

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

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Abstract

Jack pine 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 pine originating from southern sources tend to out-grow 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.

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 warbler (*Setophaga kirtlandii* [Baird] [Parulidae]), 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* [Zimmerman]) 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.



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



Figure 2. Jack pine is common in the boreal forests of northeastern Minnesota where tree form is often tall and straight. (Photo by C. Pike, 2008)

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 tend 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 the Northwest Territories of Canada (Wheeler and Guries 1987).

Genetic diversity in jack pine varies clinally across its range, but population sub-structure is evident from studies of neutral DNA (genes that are not associated with physical traits). In pines, chloroplasts are paternally inherited (via pollen). Chloroplast DNA (cpDNA) 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, Quebec, 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 (mtDNA), which is maternally inherited, revealed pronounced separations among populations (Godbout et al. 2010, Godbout et al. 2005) 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



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, a trait that also varies geographically, though the adaptive value is unknown. (Photo by C. Pike, 2010)

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 sub-structure has been attributed to different glacial refugia (Critchfield 1985) but underlying causes remain unresolved.

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



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

and Parker 2008, van Niejenhuis and Parker 1996). Seed sources originating approximately 100 mi (160 km) (1 to 2° latitude) 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 1° latitude (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 precipitation to a lesser degree (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,

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

Jack pine, <i>Pinus banksiana</i> Lamb	
Genetics	<ul style="list-style-type: none"> • Genetic diversity: high • Gene flow: high (pollen); medium (seed)
Cone and seed traits	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • Jack pine budworm, sawfly • Eastern gall rust, western gall rust, Diplopedia (young seedlings)
Palatability to browse	<ul style="list-style-type: none"> • Moderate to high browsing from white-tailed deer in the winter months
Maximum transfer distances	<ul style="list-style-type: none"> • Seed sources originating 70 to 140 miles south of the planting site (112 to 225 km; 1 to 2° latitude) display higher growth rates than local sources
Range-expansion potential	<ul style="list-style-type: none"> • Likely to shift range northward into Canada but southern range edge may persist in the United States due to its drought tolerance

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 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 red headed pine sawfly (*Neodiprion lecontei* [Fitch]) and jack pine sawfly (*Neodiprion Swaini* 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 jack pine seedlings in the Lake States (Stanosz et al. 2007; Nicholls 1990). 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.

Acknowledgments

This manuscript was reviewed and revised with input from partners from Michigan State University (Paul Bloese), USDA Forest Service (Steve Katovich, Nick LaBonte, Prasad Anantha, Katie Frerker, and Kaysee Miller), and Minnesota Department of Natural Resources (Deb Pitt and Mike Reinkainen).

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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. This sample was observed at a seed orchard in Minnesota. (Photo by C. Pike 2008)

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