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

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Abstract

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.

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 (*P. strobus* L.), jack pine (*P. 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 (e.g., 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 (e.g., figure 2).

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. (Photo by Nick LaBonte, 2021)

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 Quebec, where crown fires are relatively frequent (Flannigan and Bergeron 1998).

Figure 2. This rangewide red pine provenance trial at the Cloquet Experimental Forest in Minnesota is similar in appearance to the numerous planted stands of red pine in the Great Lakes region. (Photo by Jim Warren, USDA Forest Service, 2004)

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.

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.

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* sp. is frequently found in naturally occurring red pine stands. (Photo by Nick LaBonte, 2021)

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} ~ 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

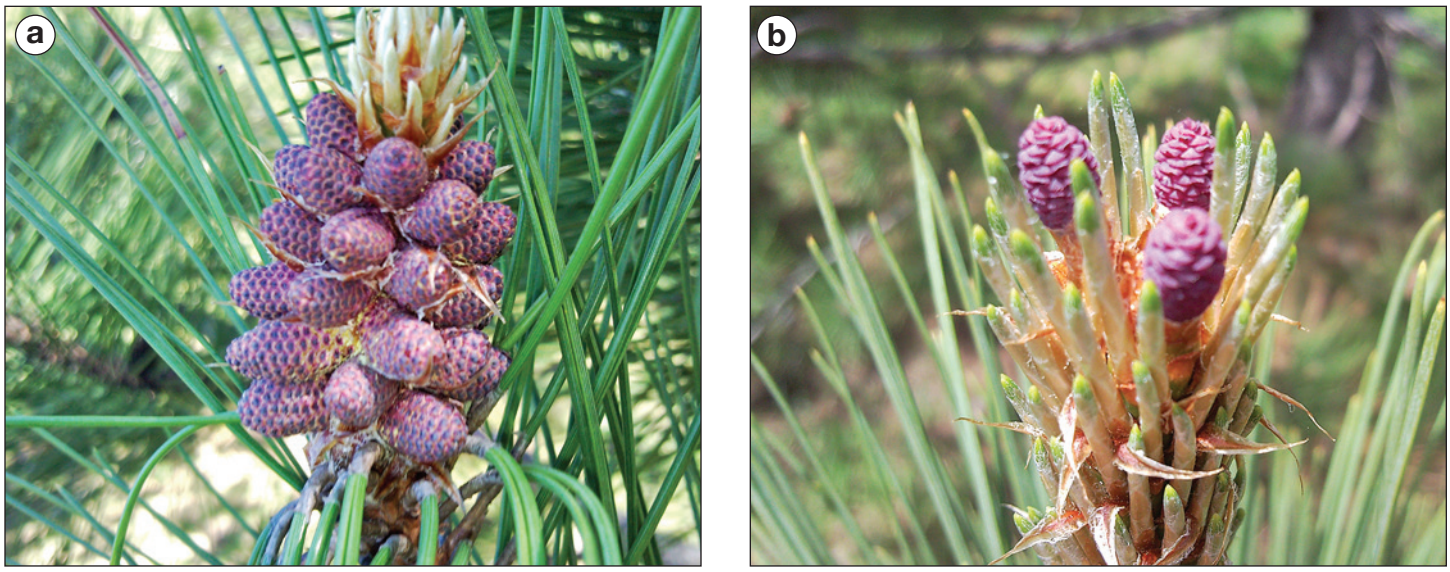

Figure 4. (a) Male and (b) female strobili of red pine in Minnesota. (Photos by Carrie Pike, USDA Forest Service, 2014)

Figure 5. Second-year cones on this red pine tree are nearly ripe enough for picking. (Photo by Nick LaBonte, 2021)

among provenances tends to be small if significant (Lester and Barr 1965), and the same sources tend to 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 Nick LaBonte, 2021)

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

Red pine, *Pinus resinosa* Aiton	
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	• Seed can be moved over a large distance (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

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* sp. 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 sp.) can kill stressed mature red pine trees. Cone beetles can cause severe damage to seed crops (Gilmore and Palik 2006).

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