh and Guyette 2004), may confer a competitive advantage to shortleaf pine because photosynthesis can take place while competing hardwoods are dormant (Guyette et al. 2007). Shortleaf pine regenerates from seed if conditions, such as bare mineral soil created through fire or scarification, prevail during seed crops (Yocom and Lawson 1977).

Genetics

Shortleaf pine is a monoecious diploid with wind-dispersed pollen and cones requiring 2 years to mature (figure 7). Trees do not produce seed until 5 to 20 years of age, which can hinder natural regeneration (Krugman and Jenkinson 2008). Seed is typically released from cone bracts in October and November. Hybridization with loblolly pine, with which it is sympatric across much of its range, is a concern because of potential losses to the genetic integrity of naturally regenerating forests or seed orchards (Stewart et al. 2010, Stewart et al.

Figure 2. Competition, especially from hardwoods, should be managed to facilitate regeneration of shortleaf pine, which is otherwise shade intolerant. In this photo, goats were brought in to help control competing vegetation from hardwood trees and shrubs. Photo by C. Pike, USDA Forest Service, 2019.

Figure 3. Restoration with tree planting is necessary to restore shortleaf pine in stands that have converted to hardwoods or other vegetation. Trees growing in this container will be outplanted in a few months. Photo by C. Pike, USDA Forest Service, 2018.

Figure 4. The lower boles of shortleaf pine trees have very thick, platy bark that can survive low- to moderate-intensity wildfires. Photo by C. Pike, USDA Forest Service, 2019.

Figure 6. Shortleaf pine seedlings form a basal crook that is an adaptive trait to protect against fire damage. Photo courtesy of Southern Regional Extension Forestry.

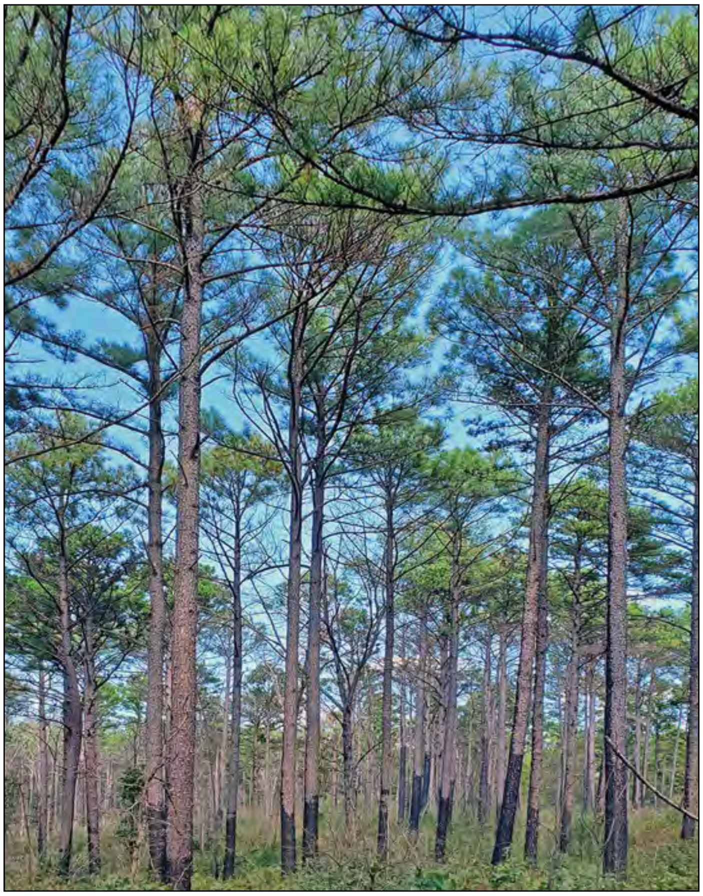


Figure 5. This stand sustained an extremely hot fire that destroyed most of the understory, while the mature shortleaf pines survived. Photo by C. Pike, USDA Forest Service, 2019.

2013, Tauer et al. 2012;). Regular burn return intervals of 3 years or less can effectively select against hybrids and loblolly pine in mixed-species stands (Stewart et al. 2015). Additional genetics research to improve marker-based identification of hybrids is needed to identify and remove advanced-generation hybrids from established seed orchards and restoration seed reserves (Stewart et al. 2016). The proportion of hybrids recruiting into regenerating stands is likely to increase with continued fire suppression (Stewart et al. 2015, Tauer et al. 2012). Climate change may also increase hybridization if phenology of flower production in loblolly and shortleaf pines becomes more synchronized (Tauer et al. 2012).

In the Missouri Ozarks, genetic variation is high with little divergence among populations sampled and no evidence of a prior genetic bottleneck (Hendrickson et al. 2018). Stewart et al. (2016) summarized prior work on isozymes and DNA markers that all describe the species as highly outcrossing with little genetic structure, increased differentiation between sources west and east of the Mississippi River, and high genetic diversity throughout the range. Hybrids with loblolly pine were more common in the western part of the range than east of the Mississippi River (Edwards and Hamrick 1995, Stewart et al. 2010), although

Figure 7. Shortleaf pine cones open to release seed with or without fire. Photo by C. Pike, USDA Forest Service, 2019.

genetic diversity between east and west were similar. Genetic improvement in shortleaf pine is promising (Gwaze et al. 2005a, 2005b), and seed orchards with improved seed are in use (Hossain et al. 2021).

Seed-Transfer Considerations

In southern Illinois, shortleaf pine sources from Ohio, Mississippi, Missouri, Arkansas, Oklahoma, and Kentucky were similar in height, diameter, and survival after 27 years (Gilmore and Funk 1976). In New Jersey, local sources had the highest survival followed by those from northeast Tennessee and Missouri, which were 8 to 10 ft (2.4 to 3.6 m) shorter than the New Jersey source (Little 1969, Wells and Wakeley 1970). Local sources were also best in Pennsylvania, but Tennessee sources were similar, followed by sources from Oklahoma and Georgia (Little 1969). Little (1969) attributed losses in survival and basal area in New Jersey and Pennsylvania sites to winter injury.

In southern range locations (Mississippi, southeast Louisiana, and southwest Georgia) southernmost sources were considerably taller than more northern sources (Wells and Wakeley 1970). Progeny tests in Arkansas revealed that shortleaf pine sources from the Ouachita National Forest had better growth than northerly sources from the Ozark National Forest (Hossain et al. 2021, Studyvin and Gwaze 2012). The same studies showed that eastern and western sources within the Ouachita National Forest did not differ significantly. North-south trends are complicated by the presence of loblolly pine hybrids in the south, which can alter the phenotype (Wells and Wakeley 1970). Local sources are best suited for areas along the northern range edge (Wells and Wakeley 1970). Seed sources originating from 5 ° to 7 °F (2.8 to 3.9 °C) warmer average annual minimum temperature have the fastest growth without sacrificing cold tolerance (Schmidtling 1994, 2001).

Insects and Diseases

Shortleaf pine is highly susceptible to southern pine beetle (*Dendroctonus frontalis* Zimmermann) and its fungal associate, *Ceratocystis minor* (Hedgecock) Hunt (Cook and Hain 1987). Southern pine beetle continues to expand its range northward and is likely to remain an impediment to southern pines into the future (Lesk et al. 2017). Cone and seed insects are often major pests in shortleaf pine seed orchards, including Nantucket pine tip moth (*Rhyacionia frustrana* Comstock), which infests conelets (Yates and Ebel 1972). The insect species *Dioryctria amatella* Hulst and *Eucosma cocana* Kearfott cause seed loss on second-year cones (Ebel and Yates 1974). Other insects associated with seed losses included seedbugs such as *Leptoglossus corculus* Say and *Tetyra bipunctata* Herrich-Schaeffer and the seed worm *Laspeyresia* spp. Sawflies (*Neodiprion* spp.) can also damage female strobili (Bramlett and Hutchinson 1965). Pales (*Hylobius pales* Herbst) and eastern pine weevil (*Pissodes nemorensis* Germar) are known to feed on bark tissue of young, vigorous seedlings (Land and Rieske 2006).

Shortleaf pine is relatively resistant to fusiform rust, (*Cronartium quercuum* f. sp. *fusiforme*) (Powers et al. 1981), the most economically important pathogen of southern pines. Root rot pathogens associated with shortleaf pine include littleleaf disease (*Phytophthora cinnamomi* Mistretta and annosus root disease (*Heterobasidion annosum* [Fr.] Bref. formerly known as *Fomes annosus*) (Berry 1968). Annosus root disease can spread onto freshly cut stumps, usually after thinning, infecting the stand for 50 years or more. Shortleaf pine can also be a host to comandra blister rust (*Cronartium comandrae* Pk.), although this pathogen is more common in the Western United States (Johnson 1997).

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Summary for *Pinus echinata*

Shortleaf pine (*Pinus echinata* Mill.) is a shade-intolerant conifer tree native to forests across southeastern and east-central North America. Shortleaf pine has declined sharply in abundance due to species conversion, absence of fire, and competition with encroaching broadleaf trees. Genetic diversity of the species is high due to high seed dispersal and pollen flow levels and low population structure. Shortleaf pine can hybridize with loblolly pine (*Pinus taeda* L.), which could accelerate if climatic shifts increasingly synchronize pollen flow and receptivity of the two species. Fire is an important component of shortleaf pine forests to reduce competition and eliminate hybridization with loblolly pine. Local seed sources are generally best in far northern and southern locales. In central and northern locales, transfer from sites that are warmer by 7 and 5 °F (4 and 3 °C) average annual minimum temperature, respectively, may have increased growth relative to local sources. Shortleaf pine is highly susceptible to southern pine beetle but is relatively resistant to fusiform rust disease. Shortleaf pine is likely to persist, or expand northward, in the future because of its high tolerance to drought and fire.

Table 1. Summary of silvics, biology, and transfer considerations for shortleaf pine.

	Shortleaf pine (*Pinus echinata*)
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• • 32–73 cleaned seeds per pound (71–161 per kg) (Krugman & Jenkinson 2008)
Insect and disease	• Southern pine beetle • Pales and eastern tip weevil • Various cone and seed insects
Palatability to browse	• Few browse issues in its current range • Northward movement to areas with different herbivores may alter its susceptibility
Maximum transfer distances	• Shortleaf pine has intermediate tolerance to seed-transfer (200–300 mi [322–483 km]) • In northern locations, local sources are best, but consider conservative application of the general rule (using seed from up to 5 °F (3 °C) warmer average annual minimum temperature • In central locations sources should be moved northward no more than 7 °F (4 °C) average annual minimum temperature • In southern locations, it is best to use local seed zones latitudinally and conservatively diversify longitudinally
Range-expansion potential	• Shortleaf pine is a good candidate for northward expansion due to drought tolerance, but insects may become problematic

Longleaf pine. Photo by David Stephens.

Pinus palustris
Longleaf Pine

Carolyn C. Pike and C. Dana Nelson

Introduction

Longleaf pine (*Pinus palustris* Mill.) is a long-lived, shade-intolerant, drought-tolerant, fire-dependent conifer species that is native across the southern portion of the Southeastern United States. Longleaf pine grows on sites ranging from poorly drained lowlands to low mountain ridges up to 2,000 ft (600 m) (Maceina et al. 2000). The species is known for its long needles (figure 1), relatively large cones and seeds, and "grass stage" juvenile growth habit. Longleaf pine ecosystems may have once occurred on 60 million acres (24 million hectares) across the Southern United States (Boyer 1990). Today approximately 3.5 million acres (1.4 million ha) of longleaf pine ecosystems remain (Kelly and Bechtold 1989), with the majority in a less than desirable state. This reduction is due to fire suppression and land conversion to nonforests or more commercially favorable pine species, such as loblolly pine (*P. taeda* L.). Longleaf pine ecosystems were considered among the most endangered in the United States (Noss et al. 1995), but recent surveys report increases in the larger (≥10 in [25 cm]) diameter size classes, reversing the previously observed decreasing trend (Oswalt and Guldin 2021).

Longleaf pine is most typically associated with sandy, acidic, infertile soils at low elevation, below 660 ft (200 m), often growing alongside other southern pines (i.e., shortleaf pine [*Pinus echinata* Mill.], slash pine [*Pinus elliottii* Engelm.], and loblolly pine). A complex, diverse, herbaceous community is associated with, and sometimes endemic to, longleaf pine ecosystems in both montane (Maceina et al. 2000, Varner et al. 2003) and low-elevation forests (Brockaway et al. 2005). Frequent fires associated with longleaf pine ecosystems sustain understory plant communities and reduce competition from xeric hardwoods (Ford et al. 2010, Maceina et al. 2000). The complexity of understory communities is determined largely by the severity and frequency of fire (Boyer 1990, Stokes et al. 2010) with wiregrass (*Aristida strictais* Michx.) as a common associate of these ecosystems (Noss 1988). Seed germination is best on bare mineral soil, which favors the likelihood that the seedling's root collar is positioned at or below the soil level to protect from future fire (Jin et al. 2019) and drought (Wilson et al. 2022).

Figure 1. Longleaf pine has exceptionally long needles. This planted seedling has recently emerged from the grass stage. Photo by K. Dumroese, USDA Forest Service, 2009.

Longleaf pine timber is relatively heavy and strong compared with other pines, with a straight grain that is desirable for the forest products industry (Alden 1997). The species is significantly more windfirm than other southern pines (Johnsen et al. 2010), and its timber is especially important for utility poles (The Longleaf Alliance 2011). Pine straw derived from longleaf pine needles is commercially valued for landscaping (The Longleaf Alliance 2011).

Extensive conservation efforts by States and partners, notably The Longleaf Alliance (https://longleafalliance.org) and America's Longleaf (https://americaslongleaf.org), have continued to advance regeneration and restoration of longleaf pine ecosystems (Brockaway et al. 2006, Guldin et al. 2015). Containerized seedlings are preferred for restoration plantings because of substantial improvements in survival over bareroot stock types (Cram et al. 2010) (figure 2). Studies on container size and nitrogen regime during nursery culture have generated specifications for quality stock (Davis et al. 2011, Jackson et al. 2012).

While in the "grass stage," longleaf pine seedlings do not grow in height, a feature that is not shared with the other southern pines (figure 3). During this development phase, which can last from 2 to 5 years or more (Boyer 1990), carbon is primarily allocated to the root system, including a characteristically large tap root. Seedlings typically emerge from the grass stage when the root collar diameter reaches 1 in (2.5 cm) (Haywood et al. 2011, Knapp et al. 2018, Wahlenberg 1946). Grass stage seedlings with good root collar diameter and position (relative to the ground line) can survive most prescribed fires depending on a variety of site conditions and fire parameters (Jin et al. 2019, Knapp et al. 2018, Pile et al. 2017). The delayed height growth relative to other southern pines (Hooker et al. 2021) can complicate their use in plantation forestry, although the volume differences may decline or disappear in mature stands (Cram et al. 2010). Efforts to shorten this stage through silviculture and genetics have been studied (Nelson et al. 2003) but reduced belowground carbon allocation may be an undesirable tradeoff (Aubrey 2022).

