CONTENTS

SPECIES 1
AUTHORS 1
REVIEW TEAM ..... Error! Bookmark not defined.
INTRODUCTION 2
2. DISTRIBUTION AND ENVIRONMENTAL ASSOCIATIONS 3
Distribution 3
CURRENT DISTRIBUTION 3
PROJECTED DISTRIBUTION AND MIGRATION POTENTIAL 4
Environmental Associations 4
CLIMATE AND ELEVATION 4
SOILS AND GEOLOGY 5
3. LIFE HISTORY TRAITS, REPRODUCTION, AND EARLY GROWTH 6
Sexual Reproduction 6
FLOWER, POLLINATION, AND FRUITS 6
SEED PRODUCTION AND DISSEMINATION 7
GERMINATION REQUIREMENTS 7
Asexual Reproduction 8
VEGETATIVE TYPES 8
VEGETATIVE REGENERATION REQUIREMENTS 9
4. TREE GROWTH AND STAND DYNAMICS 9
Plant Associations and Site Conditions 9
Successional Stages and Structural Development 10
Growth Rates and Yield Across Stages 11
5. MANAGEMENT 11
Management with Natural Regeneration 11
SILVICULTURAL SYSTEMS 11
SILVICULTURAL OPTIONS AND CONSIDERATIONS 12
SITE PREPARATION 13
Management with Planted Regeneration 13
PLANTING STRATEGIES 13
SILVICULTURAL OPTIONS AND CONSIDERATIONS 14

SITE PREPARATION 16
Tending or Intermediate Management 17
SEEDLING AND SAPLING STAGE 17
POLE AND MATURE STANDS 17
PRUNING 18
SANITATION 18
SALVAGE 18
6. GENETICS 18
Taxonomy 18
Genetic Variation 18
VARIATION WITHIN AND AMONG POPULATIONS 18
SEED TRANSFER GUIDANCE 19
TREE BREEDING 19
Genomic Resources for Forest Tree Species 20
AVAILABLE SNP ARRAYS 20
SEQUENCING RESOURCES 20
7. DISTURBANCE REGIME: INSECTS AND DISEASES 20
Dominant Insects and Diseases 20
Response to Insects and Diseases 22
2nd Order Interactions 22
Management Considerations 23
8. DISTURBANCE REGIME: WILDLAND FIRE 23
Dominant Fire Regime 23
Response to Fire 24
2nd Order Interactions 24
Management Considerations 25
9. DISTURBANCE REGIME: DROUGHT 25
Dominant Drought Regime 25
Response to Drought 25
2nd Order Interactions 26
Management Considerations 26
10. ADDITIONAL DISTURBANCES 26
Dominant Disturbances 26
Response to Disturbances 27

2nd Order Interactions **27**
Management Considerations **27**
11. GOODS AND SERVICES **28**
Goods **28**
WOOD PRODUCTS 28
NONWOOD PRODUCTS 28
Ecosystem Services **29**
BIODIVERSITY 29
FOREST CARBON AND NUTRIENT DYNAMICS 29
RECREATION 29
OTHER (ADDITIONAL CONSIDERATIONS) 29
12. URBAN FORESTRY **30**
Urban Range and Abundance **30**
Forests in Cities **30**
REPRODUCTION AND EARLY GROWTH 30
SAPLING STAGES TO MATURITY 30
Trees in Planted Urban Landscapes **31**
SAPLING STAGES TO MATURITY 31
Urban Goods and Services **31**
13. KNOWLEDGE GAPS **31**
LITERATURE CITED ..... Error! Bookmark not defined.
APPENDIX ..... Error! Bookmark not defined.
A.2 Distribution and Environmental Associations .. Error! Bookmark not defined.
A.3 Life History Traits, Reproduction and Early Growth ..... Error! Bookmark not defined.
A.4 Tree Growth and Stand Dynamics ..... Error! Bookmark not defined.
A.5 Management ..... Error! Bookmark not defined.
A.6 Genetics ..... Error! Bookmark not defined.
A.7 Disturbance Regime: Insects and Diseases ..... Error! Bookmark not defined.
A.8 Disturbance Regime: Wildland Fire ..... Error! Bookmark not defined.
A.9 Disturbance Regime: Drought ..... Error! Bookmark not defined.
A.10 Additional Disturbances ..... Error! Bookmark not defined.
A.11 Goods and Services ..... Error! Bookmark not defined.
A.12 Urban Forestry ..... Error! Bookmark not defined.

SPECIES

Scientific Name *Pinus palustris* Mill.

Other Common Names None.

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INTRODUCTION

Longleaf pine (*Pinus palustris;* figs. 1 through 5) is an iconic tree species native to the southeastern United States. Before the arrival of non-Indigenous settlers, longleaf pine occurred as the dominant tree species across an estimated 29.9 million ha (73.9 million acres) of fire-maintained forests, woodlands, and savannas, and another 7.3 million ha (18 million acres) as a codominant in mixtures with other fire-adapted tree species (Frost, 1993). Over the next three centuries, a combination of anthropogenic factors decimated longleaf pine and its associated ecosystem (Frost, 2006). Longleaf pine was initially harvested by settlers to clear land for agriculture and provide material for housing and fencing. In the early to mid-19th century, vast areas of longleaf pine were killed in turpentine orchards to supply the naval stores industry. Near the turn of the 20th century, steam-powered technology drove decades of extensive logging throughout much of the remaining longleaf pine woodlands. Recovery from exploitation was hindered by regeneration failures deriving from local seed source limitations, seedling depredation from introduced hogs, fire exclusion, and land use conversion. Longleaf pine continued to decline gradually until the 1990s, when existing extent reached its nadir of approximately 1.2 million ha (3 million acres) (Outcalt and Sheffield, 1996). Subsequently, concerns over the loss of habitat for several endemic flora and fauna prompted extensive investment and research into restoring the longleaf pine ecosystem (Landers et al., 1995). Contemporary restoration efforts have succeeded in stemming the loss of longleaf pine extent and have even produced a modest recovery. However, at the current

estimated extent of 1.8 million ha (4.4 million acres), restoration remains a work in progress (Oswalt and Guldin, 2021).

Longleaf pine is preferentially grown for its ecological, economic, and social values. Ecologically, longleaf pine is considered a foundational species in southeastern woodlands for its role in promoting understory flammability (Varner et al., 2021a). Longleaf pine is also well adapted to resist disturbances such as drought and wind, which are common throughout the region (Rutledge et al., 2021; Samuelson et al., 2019). From an economic perspective, longleaf pine is often commercially grown for sawtimber or utility poles, while its straw is highly sought as groundcover in the landscaping industry (Dickens et al., 2012; South, 2006). Beyond its ecological and economic importance, longleaf pine is viewed by many throughout the region as a cultural symbol connecting humans to their local environment (Gordon et al., 2020).

Figure 1—Examples of (A) a developing and (B) a senesced longleaf pine cone following seed dispersal in Auburn, Alabama, July 2024. U.S. Forest Service photo by John L. Willis.

Alternate Text: Photo depicting immature and senesced longleaf pine cones.

Figure 2—Longleaf pine shown (A) in the "grass stage," (B) initiating height growth, and (C) in the "bolting stage," Tuskegee National Forest, Alabama, July 2024. U.S. Forest Service photo by John L. Willis.

Alternate Text: Photo depicting the early developmental stages of longleaf pine.

Figure 3—Longleaf pine in the (A) sapling, (B) pole, and (C) mature developmental stages, Tuskegee National Forest, Alabama, July 2024. U.S. Forest Service photo by John L. Willis.

Alternate Text: Photo depicting the later developmental stages of longleaf pine.

Figure 4—Bark development of (A) "bolting," (B) sapling, and (C) mature stage longleaf pine, Tuskegee National Forest, Alabama, July 2024. U.S. Forest Service photo by John L. Willis.

Alternate Text: Photo depicting longleaf pine bark development across developmental stages.

Figure 5—A longleaf pine bolt refoliating following a prescribed fire, Blackwater River State Forest, Florida, February 2024. U.S. Forest Service photo by John L. Willis.

Alternate Text: Photo showing new needle growth appearing above dead needles on a longleaf pine.

DISTRIBUTION AND ENVIRONMENTAL ASSOCIATIONS

Distribution

CURRENT DISTRIBUTION

The current range of longleaf pine extends along the Atlantic Coastal Plain from southeastern Virginia to central peninsular Florida, and westward across the Gulf Coastal Plain from the Florida Panhandle to eastern Texas. Most existing longleaf pine lies within the Southeastern Plains and Coastal Plains ecoregions, aside from its montane extent in Georgia and Alabama (Omernik and Griffith, 2014) (fig. 6).

Figure 6—Current relative abundance of longleaf pine in the southeastern United States overlaid by the original Little's range map. U.S. Forest Service cartography by Matthew P. Peters.

Alternate Text: Map of North America showing seven levels of habitat quality for longleaf pine where the species is present in the southeastern United States and the boundaries of the range of longleaf pine as determined during the 1970s.

PROJECTED DISTRIBUTION AND MIGRATION POTENTIAL

Future climate scenarios project an expansion of suitable habitat for longleaf pine (fig. 7). Moderate and high emissions scenarios predict that large swaths of Tennessee, Kentucky, and the Ouachita region of Arkansas and Oklahoma will provide marginal habitat for longleaf pine expansion (Prasad et al., 2024). Similarly, along the Atlantic Coastal Plain, areas within Maryland and New Jersey are expected to become viable sites for future expansion. However, model projections for longleaf pine are only of medium reliability and may be further restricted by barriers to expansion, including poor competitiveness in the absence of frequent, low-intensity surface fire, and minimal resistance to ice damage (Bragg, 2016).

Figure 7—Maps showing future habitat suitability and migration potential for longleaf pine projected under (A) a moderate emissions scenario and (B) a high emissions scenario. U.S. Forest Service cartography by Matthew P. Peters.

Alternate Text: Maps of North America colored to show projected relative habitat quality for longleaf pine by the end of the 21st century. Potential habitat expands westward and northward under both model scenarios.

Environmental Associations

CLIMATE AND ELEVATION

Longleaf pine exists across an elevational gradient ranging from near sea level in the Gulf Coastal Plain ecoregions to above 600 m (2,000 feet) in Alabama and Georgia (table 1). Climatic conditions across these ecoregions are considered humid, subtropical, and have mean annual temperatures and precipitation near 18 °C (64 °F) and 1200 to 1700 mm $year^{-1}$ (47 to 67 inches $year^{-1}$), respectively.

Throughout longleaf pine's native range, maximum summer temperatures consistently reach 35 °C (95 °F) with some parts of eastern Texas and the Gulf Coast occasionally exceeding 40 °C (104 °F). Winters are mild with low temperatures near 5 °C (41 °F) and few days below freezing. At the extreme northern extent of the longleaf pine range, winter temperatures may reach lows of -15 °C (5 °F). Precipitation is influenced by proximity to the Atlantic Ocean and Gulf of America, local topography, and positioning of the Bermuda High, a semipermanent high-pressure system. Rainfall is greatest along the Gulf Coast areas of Mississippi, Alabama, and the Florida Panhandle, where a seasonal peak occurs during the late summer months due to heavy thunderstorms (Konrad and Fuhrmann, 2013). These thunderstorms result in some of the highest lightning flash densities globally and can act as an ignition source (Noss, 2018). Despite relatively high annual rainfall, the southeastern United States frequently experiences droughts with a maximum precipitation-free period of around 21 days on average (Trepanier et al., 2015). Longleaf pine's current distribution is generally limited by aridity to the west and by soil conditions and freezing temperatures inland and to the north (Croker, 1979).

