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

Carolyn C. Pike and C. Dana Nelson

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

Abstract

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.

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.).

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 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 [*P. 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).

Longleaf pine timber is relatively heavy and strong compared with other pines, with a straight grain that is desirable by 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).

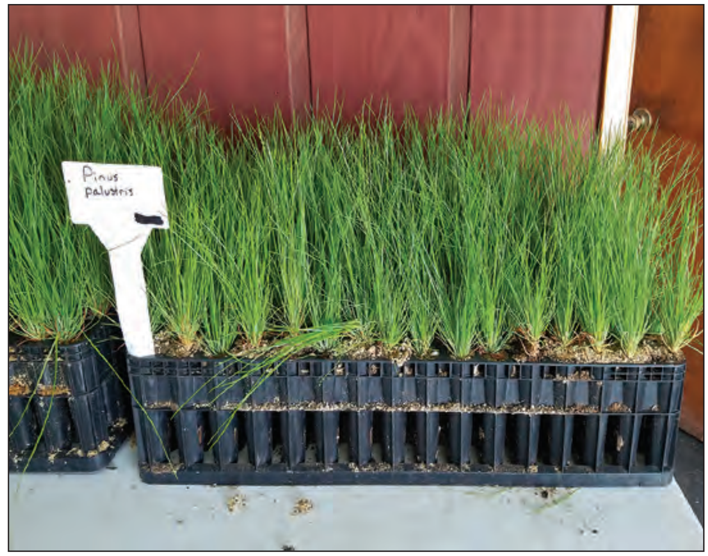

Figure 2. Longleaf pine containerized stock is generally more successful in planting than bareroot stock. (Photo by C. Pike, 2018)

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 10 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).

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).

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, 2018)

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 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 FST values of 0.041 indicate that populations are not strongly differentiated (Schmidtling and Hipkins 1998).

Longleaf pine has relatively large seeds compared with 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

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

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 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* [Zimmerman]), 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 disease 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.

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

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

Longleaf pine, *Pinus palustris* Mill.	
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• 4,900 seeds per pound (10,800 per kg) (Krugman and Jenkinson 2008) • Trees 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	• 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
Species range-expansion potential	• Longleaf pine is expected to be generally favored in a warming climate because of its adaptability to fire

Address correspondence to—

Carolyn C. Pike, Regeneration Specialist, USDA Forest Service, 767-799 Mitch Daniels Street, Pfendler Hall-Purdue University, West Lafayette, IN 47907; email: carolyn.c.pike@usda.gov; phone: 765–490–0004.

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