Figure 2. Longleaf pine containerized stock is generally more successful in planting than bareroot stock. Photo by C. Pike, USDA Forest Service, 2018.

Longleaf pine had at least one glacial refugia in southern Texas and northern Mexico (Schmidtling and Hipkins 1998), with a second refugia likely in Florida, the Caribbean, or both (Schmidtling 1999). Longleaf pine is forecast to do moderately well as the climate warms because of its tolerance to fire and drought (Wilson et al. 2022), but its shade intolerance will deter its establishment and survival in areas with encroaching hardwoods (Peters et al. 2020).

Genetics

Longleaf pine is a monoecious and diploid species with high genetic variation, in part due to its wind pollination and ample seed dispersal (Grace et al. 2004). Opportunities for tree improvement are high

Figure 3. Longleaf pine seedlings remain in the grass stage for 2 to 5 or more years depending on site conditions. Photo by C. Pike, USDA Forest Service, 2018.

for longleaf pine due to its prolific genetic variation and high-quality timber that are valued and supported by the timber industry (Samuelson et al. 2018, Schmidtling and White 1990). Seed orchards are commonly used for supplying seed for seedling production in nurseries (figure 4). Assessments of carbon isotopes δ13C, as a proxy for water use efficiency, among provenances and full-sib families demonstrates the potential to further improve drought tolerance through selection and breeding (Castillo et al. 2018, Samuelson et al. 2018). Similar to other pine species, most genetic variation occurs within populations relative to among populations as determined with allozyme (Hamrick et al. 1993) and microsatellite markers (Crane et al. 2019, Echt and Josserand 2018). Low allozyme-based F_{ST} values of 0.041 indicate that populations are not strongly differentiated (Schmidtling and Hipkins 1998).

Longleaf pine has relatively large seeds compared to other southern pines that are wind-dispersed (figure 5). The species naturally hybridizes with loblolly pine but is not likely to naturally hybridize with slash pine due to large phenological differences. Longleaf pine is not known to hybridize with shortleaf pine. The hybrid with loblolly pine is known as Sonderegger pine (*P. x sondereggeri* H. H. Chapm.) and has relatively fast early height growth compared with longleaf pine, but survival may be lower compared with loblolly pine (Schoenike et al. 1975). Seedlings that grow in height in nurseries (i.e., lacking a grass stage) are likely to be Sonderegger pines and are typically culled prior to outplanting (Schmidtling 1999).

Seed-Transfer Considerations

Seed-transfer recommendations are based largely on plant hardiness zones, or the minimum temperatures for a locale as discussed in Schmidtling (2001) and Schmidtling and Sluder (1995). In general, seedlings can be planted at locations with 5 °F (2.8 °C) lower average annual minimum temperature. This transfer distance is consistent with Wells and Wakeley (1970), who found that seeds from 150 mi (241 km) south are generally favored for planting because their growth exceeds local sources, except in northern locales where local sources may grow better. Longitudinal differences among populations (east to west) are minimal (Schmidtling 1999, 2001; Schmidtling and Hipkins 1998).

The understory plants of longleaf pine ecosystems are critical components for successful restoration of the ecosystem, including little bluestem (*Schizachyrium scoparium* [Michx.] Nash) and hairy lespedeza (*Lespedeza hirta* [L.] Hornem.) (Gustafson et al. 2018). A common garden study of six understory plant species showed that longitudinal transfer distances of 93 to 310 mi (150 to 500 km) and latitudinal transfer distances of 150 to 248 mi (150 to 400 km) were optimal (Giencke et al. 2018).

Insects and Diseases

Longleaf pine is generally less susceptible to major pests and pathogens than other southern pines, but forest pests may be less well understood in longleaf pine ecosystems and could become problematic as

Figure 4. Seed orchards are used for collecting much of the seed used for longleaf pine tree planting. Photo by C. Pike, USDA Forest Service, 2016.

Figure 5. Longleaf pine seeds are relatively large compared with other southern pines. Photo by V. Vankus, USDA Forest Service, 2023.

restoration efforts increase (Barnard and Mayfield 2009). Relative to the other southern pines, longleaf pine is less susceptible to the southern pine beetle (*Dendroctonus frontalis* Zimmermann), apparently due to its strong response to insect feeding with high resin production (Hodges et al. 1979). More recent work has suggested two alternative hypotheses relative to loblolly pine: (1) longleaf pine may have coevolved more closely with the southern pine beetle, or (2) the spatial scale of longleaf pine occurrence may play a role in reducing the impact of southern pine beetles (Martinson et al. 2007).

Brown spot needle blight, caused by the ascomycete *Lecanosticta acicola* (Thümen) A. Sydow., is the most important disease of longleaf pine, especially impacting seedlings in the grass stage (van der Nest et al. 2019). Genetic trials have shown that resistance to brown spot needle blight is heritable and could be improved by selection and breeding (Gwaze et al. 2002, Lott et al. 2011, Nelson et al. 2005). Although fusiform rust does infect longleaf pine, the species is not considered to be susceptible as infection and tree damage levels are typically quite low relative to susceptible species such as loblolly and slash pines.

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Summary for *Pinus palustris*

Longleaf pine (*Pinus palustris* Mill.) is a shade-intolerant conifer tree that occurs across the Southern United States from southeast Texas in the west to southeast Virginia in the east. The species and its associated ecosystem have declined sharply over the last several decades due to absence of fire and replacement with southern pines that have faster growth and higher reproductive potential. Genetic diversity of longleaf pine is high and population structure is low, with very little geographic-based differentiation. Seeds can be moved from a warmer to a colder hardiness zone (up to 5 °F [2.8 °C] lower average annual minimum temperature) to increase growth relative to local sources. Brown spot needle blight is the most damaging disease of longleaf pine, contributing to seedling mortality in some cases. Damage from fusiform rust and southern pine beetle are generally minor compared with damage to loblolly pine (*P. taeda* L.), a common associated species. In the future, longleaf pine is likely to increase within its current range because of its tolerance to fire, drought, and wind and the increasing restoration planting efforts, but shade intolerance will hamper its success on stands with moderate to heavy hardwood competition.

Table 1. Summary of silvics, biology, and transfer considerations for longleaf pine.

	Longleaf pine (*Pinus palustris*)
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• 4,900 seeds per pound (10,800 per kg) (Krugman and Jenkinson 2008) rees do not typically bear seeds until >20 years old • Good cone crops occur every 5 to 7 years (Krugman and Jenkinson 2008)
Insect and disease	• Southern pine beetle • Brown spot needle blight
Palatability to browse	• Browse is rarely reported in longleaf pine
Maximum transfer distances	• Tolerant of long-distance transfer, with distances >300 mi (483 km) well tolerated in many cases • Movement to cooler plant hardiness zone (5 °F [2.8 °C] lower average annual minimum temperature) is typically practiced; with added risk, movement up to 10 °F (5.6 °C) may be tolerated • No east-west transfer limits are designated
Range-expansion potential	• Longleaf pine is expected to be generally favored in a warming climate because of its adaptability to fire

Red pine tree. Photo by C. Pike, 2014.

Pinus resinosa
Red Pine

Nicholas LaBonte

Introduction

Red pine (*Pinus resinosa* Ait.) is a long-lived conifer that occurs naturally on well-drained sites in a relatively narrow band in eastern North America, including the northern Great Lakes region, the St. Lawrence River Valley, and the extreme northern Appalachians in the Northeastern United States and Maritime Canada. In natural settings, red pine may form single-species stands or occur in mixed-pine forests with eastern white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), or both. Most natural red pine stands occur on dry (but not excessively so) sites with coarse-textured soil (Hauser 2008). In the upper Great Lakes region, stands dominated by natural-origin red pine may be extensive and are often associated with sandy ridges and banks near lakes and swamps. In the Northeast, red pine typically occurs as small stands on favorable sites while at its southern range edge in southwestern Wisconsin, Pennsylvania, and West Virginia, it is limited to small, exposed areas on rocky cliffs (Stephenson et al. 1986) (figure 1). Most original red pine stands were removed by logging in the late 19th and early 20th century. Red pine is one of the most widely planted tree species in the Great Lakes region of the United States and may be found in single-species planted stands on a wide range of sites (figure 2).

Natural regeneration of red pine is governed by its intolerance of shade and its seedlings' preference for bare mineral soil or mineral soil with a thin moss or litter layer (Rudolf 1990). Fire played a major role in determining red pine's distribution and persistence historically. Mature red pines are more fire-tolerant than jack pine or white pine (Hauser 2008), but its cones are not serotinous and seeds are destroyed by intense fire. Based on dendrochronology and analysis of fire scars (figure 3), most extant old-growth red pine stands are dominated by one or two age cohorts. Fires severe enough to remove some canopy trees, but not severe enough to eliminate local red pine seed sources, were probably involved in the origin of natural stands historically (Fraver and Palik 2012) while less severe, more frequent ground fires reduced hardwood competitors. Red pine is restricted to the least fire-prone sites in the boreal forest of Québec, where crown fires are relatively frequent (Flannigan and Bergeron 1998).

Figure 1. These mature red pines near the southwestern edge of the species' native range in Wisconsin are growing with oaks and white pine on a steep, sandy slope with exposed sandstone (visible at upper left). Photo by N. LaBonte, USDA Forest Service, 2021.

Red pine seedling establishment is most likely to occur several years after a canopy-clearing fire, after the ash layer has broken down, and in conjunction with a large cone crop, which occur at 3- to 7-year intervals (Ahlgren 1976). Seedlings grow slowly following germination, but growth increases after 4 or 5 years (Rudolf 1990). Due to slow initial growth and shade intolerance, germinating red pine seedlings are not competitive with hardwood sprouts, seedlings, or shrubs, such as hazel (*Corylus* sp.). Planted red pine seedlings are more competitive than naturally regenerated seedlings, but site preparation may still be necessary to remove competition. Red pine may be browsed occasionally but is not considered a preferred species of deer in most of its range.

Figure 2. This range-wide red pine provenance trial in Minnesota is one of a series established to study genetic variation in the species. Photo by J. Warren, USDA Forest Service, 2004.

Figure 3. This old red pine growing in a mixed pine/oak forest in Wisconsin has a substantial upslope fire scar. The thick bark of red pine allows mature trees to survive low-intensity fire. Fire is a key part of the natural red pine regeneration process and is important for maintenance of mature red pine stands. A ground layer of *Vaccinium* spp. is frequently found in naturally occurring red pine stands. Photo by N. LaBonte, USDA Forest Service, 2021.

Genetics

Red pine is not closely related to any other continental North American pine species and does not naturally form hybrids with its closest relatives, Eurasian hard pines such as European black pine (*Pinus nigra* Arnold). Like other Great Lakes forest tree species, red pine migrated southwards during the last glacial maximum and occupied the southernmost Appalachian uplands in Georgia (Rudolf 1990, Walter and Epperson 2005). Chloroplast DNA evidence suggests that a second refugial population of red pine existed on now-submerged land off the coast of northeastern North America (Walter and Epperson 2005). The main landscape-scale genetic distinction in red pine is between the large western population, which has a single chloroplast haplotype, and the more diverse, but smaller, eastern population. This division is notable in both chloroplast (Walter and Epperson 2005) and nuclear (Boys et al. 2005) DNA markers.

Red pine is characterized by remarkably low genetic variation, genetic diversity, and heterozygosity based on markers from the nuclear genome. Early studies (e.g., Fowler and Morris 1977) failed to identify variation in large samples of red pine using protein-based isozyme markers. Later studies identified relatively small amounts of variation at microsatellite DNA markers (e.g., Boys et al. 2005). Red pine is monoecious (figure 4) and self-compatible. Unlike most forest trees, however, red pine seeds resulting from self-pollination show little evidence of inbreeding depression (Fowler 1964), which may indicate that many generations of inbreeding have "purged" deleterious alleles from the genome. Despite red pine's large population, long lifespan, and wind-pollinated habit, genetic differentiation at molecular markers among natural populations is much higher than in other conifers ($F_{ST} \sim 0.25$, Boys et al. 2005), likely due to facultative self-pollination. The unusually low genetic diversity of red pine is not a result of its heavy exploitation for timber; the population bottleneck likely involved a long-term reduction in population size (Fowler and Morris 1977) dating back to the last glacial maximum. Red pine's low genetic diversity is not shared by its closest extant relative, European black pine, although a study of trees from isolated stands in Spain and Morocco found high differentiation between the two regions (Rubio-Moraga et al. 2012). Given that no comparable barriers to gene flow exist within the native range of red pine, a tendency to produce offspring by self-pollination may be the reason red pine populations are so strongly differentiated.

Seed-Transfer Considerations

Studies that measured performance of red pine seed sources did not find strong relationships between movement distance and performance, but sources from the Northeastern United States (New England States) consistently underperform compared with Great Lakes sources (e.g., Wright et al. 1972). Variation among provenances tends to be small if significant (Lester and Barr 1965), and the same sources tend to

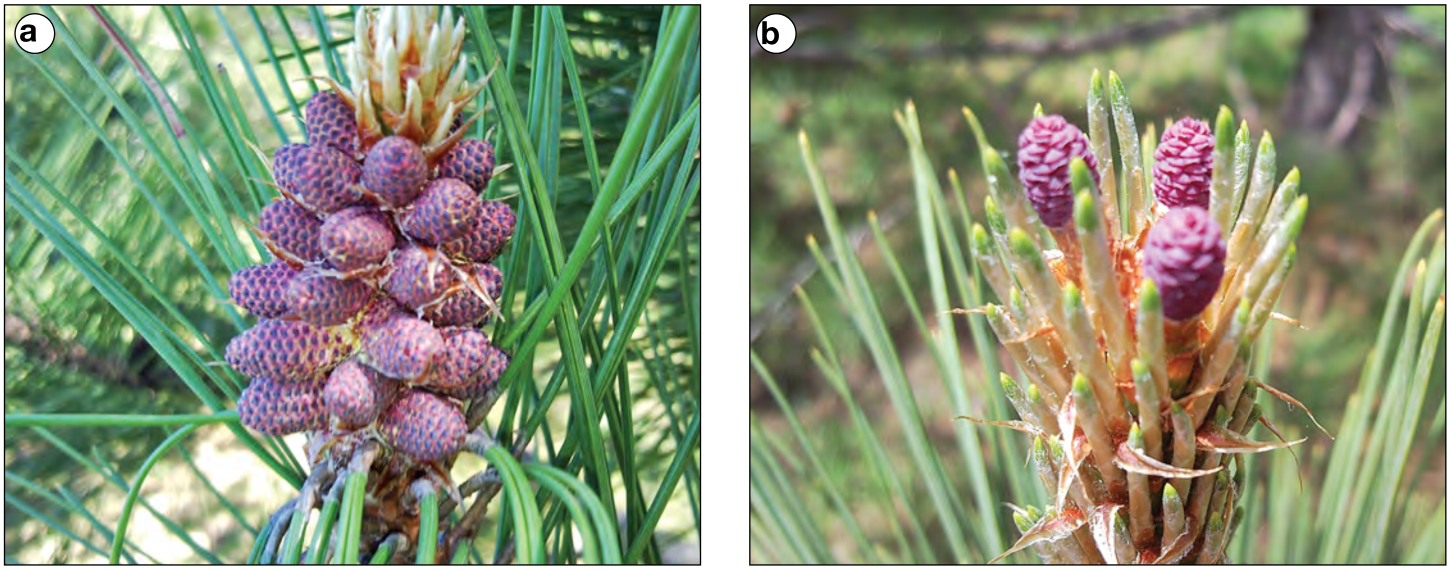

Figure 4. (a) Male and (b) female strobili of red pine in Minnesota. Photos by C. Pike, USDA Forest Service, 2014.