Table 1—Temperature, precipitation, and elevation ranges for longleaf pine in North America for 1991–2020 and two future climate scenarios for 2070–2099

Summary statistics (actual, 1991–2020)	Mean annual temperature in °C (°F)	Mean annual precipitation in millimeters (inches)	Elevation in meters (feet)
Minimum	15.2 (59)	1200 (47)	Sea level
Lower 25 percent	17.9 (64)	1320 (52)	40 (120)
Median	18.9 (66)	1400 (55)	60 (210)
Mean	18.8 (66)	1430 (56)	80 (260)
Upper 25 percent	19.6 (67)	1650 (65)	100 (330)
Maximum	23.3 (74)	1720 (68)	620 (2,030)
Summary statistics under a moderate emissions scenario (2070–2099)	**Mean annual temperature in °C (°F)**	**Mean annual precipitation in millimeters (inches)**	**Elevation in meters (feet)**
Minimum	14.8 (59)	500 (19)	Sea level
Lower 25 percent	18.4 (65)	1360 (53)	40 (140)
Median	19.9 (68)	1450 (57)	100 (320)
Mean	19.9 (68)	1450 (57)	140 (440)
Upper 25 percent	21.4 (71)	1620 (64)	200 (650)
Maximum	27.8 (82)	1880 (74)	1540 (5,060)
Summary statistics under a high emissions scenario (2070–2099)	**Mean annual temperature in °C (°F)**	**Mean annual precipitation in millimeters (inches)**	**Elevation in meters (feet)**
Minimum	13.2 (56)	530 (21)	Sea level
Lower 25 percent	19.4 (67)	1330 (53)	50 (160)
Median	21.1 (70)	1420 (56)	120 (380)
Mean	21.1 (70)	1430 (56)	170 (560)
Upper 25 percent	22.8 (73)	1600 (63)	240 (780)
Maximum	31.7 (89)	3670 (145)	1300 (4,270)

SOILS AND GEOLOGY

The Coastal Plain gradually developed over millions of years (i.e., lower Cretaceous to recent Cenozoic) as a shallow inland sea repeatedly flooded the landscape, depositing sediments carried inland from adjacent streams and generated by erosion from wave action. The oldest of these deposits are found bordering the Piedmont province, and layers of sediment and sedimentary rock thicken toward the Gulf Coast, forming a wedge (Stephenson, 1926). Parent material of the Coastal Plain includes sedimentary sandstone, siltstone, limestone, and shale. In the Piedmont, parent material includes crystalline metamorphic and igneous rock, and the adjacent Ridge and Valley ecoregion is developed on sedimentary rock with ridges forming on sandstone and chert while valleys occur on more erosion-prone shale and carbonate (Raymond et al., 1988).

Longleaf pine is associated with 5 of the 12 major soil orders, with Ultisols being the most widespread throughout the range. Ultisols are weathered, acidic soils that occur where a warm and humid climate has resulted in heavy leaching and a clay-enriched subsoil. Udults (Typic Paleudults, Plinthic Paleudults) predominate throughout the inland southeast, and wetter Aquults occur along coastal regions with the exception of peninsular Florida. Entisols, which are sandy and lack diagnostic

horizons, occur in the Georgia and Carolina sandhills and on sandy ridges of inland Florida; Quartzipsamments are most common. Along the coastal lowlands of Florida and southeastern Georgia, poorly drained Spodosols (Aquods) associated with a shallow, fluctuating water table are widespread. Longleaf pine is also infrequently found on Alfisols (Udalfs) along a loessal fringe belt east of the Mississippi River and Inceptisols (Aquepts) scattered along streams in Alabama and southern Mississippi (Craul et al., 2005; Soil Survey Staff, 2022). Soils are typically 2 to 8 m (6 to 26 feet) thick and range in texture and drainage class from coarse-textured sands that are excessively well-drained to very poorly drained clays. Most soils, however, are acidic with a high sand content and poor water-holding capacity. Heavy precipitation tends to leach nutrients and organic matter through the topsoil, resulting in poor fertility.

LIFE HISTORY TRAITS, REPRODUCTION, AND EARLY GROWTH

Sexual Reproduction

FLOWERS, POLLINATION, AND FRUIT

Longleaf pine is a monoecious tree species. Cone production can be divided into three phases: pollination, fertilization, and cone development. The entire process requires more than 2 years (27 to 29 months) and can be affected by genetics, biotic factors, and variable weather conditions, making cone production notoriously difficult to predict. During the pollination phase, male (catkins) and female (conelets) strobili differentiate inside buds in mid- to late summer (July through August of year 0). Genetics exert a strong influence over conelet production. Annual production ranges from 53 to 588 conelets tree^{-1} (Shoulders, 1967). Conelet production also varies among individuals, with certain trees consistently outproducing others (Croker, 1964; Shoulders, 1967). However, the proportion of catkins and conelets produced annually can be modified by environmental conditions during strobili primordia differentiation. Warm temperatures in mid- to late summer favor the formation of catkins over conelets (Guo et al., 2017). Catkin formation also benefits from precipitation throughout the growing season (Boyer, 1990b). In contrast, conelet formation benefits from abundant precipitation in June and July followed by an extended stretch of dry conditions (Shoulders, 1967). Wet late-summer conditions can also suppress conelet formation (Boyer, 1990b). The discordance between favorable rainfall timing for catkin and conelet formation can annually decouple pollen and conelet availability. Optimal cone production occurs when the pollen-to-conelet ratio ranges between 50 and 150; nevertheless, cone production failures have also been documented within this range (Guo et al., 2017). Conelet formation is also affected by recent production rates. For example, heavy conelet production 2 years prior (or cone production 1 year prior) can reduce conelet production in the current year (Shoulders, 1967). Other factors including insect predation and cone abortions may also significantly reduce conelet availability (McLemore, 1977; White et al., 1977). Overall, conelet availability is affected more by post-differentiation mortality than initial reproductive allocation (Boyer, 1987).

Catkins first become visible between mid-November and early December in lower crown positions (year 0) (Schopmeyer, 1974). Following emergence, catkins remain dormant until development begins between December and February (year 0 into year 1) (Boyer, 1981). Conelets emerge primarily in upper crown positions between January and February (year 1) (Schopmeyer, 1974). Catkin and conelet development increases with winter temperatures (Boyer, 1973; Chen et al., 2020). Peak pollen shedding occurs from late February to early April, but on average occurs in mid-March (year 1). Accumulated maximum air temperatures to peak pollen shed range between 1027 °C (1881 °F) and 1522 °C (2772

°F), with an average of 1342 °C (2448 °F) (Chen et al., 2020). On average, 80 percent of pollen is dispersed within 13 days after initial release (year 1) (Boyer, 1981; Chen et al., 2020). Pollination occurs between February and April (year 1); however, conelet post-pollination fertilization lags by approximately 11 months (early year 2). Fertilized conelets (2.5 cm [1 inch]) grow rapidly before reaching maturity (10 to 25 cm [4 to 10 inches] long) in September or October (year 2). Upon reaching maturity, cones change color from bright green to brown.

SEED PRODUCTION AND DISSEMINATION

Longleaf pine produces cones as early as 12 to 15 years after height growth initiation in a seed orchard and 9 to 10 years on planted old-field sites with high phosphorus availability. However, in natural stands, cone production is limited until trees reach 15 cm (6 inches) diameter at breast height (DBH) or 20 to 30 years after height growth initiates (see the next section) (Croker, 1973; Schopmeyer, 1974). Seed dispersal primarily occurs from mid-October through November and is concentrated within a 2-week period (year 2). Longleaf pine seed is wind-dispersed but limited by its relatively large seed size: width 0.68 cm (0.27 inch); length 1.03 cm (0.41 inch), and dry mass 0.06 g (0.002 ounce). Most dispersed seeds fall within 20 m (66 feet) of the parent tree (Croker and Boyer, 1975).

Approximately 1,853 cones ha^{-1} (750 cones $acre^{-1}$; 30 cones $tree^{-1}$) at a shelterwood density (62 trees ha^{-1} [25 trees $acre^{-1}$]) is the minimum threshold of cone production needed to secure adequate natural regeneration (Boyer and White, 1990). Nearly six decades of cone monitoring across 11 sites showed an average annual cone crop of 27 cones $tree^{-1}$ (Willis and Brockway, 2022). Fair cone crops (30 to 49 cones $tree^{-1}$) were recorded on average every 3.6 years, while good cone crops (50 to 100 cones $tree^{-1}$) occurred every 9.6 years (Willis and Brockway, 2022). Within-cone seed density also varies with crop size, as an average of 50, 35, and 10 sound seeds have been found in cones during good, fair, and poor seed years, respectively (Croker, 1973).

Substantial effort has been devoted to predicting longleaf pine cone and seed production. Good cone crops generally follow several consecutive years of lower cone production (Chen et al., 2022). Climatic factors influence cone production more than nonclimate factors (Chen et al., 2022; Pederson et al., 1999); however, these relationships are often complex and grow weaker with distance between sites (Bowman and Chen, 2023; Chen et al., 2018; Guo et al., 2016). Cone production increases with moderate air temperatures and heavy fall precipitation in the year preceding seed dispersal (Guo et al., 2016). Genetics also factor into cone production, as certain individual trees are inherently more fecund than others (Chen et al., 2023; Patterson, 2020). Production dynamics are further complicated by disturbance, as longleaf pine cone production increased by 71 percent 2 years after a hurricane compared to baseline conditions (Cannon et al., 2024). Collectively, these factors suggest that longleaf pine has a weak masting pattern (Bowman and Chen, 2022).

Cone production can also be influenced by canopy position, tree morphology, and forest management. Large open-grown trees produce the most cones (Croker and Boyer, 1975). However, competition density and canopy status are more informative for cone production than tree diameter. Competition reduces cone production regardless of canopy position, but more so for suppressed trees than codominant and dominant trees (Haymes and Fox, 2012). As such, thinning stands to a residual basal area of 5 to 9 m^2 ha^{-1} (22 to 39 $feet^2$ $acre^{-1}$) increases cone production (Boyer, 1979; Patterson and Knapp, 2016). Similarly, trees burned at frequent intervals (1, 2, or 5 years) produce more cones than those burned at longer intervals (7 years), or those surviving in the absence of fire (Haymes and Fox, 2012).

GERMINATION REQUIREMENTS

Longleaf pine germination is epigeal and can occur from days to months after seed dispersal (Schopmeyer, 1974). Germination soon after dispersal is an unusual phenomenon among southern pine species, and helps mitigate risk of seed depredation by birds, invertebrates, and small mammals that can compromise seedling establishment (Willis et al., 2021). High rates of depredation likely explain why longleaf pine seeds are generally absent from the soil seed bank (Cohen et al., 2004; Sharma et al., 2018). Seedling establishment is highest on mineral soil and is impeded by the presence of pine and hardwood litter (Wahlenberg, 1946; Willis et al., 2019). Newly germinated seedlings have short, blue-green primary needles. Longer green secondary needles replace the primary needles within 2 months. Longleaf pine seedlings begin life in a “grass stage” where resources are devoted to root system development, root collar growth, needle maintenance, and carbohydrate storage. The grass stage is uncommon among pine species and is considered an adaptation to recurrent surface fire, as the apical bud is protected by dense needles near the forest floor (He et al., 2012; Keeley, 2012; Pile et al., 2017; Wahlenberg, 1946). Longleaf pine seedling density is maximized in stands maintained at 7.5 to 9.1 m^2 ha^{-1} (33 to 40 $feet^2$ $acre^{-1}$) (Bigelow et al., 2024; Fan et al., 2021; Mitchell et al., 2006). Minimal height growth occurs until the root collar reaches 25 mm (1 inch) in diameter (Knapp et al., 2006; Ramsey et al., 2003).

