



**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.

# Loblolly Pine: Guidance for Seed Transfer Within the Eastern United States

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

*Regeneration Specialist, U.S. Department of Agriculture (USDA), Forest Service, Eastern Region, State, Private, and Tribal Forestry, West Lafayette, IN; Research Geneticist and Project Leader, USDA Forest Service, Southern Research Station, Lexington, KY; Research Ecologist, USDA Forest Service, Southern Research Station, Research Triangle Park, NC*

## Abstract

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.

## 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,



**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.

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 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 (Schmidting 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 (Schmidting 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* 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 (figure 3) (Grossnickle and South 2017, Porterfield 2006), performing best on mildly acidic nursery soils (South 2017). Young seedlings, whether in the nursery or



**Figure 3.** Most loblolly pine seedlings being 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.

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, 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 have 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 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 (Schmidting 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, which informs seed zone recommendations formulated by Schmidting (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 and 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 midparent (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



**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.

Sonderegger pines (Henderson and Schoenike 1981). Loblolly pine also forms natural hybrids with pitch pine (*P. rigida* Mill.) in New Jersey, Maryland, and Delaware, and with 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 (Schmidting 2001). Winter temperatures are the best predictors of height growth in loblolly pine, including AAMT and number of frost-free days (Schmidting 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 (Schmidting 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 (Schmidting 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



**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.

in the eastern seed zone, particularly for droughty sites and areas with high fusiform rust exposure, though these western sources will likely grow slower (Schmidting 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 Schmidting (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.

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

Loblolly pine ( <i>Pinus taeda</i> )	
Genetics	<ul style="list-style-type: none"> <li>• Genetic diversity: high</li> <li>• Gene flow: high</li> </ul>
Cone and seed traits	<ul style="list-style-type: none"> <li>• Average 18,000 seeds per pound (40,000/kg) (Krugman and Jenkinson 2008)</li> <li>• Cone/seed bearing may begin at 5 to 10 years; cone crops occur every 3 to 13 years (Krugman and Jenkinson 2008)</li> </ul>
Insect and disease	<ul style="list-style-type: none"> <li>• Insects: southern pine beetle</li> <li>• Diseases: fusiform rust, pitch canker, brown spot needle blight</li> </ul>
Maximum transfer distances	<ul style="list-style-type: none"> <li>• Intermediate tolerance to seed transfer (200–300 mi [322–483 km])</li> <li>• 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</li> <li>• East to west transfer is not recommended, while west to east transfer might be acceptable for some sites provided that north-south transfer guidelines are followed</li> </ul>
Palatability to browse	<ul style="list-style-type: none"> <li>• Browse is rarely reported, but white-tailed deer in northern areas of the range are known to consume needles and may threaten seed sources that are moved northward</li> </ul>
Range-expansion potential	<ul style="list-style-type: none"> <li>• Expected to have generally favorable potential in a warmer climate because of broad ecological amplitude, high abundance, and good fire tolerance</li> </ul>

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).

**Address Correspondence to:**

Carolyn Pike, 715 Mitch Daniels Blvd, Pfendler Hall, West Lafayette, IN 47907; email: carolyn.c.pike@usda.gov; phone: 765-490-0004.