Figure 5. Second-year cones on this red pine tree are nearly ripe enough for picking. Photo by N. LaBonte, USDA Forest Service, 2021.

perform best at different sites (Pike and David 2007, Wright et al. 1972). Red pine is projected to cope poorly with a changing climate according to the Tree Atlas (Peters et al. 2020). Some investigators have found subtle variation in growth traits based on latitude, with sources from the southwestern part of the range performing best, indicating that assisted gene flow may be effective in helping red pine adapt to climate change (Rahi et al. 2010, Ter-Mikaelian 2014). Limited clinal variation has been noted for average seed size and some foliar traits (Rudolf 1990). Southern seed sources tend to have larger seeds, which may explain an observation of increased vigor of seedlings from native remnant populations in West Virginia when compared to seedlings from a Maine seed source (Buell 1940). A summary of considerations for moving red pine seed is contained in table 1.

Figure 6. This red pine tree has one cone near opening (purple-brown color) and a second already open with seed release in progress in September in southwestern Wisconsin. Cones at the closed and mostly brown stage are ideal to collect. Photo by N. LaBonte, USDA Forest Service, 2021.

Insects and Diseases

Shoot blights are the most serious disease problem affecting red pine, causing damage to seedlings that grow near mature, infected red pines. In the Lake States, *Sphaeropsis sapinea* can induce mortality on mature trees (Nichols and Ostry 1997, Stanosz et al. 1997) or on seedlings infected at the nursery of origin (Stanocz et al. 2007). *Armillaria* spp. and annosum root rots (*Heterobasidion annosum* [Fr.] Bref.) also affect red pine. A wider variety of root diseases may cause damage to red pine on sites outside its natural range of adaptability, especially on heavy and/or poorly drained soils and in forests with simplified structure such as even-aged pine plantations (Ostry et al. 2012). Red pine seedlings may also be susceptible to frost damage in frost pockets (Rudolf 1990).

Insect pests of red pine can damage stressed trees and stands but are not currently major causes of red pine mortality. Several insects cause damage to young stands, including sawflies, pine shoot moths, and pine root collar weevils. Native pine engraver beetles (*Ips* spp.) can kill stressed mature red pine trees. Cone beetles can cause severe damage to seed crops (Gilmore and Palik 2006).

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Summary for *Pinus resinosa*

Red pine (*Pinus resinosa* Ait.) is one of the most widely planted tree species in temperate North America. This species is native to coniferous and mixed conifer/deciduous forests around the Great Lakes, along the St. Lawrence River, and in the Northeastern United States and Maritime Canada. Red pine is notable for lower genetic diversity and higher levels of inbreeding than most conifer trees, likely due to past population bottlenecks. Variation among red pine of different geographic origins is limited, but there is evidence that southern sources generally perform better than northern sources. Moving red pine between the Great Lakes and northeastern populations is not recommended, but otherwise, assisted migration is a good strategy for maintaining this species in a changing climate.

Table 1. Summary of silvics, biology, and transfer considerations for red pine.

Red pine (*Pinus resinosa*)	
Genetics	• Genetic diversity: low • Gene flow: medium-low due to its capacity to self-pollinate; pollen and seed dispersal presumed similar to other pines
Cone and seed traits	• Small, winged seeds • 66,000 to 156,000 seeds per pound (30,000 to 71,000 per kg) • Non-serotinous cones; most seeds drop shortly after cone opening in early fall (figures 5 and 6) • Large cone crops every 3 to 7 years
Insect and disease	• Diplodia shoot blight may be problematic in young or mature stands • Other pests include red pine shoot moth, pine root collar weevil, and pine engraver • Pathogens of concern include armillaria root disease and annosum root rot
Palatability to browse	• Not a preferred food source for white-tailed deer, but seedlings may require protection in some locales
Maximum transfer distances	• Red pine is relatively tolerant to long-distance transfers (>300 mi [483 km]) • Seed can be moved (200 to 300 mi [322 to 483 km]) without significant declines in performance • Best performing sources tend to perform well at many sites • Seed sources from New England States are not recommended for planting in the Great Lakes region
Range-expansion potential	• Likely to experience northward range shift due to increased drought stress • Requirements for natural establishment put red pine at a disadvantage for natural migration into new areas

Eastern white pine tree. Photo by C. Pike, 2018.

Pinus strobus
Eastern White Pine

Nicholas Labonte and Andrew David

Introduction

Eastern white pine (*Pinus strobus* L.) is a large, long-lived coniferous tree, occurring naturally on a wide range of sites in northeastern North America. Its native range includes nearly the entire Appalachian Mountains system from far northern Georgia through New England to Newfoundland; southern Québec and Ontario; the Cumberland and Allegheny plateaus; most of the Great Lakes Basin; and the upper Mississippi River watershed in Minnesota and Wisconsin. In scattered locations in southern Wisconsin, Iowa, Illinois, Indiana, and Kentucky, stands of native eastern white pine occur outside the main range boundary on suitable sites, usually in areas where eroded sandstone is close to the surface (McIntosh 1948). Eastern white pine is an ecological keystone species: large, long-lived white pines add habitat elements and structural complexity (figure 1) that critically support large wildlife species like osprey, bald eagle, and black bear (Latremouille et al. 2008, Rogers and Lindquist 1992).

Eastern white pine was heavily logged from colonial times (in New England) until the early 1900s (in the western Great Lakes), which has reduced its abundance and eliminated most large, old specimens. The lumber is light and easily worked but strong for its weight, which made it prized for shipmasts, construction lumber, flooring, siding, and many other uses (Peattie 1948). Eastern white pine may be considered a cultural keystone species for Indigenous societies, who use parts of the tree medicinally and recognize its importance to other beings, including bald eagles and fur-bearing mammals (Uprety et al. 2013). Eastern white pine also has symbolic significance to Native peoples as an especially majestic and distinctive tree (Uprety et al. 2013) and as a “tree of peace” to the Iroquois (Schroeder 1992).

Eastern white pine occurs on a broad range of sites in boreal and broadleaf forest ecosystems (Abrams 2001, Wendel and Smith 1990). In general, this species grows best on well-drained sites with ample fertility but competes best on sites with average to below average fertility. In the warmest parts of its range, eastern white pine occurs as groves or scattered trees within a matrix of dry-mesic to mesic-hardwood or hemlock/hardwood forest types, often in areas with steep topography (figure 2). The trees may form a supercanopy where scattered individuals exceed the height of surrounding hardwoods. White pine does not form single-species stands naturally but may dominate extensive areas in the northern part of its range

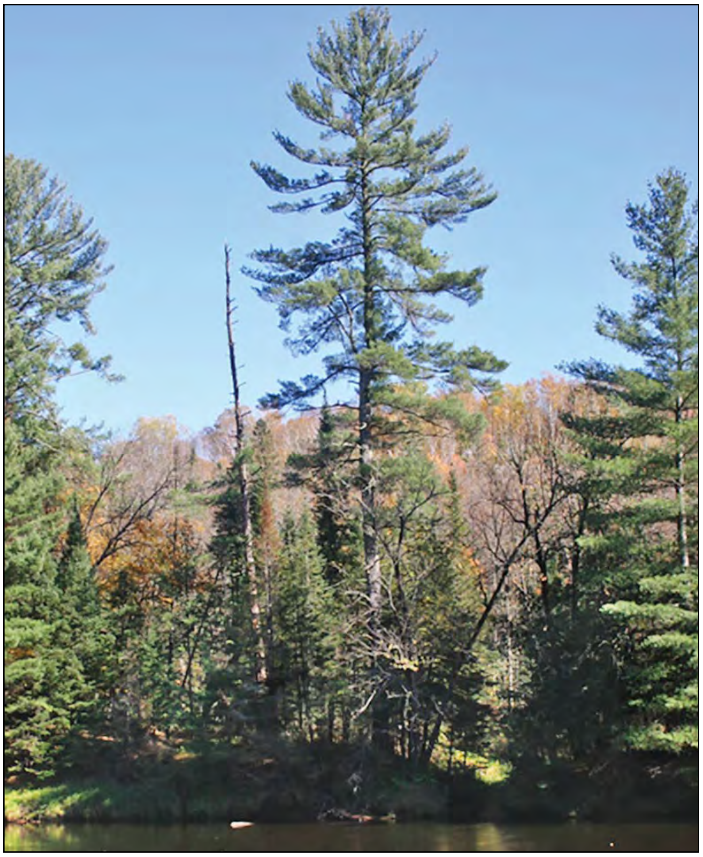

Figure 1. Eastern white pine is a large, long-lived tree species. This photo in a northern Minnesota mixed-species forest shows the typical crown outline and great height of eastern white pine. Photo by Steve Katovitch, USDA Forest Service, 2018.

Figure 2. Eastern white pine can be found growing with hardwoods, such as this sandy upland site in northern Indiana. Photo by N. LaBonte, 2022.

Figure 3. Eastern white pine cones require 2 years to mature. These first-year cones are at the start of their second growing season. Photo by N. LaBonte, 2022.

on well-drained, rocky or sandy loam soils. A good surviving example of this occurrence is the Menominee Tribal forest in northeastern Wisconsin, which escaped clearcutting during the cutover era. On drier sites, especially on outwash plains, eastern white pine is a component of mixed stands with red pine (*Pinus resinosa* Aiton) and/or jack pine (*P. banksiana* Lamb.), although it does not occur on the driest sands. In the northernmost parts of its range, eastern white pine is an element of boreal forests dominated by aspen (*Populus* spp.), birch (*Betula* spp.), fir (*Abies* spp.), and spruce (*Picea* spp.) (Engelmark et al. 2000). Finally, despite its overall preference for drier sites, eastern white pine frequently occupies less-saturated microsites within conifer swamps and may even be a dominant species in some wet forests (e.g., the Pinhook Bog in northern Indiana).

Eastern white pine is more shade-tolerant than red pine and jack pine, which allows it to persist in canopy gaps and somewhat sunny microsites such as steep slopes or rock outcrops in hardwood-dominated forests. Seeds germinate best with access to mineral soil. Eastern white pine is less resistant to fire damage than red pine when mature, and it does not have serotinous cones like jack pine, so it is adversely affected by high-intensity fires. While individual trees may be injured or killed by fire, occasional fire had an overall positive effect on maintaining the dominance of eastern white pine (often alongside red pine) in the “pineries” of the Great Lakes region by eliminating hardwood and shrub competition and maintaining ideal seedbed conditions (Heinselman 1973).

Like all pines, eastern white pine produces seed cones on a 2-year cycle. The first-year cones are relatively easy to see from the ground and may be used for advance forecasting and seed collection planning during the period between the hardening-off of new shoots in their first fall and the initiation of new growth in the spring (figure 3). When cones mature in their second year, cone scales open and disperse mature, winged seeds rapidly, usually in late August or early September (figure 4). Because of the short window between seed maturity and dispersal and the great height of seed-bearing wild trees, managed seed-production plantings are an especially important tool for maintaining a supply of eastern white pine seed (figure 5). Eastern white pine is a preferred browse species (Wendel et al. 1990) and may

Figure 4. Eastern white pine can produce heavy cone crops as seen here on the Superior National Forest in Minnesota. Photo by Ryan Pennesi, USDA Forest Service, 2020.

be damaged by white-tailed deer, moose, and hare. Protection during winter using bud-capping or other strategies may be needed for successful establishment. Fencing may be effective over small areas.

Genetics

Eastern white pine is closely related to western white pine (*Pinus monticola* Douglas ex D. Don), limber pine (*P. flexilis* James), and the five-needled pines of Mexico and will form hybrids with these relatives when in close proximity (Critchfield 1986), but there are no natural range overlaps that provide opportunities for hybridization in the wild. The most recent common ancestor of eastern white pine and its western relatives probably lived 15 to 20 million years ago (Jin et al. 2021). Eastern white pine is documented in the southern Appalachians during the last glacial maximum along with many of its present-day associates (Jackson et al. 2000); this population was probably the sole glacial refugium for the species (Nadeau et al. 2015). Large-scale genetic differences across the native range of eastern white pine likely originated as different sets of lineages colonized areas east and west of the Appalachians after glaciation. These genetic lineages are most obvious in chloroplast DNA (Zinck and Rajora 2016) but can be identified in the nuclear genome as well (Nadeau et al. 2015, Rajora et al. 2016). As a result of this recolonization process, the eastern white pine lineage in the western Great Lakes States is distinct from the northeast and southern parts of the species' range (Zinck and Rajora 2016).

Figure 5. Seed orchards are important for production of eastern white pine seed, such as this grafted eastern white pine at the USDA Forest Service, Oconto River Seed Orchard in northern Wisconsin. Photo by Paul Berrang, USDA Forest Service, 2003.

Eastern white pine retains high levels of genetic variation, genetic diversity, and heterozygosity throughout its range, even in isolated populations (Rajora et al. 1998). Most genetic variation is distributed within populations while a small, but significant, amount is distributed among populations (F_{ST} = 0.06 to 0.10 based on microsatellite and allozyme estimates) (Nadeau et al. 2015, Rajora et al. 2016). Genetic differentiation is more substantial when a larger part of the range is sampled (Zinck and Rajora 2016). Eastern white pine is an outcrossing species and suffers from inbreeding depression when self-pollinated (Johnson 1945, Patton and Riker 1958). Overall genetic diversity remains high despite intensive harvesting from 1850 to 1910, suggesting that the species did not experience a genetic bottleneck. The effect of harvesting on genetic variation in eastern white pine is unclear. Recent research indicates harvesting may have a neutral effect, reduce inbreeding (Marquardt et al. 2007), or have a negative effect on local genetic diversity (Buchert et al. 1997).