Longleaf pine seedlings persist in the grass stage for up to 15 years but may emerge in as little as 2 years (Pessin, 1934; Wakeley, 1954). However, unpublished records indicate that persistence may extend up to 24 years. Several factors affect grass stage duration and whether seedlings ultimately survive and develop into saplings. Longleaf pine growth is maximized in high-light environments such as canopy gaps or beneath low-density stands (McGuire et al., 2001; Palik et al., 1997; Pope et al., 2023). However, seedling response to light is also dependent on adequate soil moisture and nitrogen availability indicating that growth is regulated by a combination of resources (Jose et al., 2003). Grass stage seedlings and young trees (about 15 years since height growth initiation) can modify their leaf physiology and morphology, providing a degree of shade tolerance that aids survival in suppressed growing positions (Samuelson et al., 2012), but emergence from the grass stage (bolting stage) is delayed or prevented if seedlings are not released from competition (Haywood, 2007). Nevertheless, the presence of canopy cover can facilitate seedling survival in low-density stands (e.g., open woodland or shelterwood) under drought conditions (Pecot et al., 2007; Rodríguez-Trejo et al., 2003; Wahlenberg, 1946). Longleaf pine seedlings and saplings can develop within clusters of resprouting midstory oaks or in proximity to mature oak trees, suggesting the existence of facilitation on xeric sites (Johnson et al., 2021; Loudermilk et al., 2016; Magee et al., 2022; Magee et al., 2024; Wahlenberg, 1946). However, evidence of facilitation has been limited to interactions with pyrophytic deciduous oaks such as turkey oak (*Quercus laevis*), sand post oak (*Q. margaretta*), and bluejack oak (*Q. incana*). Conifers, including longleaf pine, and evergreen hardwoods do not facilitate longleaf pine development (Bigelow et al., 2024; Kara et al., 2017; Provencher et al., 2001; Willis et al., 2023). The mechanisms underlying these relationships remain unknown.

Limited branching occurs in the first few years of height growth as seedlings develop in a bottlebrush form. Once height growth is initiated, naturally established saplings can annually grow between 30 and 100 cm (12 and 39 inches) across a gradient of canopy openness (Pope et al., 2023; Wahlenberg, 1946). On abandoned fields, planted longleaf pine can grow 1.1 m (3.7 feet) annually following site preparation and herbaceous weed control (Clabo and Dickins, 2022).

Asexual Reproduction

VEGETATIVE TYPES

Longleaf pine can sprout from dormant buds while in the grass stage (Farrar, 1975; Jin et al., 2019; Knapp et al., 2018). Sprouting is supported by abundant root-stored carbohydrate reserves (Pile

et al., 2017). Seedling sprouting ability declines once height growth is initiated and is negligible when seedlings reach a height of 1.37 m (4.5 feet) (Farrar, 1975).

VEGETATIVE REGENERATION REQUIREMENTS

The long-term competitiveness of resprouted grass stage seedlings is currently unknown.

4. TREE GROWTH AND STAND DYNAMICS

Plant Associations and Site Conditions

The principal longleaf pine cover types are Longleaf Pine (Society of American Foresters Type 70), Longleaf Pine-Scrub Oak (Type 71), and Longleaf Pine-Slash Pine (Type 83) (Eyre, 1980). Longleaf pine is also a minor component of several other forest types within its range: Sand Pine (Type 69), Shortleaf Pine (Type 75), Loblolly Pine (Type 81), Loblolly Pine-Hardwoods (Type 82), Slash Pine (Type 84), and South Florida Slash Pine (Type 111). Community composition in longleaf pine-associated forests is influenced by a multidimensional gradient of disturbance regimes, edaphic conditions, and climate. The longleaf pine ecosystem exhibits considerable variation in species associations and diversity due to differences in soil texture, soil moisture, and latitude across its range (Peet, 2006). The presence of plant species, most notably hardwoods, is also influenced by the frequency and intensity of fire, with hardwood dominance decreasing as fire return intervals shorten (Heyward, 1939; Whelan et al., 2021).

The range of longleaf pine has been classified into 135 different vegetation associations which are described in detail by Peet (2006) and summarized here. On the most xeric sites, including sandhills and river dunes, longleaf pine can be found growing among pyrophytic and other xeric oaks. These sites are characterized by open stand structures with bare sand, sparse herbaceous cover, and the presence of xerophytic shrubs in the understory (Kirkman and Giencke, 2017). Fire return intervals are less frequent compared to other Coastal Plain sites due to the lack of fuel accumulation (Peet, 2006). Turkey oak is one of the most common associated species on xeric sites. Bluejack oak and sand post oak can also be found on xeric sites and become more prevalent in the Western Gulf region (Peet, 2006). On silty, subxeric upland sites, oak species become a more dominant component of stand composition, with the species of oak heavily influenced by soil moisture and fire regime (Cavender-Bares et al., 2004).

Longleaf pine is dominant in mesic uplands characterized by well-drained loamy soils with a clay subsoil (Kirkman and Giencke, 2017). These sites typically have a high understory diversity that is maintained by frequent fire and support less oak than more xeric sites (Palmquist et al., 2014; Peet, 2006). In the understory, wiregrass species (*Aristida stricta* and *A. beyrichiana*) predominate from southeastern Mississippi to North Carolina while bluestem grass species (*Schizachyrium* spp. and *Andropogon* spp.) predominate in the range farther west in Louisiana and Texas and inland in Alabama, Georgia, North Carolina, and South Carolina. Bluejack oak, blackjack oak (*Q. marilandica*), and post oak (*Q. stellata*) are occasionally found in the Atlantic Coastal Plain. Loessal soils adjacent to the Mississippi River in Louisiana and Mississippi tend to promote hardwood dominance but can support longleaf pine under specific microsite conditions (e.g., eroded ridges). Pine flatwoods are characterized by a high water table and can sustain high plant diversity. On these sites, longleaf pine codominates with slash pine (*P. elliottii*) and in wetter areas, pond pine (*P. serotina*). Flatwoods characteristically contain a minor component of oaks except for runner oaks (*Q. pumila*) and dwarf live oaks (Q. *minima*). In addition to grasses, the flatwoods understory may contain gallberry (*Ilex glabra*), saw palmetto (*Serenoa repens*), and a high diversity of forbs (Kirkman and Giencke, 2017; Peet, 2006). West of the Mississippi River,

longleaf pine can be found in wet savannas dominated by bluestem, muhly (*Muhlenbergia* spp.), and toothache grass (*Ctenium aromaticum*) in the understory.

Longleaf pine occurs on montane sites in pure stands and in mixtures with shortleaf pine (*P. echinata*), oaks, and hickories in the Blue Ridge and Piedmont ecoregions. Montane forests represent broad ecotones between ecoregions with vegetation associations more commonly associated with mesic uplands like blackjack oak, sand hickory (*Carya pallida*) (Varner et al., 2003a), and bluestem grasses, combined with species characteristic of the ecoregion. For example, montane woodlands on the Piedmont contain mountain laurel (*Kalmia latifolia*) and sparkleberry (*Vaccinium arboreum*) (Kirkman et al., 2007; Peet, 2006).

Successional Stages and Structural Development

Historically, longleaf pine was found in open, park-like structures with overstories of large diameter trees and understories dominated by grasses. Much of the information on historical stand compositions comes from either isolated stands that have maintained a frequent fire regime, or from historical records. Stand development of longleaf pine forests reflects interactions between both large-scale disturbances (e.g., hurricanes, ice storms, and insect outbreaks) and small-scale disturbances (e.g., frequent, low-intensity fire) (Platt and Rathbun, 1993). Without these disturbances, longleaf pine would be replaced on the landscape on all but the most xeric sites. Historical longleaf pine stands were multi-aged with the oldest age-classes exceeding 250 years (Noel et al., 1998; Varner and Kush, 2004; Varner et al., 2003b).

Fire return interval and localized intensity generally determine stand structure in smaller diameter classes; where frequent fire exposes mineral soil required for germination but also causes mortality of younger, more vulnerable seedlings. However, in most scenarios, the beneficial effects of prescribed fire on local competitors outweigh the potential risks to small seedlings. Overstory gaps created from varying degrees of disturbance result in spatially aggregated clusters of small diameter trees further from gap edges that later experience density-dependent mortality (Grace and Platt, 1995; Hammond et al., 2016). These clusters have a characteristic dome shape, where increased growing space near gap center increases height growth compared to trees near the gap edge (Brockway and Outcalt, 1998). Frequently burned stands feature a minimal midstory, which promotes a reverse-J or U-shaped diameter distribution characteristic of uneven-aged stands (Noel et al., 1998; Varner et al., 2003b).

Even-aged monocultures of longleaf pine are common throughout its native range. Stand development in monocultures is like that of other commercially important southern pine species. Depending on planting density, longleaf pine monocultures can sustain higher densities compared to stands naturally regenerated with a frequent fire regime, resulting in earlier crown closure and stem-exclusion. During stem-exclusion, diameter distributions are generally unimodal and progressively flatten and become negatively skewed as differentiation and density dependent mortality occur (Harrington, 2006; Oliver and Larson, 1996).

Longleaf pine is intolerant to competition for light, moisture, and nutrients (Harrington, 2006). Across much of the Coastal Plain, soil moisture appears to be the most limiting factor to longleaf pine growth (Peet, 2006). This said, longleaf pine tolerates low soil moisture better than any of the southern pines and outperforms other southern pine species on xeric sites (Shoulders, 1983). Decoupling the interaction between growth limiting factors can be challenging. For example, the domed structures of natural regeneration established beneath overstory gaps are hypothesized to be driven by a combination of reduced fire intensity, root competition for belowground resources, and shading (Brockway and Outcalt, 1998; McGuire et al., 2001; Pecot et al., 2007; Robertson et al., 2019).

Growth Rates and Yield Across Stages

Longleaf pine growth and yield is sensitive to site variability, land use history, stand density, and silvicultural practices (Boyer, 1983; Boyer 1990b). Site productivity also varies with precipitation, slope, and available soil moisture (Shoulders and Tiarks, 1980). Estimates of longleaf pine site index provide a range of site indices between 15 and 29 m (50 and 96 feet) (base age 50) for planted and natural stands (Farrar, 1993; Harrington, 1990). However, planted stands are likely to achieve greater site indices compared to naturally regenerated stands.

The growth and yield dynamics of longleaf pine has received less attention than that of other commercially managed southern pines. Early growth and yield work in longleaf pine is summarized by Farrar (1990). Lauer and Kush (2011) developed a variable density stand-level model to estimate growth and yield of naturally regenerated even-aged longleaf pine. Models to predict individual tree diameter, height, and volume for both planted and natural stands were developed by Gonzalez-Benecke et al. (2012). Systems of equations for estimating stand-level survival and volume have also been developed for thinned and unthinned monocultures (Farrar and Matney, 1994; Gonzalez-Benecke et al., 2012). Predicted total volume (inside bark) yields for stands at two site index classes are estimated from a system of equations (Gonzalez-Benecke et al., 2012).

There are a wide range of planting options recommended for longleaf pine based on management objectives (see subsequent discussion on planting strategies). The maximum basal area across a range of densities (and diameters) in pure longleaf stands is approximately 44.7 m^2 ha^{-1} (215 $feet^2$ $acre^{-1}$). Stands reach the zone of imminent mortality (sensu Drew and Flewelling, 1979) at 22.2 m^2 ha^{-1} (107 $feet^2$ $acre^{-1}$); crown closure occurs at approximately 14.5 m^2 ha^{-1} (63 $feet^2$ $acre^{-1}$), assuming the exponent in Reineke's stand density index equation was set to approximately -2 (Kara et al., 2018; Kush, 2016; Reineke, 1933). Like all tree species, thinning before stand density reaches the zone of imminent mortality is required to maximize volume production under a traditional even-aged rotation (Dean and Baldwin, 1996).

5. MANAGEMENT

Management with Natural Regeneration

SILVICULTURAL SYSTEMS

Longleaf pine is a flexible species that can be regenerated under any silvicultural system that balances seed source proximity, resource availability, and fuel continuity to support frequent fire. Even-aged systems such as clearcutting and seed tree harvests provide ample light to meet the requirements of longleaf pine, but most variants of these systems do not account for seed and litter dispersal limitations (Blaydes et al., 2023; Croker and Boyer, 1975) and cause substantial damage to advance regeneration (Croker and Boyer, 1975; Mitchell et al., 2006). Consequently, neither system is optimal for naturally regenerating longleaf pine. In contrast, a uniform shelterwood harvest initially retains a portion of the overstory, enabling even seed and litter distributions (Croker, 1956; Croker and Boyer, 1975). Light availability is more limited under a uniform shelterwood harvest, compared to a clearcut or seed tree harvest, but is sufficient to promote longleaf pine recruitment (Samuelson and Stokes, 2012). Reduced light availability can also indirectly benefit grass stage longleaf pine seedlings by reducing the growth of more light-acquisitive species, keeping them within the range of surface fire. Collectively, these factors make uniform shelterwood harvesting an effective even-aged method for naturally regenerating longleaf pine (Boyer and Farrar, 1981; Brockway and Outcalt, 2017).

