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

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Abstract

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 moderate 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 its 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.

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 Mountain 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

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

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 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 (e.g., 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 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.) (e.g., 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).

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

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

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 Nick LaBonte, 2022)

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, northern Wisconsin. (Photo by Paul Berrang, USDA Forest Service, 2003)

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 eastern white pine 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 seed (figure 5). Eastern white pine is a preferred browse species (Wendel et al. 1990) and may 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.

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)

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 became postglacial colonizers east and west of the Appalachians. 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).

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, Northeastern United States, Michigan, and southern Ontario sources 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 rangewide tests (Joyce and Rehfeldt 2013), which indicates that obtaining seed from up to several hundred miles south of the planting site is a good practice. 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 more than 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).

Insect and Disease

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 lifecycle 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).

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

Eastern white pine, ***Pinus strobus*** **L.**	
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	• 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

Eastern white pine harbors naturally occurring resistance to white pine blister rust. Thus, 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, even though 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 improved blister-rust resistant lines are suitable for planting in high-risk areas if they are available.

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

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 credit: Paul Berrang, USDA Forest Service, 2007)

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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