Seed-Transfer Considerations

There is extensive literature on eastern white pine provenance testing, and the results of the many studies tell a consistent, but complex, story about the deployment of eastern white pine seed. In general, a few seed sources outrank others in height growth in a wide variety of locations, and local sources may not display the most rapid growth. In the Lower Peninsula of Michigan, seed sources from the western and central Lower Peninsula grew faster than sources from the Upper Peninsula or the Lake Huron side of the Lower Peninsula (Wright et al. 1969). In the Northeastern United States, seed sources from the southern Appalachians had the greatest height after 10 years as far north as Pennsylvania, but New York and Pennsylvania sources did better farther north in Massachusetts and Maine (Garrett et al. 1973). In Iowa and Ohio, sources from lower Michigan, Tennessee, and Georgia were the best performers after 16 years of growth (Funk 1979). Michigan provenances also performed well in Maryland (Genys 1983). In Québec, sources from the Northeastern United States, Michigan, and southern Ontario performed well, although some provenances from these areas were not top performers (Beaulieu et al. 1996). The tendency of some lower Michigan provenances to grow rapidly extends as far as Germany (Stephan 2004).

In northern locations such as the upper Great Lakes, southern seed sources of eastern white pine are vulnerable to cold damage, but sources may move hundreds of miles north before a cold-hardiness penalty to survival and growth is observed (Lu et al. 2003). In multiple genetic trials, sources from south of the planting site were the best performers (Fowler and Heimburger 1968, Funk 1971, King and Nienstaedt 1968). Synthesizing climate models and eastern white pine provenance tests, Joyce and Rehfeldt (2013) illustrated potential seed movement zones under different warming scenarios. In general, their acceptable movement distance was longest in the Appalachian Mountains and somewhat shorter (~200 mi [322 km]) near eastern white pine's range limit in the western Great Lakes, where a strong climatic gradient creates a floristic tension zone between the boreal and temperate forests. Summer warmth (degree days) and mean minimum temperature are both predictive of performance of eastern white pine seed sources in range-wide tests (Joyce and Rehfeldt 2013). Summer moisture stress, snowfall, and vulnerability to storm and cold damage in spring and fall are all likely to influence eastern white pine radial growth (Chhin et al. 2018). Eastern white pine's shade tolerance and ability to grow on a range of sites enhances its adaptability to climate change according to the Climate Change Tree Atlas (Peters et al. 2020). The ability to establish and grow on a wide range of sites may allow eastern white pine to migrate more effectively than similar species like red pine or jack pine that are dependent on specific site conditions for recruitment. In addition, eastern white pine's high genetic diversity and large native range give it evolutionary tools, in the form of genetic variation and adaptive potential, that make it more likely to thrive in a changing climate than most other northeastern North American conifers.

In summary, white pine seed can be transferred over large distances without negative impacts on survival and growth with a few caveats (table 1). Sources from south of the planting site are likely to perform as well or better than local sources, and sources in excess of 200 mi (322 km) from the planting site are susceptible to cold damage if they are brought north of the ecological tension zone. Broadly speaking, transfer within the boreal and mixed-broadleaf biomes is acceptable but transfer between the two, near the tension zone, should be limited to 200 mi (322 km).

Insects and Diseases

Eastern white pine is affected by numerous native and nonnative pathogens and insects which have contributed to reducing its ecological and economic value in the post-cutover era (Wendel and Smith 1990). White pine blister rust, introduced in the early 1900s, is a damaging, nonnative disease that spends part of its life cycle on gooseberry and currant shrubs in the genus *Ribes*, where it causes minor foliar symptoms, and completes reproduction on five-needle pines as a parasite of live tissue. In susceptible pines, infections cause needle and twig dieback and necrotic bark cankers that can be large enough to girdle branches (figure 6) or kill young trees outright. These cankers produce characteristic bright orange fruiting structures in spring. Risk of pine infection is highest in areas where *Ribes* species are abundant with cool, humid conditions prevalent in late summer and early fall (Ostry et al., 2010).

Eastern white pine harbors naturally occurring resistance to white pine blister rust —i.e., an effective disease response can be passed from parent trees to offspring (Pike et al. 2018). While it was initially thought that the species was uniformly susceptible, refinements to resistance screening protocols revealed that blister rust resistance could be improved through breeding in eastern white pine, despite the fact that it does not possess major gene resistance as found in some western North American white pines (King et al. 2010, Merrill et al. 1986). Prevailing weather conditions and local climate are only conducive enough to blister rust spread and development to limit eastern white pine establishment in localized areas of eastern North America, such as the Lake Superior shoreline in Minnesota and Wisconsin, but lineages more resistant to blister rust are suitable for planting in high-risk areas if they are available.

Figure 6. Eastern white pine shows branch flagging due to white pine blister rust as seen in this stand on the Superior National Forest in Minnesota. Photo by Paul Berrang, USDA Forest Service, 2007.

Root rots caused by *Armillaria mellea* and *Heterobasidion annosum* can also damage eastern white pine (Costanza et al. 2018), especially in areas where hardwood (*Armillaria*) and conifer (*Heterobasidion*) stumps are present near young eastern white pines. The dyer's polypore (*Phaeolus schweinitzii*) is a native fungus that causes a destructive, brown butt rot in mature eastern white pine (Wendel and Smith 1990).

The most damaging insect to affect eastern white pine is the white pine weevil (*Pissodes strobi*), which can result in multiple leaders and a rounded crown, especially in low-density, open-grown areas (Wendel and Smith 1990). Adults typically fly less than 35 ft (10.7 m) above the ground and seek out robust terminal leaders associated with fast-growing trees. The adult lays eggs near the terminal shoot where subsequent feeding by larvae kills the terminal resulting in decreased growth, multiple leaders, and rounded crown, (Ostry et al., 2010). Trees taller than 35 ft (10.7 m) or those with decreased leader diameter due to shaded or partially shaded conditions typically are not impacted. Other impactful insect pests include several additional species that attack shoots and twigs: European pine shoot moth (*Rhyacionia buoliana*), eastern pine shoot borer (*Eucosma gloriosa*), and white pine aphid (*Cinara strobi*); defoliating sawflies (*Neodiprion pinetum* and *Diprion similis*); insects that attack wood and vascular tissue, including Zimmerman pine moth (*Dioryctria zimmermani*) and pine root collar weevil (*Hylobius radices*); and the white pine cone borer (*Eucopina tocullionana*), a moth that specifically attacks developing cones and can devastate seed crops thereby negatively affecting natural regeneration and cone crops in seed orchards (Costanza et al. 2018, Goulding et al. 1988). In addition to these biological agents, eastern white pine is susceptible to ozone damage, although this is a problem localized to areas near major cities and is not a concern in most of the native range (Costonis and Sinclair 1969).

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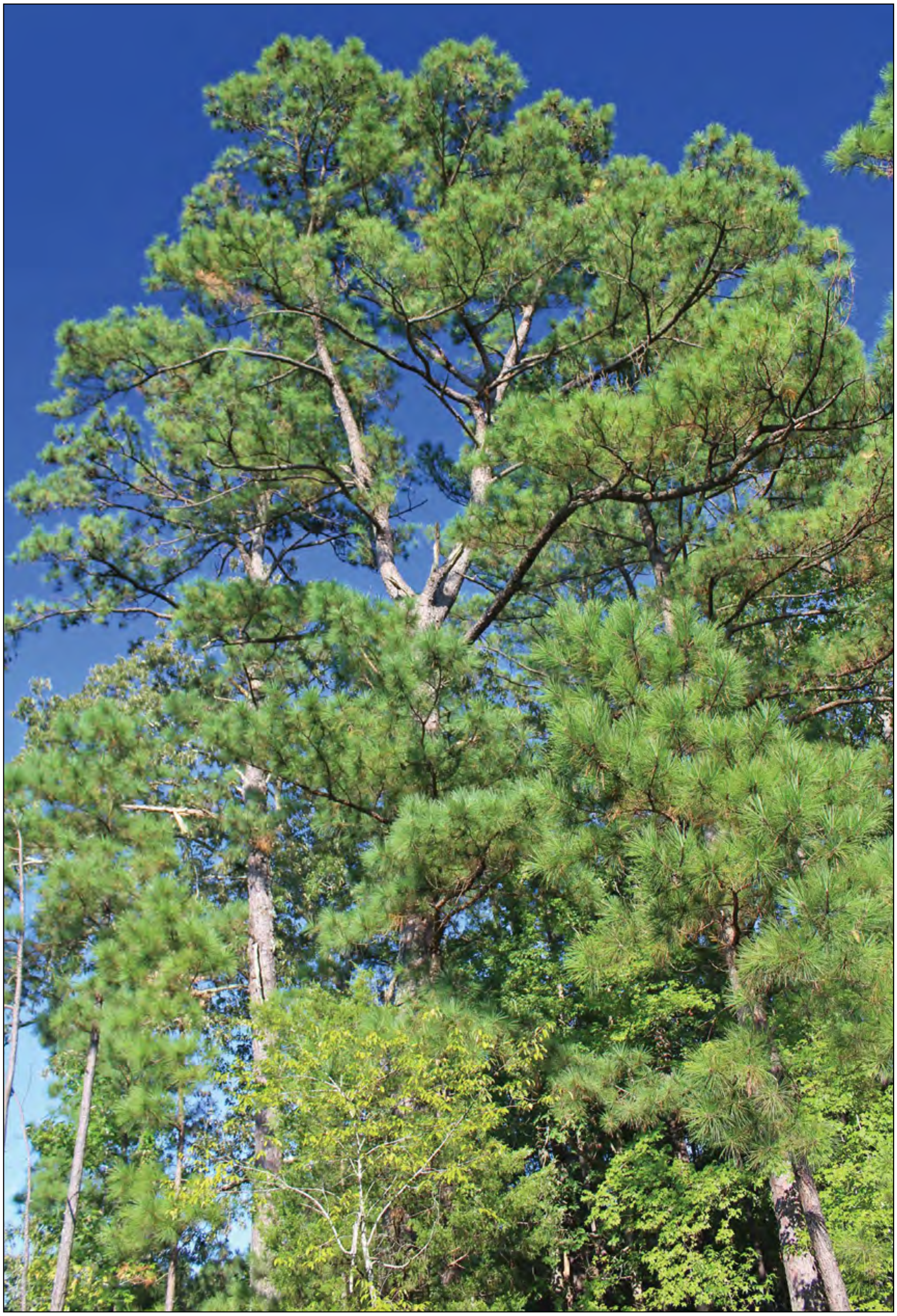
Summary for *Pinus strobus*

Eastern white pine (*Pinus strobus* L.) is an iconic component of cool-temperate, mixed broadleaf/conifer forests and southern boreal forests in eastern North America. This species has higher shade tolerance and broader site preferences than most northeastern North American conifers. Genetic diversity of eastern white pine is high at the species and population levels as expected given life-history characteristics: i.e., a wind pollinated, obligate outcrosser with a long lifespan. Seeds sourced from far south of the planting site tended to perform best in progeny tests, suggesting long-distance seed-transfer is possible. Sources from the southern Appalachians, however, experienced cold damage at northern test sites. Transfer distances of 200 mi (322 km) northward are considered safe for assisted migration, although longer transfers may be safe if they do not cross the floristic tension zone between the boreal and temperate forest. There are no known population-level differences for resistance to common insects or diseases or resistance to herbivory, but assisted migration is best avoided in areas with severe white pine blister rust, where local sources selected for blister rust resistance will remain optimal.

Table 1. Summary of silvics, biology, and transfer considerations for eastern white pine.

	Eastern white pine (*Pinus strobus*)
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Cones not serotinous, 0 to 73 winged seeds per cone • Most seeds release in late August to early September • 26,500 seeds per pound (58,400 seeds per kg)
Insect and disease	• Major pests: white pine blister rust and white pine weevil • Others: heterobasidion root disease, armillaria root rot, white pine cone borer, white pine sawfly
Palatability to browse	• A preferred food of white-tailed deer in winter over much of its range; also targeted by rabbit, hare, and moose • White pine may be heavily browsed
Maximum transfer distances	• ntermediate tolerance to seed-transfer (200–300 mi [322–483 km]) • Seed sources originating up to 200 mi (322 km) south of the planting site will likely perform as well or better than local sources; longer distance transfer possible in certain areas (see text) • Unique gene pool in western Great Lakes; seed-transfer southward not recommended
Range-expansion potential	• Likely to expand northward; may lose habitat in southern part of range • Shade tolerance and broad site preferences may create opportunities for persistence and even localized population expansion



Loblolly pine trees. Photo by Kevin Potter, 2023.

Pinus taeda
Loblolly Pine

Carolyn C. Pike, C. Dana Nelson, Kevin Potter

Introduction

Loblolly pine (*Pinus taeda* L.) is a widely distributed, long-lived, intermediate shade-tolerant conifer with a broad ecological amplitude. The species has the highest commercial value of any tree species in the United States due in part to its fast growth, broad adaptability, and strong apical dominance (figure 1). The growth and form characteristics of the species have been further enhanced by extensive breeding programs (Cumbie et al. 2012). For example, the program led by North Carolina State University is in its fourth breeding cycle and is currently planning for a fifth cycle (Isik and McKeand 2019). The present value of efforts to breed improved loblolly pines and to deploy genetic gains to landowners is estimated to exceed $1.7 billion, reflecting an increase of $1,594 per acre ($3,937 per ha) across over 1 million acres (404,685 ha) of improved seedlings planted each year (McKeand et al. 2021). Loblolly pine forests comprise more than half of the standing pine volume in the Southern United States (Baker and Langdon 1990), and it is the most planted tree in the country (Abrahams 2023). The wood of loblolly pine is valued for construction because of its high density (Alden 1997) and concomitant high strength and stiffness. The species is also a prime candidate for carbon markets because of its high growth rates and preferred status as a plantation species across much of the region's coastal and piedmont forest sites (Huang et al. 2004).

Loblolly pine is native across the Southern United States, and it is grown successfully on other continents (Baker and Langdon 1990), including South America, Australia, Asia, and Africa (Schmidtling 2001). As with other southern pines, its natural distribution is limited in the north by lower winter temperatures and in the west by lower precipitation (Schmidtling 2003). In noncommercial stands, loblolly pine occurs on sites with higher soil moisture than other southern pines and may grow in pure or mixed stands with hardwoods that have relatively long intervals between fire events (figure 2) (Baker and Langdon 1990). In its northern range, loblolly pine occurs with shortleaf pine (*Pinus echinata* Mill.) as far north as New Jersey (Crocker et al. 2017), Maryland, and southern Illinois (Crocker et al. 2009). The rapid early growth of loblolly pine exceeds that of longleaf pine (*P. palustris*

Figure 1. This loblolly pine tree growing in an unmanaged forest in North Carolina demonstrates the strong apical dominance of the species. Photo by K. Potter, USDA Forest Service, 2023.

Figure 2. In wild stands, loblolly pine trees vary in height and diameter and often grow in stands mixed with hardwood trees, as seen in this stand in North Carolina. Photo by K. Potter, USDA Forest Service, 2023.