A uniform shelterwood can be applied in either two or three cuts depending on initial stand conditions. Three cuts are recommended in high-density stands (more than 18 m^2 ha^{-1} [78 $feet^2$ $acre^{-1}$]), while the two-cut variant can be applied in stands that have been maintained at a low density (Brockway et al., 2006). The three-cut method begins 10 years before harvest with a preparatory cut (13.8 to 16.1 m^2 ha^{-1} [60 to 70 $feet^2$ $acre^{-1}$] average residual density) to promote residual tree crown development (Boyer and Peterson, 1983; Croker and Boyer, 1975). Five years following the preparatory cut, the seed cut (6.9 m^2 ha^{-1} [30 $feet^2$ $acre^{-1}$]) is applied, targeting the most dominant cone producing trees for retention. Residual seed trees are retained until at least 15,000 seedlings ha^{-1} and 1,250 saplings ha^{-1} (6,073 seedlings $acre^{-1}$ and 506 saplings $acre^{-1}$) have established, at which point the seed trees are harvested to release advance regeneration (Croker and Boyer, 1975). In situations where accelerating the development of structural and age class diversity are desired, seed trees can be retained indefinitely under an irregular shelterwood system. However, delaying or forgoing the removal cut inhibits regeneration development (Boyer, 1993). The two-cut variant begins at the seed cut and follows the same subsequent protocols. Both shelterwood variants can be applied across the stand (even-aged), in progressive strips (uneven-aged), or in groups (uneven-aged) to produce age class diversity (Boyer and White, 1990).

Favorable conditions for longleaf pine regeneration can also be created under a variety of selection systems (Brockway et al., 2014; Guldin, 2006; McConnell, 2002). Single tree harvest gaps (less than 0.1 ha [0.3 acre]) are effective at providing fuel connectivity and mitigating seed dispersal limitations but provide only modest increases in light and soil nutrient availability (Brockway and Outcalt, 1998; Palik et al., 2003). In contrast, group selection gaps (0.1 to 1.0 ha [0.3 to 2.5 acres]) provide greater light and soil nutrient availability than single tree selection gaps, but can limit seed dispersal and fuel continuity, and increase competition with woody and herbaceous vegetation (Jack et al., 2006; McGuire et al., 2001; Pecot et al., 2007). Longleaf pine growth is maximized near the gap center and increases with gap size up to 36 m (118 feet) from the edge (McGuire et al., 2001; Palik et al., 2003). Both single tree and group selection harvests are effective for establishing longleaf pine seedlings and saplings (Brockway and Outcalt, 2017); however, consensus on the optimal gap size for promoting longleaf pine natural regeneration has yet to be reached. The Stoddard-Neel system provides another stocking control option for accomplishing multiple ecological objectives (Moser et al., 2002). At its core this system is a form of variable retention silviculture that results in a heterogeneous, multi-aged structure (Mitchell et al., 2006). The Stoddard-Neel system utilizes single tree and small group selection techniques with a focus on retaining adequate fine fuels for prescribed fire and releasing advance regeneration for canopy recruitment. No structural guidelines (e.g., diameter distribution, residual volume or basal area) are typically used to guide the marking process, though removals are limited by a form of volume regulation (Mitchell et al., 2006). Key components of the system are (1) the application of frequent (every 1 to 3 years) prescribed fire, (2) continual maintenance of a forest canopy, (3) continuous accumulation of advance regeneration cohorts to foster the multi-aged structure, (4) incorporating overstory spatial heterogeneity and retaining some trees with natural defects, (5) conservative volume removals and retention of relatively high basal areas, (6) a focus on maintaining habitat features for a broad range of wildlife species, and (7) perpetuation of a healthy and diverse groundcover plant community (Jack and McIntyre, 2018).

SILVICULTURAL OPTIONS AND CONSIDERATIONS

Shelterwood, Stoddard-Neel, and selection harvests are viable options for naturally regenerating longleaf pine. However, each method has its own advantages and drawbacks. The shelterwood method does not require a stand inventory or skid trail system, is easy to mark, and presents a low risk of logging damage to residual seed trees. Shelterwood harvests also provide more volume per entry than either Stoddard-Neel or selection harvests. Alternatively, unless irregular shelterwood, strip shelterwood, or group shelterwood is utilized, shelterwood harvesting is incompatible with wildlife objectives requiring

mature forest structure. Shelterwood harvests are also vulnerable to wind damage following the seed cut (Polinko et al., 2022).

Stoddard-Neel and selection harvests allow for perpetual canopy cover, making them ideal for mature forest habitat conservation and aesthetic value. Frequent stand entries also allow for a continuous income stream from high-value timber. Nevertheless, stands managed with these systems require frequent inventory and marking, an established skid trail network, and an experienced logging workforce to minimize residual tree damage. Selection managed timber sales can also be difficult to implement on small parcels due to the relatively small volume removed per entry, compared to even-aged harvests, and lack of markets for large diameter southern pine.

SITE PREPARATION

Seedbed preparation is important for securing natural regeneration, as longleaf pine seedling establishment benefits from mineral soil availability (Willis et al., 2019). Potential tools for exposing mineral soil include mechanical soil manipulation (chopping, disking, scarification) or prescribed fire. Either option must be conducted no more than 1 year before seedfall to be effective. The two most common windows for site preparation burning are the winter or fall before seedfall. Burning in the winter presents a lower risk to existing advance regeneration. However, seedling survival and growth are highest after fall burns (Croker and Boyer, 1975). Mechanical options are more appealing for summer seedbed preparation. Timely seedbed preparation is particularly important during years with high cone production due to their relative infrequency.

Management with Planted Regeneration

PLANTING STRATEGIES

There are several longleaf pine planting spacing options based on specific landowner objectives and local timber or nontimber forest product (e.g., pine straw) markets. For example, high-density plantings can reduce time to canopy closure for pine straw raking. In contrast, planting at a low density can be beneficial for wildlife habitat objectives assuming timely prescribed fire and thinning are utilized as the stand develops (Hausle et al., 2023; South, 2006). However, it should be recognized that branch retention and size increase in low-density plantings in the absence of fire, which negatively affects timber quality (McGuire et al., 2021). Longleaf pine seedling survival is generally lower than loblolly or slash pine (e.g., Haywood et al., 2015); hence longleaf pine is often planted at a higher density to compensate for low survival and to provide management flexibility. Land use history should also be considered before planting. When planting on former agricultural fields, pastures, or hay cutting fields, higher planting densities are recommended due to enhanced site fertility, which can promote competition and a high prevalence of stem defects (often 40 to 60 percent of trees) (Dickens et al., 2018). Higher planting densities (e.g., 1,495 to 1,793 trees ha^{-1} [605 to 726·$acre^{-1}$]) will produce more trees per hectare with fewer stem defects (e.g., forks, ramicorn branches, or sweep) than lower planting densities of 1,235 to 1,346 trees ha^{-1} (500 to 545·$acre^{-1}$). Cutover sites (i.e., areas where the previous crop was trees for one or more rotations) generally have low fertility and woody vegetation competition that will reduce the growth rate of longleaf pine. These sites can be planted at lower planting densities 1,344 to 1,495 trees ha^{-1} (545 to 605·$acre^{-1}$), as the stem defect rate is often lower on these sites due to slower growth rates. Rotation age and potential number of stand entries need to be considered when deciding on planting density. Longleaf pine stands, depending on the number of stems with no visible defect in the first 10 to 12 m (33 to 39 feet) or higher, may be thinned once or multiple times. Higher planting densities tend to permit more than one thinning. Due to the size of modern logging equipment, planting row widths need to be at least 2.75 m (9 feet) wide. Many foresters, planters, and landowners

start with 3.0 m (10 foot) rows as a minimum row width because width is rarely consistent in handplanting.

Underplanting longleaf pine seedlings beneath the canopy of a different southern pine (e.g., loblolly or slash pine) is a restoration strategy for converting stand composition (Kirkman et al., 2007). Prior to planting, intervals of prescribed fire and thinning should be used to establish an understory that promotes light availability and creates uniform, herbaceous fuel conditions (Haywood et al., 2001; Outcalt and Brockway, 2010). Frequent fire is imperative for maintaining the competitiveness of underplanted longleaf pine seedlings among abundant natural regeneration. Juvenile longleaf pines adapt to low light environments by utilizing short periods of high light intensity and sunflecks to sustain growth (Gilbert et al., 2014; Samuelson and Stokes, 2012). Underplanting treatments can retain mature pines, ephemerally or indefinitely, to provide overstory structure and litter inputs to support ecological function (Willis et al., 2024a). Optimal overstory basal area depends on site conditions and the relative importance of seedling survival and growth after planting. For example, on a xeric site, seedling survival increased with canopy basal area up to 16 m^2 ha^{-1} (70 $feet^2$ $acre^{-1}$) (Knapp et al., 2015). However, after establishment, height growth was best under a 5 m^2 ha^{-1} (22 $feet^2$ $acre^{-1}$) or less overstory. The opposite pattern occurred on a mesic site where survival decreased with increasing overstory basal area. Meanwhile height growth was unaffected by a reduction in basal area from 9 to 5 m^2 ha^{-1} (39 to 22 $feet^2$ $acre^{-1}$) or less (Knapp et al., 2015).

SILVICULTURAL OPTIONS AND CONSIDERATIONS

Approximately 100 million longleaf pine seedlings are produced annually (Enebak, 2022). Most seedlings are grown in containers (95 percent) rather than nursery beds as bareroot seedlings (South et al., 2016). Bareroot longleaf pine seedlings are marketed as 1-0 stock, and their establishment success depends on cultural and post-planting conditions that cannot always be controlled (Barnett and McGilvray, 2000). This risk is diminished for all species by growing seedlings in containers, but the cost of container-grown seedlings is more than double that of bareroot stock (South et al., 2016). Container-grown longleaf pine seedlings afford several benefits such as a longer pre-plant storage period and a wider planting window (Grossnickle and El-Kassaby, 2016). Once planted, containerized longleaf pine seedling survival exceeds that of bareroot stock primarily because the plug insulates roots from planting stress and dry conditions (Grossnickle and El-Kassaby, 2016; South et al., 2016).

Planting high-quality seedlings is important for longleaf pine artificial regeneration success. Root collar diameter, the primary indicator of seedling quality, should be at least 10 mm (0.4 inch) for bareroot seedlings and 6.4 mm (0.3 inch) when grown in most cavity sizes (Brockway et al., 2006; Dumroese et al., 2013). For relatively small cavities (i.e., 100 cm^3 [6.1 $inches^3$]), root collar diameter should be greater than 4.7 cm (0.2 inch). Attention to the ratio between root collar and cavity diameter (i.e., root-bound index) is advised as a value greater than 27 is correlated with suboptimal root growth after planting (South and Mitchell, 2006).

Another attribute indicative of high seedling quality is the number of woody first-order lateral roots that have emerged from the taproot. A standard value for this attribute is not available because the depth at which bareroot seedling taproots are pruned during lifting and the cavity length of container-grown seedlings vary. However, under normal bareroot nursery conditions, seedlings should have at least six of these roots (Brockway et al., 2006; South et al., 2023). Because first-order lateral roots are obscured by the root plug, this attribute is not useful for assessing container-grown longleaf seedling quality. However, depending on cavity size, these seedlings typically have five to nine of these roots that persist after planting (Sung and Haywood, 2016; Sword Sayer et al., 2009). The presence of abundant white root tips and ectomycorrhizae is also indicative of high seedling quality (Dumroese et al., 2013) but may be of little benefit to post-planting seedling performance (Cram, 2019) because established

seedling performance is likely enhanced more by native rather than introduced ectomycorrhizal symbionts (Karlsen-Ayala et al., 2022).