## References

- Abrahams, A. 2023. Personal communication. Assistant professor, Auburn University, Auburn, AL.
- Acosta, J.J.; Fahrenkrog, A.M.; Neves, L.G.; Resende, M.F.R.; Dervinis, C.; Davis, J.M.; Holliday, J.A.; Kirst, M. 2019. Exome resequencing reveals evolutionary history, genomic diversity, and targets of selection in the conifers *Pinus taeda* and *Pinus elliottii*. *Genome Biology and Evolution*. 11(2): 508–520. <https://doi.org/10.1093/gbe/evz016>.
- Alden, H.A. 1997. Softwoods of North America. Gen. Tech. Rep. FPL–GTR–102. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 151 p.
- Baker, J.B.; Langdon, O.G. 1990. *Pinus taeda* L. loblolly pine. In: Burns, R.M.; Honkala, B.H., tech. cords. Silvics of North America, vol 1, conifers. Ag. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 497–512. [https://www.srs.fs.usda.gov/pubs/misc/ag\\_654/volume\\_1/Pinus/taeda.htm](https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_1/Pinus/taeda.htm).
- Bannister, P.; Neuner, G. 2001. Frost resistance and the distribution of conifers. In: Bigras, F.J.; Colombo, S.J., eds. Conifer cold hardiness. Dordrecht, The Netherlands: Kuwer Academic Publishers: 3–22. [https://doi.org/10.1007/978-94-015-9650-3\\_1](https://doi.org/10.1007/978-94-015-9650-3_1).
- Bradley, J.C.; Will, R.E.; Stewart, J.F.; Nelson, C.D.; Guldin, J.M. 2016. Post-fire resprouting of shortleaf pine is facilitated by a morphological trait but fire eliminates shortleaf x loblolly pine hybrid seedlings. *Forest Ecology and Management*. 379: 146–152. <https://doi.org/10.1016/j.foreco.2016.08.016>.
- Bridgwater, F.; Kubisiak, T.; Byram, T.; McKeand, S. 2005. Risk assessment with current deployment strategies for fusiform rust-resistant loblolly and slash pines. *Southern Journal of Applied Forestry*. 29(2): 80–87. <https://doi.org/10.1093/sjaf/29.2.80>.
- Carson, S.D.; Carson, M.J. 1989. Breeding for resistance in forest trees - a quantitative genetic approach. *Annual Review of Phytopathology*. 27(23): 373–395. <https://doi.org/10.1146/annurev.py.27.090189.002105>.
- Cram, M.M.; Outcalt, K.W.; Zarnoch, S.J. 2010. Growth of longleaf and loblolly pine planted on South Carolina sandhill sites. *Southern Journal of Applied Forestry*. 34(2): 79–83. <https://doi.org/10.1093/sjaf/34.2.79>.
- Crocker, S.J.; Barnett, C.J.; Butler, B.J.; Hatfield, M.A. et al. 2017. New Jersey forests 2013. Resour. Bull. NRS-109. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 90 p.
- Crocker, S.J.; Brand, G.J.; Butler, B.J.; Haugen, D.E. et al. 2009. Illinois' forests 2005. Resour. Bull. NRS-29. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 114 p.
- Cumbie, P.W.; Isik, F.; McKeand, S.E. 2012. Genetic improvement of sawtimber potential in loblolly pine. *Forest Science*. 58(2): 168–177. <https://doi.org/10.5849/forsci.09-060>.
- Echt, C.S.; Deverno, L.L.; Anzidei, M.; Vendramin, G.G. 1998. Chloroplast microsatellites reveal population genetic diversity in red pine, *Pinus resinosa* Ait. *Molecular Ecology*. 7(3): 307–316. <https://doi.org/10.1046/j.1365-294x.1998.00350.x>.
- Eckert, A.J.; van Heerwaarden, J.; Wegrzyn, J.L.; Nelson, C.D.; Ross-Ibarra, J.; González-Martínez, S.C.; Neale, D.B. 2010. Patterns of population structure and environmental associations to aridity across the range of loblolly pine (*Pinus taeda* L., Pinaceae). *Genetics*. 185: 969–982. <https://doi.org/10.1534/genetics.110.115543>.
- Edwards, M.A. 1987. Natural regeneration of loblolly pine. A loblolly pine management guide, Gen. Tech. Rep. SE-47. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 17 p.
- Edwards, M.A.; Hamrick, J.L. 1995. Genetic variation in shortleaf pine, *Pinus echinata* Mill. (Pinaceae). *Forest Genetics*. 2(1): 21–28.
- Florence, L.Z.; Hicks, R.R.J. 1980. Further evidence of introgression of *Pinus taeda* with *P. echinata*: electrophoretic variability and variation in resistance to *Cronartium fusiforme*. *Silvae Genetica*. 29(3): 41–43.
- Grossnickle, S.C.; South, D.B. 2017. Seeding quality of southern pines: influence of plant attributes. *Tree Planters' Notes*. 60(2): 29–40.
- Hamrick, J.L.; Platt, W.J.; Hessing, M. 1993. Genetic variation in longleaf pine. In: Hermann, S.M., ed. Proceedings of the Tall Timbers Fire Ecology Conference, No. 18. Tallahassee, FL: Tall Timbers Research Station: 193–203.
- Henderson, L.T.; Schoenike, R.E. 1981. How good is Sonderegger pine? *Southern Journal of Applied Forestry*. 5(4): 183–186. <https://doi.org/10.1093/sjaf/5.4.183>.
- Hooker, J.M.; Oswald, B.P.; Stovall, J.P.; Weng, Y.; Williams, H.M.; Grogan, J. 2021. Third year survival, growth, and water relations of west Gulf coastal plain pines in east Texas. *Forest Science*. 67(3): 347–355. <https://doi.org/10.1093/forsci/xfab005>.
- Huang, C.H.; Bates, R.; Kronrad, G.D.; Cheng, S. 2004. Economic analyses of sequestering carbon in loblolly pine, cherrybark oak, and northern red oak in the United States. *Environmental Management*. 33(SUPPL. 1): 187–199. <https://doi.org/10.1007/s00267-003-9129-y>.
- Isik, F.; McKeand, S.E. 2019. Fourth cycle breeding and testing strategy for *Pinus taeda* in the NC State University Cooperative Tree Improvement Program. *Tree Genetics and Genomes*. 15(70). <https://doi.org/10.1007/s11295-019-1377-y>.
- Iverson, L.; Schwartz, M.W.; Prasad, A. 2004. Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*. 19: 787–799. <https://doi.org/10.1007/s10980-005-3990-5>.