Mill.) on South Carolina sandhill plains at least until 19 years of age (Cram et al. 2010). Adult trees have thick bark and relatively high fire tolerance (USDA NRCS 2023), but seedlings are relatively intolerant of fire compared with shortleaf, longleaf, and slash (*P. elliottii* Engelm.) pines (Bradley et al. 2016, Pile et al. 2017). Seed germination is optimal on bare mineral soil (Edwards 1987).

Loblolly pine seedlings are grown in nurseries as both bareroot and containerized stock types (Grossnickle and South 2017, Porterfield 2006) (figure 3), performing best on mildly acidic nursery soils (South 2017). Young seedlings, whether in the nursery or in the field, may be sensitive to winter cold snaps when temperatures drop below 25 °F (-4 °C) (Pickens and Crate 2018). Loblolly pine's range is predicted to shift northward as the climate warms over the next few decades because of its high abundance, fecundity, and adaptability (Iverson et al. 2004, Peters et al. 2020), while being limited by its current cold hardiness level (i.e., USDA Plant Hardiness Zone 7, or approximately 0 to 10 °F [-17.8 to 12.2°C]) (Bannister and Neuner 2001). Shade tolerance of loblolly pine is greater than other southern pines, which is advantageous for its adaptability to climate change (Peters et al. 2020).

Genetics

Loblolly pine is a monoecious diploid species with high genetic variation typical of outcrossing, wind-pollinated tree species, despite a prior genetic bottleneck occurring during the last glacial period (Acosta et al. 2019). The species' postglacial period recovery of genetic diversity is in stark contrast to red pine (*Pinus resinosa* Aiton) that also experienced a bottleneck during the same glacial maximum but today harbors low genetic diversity (Echt et al. 1998). The fact that loblolly pine was able to recover from a dramatic reduction in population size and maintain high levels of genetic diversity is promising for its ability to respond to challenges like climate change and to adapt successfully to novel future conditions (Acosta et al. 2019). Loblolly pine's fast growth rate and wide adaptability has led to extensive selection and breeding efforts for coastal Atlantic, Piedmont, and western Gulf populations (Hooker et al. 2021, Sierra-Lucero et al. 2002). Similar to other *Pinus* species, most genetic variation for loblolly pine occurs within populations, rather than among populations as determined with protein (i.e., allozymes) (Hamrick et al. 1993) and DNA-based markers (Eckert et al. 2010, Lu et al. 2016). Evidence from allozymes, monoterpenes, and fusiform rust resistance suggest that loblolly

Figure 3. Most loblolly pine seedlings that are planted across the Southern United States are grown as bareroot stock, but containerized seedlings are increasingly common. Photo by C. Pike, USDA Forest Service, 2018.

pine existed in two refugia during the last glacial period: one in south Florida and/or the Caribbean and one in south Texas and/or northeast Mexico. These refugial populations likely migrated north during the Holocene and merged near the Mississippi River (Schmidtling et al. 1999).

Loblolly pine populations west of the Mississippi River are characterized with slower growth, but they have greater resistances to drought and fusiform rust (Wells and Wakeley 1966) than populations east of the river, informing seed zone recommendations formulated by Schmidtling (2001). Specifically, the three seed zones are: (1) east of the Mississippi River, (2) between the Mississippi River and east of the borders between Texas/Oklahoma and Louisiana/Arkansas, and (3) west of the borders between Texas/Oklahoma and Louisiana/Arkansas. Genetically improved seed from seed orchards (figures 4 and 5), including mass control-pollinated and control-pollinated full-sib, is the primary source of seed for reforestation (McKeand et al. 2021).

Loblolly pines have medium-sized cones (figure 6) compared with other *Pinus* species with wind-dispersed seeds (Krugman and Jenkinson 2008). Growth rates of hybrids with longleaf pine, known as Sonderegger pine (*P. x sondereggeri* H. H. Chapm.), are relatively high compared with the mid-parent (parental species' mean), but survival is higher for loblolly pine than the hybrid or the longleaf pine parent (Schoenike et al. 1975). Further work has shown no significant differences in height, diameter, volume, or fusiform rust severity between loblolly and Sonderegger pines (Henderson and Schoenike 1981). Loblolly pine also forms natural hybrids with pitch pine (*P. rigida* Mill.) in New Jersey, Maryland, Delaware, and pond pine (*P. serotina* Michx.) in New Jersey, Maryland, Delaware, and North Carolina (Baker and Langdon 1990). Hybridization occurs with shortleaf pine throughout the species' ranges, with higher rates west of the Mississippi River (Edwards and Hamrick 1995, Xu et al. 2008). The introgression between the species is thought to contribute to fusiform rust resistance of loblolly pine in this region (Florence and Hicks 1980).

Seed-Transfer Considerations

Seed-transfer recommendations for loblolly pine (and other southern pine species) are based largely on plant hardiness zones, or the average annual minimum temperatures (AAMT) for a locale, as supported by seed source study results (Schmidtling 2001). Winter temperatures are the best predictors of height growth

Figure 4. The wide spacing in loblolly pine seed orchards, as shown here in Georgia, is used to maximize seed production and to provide full access to crowns for cone collecting with a mechanical lift. Photo by C. Pike, 2018.

Figure 5. This seed orchard in Delaware is the most northerly seed orchard of loblolly pine in the United States. Seed orchards like this one may be used to increase seed production for planting in more northerly climates. Photo by R. Overton, USDA Forest Service, 2007.

in loblolly pine, including AAMT and number of frost-free days (Schmidtling 1994, 2001). Seedlings generally can be transferred from areas with AAMT within 5 °F (2.8 °C) of the planting location, although they can be moved as far as 10 °F (5.6 °C). The risk of cold damage increases for northward transfers, while growth decreases in southward transfers (Schmidtling 1994, 2003). Seeds from 150 mi (241 km) south of the planting site are generally favored because their growth exceeds local sources except in northern areas where local sources may be best (Schmidtling 2001).

Loblolly pine seed sources from the eastern seed zone (east of the Mississippi River) should not be planted in the western seed zones because of the risks posed by drought and fusiform rust. Western seed sources can be planted in the eastern seed zone, particularly for droughty sites and areas with high fusiform rust exposure, though these western sources will likely grow slower (Schmidtling 2003). Loblolly pine is also sensitive to photoperiod, with northerly populations being more sensitive than southerly populations (Perry et al. 1966). For this reason, movement from central to northern areas for assisted range expansion or assisted species migration (Williams and Dumroese 2014) should not exceed previously recommended maximum transfer distances, while transfers of less than 200 mi (322 km) are not likely to exhibit negative effects attributable to photoperiod alone. Loblolly pine is not recommended for planting in Illinois north of U.S. Route 40 (which runs near and parallel to Interstate 70 at roughly 39° N latitude) (Gilmore 1980) because of low minimum winter temperatures. In Maryland, local seed sources are recommended for planting (Little 1969), which is also consistent with Schmidtling (2001). Local sources should be favored along the edge of the northern range for assisted migration beyond the current range limit for assisted range expansion or assisted species migration. A summary of considerations for moving loblolly pine seed is contained in table 1.

Insects and Diseases

Loblolly pine generally outgrows longleaf and shortleaf pines but is more susceptible to pests, specifically southern pine beetle, fusiform rust (Moser et al. 2003), and pitch canker (caused by *Fusarium circinatum*). Breeding for resistance to fusiform rust (Carson and Carson 1989) has been occurring for decades with different deployment strategies (e.g., full-sib vs. half-sib families) depending on disease severity (Bridgwater et al. 2005). Western sources of loblolly pine have evolved a higher degree of resistance to fusiform rust compared with eastern sources. Like other southern pines, decadent stands with low vigor may be preferentially attacked and negatively impacted by bark beetles. Brown spot needle blight (caused by *Lecanosticta acicola*) is a primary pathogen on needles of trees in *Pinus* species across the globe and a major concern for the southern pines grown in plantations (van der Nest et al. 2019).

Figure 6. Loblolly pine cones are medium-sized and typically release seeds while still on the tree. This habit requires that cones be handpicked before the seeds are released. Photo by C. Pike, USDA Forest Service, 2023.

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Summary for *Pinus taeda*

Loblolly pine (*Pinus taeda* L.) is the most commercially valuable conifer in the United States. This native species is grown widely across the Southern and Central States. Genetic diversity of this species is high, and population structure is low with some east-west differentiation. Loblolly pine seeds and seedlings for planting are typically moved from a 5 °F (2.8 °C) warmer hardiness zone to a cooler zone to maximize growth potential. Fusiform rust (caused by *Cronartium quercuum* f.sp. fusiforme) can be a lethal pathogen to loblolly pine if not managed properly, while southern pine beetle (*Dendroctonus frontalis*) is a significant pest on older, more decadent stands. Loblolly pine is expected to perform well under climate change because of its high abundance, moderate shade tolerance, and broad adaptability.

Table 1. Summary of silvics, biology, and transfer considerations for loblolly pine.

Loblolly pine (*Pinus taeda*)	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Average 18,000 seeds per pound (40,000/kg) • Trees grow 5 to 10 years to seed bearing; cone crops occur every 3 to 13 years
Insect and disease	• Insects: southern pine beetle • Diseases: fusiform rust, pitch canker, brown spot needle blight
Maximum transfer distances	• Intermediate tolerance to seed-transfer (200–300 mi [322–483 km]) • Movement from warmer (5 °F [2.8 °C]) plant hardiness zones is typically practiced; movement from up to 10 °F (5.6 °C) warmer may also be tolerated • East to west transfer is not recommended, while west to east might be acceptable for some sites, provided that north-south transfer guidelines are followed
Palatability to browse	• Browse is rarely reported, but white-tailed deer in northerly locales are known to consume needles and may threaten seed sources that are moved northward
Range-expansion potential	• Expected to have generally favorable potential in a warmer climate because of broad ecological amplitude, high abundance, and good fire tolerance

Flowers of the black cherry tree. Photo by Rob Routledge, Sault College.

Prunus serotina
Black cherry

Nicholas LaBonte

Introduction

Black cherry (*Prunus serotina* Ehrh.) is a medium-to-large, early-successional hardwood tree that grows on a variety of well-drained soils throughout the Eastern United States, usually as a minor component of mixed hardwood forests. It grows best on well-draining, rich, loamy, or sandy soils (Marquis 1990), although it is often found in old field environments with degraded, rocky, sandy, or clay soil. On suboptimal sites, black cherry rarely attains commercial size or form. The species is considered shade intolerant; although its seedlings can persist for years in shade and respond to release (Auclair and Cottam 1971), they are not competitive with more shade-tolerant species in partially shaded growing conditions (Marquis 1979). A mature black cherry's very dark, scaly, "burnt potato chip" bark is distinctive (figure 1). Black cherry produces racemes of small, mildly fragrant white flowers in late spring or early summer (figure 2) that mature into small, dark purple drupes in early fall (figure 3). Leaves and twigs have a distinctive bitter almond or cherry scent due to cyanogenic glycosides, including amygdalin (Telichowska et al. 2020).

Black cherry is sympatric with several other native *Prunus* species in different parts of its range along with commonly cultivated *Prunus* species (e.g., peach, plum, cherry, and apricot) introduced from Europe and Asia. It is only distantly related to the sympatric native pin cherry

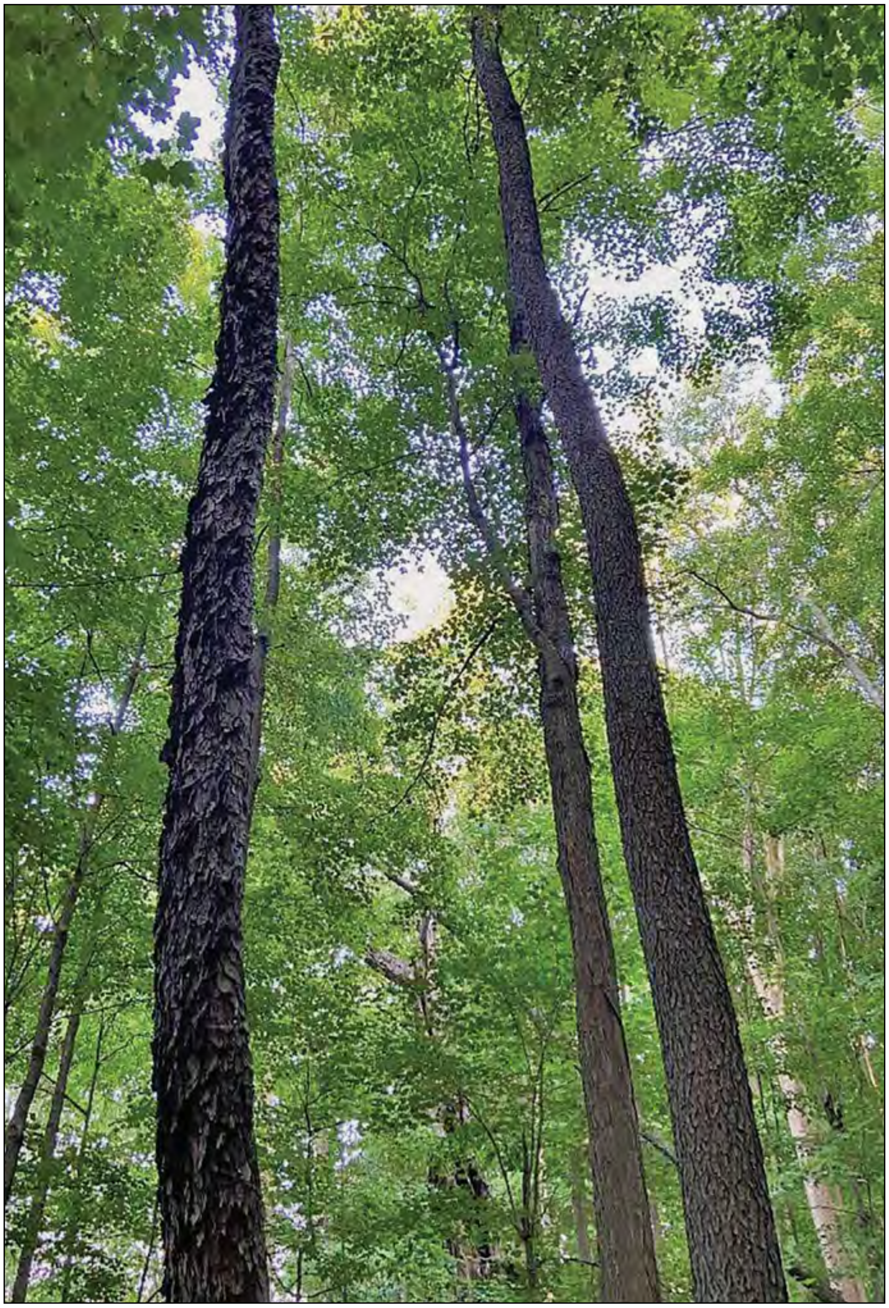

Figure 1. The two black cherry trees in this photo are in a mesic hardwood forest in southeast Wisconsin dominated by sugar maple. These trees show the black cherry's dark, scaly bark and long, branchless boles in a heavily shaded environment. The tree on the left has scalier/shaggier bark than typical black cherry. Photo by N. LaBonte, USDA Forest Service, 2023.