Indices of balance between the root system and shoot such as root-to-shoot ratio and root-to-weight ratio are also useful predictors of establishment success on xeric sites (Grossnickle and South, 2017; Jackson et al., 2012; South et al., 2016). However, these indices vary by nursery because they are affected by cultural practices that manipulate foliage and taproot length (i.e., foliage clipping, undercutting). A recent evaluation of commercially grown containerized longleaf pine seedlings yielded root-to-shoot and root-to-weight ratios of 0.39 to 0.77 and 0.28 to 0.44, respectively (Sung and Haywood, 2016). Establishment success is expected to increase with greater values of these ratios unless root system and cavity size yielded a root-bound index less than 27 (South, 1998; South and Mitchell, 2006).

Container type is another important factor to consider if containerized seedlings are used for reforestation. Positive correlations exist between container cavity volume, seedling stature, and grass stage emergence (Haywood et al., 2012; Knapp et al., 2018; South et al., 2005). Thus, cavity volume not only affects seedling quality during production but also affects post-planting growth. A cavity volume as small as 100 cm^3 may be considered if the primary objective is seedling survival (Barnett and McGilvray, 2000). Comparisons of grass stage emergence among seedlings grown in cavities with volumes ranging between 60 cm^3 (3.7 $inches^3$) and 336 cm^3 (20.5 $inches^3$) suggest that cavities at least 170 cm^3 (10.4 $inches^3$) in volume are superior in grass stage emergence by the end of the second growing season (Haywood et al., 2012; Sung et al., 2010; Sung et al., 2019). In addition to cavity size, the root pruning nature of cavities may affect regeneration success by influencing root system morphology. Root pruning decreases the likelihood of lateral root deformities such as caging and spiraling that can constrict taproot development (Pickens and Crate, 2019; Sung and Haywood, 2016; Sung et al., 2019). By preserving taproot development and first-order lateral root symmetry, root pruning may reduce the occurrence of toppling among saplings during high wind (Pickens and Crate, 2019; South et al., 2001). Past research demonstrated that chemical (i.e., copper-coated cavity walls) or mechanical (i.e., air vents) root pruning consistently increased taproot mass (Dumroese et al., 2013; Sung and Haywood, 2016). However, variable juvenile growth responses across diverse locations suggest that site factors can mitigate the effects of root pruning.

Throughout the longleaf pine native range, planting tends to start in late fall but should not commence until there is sufficient soil moisture in the mineral soil zone (0 to 20 cm [0 to 8 inches] or more) (Grossnickle and El-Kassaby, 2016). For most of the Coastal Plain region, containerized plantings can start as early as mid-September, which can result in extra root growth and less time in the grass stage compared to winter plantings, but hot, dry periods in September have led to poor survival necessitating replanting (Barnett and McGilvray, 2000; Larson, 2002). To maximize survival, containerized plantings often start in early November (assuming good soil moisture) and should be completed by late February within most of longleaf pine's native range. Planting on higher elevation montane sites or in North Carolina and Virginia should be finished by early April (Wakeley, 1954). Bareroot seedlings tend to be planted starting in mid-December. Additionally, bareroot seedlings need to be lifted from the nursery and planted within 48 hours for best survival. Trials have found that when bareroot seedlings are lifted and refrigerated for more than 5 to 7 days prior to planting, seedling survival is often poor (10 to 50 percent) (Barnett et al., 1990). Bareroot planters should have no more than 1 to 1.5 days of seedlings at any point in time. Once longleaf pine seedlings are lifted or removed from their trays and picked up by the planters, they need to be properly stored prior to planting, preferably in a refrigerated truck at 1.1 to 3.3 °C (34 to 38 °F) until the day of planting (Barnett and McGilvray, 2000). Seedlings with small root collar diameters generally do not store as long as those with root collar diameters greater than 1.3 cm (0.5 inch) (White, 1981).

Longleaf pine seedlings can be planted by hand using tube dibbles, bar dibbles, or hoe-dads, or by machine. Bareroot seedling root collars should be planted at ground level to 1.2 cm (0.5 inch) below

ground level with shallow planting often reducing survival (Barnett et al., 1990; Smith, 1954). Planting depth considerations for containerized seedlings may need to accommodate post-planting soil movement on some sites. For example, on sites with high slope and mineral soil exposure, shallow planting that temporarily exposes less than 2.5 cm (1 inch) of the root plug may be warranted when there is a high probability that soil movement will promptly eliminate root plug exposure (Hainds, 2004). One drawback of this planting method is the risk of delayed or minimal soil movement, which may limit available water and expose the root plug to lethal temperatures in fire. To avoid excessive grass stage seedling mortality (potentially as great as 90 percent), fire should be avoided with shallow plantings until soil covers the plug or the average seedling root collar diameter is greater than approximately 1.9 cm (0.75 inch) (Jin et al., 2019). If soil movement is not a concern, containerized seedlings should be planted with the root collar at ground level.

SITE PREPARATION

Proper site preparation addressing limiting soil conditions and competing vegetation can greatly improve artificial regeneration success (Addington et al., 2012; Crouch et al., 2020; Johnson and Gjerstad, 2006). After planting, there are few options to control woody or herbaceous vegetation, which can greatly extend the duration of the grass stage (Boyer, 1990a; Willis et al., 2023). On cutover sites, woody competition needs to be controlled prior to planting to give longleaf pine seedlings a “free to grow” environment in which they capture sufficient sunlight, water, and nutrients. Pre-plant mechanical site preparation treatments (disking, bedding, 3-in-1 plow, and drum chopping) do not provide long-term woody control. Labeled site preparation forest herbicides are the most efficient and cost-effective method for pre-plant long-term woody vegetation control. Former pastures, hay fields, and agricultural fields can have a plow or traffic hardpan (a very dense soil layer restricting root development and soil drainage) that should be ripped or subsoiled to a depth of at least 45 cm (18 inches) to improve conditions for root exploration. Scalping is another method used on level to nearly level old-field sites (often turf grass fields) to provide seedlings short-term weed-free conditions, limit disease and insect damage potential, and improve soil moisture availability (Johnson and Gjerstad, 2006). Mechanical site preparation should be done during dry periods several months before planting. When completed by May or June, ripping or subsoiling allows rips to settle and reduces air pockets prior to planting in the dormant season. Ripping or subsoiling and scalping should follow the land’s contour to reduce erosion potential and utilize the interval of planting row width so seedlings can be planted in the prepared rows.

Applying first-year post-plant herbaceous weed control, using labeled forest herbicides over the top of seedlings at the right dose and timing, can significantly improve survival and growth in droughty springs and growth in years of normal rainfall (Dickens et al., 2024; Minogue et al., 1991; Nelson et al., 1985). Herbaceous weed control applications also lead to long-term individual tree and stand growth improvements (Clabo and Dickens, 2022; Freeman and Jose, 2009). Post-plant herbicides labeled for over-the-top applications on longleaf pine can be sprayed in a 1.2- to 1.8-m (4- to 6-foot) wide band when broadleaf weeds are the primary competition, or broadcast over the entire stand when grasses or invasive herbaceous plants are the main competitors. Most herbaceous weed control herbicides used over the top of longleaf pine seedlings are soil active pre-emergence (before the weeds start to grow) or early post-emergence (weeds recently germinated). It is best to apply these herbicides when the herbaceous weeds are less than 15 to 30 cm (6 to 12 inches) tall and where planting rows can still be easily seen. Imazapyr and hexazinone should not be applied over longleaf seedlings for at least 2 months after planting, due to mortality concerns, even at their lowest dosage (e.g., Clabo and Dickens, 2022). Once new root growth has begun and seedlings show no outward signs of stress, over-the-top applications of herbicides at labeled rates are possible. Sulfometuron methyl should not be applied to longleaf pine when soil pH is over 6.2. Soil pH values above this threshold can occur on some former agricultural fields (i.e., former peanut fields). Cutover sites generally have more acidic soils (pH 4.2 to 5.3). It is wise to test soil pH where it may be in question. Often sulfometuron methyl and hexazinone

are tank mixed for broader spectrum weed control. Other longleaf herbaceous weed control herbicides such as aminopyralid and clopyralid control fewer weed species than imazapyr, hexazinone, and sulfometuron methyl but are not affected by soil pH. Where grass is the only competitor with seedlings after planting, grass-selective herbicides such as clethodim and sethoxydim can be applied over the top of longleaf pine seedlings. For more information on herbicides and longleaf pine establishment, please refer to the publications listed in University of Georgia (2022a) and University of Georgia (2022b).

Tending or Intermediate Management

SEEDLING AND SAPLING STAGE

Regardless of whether a new stand or age cohort is established using natural regeneration or planting, attention will soon turn to intermediate treatments to produce desirable stand conditions. Longleaf pine seedlings should be surveyed in the fall of the first year following treatment to determine regeneration stocking. Overstocking is rarely a concern at the seedling and sapling stages, as frequent prescribed fire generally moderates seedling density by removing the smallest individuals. However, the potential for overstocking exists following a bumper seed year leading to the development of "dog-hair thickets." In such situations, a precommercial thinning is recommended to prevent future stagnation.

Fire is critical during the seedling and sapling stage, and especially in planted monocultures or in natural stands containing seed sources of loblolly pine. Newly established cohorts should be examined for brown spot needle blight (caused by *Lecanosticta acicola*) 2 to 3 years after establishment. A good discussion of this disease can be found in Croker and Boyer (1975). If present, brown spot needle blight is a sign that prescribed fire needs to be applied to remove the diseased needles.

Fire should be applied within 3 years of planting or establishment via natural regeneration, and every 2 to 3 years subsequently. Most prescribed fires in the southeastern United States are conducted in the dormant or early growing season (Cummins et al., 2023). However, growing season burning is often incorporated into the burning regime to control woody competition and promote herbaceous vegetation. Prescribed fire could be applied to vigorous grass stage longleaf pine as early as the second year after planting under normal fuel conditions and while carbohydrate reserves are plentiful in spring and early summer to support foliage regrowth (Sayer et al., 2020a; Sayer et al., 2020b).

In the absence of fire, encroachment from hardwoods and other pines can be a serious issue. A brief examination of a 17-year-old unburned longleaf pine monoculture found 180 stems ha^{-1} ($73 \cdot acre^{-1}$) and 2.3 $m^2\,ha^{-1}$ (10 $feet^2\,acre^{-1}$) of longleaf pine, 1130 stems ha^{-1} ($457 \cdot acre^{-1}$) and 16.5 $m^2\,ha^{-1}$ (72 $feet^2\,acre^{-1}$) of loblolly pine, and 1295 stems ha^{-1} ($524 \cdot acre^{-1}$) and 13.3 $m^2\,ha^{-1}$ (58 $feet^2\,acre^{-1}$) of various hardwoods (Kush 2016).

POLE AND MATURE STANDS

Prescribed fire should be applied frequently throughout the life of the stand to prevent woody species encroachment. Moreover, continued use of prescribed fire will be critical if future management plans involve natural regeneration. Croker and Boyer (1975) provide a detailed discussion of treatment options for natural regeneration using the shelterwood method. Farrar (1996) provides similar information if uneven-aged management is the goal.

In even-aged stands, pine straw raking primarily occurs between canopy closure and the age of first thinning. Frequent applications of prescribed fire and herbicide are required to maintain the "clean" understory condition desired by industry. Fertilization can improve or maintain straw production on cut-over sites, or on sites with marginal soils, but has little effect on old-field sites with a legacy of nutrient additions (Dickens et al., 2020).

PRUNING

Longleaf pine can produce high-quality utility poles because of its ability to readily self-prune. However, many new stands are planted at relatively low density to promote open-forest habitat (Wheeler et al., 2020). Saplings established in low-density stands retain branches longer than they would in dense stands, as happens with natural regeneration. Mechanical pruning to improve timber quality is unadvisable until trees reach 6 to 9 m (20 to 30 feet) height and is rarely used due to labor costs. However, prescribed fire can be used to kill lower branches early in stand development (McGuire et al., 2021; Sayer et al., 2020a).