- Krugman, S.L.; Jenkinson, J.L. 2008. *Pinus* L. In: Bronner, F.; Karrfalt, R.P., eds. The woody plant seed manual. Ag. Handb. 727. Washington, DC: U.S. Department of Agriculture, Forest Service: 809–847.
- Lu, M.; Krutovsky, K.V.; Nelson, C.D.; Koralewski, T.E.; Byram, T.D.; Loopstra, C.A. 2016. Exome genotyping, linkage disequilibrium and population structure analysis in loblolly pine (*Pinus taeda* L.). BMC Genomics. 17: 730. <https://doi.org/10.1186/s12864-016-3081-8>.
- McKeand, S.E.; Payn, K.G.; Heine, A.J.; Abt, R.C. 2021. Economic significance of continued improvement of loblolly pine genetics and its efficient deployment to landowners in the southern United States. Journal of Forestry. 119(1): 62–72. <https://doi.org/10.1093/jofore/fvaa044>.
- Moser, W.K.; Treiman, T.; Johnson, R. 2003. Species choice and the risk of disease and insect attack: evaluating two methods of choosing between longleaf and other pines. Forestry. 76(2): 137–147. <https://doi.org/10.1093/forestry/76.2.137>.
- Perry, T.O.; Wang, C.-W.; Schmitt, D. 1966. Height growth for loblolly pine provenances in relation to photoperiod and growing season. Silvae Genetica. 15(3): 61–64.
- Peters, M.P.; Prasad, A.M.; Matthews, S.N.; Iverson, L.R. 2020. Climate change tree atlas, Version 4. Delaware, OH: U.S. Department of Agriculture, Forest Service, Northern Research Station and Northern Institute of Applied Climate Science. <https://www.fs.usda.gov/nrs/atlas/>. (November 2023)
- Pickens, B.; Crate, S. 2018. Cold weather injury to southern yellow pine seedlings. TRB-011. Raleigh, NC: North Carolina Forest Service. 3 p.
- Pile, L. S.; Wang, G.G.; Knapp, B.O.; Liu, G.; Yu, D. 2017. Comparing morphology and physiology of southeastern US *Pinus* seedlings: implications for adaptation to surface fire regimes. Annals of Forest Science. 74(4). <https://doi.org/10.1007/s13595-017-0666-6>.
- Porterfield, D. 2006. Growing loblolly pines from seed in pots. Forestry Notes. Oklahoma City, OK: Oklahoma Department of Agriculture, Food, and Forestry - Forestry Services Division. 2 p.
- Schmidting, R.C. 1994. Use of provenance tests to predict response to climatic change: loblolly pine and Norway spruce. Tree Physiology. 14(7–9): 805–817. <https://doi.org/10.1093/treephys/14.7-8-9.805>.
- Schmidting, R.C. 2001. Southern pine seed sources. Gen. Tech. Rep. SRS-44. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 25 p. <https://doi.org/10.2737/SRS-GTR-44>.
- Schmidting, R.C. 2003. Determining seed transfer guidelines for southern pines. In: Riley, L.E.; Dumroese, R.K.; Landis, T.D., eds. National proceedings: forest and conservation nursery associations. Moscow, ID: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 8–11.
- Schmidting, R.C.; Carroll, E.; Lafarge, T. 1999. Allozyme diversity of selected and natural loblolly pine populations. Silvae Genetica. 48(1): 35–45.
- Schoenike, R.E.; Hart, J.D.; Gibson, M.D. 1975. Growth of a nine-year-old Sonderegger pine plantation in South Carolina. Silvae Genetica. 24(1): 10–11.
- Sierra-Lucero, V.; McKeand, S.E.; Huber, D.A.; Rockwood, D.L.; White, T.L. 2002. Performance differences and genetic parameters for four coastal provenances of loblolly pine in the southeastern United States. Forest Science. 48(4): 732–742. <https://doi.org/10.1093/forestscience/48.4.732>.
- South, D.B. 2017. Optimum pH for growing pine seedlings. Tree Planters' Notes. 60(2): 49–62.
- U.S. Department of Agriculture, Natural Resources Conservation Service [USDA NRCS]. 2023. PLANTS Database. <http://plants.usda.gov>. (October 2023)
- van der Nest, A.; Wingfield, M.J.; Janousek, J.; Barnes, I. 2019. *Lecanosticta acicola*: a growing threat to expanding global pine forests and plantations. Molecular Plant Pathology. 20(10): 1327–1364. <https://doi.org/10.1111/mpp.12853>.
- Wells, O.O.; Wakeley, P.C. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. Forest Science, monograph 11. 40 p.
- Williams, M.I.; Dumroese, R.K. 2014. Planning the future's forests with assisted migration. In: Sample, V.A.; Bixler, R.P., editors. Forest conservation and management in the Anthropocene: conference proceedings. Proceedings. RMRS-P-71. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 133–144.
- Xu, S.; Tauer, C.G.; Nelson, C.D. 2008. Natural hybridization within seed sources of shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*Pinus taeda* L.). Tree Genetics and Genomes. 4: 849–858. <https://doi.org/10.1007/s11295-008-0157-x>.