(*Prunus pensylvanica* L. f.) and the widely planted domestic stone fruits (Shi et al. 2013). Hybridization has not been documented with these species or the more closely related sympatric chokecherry (*Prunus virginiana* L.), which is a thicket-forming shrub.

Black cherry's glacial refugia are not entirely clear. Its broad current distribution in Mexico indicates that it was able to migrate south quite effectively as the climate cooled (Guzman et al. 2018, McVaugh et al. 1952), and it still occurs near a site in Texas where seed remains have been found in Pleistocene packrat middens (Van Devender 1979). Analysis of chloroplast DNA in its northern range hints at several refugia east and west of the Appalachian Mountains (Pairon et al. 2010). Its persistence in likely Pleistocene refugia indicates its potential to adapt to climate changes and migrate to nearby suitable habitats if necessary, although the Climate Change Tree Atlas identifies insects and diseases as potential complicating threats in the future (Peters et al. 2020).

Black cherry will likely be able to expand its range in some areas given current evidence and its large native range, adaptability, and dispersal ability (Segura et al. 2018). In the areas where it is most abundant, however, black cherry may struggle to benefit from climate change due to other factors that are currently causing it to diminish in importance. In its core commercial range on the Allegheny Plateau, black cherry is a dominant canopy species (up to 50 percent of basal area in some areas) and produces large veneer logs and sawlogs more consistently in this area than anywhere else in its native range. Black cherry reproductive success has declined dramatically in these areas, however, due to plant/disease feedbacks at high densities and changes in nitrogen deposition rather than climate stress (Royo et al. 2021).

Figure 2. Black cherry flowers can proliferate across eastern forests in the spring. Photo by Richard Gardner, bugwood.org.

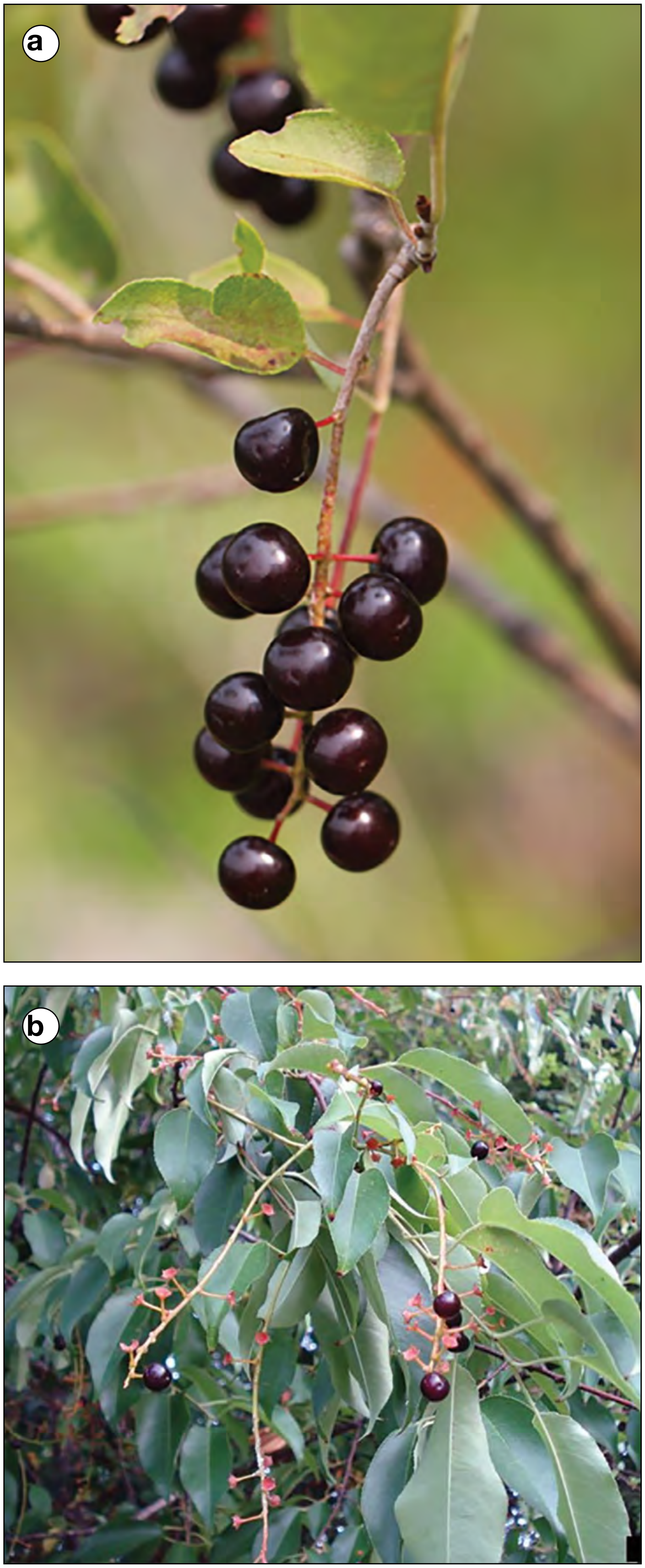

Figure 3. Black cherry fruits (a) are a favored food source for birds in the Eastern United States. The leaves of black cherry (b) are relatively small in stature, but crowns produce dense shade during the active growing season. Photo (a) by Franklin Bonner, USDA Forest Service (retired), 2010, and (b) by Steve Katovich, USDA Forest Service, 2019.

Genetics

Black cherry is a monoecious tetraploid (2n = 4x = 32) with a relatively small genome of 490 Mb (Jung et al. 2019). Its nectar-producing flowers are visited by a variety of generalist insects (McLaughlin et al. 2022), and ground-dwelling Andrenid miner bees seem to be the most important pollinators. Black cherry is primarily outcrossing and can generally be considered self-incompatible (Gordillo-Romero et al. 2020). Its fleshy fruits are eaten and dispersed in the digestive tracts of a variety of animals, and it is likely that birds are an effective means of long-distance seed dispersal. Black cherry apparently does not hybridize readily with its closest relatives, so hybridization is not a concern for seed movement considerations.

Studies of genetic structure in black cherry revealed weak differentiation among populations with relatively low F_{ST} (a measure of population differentiation) estimates using 8 nuclear microsatellite loci: 0.06 for trees sampled within the native range of black cherry and 0.09 for invasive populations in Europe (Pairon et al. 2010) (table 1). A smaller study with five microsatellite markers found high heterozygosity (0.7 to 0.8) and slightly lower allelic richness (30 to 40 vs. 40 to 50 unique alleles observed) in western range limit compared with core range populations (Beck et al. 2014), which indicates high genetic diversity on the black cherry genome. A large study using 12 microsatellite markers and DNA from herbarium specimens found limited isolation by distance, indicative of high gene flow and limited genetic structure (Konrade et al. 2018). A microsatellite marker study of black cherry in South America, where it is introduced and naturalized, also showed high heterozygosity and low population differentiation (Guadalupe et al. 2015), although Ecuadorian populations likely only contain a subset of the genetic diversity found in native Mexican populations based on chloroplast haplotype analysis (Downey et al. 2000).

Seed-Transfer Considerations

A meta-analysis of common garden studies of five major hardwood species in the Northeastern United States found that black cherry was more sensitive to climatic variables than other species tested (red oak [*Quercus rubra* L.], black walnut [*Juglans nigra* L.], yellow birch [*Betula alleghaniensis* Britton], and red maple [*Acer rubrum* L.]), especially for mean coldest month and warmest month temperatures (Leites et al. 2019). This finding indicates that black cherry seed should not be moved as far north as some other native hardwoods for assisted migration because of heightened sensitivity to both cold winter and hot summer temperatures. The distinct morphology of black cherry subspecies from dramatically different climates (Guzman et al. 2018) indicates that locally adapted genetic strains of this species have developed despite pervasive gene flow. Local adaptation is probably less pronounced in the relatively homogenous Northeastern United States versus the arid-to-tropical, mountainous extreme south and west of black cherry's sprawling native range, but investigators have observed adaptive differences in black cherry from high and low elevations in the Appalachian Mountains (Barnett and Farmer 1980).

In earlier studies, black cherry has showed strong site by provenance interactions and poor performance of sources that had been moved more than 5 degrees latitude north or south of the planting site (Carter et al. 1983, Genys and Cech 1975), which indicate a level of local adaptation. Sources from locations south of the planting site within 210 mi [338 km] or 3 degrees latitude are generally strong performers (e.g., Walters 1985), although some sources from 350 miles [563 km] or 5 degrees latitude south of the planting site may perform well. Sources from 200 to 250 miles (322 to 402 km)—3 degrees of latitude—south of the planting site will likely be the best performers at a given location, but moving sources farther than this is risky. Collections from parent trees with superior phenotypes do not necessarily exhibit significantly better performance than collections from average parent trees (Pitcher 1982).

Insects and Diseases

Many native insects and diseases affect black cherry. The species is a preferred food source of the eastern tent caterpillar (*Malacosoma americanum* F.), which can cause defoliation, reduced growth, and occasionally mortality due to repeated attacks (Marquis 1990). Cherry scallop shell moth (*Rheumaptera prunivorata* F.) can also cause defoliation. Black cherry is vulnerable to several stem borers that can damage the wood and leave distinctive pitch spots on the outer bark (Kulman 1964), including the peach bark beetle (*Phloeotribus liminaris* Harris), lesser peachtree borer (*Synathedon pictipes* Grote & Robinson), and cambium miner (*Phytobia pruni* Gross).

The most recognizable fungal disease of black cherry is black knot, caused by *Apiosporina morbosa* (Schwein.) Theiss. & Syd., which causes large, woody black swellings on stems and can destroy the timber value of trees. Leucostoma canker (*Cytospora leucostoma* [Pers.] Sacc.) is a fungus that causes cankers and branch mortality, often in association with cambium miner feeding (Gross 1967). Several species of generalist wood decay fungi, including *Armillaria mellea* (Vahl) P.Kumm. and *Laetiporus sulphureus* (Bull.) Murrill, attack the wood of mature black cherry trees. Due to its typical canopy position and somewhat weak branch structure, black cherry

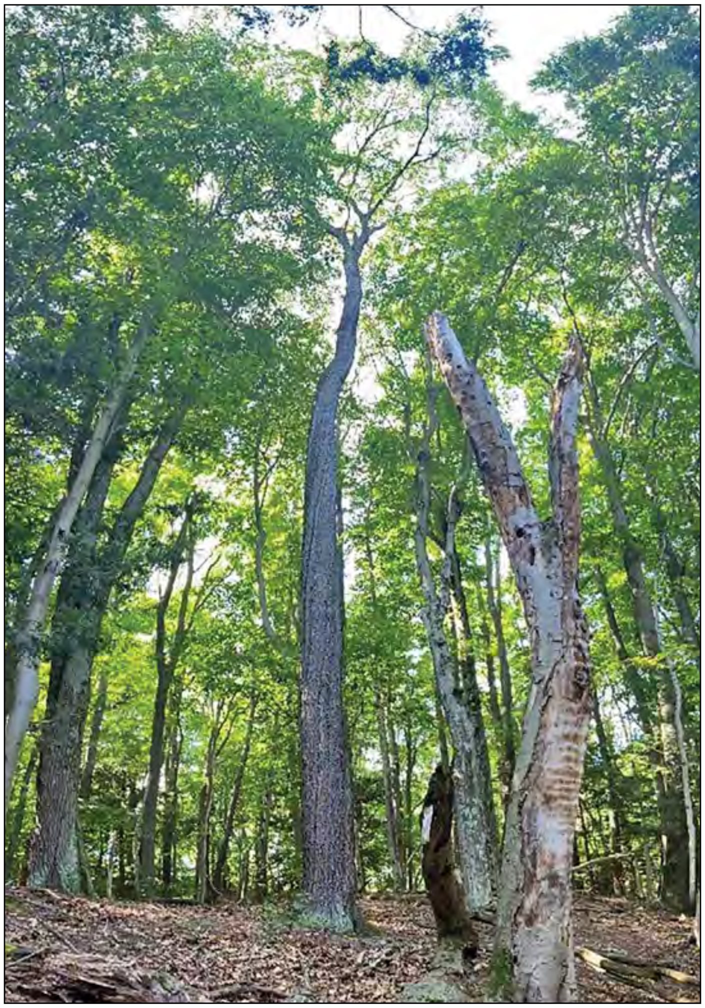

Figure 4. This large black cherry is growing in southwestern Michigan in a forest with deep, sandy soils. The forest is dominated by American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carrière). This tree, growing among others with storm damage, demonstrates crown form and canopy position typical of good-quality stands in most of black cherry's range. Photo by N. LaBonte, USDA Forest Service, 2023.

is often damaged by storms (figure 4). These injuries provide infection courts for decay fungi (Campbell and Davidson 1940, Downs 1938), although most wounds can be compartmentalized. Increased frequency of severe storms and ice storms in a changing climate could increase economic losses of black cherry due to these opportunistic native fungi.

White-tailed deer (*Odocoileus virginianus* Zimmermann) do not prefer black cherry as browse compared with many commonly co-occurring species (Sample et al. 2023), which allows black cherry to regenerate well (relative to other hardwoods) in areas with heavy browse pressure. Browsing can be a serious problem, however, in areas with high pressure where preferred trees are uncommon. Although the defensive hydrocyanic acid-producing compounds in the leaves are highly poisonous to cattle (Smeathers et al. 1973) and other livestock, deer and rabbits are either not as vulnerable to harm from these compounds or do not consume enough at one time to be harmed.

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Summary for *Prunus serotina*

Black cherry (*Prunus serotina* Ehrh.) is a shade-intolerant hardwood tree that is found occasionally to frequently in a variety of hardwood forest types across the Eastern United States and extreme southeastern Canada, as well as parts of Mexico. Valued for its colorful, dense, and highly workable wood, black cherry is also a notable source of soft mast for wildlife. Black cherry regenerates readily on disturbed sites when adequate seed crops are present. In the heart of its commercial range, however, well-documented regeneration problems occur due to complex and unique circumstances. Black cherry has high genetic diversity due to high levels of seed dispersal and pollen flow, while population structure is low. Common garden studies revealed that black cherry is somewhat more sensitive to seed-transfer than some other hardwoods with similarly expansive ranges and high genetic diversity. Seed-transfer distances of 200 miles (322 km) from south to north are considered safe to maximize growth. Black cherry is affected by a variety of native damaging insects and fungal diseases that reduce its economic value. Under climate change, black cherry is likely to expand its range northward but may suffer from increased stress and insect attacks in parts of its range.