SANITATION

No research has been reported on the direct effects of sanitation logging on longleaf pine.

SALVAGE

No research has been reported on the direct effects of salvage logging on longleaf pine.

GENETICS

Taxonomy

Natural hybridization is common between longleaf pine and loblolly pine, producing the Sonderegger pine (*P.* × *sondereggeri* H.H. Chapm.), also called southern pine hybrid (Boyer, 1981). Natural hybridization between longleaf pine and slash pine is unlikely, based on differences in dormancy and heat requirements for flowering between species (Boyer, 1981). Artificial crosses between longleaf and loblolly pines and between longleaf and slash pines can be achieved, but not with other pine species (Snyder et al., 1977).

Genetic Variation

VARIATION WITHIN AND AMONG POPULATIONS

Molecular genetic studies using protein (allozyme) or DNA (microsatellite or short simple repeat [SSR]) markers have found high levels of genetic diversity in longleaf pine but little genetic divergence between populations (Dubai, 1985; Schmidtling and Hipkins, 1998). In particular, Dubai (1985) and Schmidtling and Hipkins (1998) used allozymes to measure diversity in longleaf pine seed orchards and old-growth stands, finding low differentiation among populations, with western seed sources showing higher allozyme diversity. Later, Echt and Josserand (2018) developed 10 informative SSR markers for fingerprinting (individually identifying) longleaf pine trees. They also developed chloroplast SSRs that Crane et al. (2019) used to screen longleaf pine seed orchard trees and their open-pollinated seedlots for hybrids with loblolly pine. Analysis of chloroplast SSR markers (i.e., paternally inherited in southern pines [Wagner et al., 1992] and most conifers) showed no interspecies hybrids among the 250 orchard clones tested and fewer than 3 percent of their tested seedlots showed a hybrid fingerprint. More recently, restriction site associated DNA (RAD) markers were developed for longleaf pine and examined for evidence of genetic differentiation between sampled locations (Petersen, 2019). Marker data were used to statistically cluster about 80 percent of the individuals, representing six of the eight sampled locations. Trees sampled from Louisiana and Florida did not fall into any cluster, indicating that more trees would need to be sampled to fully resolve the rangewide population genetic structure of longleaf pine (Petersen, 2019).

Using data from the iconic Southern Pine Seed Source Study, Wells and Wakeley (1970) demonstrated that significant geographic variation exists in longleaf pine survival, initiation of height growth from the grass stage, growth characteristics, and disease resistance. Snyder et al. (1977) found that trees originating from the central Gulf Coast were more productive than trees from other sources on most Coastal Plain sites ranging from Georgia to east-central Louisiana. Studies of various traits in longleaf pine have shown marked genetic differentiation between populations (Johnson et al., 2015; Petersen, 2019; Samuelson et al., 2018). For example, Samuelson et al. (2018) found a wide range in foliar water use efficiency, with trees from the Piedmont and Montane Uplands having a higher water use efficiency than trees from the western Gulf Coastal Plain and a portion of the eastern Gulf Coastal Plain. Similarly, a preliminary analysis of longleaf pine provenance tests in Virginia indicated provenance variation in water use efficiency (Johnsen et al., 2015). Overall, the provenance tests indicate that trees from coastal areas usually outgrow those from inland areas at all but the coldest locations. The information from these molecular and field-based experiments related to variation among and within populations is essential to the development of seed transfer guidelines. Results suggest that neutral genetic variation as shown by molecular markers is widely shared, indicating the ongoing exchange of genes between populations, while phenotypic trait variation (e.g., height growth and survival) is more strongly differentiated between populations, indicating selection for local adaptation.

SEED TRANSFER GUIDANCE

Schmidtling (2001) developed and published a handbook on how to select appropriate longleaf pine seed sources for reforestation, replacing the previous booklet published by Lantz and Kraus (1987). Both versions were mainly based on geographic variation and their association with the U.S. Department of Agriculture Plant Hardiness Zones rather than climate projections. The primary data consisted of a study where 20 seed sources of longleaf pine were grown for two decades at seven locations in Georgia and Florida (Schmidtling and Sluder, 2000). The best-fitting models showed that the average annual minimum temperature was the variable with the highest north-south variation and the best predictor of tree height (Schmidtling and Sluder, 2000). Evidence also suggests that moving seeds northwards (240 km [150 miles]) could improve height growth, and avoiding moves of more than about 6 °C (10 °F) lower in terms of average annual minimum temperature would limit risk of cold damage (Pike and Nelson, 2024; Schmidtling and Sluder, 2000).

TREE BREEDING

The U.S. Forest Service's Southern Region (Region 8) Genetic Resource Management Program oversees 218 ha (540 acres) of longleaf pine seed orchards, 109 ha (270 acres) of longleaf pine seed production areas, and 35 longleaf pine progeny trials (Crane et al., 2019). Region 8's Erambert and Black Creek seed orchards, located in southern Mississippi, contain first- and second-generation orchard blocks, respectively (Crane et al., 2019; Johnson, 1996). The first series of progeny tests were established in 1988 and measured in 1998, which allowed the Mississippi Forestry Commission to rogue the seed orchards under an agreement with Region 8 (Byram et al., 1998).

Hamrick et al. (1993) reported moderate narrow-sense heritability in longleaf pine for height at 15 years (0.53) and 21 years (0.58), branch angle (0.43), dorsal stomata (0.39), brown spot incidence (0.44), and January bud length (0.62); they reported high narrow-sense heritability for diameter (0.72), volume (0.82), and proportion of trees rust-free at 21 years (0.78). Bey and Snyder (1978) reported on a progeny test of 226 superior tree selections from 9 geographic seed sources across the Southeast, showing the central Gulf Coast source to be superior in survival and growth, with higher genetic gains expected from selection of families in some sources compared to others (Bey and Snyder, 1978). Elite x elite controlled-pollinated crosses showed the best performance in survival, brown spot incidence, and

wood volume production compared to crosses among non-elite parents or open-pollinated families (Bey and Snyder, 1978). Gwaze et al. (2003) and Nelson et al. (2005) reported on appreciable expected gains in early height growth and brown spot resistance from selection in the advanced generations of the Bey and Snyder population. Nelson et al. (2003) estimated that few genetic loci account for the genetic differences in first-year height growth (a measure of the grass stage trait) between longleaf and loblolly pines, indicating a high degree of similarity. These authors argued that breeding programs aimed at improving the early height growth of longleaf pine must recognize that reducing the grass stage may negatively impact long-term fitness in traditional longleaf pine environments by making the seedlings susceptible to fire-induced mortality.

Genomic Resources for Forest Tree Species

AVAILABLE SNP ARRAYS

At the present time, a single nucleotide polymorphism (SNP) array for longleaf pine has not been developed, although researchers at North Carolina State University have led the development of a SNP array for loblolly pine (PITA 50K Axiom Array; Caballero et al., 2021); given the close relationship between loblolly and longleaf pines (inferred from crossing studies, e.g., Snyder et al. 1977), this resource is likely to prove useful for longleaf pine.

SEQUENCING RESOURCES

Currently, for the southern pines there are sequence resources only for loblolly pine as its genome and transcriptome (expressed genes) have been comprehensively sequenced (Lorenz et al., 2012; Neale et al., 2014; Wegrzyn et al., 2014; Zimin et al., 2017). As sequencing and bioinformatic technologies continue to improve, obtaining whole genome sequences for large, complex genomes—such as the pine species—may become commonplace.

DISTURBANCE REGIME: INSECTS AND DISEASES

Dominant Insects and Diseases

Native bark beetles (Coleoptera: Scolytinae) represent the primary group of insects affecting longleaf pine, of which the southern pine beetle (*Dendroctonus frontalis*) is the most aggressive tree-killer (table 2). Southern pine beetle occurs throughout the native range of longleaf pine and other southern pines, with loblolly and shortleaf pine stands being the favored hosts (Coulson and Klepzig, 2011). Outbreaks of this beetle occurred every 6 to 10 years over a 40-year period from the 1960s through the 1990s (Clarke et al., 2016), and range expansion into the northeastern United States has recently occurred in association with warming winters (Dodds et al., 2018; Lesk et al., 2017). Southern pine beetle outbreaks across the southeastern United States have declined in the 21st century, which may be attributed to management as well as changed stand and landscape conditions rather than climatic factors or natural enemies (Asaro et al., 2017; Clarke et al., 2016; Lombardo et al., 2022). In addition to hosting southern pine beetle, longleaf pine may host a variety of other native bark beetles and weevils including the black turpentine beetle (*Dendroctonus terebrans*), southern pine engraver (*Ips* spp.), pales weevil (*Hylobius pales*), pitch-eating weevil (*Pachylobius picivorus*), southern pine root

weevil (*Hylobius aliradicis*), and eastern pine weevil (*Pissodes nemorensis*). The collective of bark beetles and the eastern pine weevil is usually associated with damaged or stressed trees, especially lightning-struck trees (Outcalt, 2008). Outbreaks of these bole-infesting beetles are commonly associated with severe droughts (McNichol et al., 2019), storms, and other widespread damage events (Coulson and Klepzig, 2011). Longleaf pine seedlings are vulnerable to tap root or root collar injury caused by the group of regeneration weevils (pales, pitch-eating, and pine root weevil) on recently cutover lands (Doggett and Smith, 1992).

Longleaf pine seedlings in the grass stage are highly susceptible to brown spot needle blight, which causes premature defoliation, stunted growth, prolonged grass stage duration, and eventual mortality with repeated defoliation (Siggers, 1932; Wakeley, 1970). The causal fungal pathogen is widely distributed in North America, Europe, Asia, and Colombia with a recent rise in its relative impact in southern pines (Aglietti et al., 2021; Pandit et al., 2020; Tubby et al., 2023; van der Nest et al., 2019). This pathogen is predicted to expand farther under projected changes in environmental conditions (Tubby et al., 2023) and is especially prevalent in longleaf pine nurseries, where rain splash allows for the spread of conidial fungal spores that increase local inoculum buildup (Phelps et al., 1978).

Table 2—Significant insects and diseases of longleaf pine by tree structure and relative impact

Degree of impact	Roots	Bole (bark, phloem, and xylem)	Foliage, shoots, and twigs	Flowers, fruits, and seeds
Greatest	N/A	Southern pine beetle (*Dendroctonus frontalis*)—most economically and ecologically important native bark beetle	Brown spot needle blight, caused by *Lecanosticta acicula*—most important disease of longleaf pine seedlings in grass stage	N/A
Moderate	Pales weevil (*Hylobius pales*)—tap root injury on recently cutover land	Southern pine engraver (*Ips* spp.)—secondary agents attacking stressed and weakened trees Black turpentine beetle (*Dendroctonus terebrans*)—attacks tree bases and roots	Pitch canker, caused by *Fusarium circinatum*—greatest impact in nurseries	Southern pine coneworm (*Dioryctria amatella*)—greatest impact in seed orchards

Low	Heterobasidion root disease, caused by *Heterobasidion irregulare*—associated with declining trees	Fusiform rust, caused by *Cronartium quercuum*—can result in deformities in older trees and can girdle younger trees	Redheaded pine sawfly (*Neodiprion lecontei*)—seedling and sapling mortality with heavy repeated defoliation Nantucket pine tip moth (*Rhyacionia frustrana*)—affects terminal shoots	N/A

N/A: not applicable.

Response to Insects and Diseases

Compared to loblolly pine, longleaf pine has lower southern pine beetle-induced mortality (Clark et al., 2016; Friedenberg et al., 2007; Snow et al., 1990). However, reduced mortality may result from stand or landscape conditions and host selection by early colonizers rather than lower tree susceptibility; longleaf pine constitutive resin flow and capacity to replace depleted resin are similar to loblolly pine, suggesting that it is just as likely to be attacked and killed by southern pine beetle (Friedenberg et al., 2007; Martinson et al., 2007; Willis et al., 2024). Successful southern pine beetle attacks require outpacing tree resin exudation while excavating entry holes, which results in the characteristic pitch tubes on the bark (Coulson and Klepzig, 2011).

Brown spot needle blight-infected needles have three distinct zones: necrotic tips with a scorched appearance, a mottled middle zone, and a green basal portion (Siggers, 1932). Heavily infected longleaf pine seedlings, initially evaluated at 3 to 4 years after planting, had reduced growth and yield after 30 years (Wakeley, 1970).

Second-Order Interactions

Fire regime, stand structure, site conditions, and disturbance history interact to affect populations of the southern pine beetle guild (southern pine beetle, black turpentine beetle, and southern pine engraver) in longleaf pine stands (Ritger et al., 2023). Conversely, southern pine beetle outbreaks have a direct effect on composition, structure, and fuel dynamics (Coleman et al., 2010). On xeric sites, frequent burning at 2-year intervals reduced southern pine engraver trap catches; however, burning did not affect southern pine beetle trap catches (Ritger et al., 2023; Sullivan et al., 2003). Fire exclusion for more than a decade was positively associated with six-spined engraver (*Ips calligraphus*) trap catches (Ritger et al., 2023). Heavy fuel loads in fire-excluded areas may also result in smoldering-related reduction of longleaf pine defenses and increased mortality, especially during post-fire drier periods (Slack et al., 2016). Following southern pine outbreaks, higher fuel loading is expected, potentially altering fire behavior (Coleman et al., 2010; Xie et al., 2020). As snags begin to fall, coarse fuels increase and may continue to do so for a decade or more (Conner and Saenz, 2005; Xie et al., 2020). Post-outbreak stand structural and compositional shifts may also change the fire-carrying fuel types, fuelbed depth, and fine fuel distribution (Waldrop et al., 2007; Xie et al., 2020). Simulations of fire

behavior indicate that stands containing beetle kill produce higher rates of fire spread and flame length than uninfested stands (Xie et al., 2020).

Severe droughts may incite southern pine engraver outbreaks and result in tree mortality (Connor and Wilkinson, 1983; McNichol et al., 2019; Negrón et al., 2009). However, direct linkages between drought and southern pine beetle outbreaks are not well established (Kolb et al., 2016; McNichol et al., 2019). Longleaf pine mortality rates following southern pine engraver outbreaks during droughts is also not well documented (McNichol et al., 2019). Soil type and site conditions differentially affect southern pine engraver activity and may result in greater tree mortality on xeric sites due to higher population pressure, especially in the absence of fire (Ritger et al., 2023).

Management Considerations

Species selection for planting is critical and should consider potential tradeoffs between high early returns versus enhanced insect and disease incidence. Longleaf pine may provide lower risk potential given its relative resistance to insects and diseases (Moser et al., 2003). When feasible, sanitation cuts to remove stressed, weakened, or damaged trees may reduce the impacts of the southern pine beetle feeding guild. During outbreaks, however, healthy trees are attacked (Coulson and Klepzig, 2011). The most effective strategy for preventing southern pine beetle infestations is to maintain healthy vigorous stands by avoiding stocking levels more than 27.5 m^2 ha^{-1} (120 $feet^2$ $acre^{-1}$) basal area, via properly timed thinning, resulting in residual stand stocking levels of less than 18.4 m^2 ha^{-1} (less than 80 $feet^2$ $acre^{-1}$) of basal area, or 5.5 to 6.1 m (18 to 20 feet) spacing between stems (Nowak et al., 2015). Actively expanding southern pine beetle infestations are managed using cut-and-remove or cut-and-leave treatments, depending on the area affected and market availability (Billings, 2011; Clarke et al., 2016). The cut-and-leave treatment is intended for suppressing small (fewer than 50 infested trees) unmerchantable areas and is conducted in the summer months to disrupt spot growth and reduce emerging beetle survival potential (Billings, 2011; Clarke et al., 2016).

Screening planting material and seed sources for disease resistance is essential for preventing losses to brown spot needle blight (Anderson and Walkinshaw, 1986; Carey et al., 2005; Lott et al., 1996; Powers et al.,1981; Sims et al., 2023; Snow et al., 1990). Brown spot needle blight-resistant seed sources can be used in nurseries to reduce infection potential without increasing susceptibility to fusiform rust (Lott et al., 1996). The Resistance Screening Center in Asheville, North Carolina, provides screening services to test seedlots and seedlings(Cowling and Young, 2013). Currently, tree improvement and progeny testing are components of America's Longleaf Pine Restoration Initiative (Bollinger et al., 2024). Screening selections from tree improvement programs allows for the identification of longleaf pine families to deploy, identification of susceptible and resistant selections, and culling seed orchards (Cowling and Young, 2013).

DISTURBANCE REGIME: WILDLAND FIRE

Dominant Fire Regime

Fire is a dominant ecological process across the southeastern United States and especially in longleaf pine ecosystems. The natural range of longleaf pine harbors a high lightning strike frequency and centuries of human fire use (Stambaugh et al., 2017). Based on reconstructions from fire scar evidence, longleaf pine has perhaps the most frequent fire return interval (about 1 to 5 years) of any forested ecosystem in North America (Rother et al., 2020; Stambaugh et al., 2017). Indeed, Stambaugh et al. (2011) found multiple examples of subannual fires (multiple scars in a single annual ring).

Evidence suggests that fires regularly occurred in the growing (May through September) and dormant (primarily December through March) seasons (Stambaugh et al., 2017).

Fire behavior in longleaf pine stands is typically characterized as low-intensity surface fires with high frequency. Fires spread in longleaf pine stands through mixtures of dead fuels (litter, cones, woody debris) and live fuels including herbaceous material, woody shrubs, and vines. Longleaf pine litter and cones are among the most flammable of all species in North America (Fonda and Varner, 2004; Varner et al., 2021b; Varner et al., 2022; Willis et al., 2024b). The leaf litter of other common species in longleaf pine ecosystems, particularly the pyrophytic oaks (turkey oak, southern red oak [*Quercus falcata*], post oak, blackjack oak) and saw palmetto, are similarly flammable (Varner et al., 2021b) as are several herbs, including wiregrass (Fill et al., 2016). Longleaf pine stands existing on flatwood sites increase in fire intensity with time since fire, functioning as a shrub fuel with slow rates of spread and high fire intensity (Brose and Wade, 2002). Outside of the flatwoods, fire exclusion hastens the loss of flammable litter and herbaceous fuels, resulting in poor fire spread and decreased intensity like the mesophication of many eastern U.S. forests.

The contemporary fire regime of extant longleaf pine is dictated largely by managed prescribed fire, at intervals approximating their pre-European frequencies. States with substantial longleaf pine occurrence account for approximately 60 to 70 percent of the prescribed burned area in the United States. Within longleaf pine's range, hotspots of prescribed fire are located on private lands (primarily hunting reserves for large bobwhite quail [*Colinus virginianus*], but also property of many nonindustrial private landowners) and large public lands (national forests, military installations, wildlife refuges, and parks) (Cummins et al., 2023). Burning is primarily conducted in February, March, and April following cold front passage (cool, predictable winds following discrete precipitation events) (Cummins et al., 2023).

Response to Fire

Longleaf pine's ability to withstand fire-caused injury is noteworthy across its life history. For grass stage seedlings, the geometry of the foliage around the apical bud provides thermal protection from radiant and convective heat (Knapp et al., 2018). This unique foliage architecture often enables terminal bud survival and subsequent sprouting despite needle consumption (Varner 2021b). Seedlings of longleaf pine also can resprout from axillary buds located above the cotyledon before reaching a height of 1.37 m, and saplings can quickly refoliate the crown to replace needles consumed by fire (Farrar, 1975; Knapp et al., 2018; Sayer et al., 2020a; Sayer et al., 2020b; Stone and Stone, 1943). Seedlings rapidly gain fire resistance after height growth initiation by accumulating stem bark, enabling the heat-sensitive vascular cambium to survive (Jackson et al., 1999). Though the grass stage and rapid bark development improve survival, seedlings and saplings still experience the greatest fire-caused mortality under typical burning situations (review in Glitzenstein et al., 2021). Grass stage seedlings are particularly vulnerable to fire-induced mortality when grown under shade (Willis et al., 2025). Pole-sized and adult trees are remarkably resistant to heating caused by surface fire. Mature longleaf pines generally survive complete crown scorch, with a brief period of defoliation, and recover foliage from surviving meristems within 8 weeks of fire (Johansen and Wade, 1987; Varner et al., 2021b).

Second-Order Interactions

The primary second-order interaction in longleaf pine ecosystems is between fire and bark beetles. Fire not only incites bark beetle attacks in weakened trees but also represents a substantial threat to living trees within beetle-infested stands. Southern pine beetle can kill pines over large areas, leading to acute issues with immediate crown fuel drying, then additions of fine and large woody fuels from dead

trees. In practice, identification of beetle-killed trees is rapid, and treatment of mortality spots within stands becomes a priority. Salvage of dead trees is common except in the most remote locations.

Management Considerations

Given its evolved traits, longleaf pine is capable of surviving fire across its life history, with some important exceptions. Substantial arguments exist over burning young grass stage seedlings. Knapp et al. (2018) found that seedlings with root collar diameters of more than 15 mm (0.6 inch) had a greater than 50 percent probability of survival, with reduced survival during growing season fires. Similarly, the wisdom of burning when seedlings begin height growth, from the sapling to small pole stage, is debated. The best data to date suggests remarkable resilience, but expectations of 10 to 20 percent mortality are warranted (Glitzenstein et al., 2021). In naturally regenerated stands, this level of mortality is often desired, but in planted stands, particularly those with low planting density (e.g., 1235 to 1346 trees ha^{-1} [500 to 545·$acre^{-1}$]), mortality is undesirable. Fires in young stands where some mortality is acceptable often receive a collateral benefit of accelerated pruning (McGuire et al., 2021). Substantial adult mortality may occur when fire is reintroduced into stands with a legacy of fire exclusion. Fires in these situations typically smolder into deep forest floor accumulations at the base of large pines, consuming fine roots and possibly resulting in acute physiological stress (O'Brien et al., 2010; Varner et al., 2009) and eventual mortality (Varner et al., 2007).

DISTURBANCE REGIME: DROUGHT

Dominant Drought Regime

Longleaf pine exists as a dominant or codominant species across a gradient of plant-available soil water. As available moisture decreases, longleaf pine increases in prevalence, resulting in its dominance on xeric, drought-prone sites (Peet, 2006). Late summer droughts are common throughout the biological range of longleaf pine (Foster and Brooks, 2001; Stambaugh et al., 2021). An exception to this pattern arises in the western Gulf Coastal Plain, where drought occurrence is considered seasonally random (Hanson and Weltzin, 2000). Droughts are expected to become more frequent and intense in the future with rising temperatures and evapotranspiration (Kunkel et al., 2013; Williams et al., 2017).

Response to Drought

Longleaf pine survives drought through a combination of avoidance and tolerance traits and is considered the primary southern pine best adapted to xeric conditions (Willis et al., 2024a). Water stress is mitigated in all but extreme conditions, in part due to a large investment in a heavy root system (Addington et al., 2004; Samuelson et al., 2012; Samuelson et al., 2019). Longleaf pine maintains a high root-to-shoot ratio (0.54) and tap root exploration potential (4.8 m [15.7 feet]) and can redistribute soil moisture via hydraulic lift (Canadell et al., 1996; Espeleta et al., 2004; Heyward, 1933). In addition to root system investment, longleaf pine conserves water during drought by reducing stomatal conductance (Samuelson et al., 2019). Vapor pressure deficit regulates longleaf pine stomatal function when soil water is plant-available, but little stomatal control exists once soil water reaches the permanent wilting point (Mendonca et al., 2023). Stomatal closure and turgor loss of foliage occur at relatively low values (-2.9 and -3.0 MPa, respectively), indicating a high degree of drought tolerance

(Samuelson et al., 2019). Longleaf pine needle shoot phenology is largely unaffected by drought (Mendonca et al., 2022).