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

Black cherry (*Prunus serotina*)	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Fleshy fruit with single seed • About 2,000 cleaned seeds per pound (4,000 per kg) • Can be stored in freezer or refrigerator for 3 to 5 years if dried to 4–6% moisture
Insect and disease	• Eastern tent caterpillar and cherry scallop shell moth are major defoliators; peachtree borer and peach bark beetle attack stems • Vulnerable to generalist decay fungi; black knot fungus causes defects
Palatability to browse	• Not a preferred browse species, but browsing can be a problem when pressure is high and preferred species are absent
Maximum transfer distances	• Relatively sensitive to seed-transfer: distances less than 300 mi [483 km] are safe • Use caution with transfers greater than 250 miles (402 km)
Range-expansion potential	• Black cherry is likely to expand in some areas due to excellent seed dispersal, but decline in other areas where it is currently abundant due to stress from insects, diseases, and drought

Northern red oak tree. Photo by C. Pike, 2023.

Quercus rubra
Northern Red Oak

Carolyn C. Pike and Philip A. O'Connor

Introduction

Northern red oak (*Quercus rubra* L.) is a long-lived, mesic hardwood that is widely distributed across the eastern half of North America from Maine and the Canadian Maritimes, west to Minnesota, and as far south as Arkansas, Alabama, and Georgia. Studies of pollen records suggest that *Quercus* refugia were likely scattered across the lower Mississippi Valley and northern Florida followed by rapid recolonization concurrent with ice sheet retreat 18,000 years before present (Davis 1983). Northern red oak is associated with deep, well-draining soils but can tolerate a range of soil textures from loams to silty clay loams. Northern red oak is generally associated with north or easterly aspects and lower elevations. Regeneration of northern red oak can occur from seed (acorns) (figure 1), and stumps can also coppice. Leaves of northern red oak have pointy tips (figure 2) which are readily distinguished from the rounded tips of white oak (*Quercus alba* L.) leaves. The bark of northern red oak trees is variable but is generally dark gray with shallow fissures (figure 3). Northern red oak readily hybridizes with other species in the *Lobatae* section including scarlet oak (*Q. coccinea* Muenchh.), northern pin oak (*Q. ellipsoidalis* E.J. Hill), bear oak (*Q. ilicifolia* Wangenh.), shingle oak (*Q. imbricaria* Michx.), blackjack oak (*Q. marilandica* Muenchh.), water oak (*Q. nigra* L.), pin oak (*Q. palustris* Muenchh.), willow oak (*Q. phellos* L.), black oak (*Q. velutina* Lam.), and Shumard oak (*Q. shumardii* Buckl.) (figure 4). Hybrids can sometimes be difficult to detect morphologically (Aldrich et al. 2003) and may require molecular assessments to confirm. Hybridization does not occur with species in the white oak section (*Leucobalanus*).

Northern red oak is intermediate in its shade tolerance and can tolerate light shade (Gottschalk 1994, Phares 1970). Shelterwoods are a common silvicultural practice in northern red oak stands (Dey and Parker 1996), though regeneration success can be unreliable if a strong cohort of seedlings is absent before, or immediately after, the first cut. Fencing is often required to protect seedlings from herbivory (Miller

Figure 1. Acorns of northern red oak are oblong with a flat, scaly cap. Photo by C. Pike, USDA Forest Service, 2018.

et al. 2004, Redick et al. 2020), while management to control competing vegetation (yellow poplar [*Liriodendron tulipifera* L.], red maple [*Acer rubrum* L.], or sugar maple [*Acer saccharum* Marshall]) may also be needed to enable northern red oak to survive or thrive (Morrissey et al. 2010). Northern red oak is the most-planted hardwood tree in the Northeastern United States (Pike et al. 2018) and suitable for planting across a variety of site types, including riparian areas and reclaimed minelands (Adams 2017). The species is more commonly propagated as a bareroot seedling because of its prodigious root system (figure 5).

Figure 2. Leaves of northern red oak are oblong with toothed lobes and sharply pointed leaves. Photos by Mark Coggeshall, USDA Forest Service, 2021.

Genetics

Genetic structure of neutral DNA markers in northern red oak is more prominent latitudinally than longitudinally (Birchenko et al. 2009, Magni et al. 2005), likely due to the northward recolonization that followed glacial recession that was more rapid compared to other deciduous tree species (Davis 1983). Genetic diversity and gene flow in northern red oak is very high. The species is a complete outcrosser, and inbreeding is very low in natural stands (Schwarzmann and Gerhold 1991, Sork et al. 1993). The exceptionally high genetic diversity of northern

Figure 3. The bark of northern red oak is dark gray and scaly with ridges, but the species lacks the deeper fissures of others in the red oak family. Photo by Mark Coggeshall, USDA Forest Service, 2021.

red oak (compared to other hardwoods) is due, in part, to its ability to hybridize with other species in the *Lobatae* section, a feature that has resulted in weak phylogenetic structure, or weak differentiation, from other taxa in the red oak family (Magni et al. 2005). Despite its high gene flow, caching habits of its primary seed dispersers (squirrels) can create fine-scale genetic structure locally (Sork et al. 1993).

Figure 4. Northern red oak can naturally hybridize with other trees in the red oak family, such as Shumard oak (*Quercus shumardii*). The hybrids, as shown in this image, can be difficult to detect morphologically as hybrids may resemble one parent or have traits of both. Photo by Mark Coggeshall, USDA Forest Service, 2021.

Northern red oak is monoecious, wherein trees may produce both male and female reproductive structures on the same individual. Pollen is wind-dispersed, and acorns can be animal dispersed, primarily by gray squirrels, fox squirrels, and blue jays. The timing of pollen shed and female receptivity may be asynchronized among trees within a seed orchard or stand. This asynchronous phenology, in

Figure 5. Northern red oak seedlings have prodigious root systems that thrive in bareroot culture but may also be grown in large containers. Photo by Mark Coggeshall, University of Missouri, 2013.

which the same subset of trees share pollen from year to year, contributes to the presence of a Wahlund effect in which pollen is not shared equally among trees (Alexander and Woeste 2017, Jones et al. 2006, Moran and Clark 2012). Such effects can reduce expected levels of genetic diversity but can be offset by mixing seed from many sources and stands within a seed lot.

Seed-Transfer Considerations

Most phenotypic variation in northern red oak is generally not attributed to provenance of seed source (Deneke 1974, Kriebel et al. 1976, Kriebel et al. 1988, Leites et al. 2019) (figure 6). For example, family differences in acorn size and first-year seedling growth superseded differences among provenances, except for extreme far northern seed sources (Kriebel 1965). Even though provenance accounted for low levels of variation in older provenance trials, physiological differences in young seedlings planted in common gardens in Minnesota were detectable between northern seed sources grown in a common garden (Etterson et al. 2020). Geographic clines (north to south) are also evident for phenological traits such as date of flushing and timing of leaf coloration in the fall, although elevation, and to a lesser extent longitude, of seed origin can also affect leaf flushing and coloration (Schlarbaum and Bagley 1981). Older northern red oak trees from southern and western provenances had thicker bark than those from northern and eastern provenances, which is likely a fire adaptation attributed to sources originating from drier portions of its range (Russell and Dawson 1994). Radial growth in natural stands was most significantly correlated with early-season moisture from May through July (LeBlanc and Terrell 2011).

No studies to date have empirically assessed seed-transfer distances, but northern red oak is highly tolerant of long-distance seed-transfers (Schlarbaum 2021). A reassessment of older provenance trials revealed local adaptation in which southern sources were best in mild environments and northern sources were most suited to cool environments (Leites et al. 2019). Height growth in common gardens was most strongly correlated with maximum summer temperatures; correlations with minimum temperatures and growing season length were not significant (Leites et al. 2019). Assisted migration (i.e., moving seed sources at least one zone northward) may help offset adaptation lags. Western edge populations that are adapted to drier climates may be favored for areas where droughts are predicted to be more prevalent. Northward transfer distances of 200 mi (320 km), or roughly 3 degrees latitude, is likely a safe recommendation to avoid phenological mismatches but has not been explicitly tested. This distance is also recommended for conifers such as white spruce (*Picea glauca* [Moench] Voss), where genetic diversity is high among families but low among provenances (Thomson et al. 2010). Considerations for seed-transfer are summarized in table 1. Northern red oak is well suited for planting in the future because of its high genetic diversity, plasticity, fecundity from high seed production, and ability to regenerate from both stumps and seed. It also has strong juvenile growth allowing it to quickly establish on a new site.

Insects and Diseases

Red oak is often defoliated by insects, such as the nonnative spongy moth (*Lymantria dispar* L.). Periodic outbreaks of native defoliators such as fall cankerworm (*Alsophila pometaria* Harris), and

Figure 6. This range-wide provenance trial (17 years from planting) is one of several common gardens analyzed to study the geographic patterns of variation in northern red oak. Photo by Mark Coggeshall, University of Missouri, 2008.

forest tent caterpillar (*Malacosoma disstria* Hubner), can feed on northern red oak in the spring leading to stress and predisposition to decline from other factors (Asaro and Chamberlin 2019). Drought events can stress northern red oak, rendering it more vulnerable to red oak borer (*Enaphalodes rufulus* Haldeman) and two-lined chestnut borer (*Agrilus bilineatus* Weber), especially following defoliation events. Oak wilt (*Bretziella fagacearum* [Bretz] Z.W. de Beer, Marincowitz, T.A. Duong, & M.J. Wingfield, previously known as *Ceratosystis fagacearum*) is also a concern and can limit management efforts from mid-March through mid-July due to activity of insect vectors like bark beetles and ambrosia beetles (Scolytinae) and picnic beetles and sap beetles (Nitidulidae). Oak borers are active in late spring/early summer and will attack wounded (pruned) trees and others in close proximity. Bacterial leaf scorch (*Xylella fastidiosa*) of northern red oak has symptoms similar to oak wilt, but trees will decline in health over several years before they succumb and die (Wells et al. 1987).

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Summary for *Quercus rubra* L.

Northern red oak (*Quercus rubra* L.) is a large-seeded hardwood that grows in forests across eastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow and from hybridization with other species in the red oak section. Hybridization occurs readily across its range except in the northern parts of the range where other species in the red oak family are less common. Northern red oak is expected to thrive in a future climate because of its genetic diversity and inherent plasticity. Common garden studies revealed relatively weak clines for growth traits. No empirical transfer distances have been suggested, but distances of 200 mi (320 km), or roughly 3 degrees latitude northward, is a safe recommendation to avoid phenological mismatches. Oak wilt, a pathogen of concern, is slowly spreading across its range and may become more problematic in the future. Several insects impact northern red oak but are generally more problematic in older stands or stands that are weakened by other causes.

Table 1. Summary of silvics, biology, and transfer considerations for northern red oak.

	Northern red oak (*Quercus rubra*)
Genetics	• Genetic diversity: high • Gene flow: high to moderate • Does not readily inbreed and will not self-cross • Readily hybridizes with other oaks in the red oak section
Cone and seed traits	• Large seeded: 75 to 255 cleaned seeds per pound (165 to 561 per kg) (Bonner 2012) • Mammal dispersed
Insect and disease	• Defoliating insects: gypsy moth, two-lined chestnut borer • Pathogens: oak wilt is a growing pathogenic threat
Palatability to browse	• High risk of browse from deer: seedlings often require protection
Maximum transfer distances	• Relatively tolerant to long-distance transfers (300 mi [483 km]), but no empirical transfer distances have been calculated • • Transfer of 200 mi (322 km) (3° latitude from south to north) is likely well tolerated
Range-expansion potential	• High potential for northward expansion • Likely to maintain populations in current range

Tamarack tree. Photo by Steve Katovich.

Mini Seed-Transfer Profiles of Relevant Minor Tree species

Nicholas LaBonte and Carolyn C. Pike

Introduction

Common garden studies and investigations into population genetics have only been conducted for a relatively small subset of tree species in North America. As the climate changes and assisted migration becomes a more widespread tactic to improve adaptation of future forests, guidance to inform safe transfer distances for many tree species may not be available. In these instances, generic seed-transfer guidelines would be employed when empirical data are unavailable. The development of new common gardens, such as those recently installed for white oak (*Quercus alba* L.) across the Eastern United States, will lead to new information on seed-transfer that will replace outdated guidelines. Advances in biotechnology have lowered the costs for genome-wide studies that can be used to elucidate gene flow and population genetics; additional research for many species is ongoing and will also provide new information on patterns of genetic variation across the landscape.

This chapter summarizes information using a combination of established literature, when available, and inferences derived from life-history traits to describe genetic diversity and gene flow of several minor tree species. It also describes insect, disease, and herbivory challenges that may impact the planting success of these species. Lastly, for some species it suggests using seed-transfer guidelines from closely related species that have been more extensively studied. Recommendations for these minor species are summarized in table 1.

Acer saccharinum L.: Silver maple

Silver maple is a large, fast-growing tree found in floodplains across the Eastern United States. This species is especially abundant in the mid-Mississippi River Valley and is commonly planted in residential settings (figure 1). Silver maple is considerably less shade tolerant than other maples, such as red maple (*Acer rubrum* L.). A study of silver maple and red maple found that several chloroplast haplotypes were shared between the two species, and that silver maple had fewer haplotypes than red maple (Saeki et al. 2011). These differences are likely attributable to red maple's extensive plasticity and wide geographic range. A common garden study of several silver maple seed sources growing in southern Illinois found that southern provenances (Mississippi) performed much better than northern provenances (New Hampshire), which was attributed to a longer growing season (earlier budbreak and later budset) (Ashby et al. 1992). Silver maple is wind pollinated, meaning gene flow is likely also high, although there is no published research on this topic. Based on its large population size, broad distribution, and evidence of genetic differences from provenance trials, the species most likely has high genetic diversity. Seed-transfer guidelines for sugar maple (*Acer saccharum* Marshall) should be applicable to silver maple without risk of maladaptation. No major pests or outbreaks have been reported on silver maple in recent years.

Figure 1. These silver maple trees growing in a residential landscape (Illinois) show a very heavy seed crop in May as new foliage is beginning to emerge. Photo by N. Labonte, 2022.

Betula papyrifera Marshall: Paper birch

Paper birch is an early successional species with a large native range occurring most often in rocky habitats or wetlands across northeastern North America. Its pollen and seed are both dispersed by wind and can travel long distances. Seed-source tests in the western part of the paper birch range (British Columbia) showed strong adaptation to local conditions (Benowicz et al. 2001), though climatic variability is much greater over short distances in the West than in the Great Lakes region. Paper birch, a hexaploid, has high heterozygosity in natural populations and low genetic differentiation in the Eastern United States (Thomson et al. 2015). A second, externally similar birch species, heartleaf birch (*Betula cordifolia* Regel), which is sometimes considered a variety of paper birch, occurs in northeastern North America and tends to have a lower number of chromosome copies than paper birch (DeHond and Campbell 1989, Wang et al. 2021). A common garden study in eastern Canada found slightly better 1-year height growth by populations originating from lower latitudes than the planting site (Oke and Wang 2013). Care should be taken to identify paper birch for seed collection because paper birch can hybridize with yellow birch (*Betula alleghaniensis* Britt.) (Barnes et al. 1974) and sweet birch (*Betula lenta* L.) where the species coexist (Thomson et al. 2015). Seed-transfer guidelines for yellow birch should be applicable to paper birch in the Great Lakes region, and likely to other parts of the range. Few pests affect young birch trees, but bronze birch borer (*Agrilus anxius* Gory) pact older trees. Forest health is often compounded in even-aged, older, mature stands (figure 2).

Figure 2. Paper birch is a relatively short-lived, early-successional tree. Photo by C. Pike, 2017.

Celtis occidentalis L.: Hackberry

Based on its life history and abundance within its native range, it is likely that hackberry has high genetic diversity and high gene flow. Hackberry is wind pollinated, and its seeds are eaten and dispersed by birds. Both wind and bird dispersal tend to lead to effective long-distance pollen and seed-mediated gene flow. Seed-transfer guidelines for black cherry (*Prunus serotina* Ehrh.) would likely provide a reasonable approximation for hackberry. Several insects and pathogens may infect hackberry (Krajicek and Williams 1990), but no large-scale forest health issues have been reported in recent years.

Fagus grandifolia Ehrh.: American beech

American beech commonly inhabits the forest understory in mesic forests across the Eastern United States because of its high degree of shade tolerance and recruitment ability. American beech propagates by seed and clonally via root sprouts, which affects the genetic architecture of stands (Houston and Houston 1994). Genetic diversity, using enzymes, is high, but populations are more substructured than other wind-pollinated trees (Kitamura and Kawano 2001), which is an indicator of lower-than-expected gene flow. This substructuring is likely the result of different reproductive strategies: some American beech populations rely almost exclusively on sprouting with little seedling recruitment, while recruitment is more common for populations in other forest types (Kitamura et al. 2001). These different modes of reproduction can sustain rare alleles and reinforce differences in genetic origin that resulted from prior glacial refugia. As a result, differences among populations that would normally disappear with wind pollination are sustained on the landscape. Seed-transfer has not been explicitly studied, but guidelines for red oak (*Quercus rubra* L.), which is also a large-seeded masting species that can sprout from stumps, may be a reasonable surrogate. In recent years, success in resistance breeding to beech bark disease (Ćalić et al. 2017) has led to an increase in demand for resistant seed for restoration where disease pressure is high. Beech leaf disease, a recently emerged pest associated with a nematode (*Litylenchus crenatae* subsp. *mccannii*), is currently a major threat to beech populations in the Eastern United States, but the biology is not yet fully understood (Burke et al. 2020).

Larix laricina (Du Roi) K. Koch: Tamarack

Tamarack is characteristically a species of wet forests, growing with lowland hardwoods and northern white cedar (*Thuja occidentalis* L.) on richer sites and black spruce (*Picea mariana* [Mill.] Britton, Sterns, & Poggenb.) on poorer sites. Tamarack can also form nearly pure stands (figure 3). Tamarack is a wind-pollinated conifer with a large native range. Populations are generally not well-structured, implying that gene flow is relatively high and consistent with other conifers (Cheliak et al. 1988, Knowles et al. 1992, Liu and Knowles 1991, Napier et al. 2020). Common garden and provenance tests have shown either a slightly better height growth and survival by southern sources compared with northern sources (Farmer et al. 1992) or variation among seed sources with no clear geographic pattern (Cech et al. 1977, Jeffers 1975). Given this information, tamarack seed collections should emphasize diversity and include sampling from as many stands as possible. Assisted migration of tamarack may help northern populations adapt to increased drought and insect pressure under climate change. Seed-transfer guidelines for black spruce should be a close approximation to tamarack.

Although still widespread in the Great Lakes region, tamarack has declined in importance due to logging,

Figure 3. Tamarack often grows in pure stands, such as trees on this peatland in southern Wisconsin. Photo by N. Labonte, 2022.

forest conversion to other land uses, and mortality caused by larch sawfly (*Pristiphora erichsonii* Hartig), eastern larch beetle (*Dendroctonus simplex* LeConte) (Minnesota Department of Natural Resources 2013), and larch casebearer (*Coleophora laricella* Hübner) (Ward et al. 2021). Climate change may increase the number of broods per year of the insect (McKee and Aukema 2014, 2015) and may be especially important for tamaracks growing along southern range edges.

Thuja occidentalis L.: Northern white cedar

Northern white cedar is a long-lived, culturally significant species. It is most often found in swamp forests and riparian areas but also occurs on exposed, dry, rocky cliff sites. Northern white cedar reproduces by seed (figure 4) or clonally by layering when branches and trunks readily form new roots when in contact with a wet substrate. Northern white cedar has, like most conifers, high genetic diversity and gene flow among populations (Pandey and Rajora 2012). Isolated populations show higher genetic differentiation than stands in areas where the species is abundant (Lamy et al. 1999, Pandey and Rajora 2012, Xu et al. 2012). No common garden studies or provenance tests incorporating sources from a large portion of the native range have been reported in the literature. Common garden studies of northern white cedar from cliffs and swamps found no evidence of ecotype differentiation (Matthes-Sears and Larson 1991). Seed should be collected from multiple stands, especially in areas where stands are relatively isolated, to ensure that the seed source has adequate genetic diversity. Seed-transfer guidelines for black spruce should be a close approximation to northern white cedar. Northern white cedar has no notable pests or diseases but is a preferred browse species by white-tailed deer (*Odocoileus virginianus* Zimmermann).

Figure 4. White cedar cones usually ripen in early September in southern Wisconsin. Photo by N. Labonte, 2022.

Tsuga canadensis (L.) Carrière: Eastern hemlock

Eastern hemlock is a large, long-lived, wind-pollinated species with a large native range. It has distinctly low within-population genetic diversity, heterozygosity, and among-population gene flow compared with species with similar life-history characteristics (Hawley et al. 2000, Potter et al. 2008, Potter et al. 2012). Eastern hemlock can self-pollinate when population sizes are small, which has likely contributed to low heterozygosity and decreased gene flow. The small remnant populations of eastern hemlock in Minnesota have low genetic diversity and high differentiation (Ellingson 2017), probably due to isolation and inbreeding of current and founding populations (Potter et al. 2012). In locations where the local populations are small and isolated, seed should be sourced from the nearest location where the species is abundant to ensure genetic diversity and increase the adaptability of seedlings produced. Resistance breeding and gene conservation have been the focus areas for hemlock management. No common gardens designed to test seed-transfer have been established to date.

Eastern hemlock is heavily impacted by two pests that can co-occur on trees: hemlock woolly adelgid

(*Adelges tsugae* Annand) and elongate hemlock scale (*Fiorinia externa* Ferris) (Preisser et al. 2011). The woolly adelgid, a homopteran, is a significant pest and has led to the decline of large trees across the range of eastern hemlock. Both insects are relatively slow moving but continue to advance across the range of eastern hemlock, threatening ecosystems where eastern hemlock is dominant.

Tilia americana L.: American basswood

American basswood, or linden, is a shade-tolerant species that is associated with sugar maple in mesic hardwood forests throughout the Northeastern United States and adjacent parts of Canada (figure 5). American basswood is most important as a canopy species in the upper Mississippi Valley and northern Great Lakes, where American beech is rare or not present as a competitor in the understory. American basswood produces nectar-rich flowers pollinated by a variety of nocturnal and diurnal insects, and its relatively large, dry fruits are dispersed by gravity.

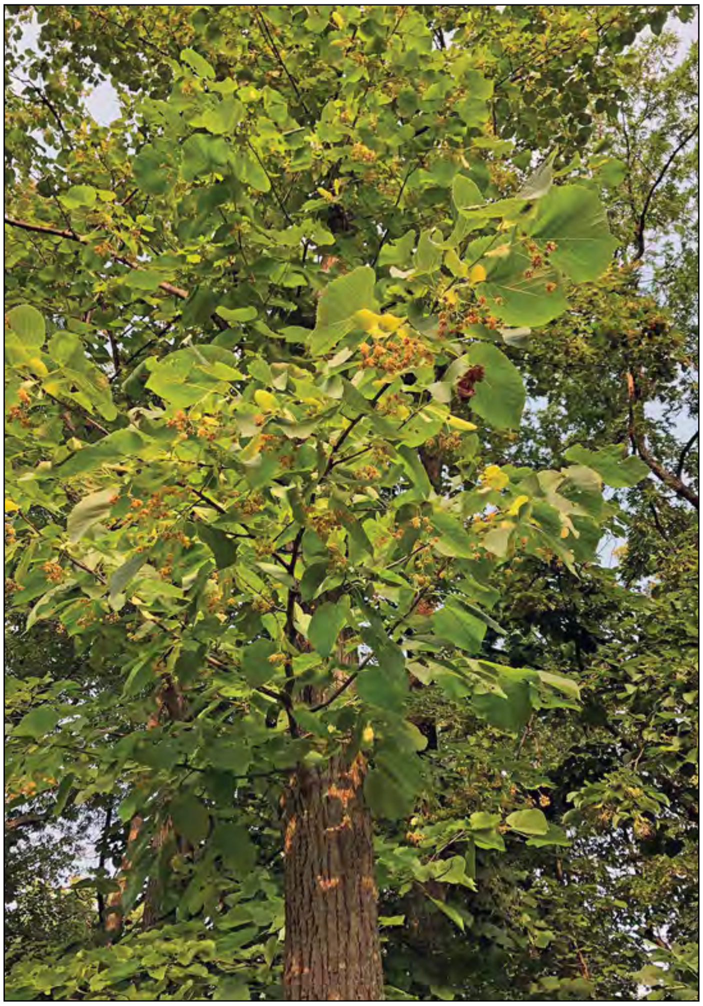

Figure 5. American basswood often occurs as a large tree in dry-mesic hardwood forests in southeastern Wisconsin. Photo by N. Labonte, 2022.

A phylogenetic study of American basswood chloroplast DNA found several intermixed haplotypes across its northeastern range. The species is also morphologically variable. Both factors suggest high genetic diversity (McCarthy and Mason-Gamer 2017). Gene flow, however, is more difficult to determine for American basswood. Insect pollinators do not necessarily constrain gene flow, but gravity-dispersed seeds do. It is possible that American basswood has lower gene flow than species with more effective seed-dispersal mechanisms, such as black cherry or red oak. Studies of closely related European species (Danusevicius et al. 2021, Erichsen et al. 2019) found high genetic diversity and high gene flow, even among fragmented populations. Seed-transfer guidelines developed for sugar maple should also be suitable for American basswood. The basswood thrips (*Thrips calcaratus* Uzel) is reportedly a pest in the Great Lakes region (Werner et al. 2005), but few other insects and diseases affect basswood trees.

Quercus alba L., *Q. macrocarpa* Michx., *Q. bicolor* Wild.: White oaks

Like red oak, trees in the white oak group show high heterozygosity, gene flow, and genetic diversity in surveys of wild populations (Craft and Ashley 2006). Common gardens of white oak (figure 6) did not reveal clear geographic trends (Huang et al. 2016), but the sample size and number of gardens was relatively small. In contrast, a common garden of bur oak (figure 7) showed geographic variation in performance, with sources from the near-south of the planting site and local sources performing best (Dicke and Bagley 1980). Species in the white oak group may hybridize with each other in the wild, but species are maintained by specific ecological adaptations of each lineage (Hipp et al. 2019). Seed-transfer recommendations for red oak could be applied to trees in the white oak group, unless newly established common gardens provide refined information.

Figure 6. This common garden of white oak is now used as a seed orchard. Photo by Mark Coggeshall, University of Missouri, 2015

Figure 7. These bur oak acorns are about 1 month prior to ripening, in July, in southeastern Wisconsin. Photo by N. Labonte, 2022.

Ulmus americana L.: American elm

American elm is associated with floodplain forests across the Eastern United States and was once a common tree in urban environments until Dutch elm disease arrived in the 20th century and decimated those populations. American elm is a tetraploid species (Whittemore and Olsen 2011) that likely possesses high genetic diversity and gene flow (Brunet and Guries 2017), but population genetics have not been explicitly studied. The number of large mature individuals in natural floodplain forests has declined, but smaller seedlings and saplings remain common in the understory (Marks 2017). Seed-transfer guidelines are not established, but the high genetic diversity of American elm likely allows for long-distance movement of 200 to 300 miles (322 to 482 km) or further. Cultivars with increased resistance to Dutch elm disease are available (Haugen and Bentz 2017). In addition, development of seed sources with improved resistance and high genetic diversity for restoration purposes is also underway (Pinchot et al. in press). Elm yellows, a mycoplasma, remains a threat to elm populations as well (Marcone 2016).

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Summary of Minor Tree Species

For species with high gene flow and high genetic diversity, sampling many individuals from a local population (a large stand) will capture a large amount of genetic diversity. For species with moderate or low gene flow and moderate or high genetic diversity, sampling individuals from several local populations (stands) and pooling is recommended to obtain a genetically diverse seed collection. For species with moderate or low gene flow and low genetic diversity, obtaining a sample with high genetic diversity will be difficult and unlikely to affect successful outcomes because natural populations of the species have low diversity.

Table 1. Summary of genetic characteristics of minor tree species.

Species	Genetic diversity	Gene flow	Notes
Acer saccharinum: Silver maple	Likely high but unconfirmed	Unknown	Introgression with red maple may occur at range margins but limited studies on genetics.
Betula papyrifera: Paper birch	High	High	Introgression with yellow birch and sweet birch. Pests associated with decadent stands include bronze birch borer and leaf miners.
Celtis occidentalis: Hackberry	Likely high but unconfirmed	High (inferred based on pollination, seed dispersal, distribution, and life history characteristics)	Not studied; gene flow inferred from seed dispersal mechanism (similar to black cherry).
Fagus grandifolia: American beech	High	Moderate-high because of clonal and seed based reproduction	Limited gene flow where root sprouts are common. Recruitment by seedlings may be high. Beech bark disease and beech leaf disease are major pests.
Larix laricina: Tamarack	High	Moderate-high	Limited gene flow where uncommon. Major pests include larch beetle, casebearer, and sawfly
Thuja occidentalis: Northern white-cedar	High	Moderate-high	Limited gene flow where uncommon. Heavily browsed by white-tailed deer.
Tsuga canadensis: Eastern hemlock	Moderate	Moderate	Self-pollination in isolated stands. Major pests include hemlock woolly adelgid and elongate hemlock scale
Tilia americana: American basswood	High	Moderate-high	Evidence for high diversity based on chloroplast DNA.
Quercus alba, Q. macrocarpa, Q. bicolor: White oak, bur oak, and swamp white oak	Very high	High	Evidence for high diversity based on chloroplast DNA.
Ulmus americana: American elm	Very high	High	Tetraploids are common, and diploids/triploids are described. Elm yellows, a phytoplasm, and Dutch elm disease are major pests.