While stomatal regulation is an important mechanism for conserving water, shifts in hydraulic and crown architecture also influence drought resistance across a soil water gradient. Longleaf pines established on xeric sites are shorter in stature, have a higher ratio of root area to leaf area, and retain a larger fraction of leaf area under drought conditions than those established on mesic sites (Addington et al., 2006; Wright et al., 2013). Moreover, photosynthetic capacity and water use efficiency are proportionally better maintained by trees established on xeric sites compared to trees established on mesic sites (Wright et al., 2013).

Second-Order Interactions

Drought effects on longleaf pine can be tempered by edaphic conditions, stand density, and tree age. Sites on sandy or rocky soils are subject to more intense drought than sites with finer textured soils because of the effects of soil texture on plant-available water. Stand density can also modify drought intensity because competition for water at high stand densities reduces stand growth and increases tree mortality (Klockow et al., 2020). Germinants of longleaf pine are initially more susceptible to drought than those of loblolly pine (Hart et al., 2020). Nevertheless, as grass stage seedlings develop, drought vulnerability is quickly reduced by rapid tap root growth (0.8 cm day^{-1} [0.3 inch day^{-1}]) (Allen, 1958). Drought resilience (i.e., growth after drought) also increases with age, as growth among longleaf pines 80 years or older recovered faster than those less than 55 years old (Goode et al., 2019).

Management Considerations

Maintaining low-density stands (e.g., lower range of full stocking or woodland structure) via thinning or harvesting is recommended for increasing drought resistance (i.e., growth during drought) and resilience (Steckel et al., 2020). Thinning generally mitigates the effects of droughts on conifers by accelerating recovery (Sohn et al., 2016, but see Bottero et al., 2017), yet the response of longleaf pine to thinning has been mixed. Longleaf pine drought resistance and resilience increase at higher levels of basal area removal (Dues, 2023). Moreover, the benefits of thinning were enhanced on excessively drained soils (Dues, 2023). Nevertheless, Goode et al. (2019) found no difference in post-drought growth between longleaf pine established within managed (304 trees ha^{-1} [123·$acre^{-1}$], 3- to 5-year fire return interval) and unmanaged stands (694 trees ha^{-1} [280·$acre^{-1}$], fire-excluded) on a xeric site. This suggests that additional factors may override the effects of density management. Furthermore, frequent applications of prescribed fire to control vegetative competition may generally aid stemwood production in low-density stands. However, the effect of fire frequency on longleaf pine drought resistance and resilience remains unknown.

ADDITIONAL DISTURBANCES

Dominant Disturbances

Weather-related disturbances (hurricanes, tornadoes, and lightning) are the primary cause of longleaf pine mortality (Ojha et al., 2021). On average, tropical storm intensity winds have a return interval of approximately 6 years throughout much of longleaf pine's geographic range (Cannon et al., 2023; Zeng et al., 2009). Historically, hurricanes (Saffir-Simpson wind scale categories 1 to 5) occur within the southeastern United States every 13 years (Keim et al., 2007). Severe hurricanes (Saffir-

Simpson 3 to 5) occur every 58 years and are more common along the Gulf Coast from Texas to Alabama (Jagger and Elsner, 2006; Keim et al., 2007). Tornadoes and intense thunderstorms annually impact southeastern forests, with areas of Mississippi and Alabama experiencing an increased probability of tree damage (Fortuin et al., 2022). In contrast to hurricanes and tropical storms, ice storms are more common in inland locations and occur every 10 to 15 years (Bragg et al., 2003). Lightning strikes frequently cause single tree mortality but can occasionally kill small groups of trees (Palik and Pederson, 1996). The odds of lightning-induced mortality increase with tree height (Outcalt, 2008).

Response to Disturbances

While not immune to wind damage, longleaf pine is the most wind-resistant southern pine (Johnsen et al., 2009; Rutledge et al., 2021; Willis et al., 2024a). Traits including an open crown structure, relatively high wood specific gravity, high modulus of rupture and elasticity, a large tap root, and an extensive root system help longleaf pine withstand windstorms (Garms and Dean, 2019; Samuelson et al., 2017). Longleaf pine growing in wind-prone coastal areas are also generally shorter in height and develop shorter needles than those growing in more sheltered locations, likely further reducing drag (Patterson et al., 2016).

In contrast to wind, longleaf pine has low inherent resistance to ice damage (Bragg, 2016; Lu et al., 2020; Willis et al., 2024a). Longleaf pine ice vulnerability is derived from its high needle and branch surface areas, which enable ice buildup capacity. Thick branches also allow longleaf pine to accumulate more ice before snapping, thus increasing the risk of stem injuries (McKellar, 1942).

Second-Order Interactions

Tree-level wind resistance is primarily affected by tree size. Wind vulnerability increases consistently with tree height (Bigelow et al., 2021; Johnson et al., 2009). Stand-level wind resistance is influenced by soil conditions, topography, stand density, and adjacent stand conditions (Wilson, 2004). Longleaf pine is resistant to wind across many soil types compared to other southern pines, but this advantage diminishes on poorly drained soils (Rutledge et al., 2021). Trees growing on exposed positions, such as ridgetops and windward slopes, have elevated risk to wind damage (Everham and Brokaw, 1996). Indeed, models containing slope, valley depth, soil erodibility factor, bedrock depth, temperatures, and precipitation levels account for 53 percent of the deviation in pine damage during tornadoes and thunderstorms (Fortuin et al., 2022). Longleaf pines grown under closed canopy conditions are particularly vulnerable to wind damage after thinning or harvesting (Polinko et al., 2022; Stanturf et al., 2007). Similarly, trees growing near open fields, canopy gaps, or timber harvests have an elevated risk of wind damage (Gardiner, 2021).

Ice resistance can differ by tree size, canopy position, and wind conditions. Smaller diameter longleaf pines (DBH less than 9.9 cm [3.9 inches]) have greater ice resistance than larger trees (15.0 to 24.9 cm [5.9 to 9.8 inches]) (Bragg, 2016). Ice-induced stem breakage increases once the height-to-diameter ratio surpasses 80 (Harrington, 2020). Trees developing in sheltered canopy positions are less likely to be killed or injured by ice than those in dominant growing positions (Lu et al., 2020). Windstorms can also intensify the effects of ice on tree injury and mortality (Bragg et al., 2003).

Management Considerations

Forest management can augment the inherent wind resistance of longleaf pine. In even-aged stands, longleaf pine wind resistance can be improved by shortening rotation length, thereby limiting

average tree size. Wind-firmness may also be improved by planting on wide spacings and maintaining low-density stands to encourage the development of highly tapered stems (Whelan et al., 2024). Thinning and harvesting treatments can be staggered over time and across the landscape to hedge against any single wind event (Stanturf et al., 2007). Longleaf pine wind resilience is enhanced by maintaining multiple cohorts in an uneven-aged structure (Polinko et al., 2022). Stocking within uneven-aged stands can be shifted to decrease the density of large diameter trees by selecting a smaller "d" or larger "q" value, holding "B" constant, within the BDq regulation method. Limiting maximum tree size will also help reduce the size of canopy gaps created during harvests, which will reduce internal edge effects. Within the context of uneven-aged management, wind resistance and resilience has not been shown to vary among stocking regulation methods (e.g., BDq, Volume Control Guiding Diameter Limit, Diameter Limit Cutting) (Polinko et al., 2022).

Management can also reduce vulnerability to ice damage. Precommercial thinning increases longleaf pine ice resistance by allowing trees to develop a lower height-to-diameter ratio (Harrington, 2020). Regeneration systems that retain continuous canopy cover (e.g., irregular shelterwood or uneven-aged management) may also improve ice resilience at the stand level, as younger cohorts will be partially sheltered from ice damage.

GOODS AND SERVICES

Goods

WOOD PRODUCTS

Longleaf pine can provide any wood product derived from pine species. Traditionally, longleaf pine has been managed for utility poles because of its ability to self-prune, which adds economic value compared to sawtimber. Results from a long-term study found that nearly 75 percent of longleaf pine pole-size trees would be classified as poles from naturally regenerated stands (Kush, 2016). Pole production ratios in planted monocultures remain unknown.

NONWOOD PRODUCTS

The primary nonwood product of longleaf pine is its needles. Historically, the needles were used to manufacture handwoven baskets. Today, pine straw raking is a major agroforestry income source, especially from young monocultures that are 10 to 20 years old. Stands managed for pine straw production need to be clear of competing vegetation, especially invasive species, so the straw is easy to rake and free of debris, as buyers are willing to pay more for clean straw. If prescribed fire has been lacking or infrequent, mowing and herbicide use will be needed to prepare the stand for raking. Dyer et al. (2012) provided an equation for calculating pine straw production based on basal area, tree density, site index, and age. Megalos et al. (2019) is an extensive resource for most aspects of pine straw production.

Silvopasture is another agroforestry venture where longleaf pine can be effectively utilized. Traditionally, silvopasture involves managing grazing domesticated animals within a woodland setting where trees are planted in rows of two or three on a spacing of 2.4 by 3.0 m (8 by 10 feet) with 9.1 m (30 feet) between the next series of rows. Prescribed fire is critical for managing this system. The U.S. Department of Agriculture, National Agroforestry Center (n.d.) has extensive resources on this topic.

Floral and decorative products are abundant in longleaf pine ecosystems. Longleaf pine cones are highly sought after due to their large size. The leaves of turkey oak, a hardwood associate of longleaf

pine on xeric sites, are a common component of many floral arrangements. Native grasses and forbs are also frequently included in dried-flower arrangements.

Ecosystem Services

BIODIVERSITY

Beyond the direct provision of forest products, longleaf pine woodlands and savannas provide a variety of ecosystem services. Longleaf pine woodlands are notable for their high vascular plant diversity. Walker (1993) found 187 rare vascular plant taxa associated with longleaf pine ecosystems. Walker and Peet (1984) reported that longleaf pine savannas supported 42 plant species per square quarter meter, while Peet and Allard (1993) found up to 140 species·1000 m^{-2} (13 species·1,000 $feet^{-2}$) in mesic woodlands. The high characteristic understory diversity and biomass of grasses and forbs impede but do not prevent invasive species colonization (Drew et al., 1998). High forb and flowering shrub diversity across a range of stand ages and sites enables longleaf pine ecosystems to sustain high pollinator diversity, particularly bees (Dixon et al., 2022; Moylett et al., 2020; Ulyshen et al., 2024).

Longleaf pine ecosystems are also notable for supporting several rare floral and faunal species. Most notable are the red-cockaded woodpecker (*Dryobates borealis*), gopher tortoise (*Gopherus polyphemus*), Bachman's sparrow (*Peucaea aestivalis*), Louisiana pine snake (*Pitouphis ruthveni*), eastern indigo snake (*Drymarchon couperi*), eastern diamondback rattlesnake (*Crotalus adamanteus*), and gopher frog (*Rana capito*). Numerous invertebrates and dozens of rare plants are also compatible with longleaf pine woodlands and typical management activities (Noss, 2018). Wet longleaf savannas also contain an extremely high diversity of endemic carnivorous plant species, including several species of pitcher plants (*Sarracenia* spp.), sundews (*Drosera* spp.), and butterworts (*Pinguicula* spp.) and the Venus flytrap (*Dionaea muscipula*).

FOREST CARBON AND NUTRIENT DYNAMICS

Forest carbon sequestration and carbon stability in stands of longleaf pine are noteworthy, given its high specific gravity; long lifespan; resistance to fire, disease, and insects; wide site tolerance; and ability to grow in dense stands (Kush et al., 2004). Even with frequent burning, longleaf pine stands can retain substantial aboveground and belowground carbon (Dixon et al., 2022; Kush et al., 2004).

RECREATION

Longleaf pine stands are highly sought after for hunting opportunities, especially for northern bobwhite quail. Hunting properties managed for quail habitat span the range of longleaf pine, with concentrations in northern Florida, southern Georgia, eastern Alabama, and the Coastal Plain of South Carolina where they contribute substantially to local economies (Nimlos et al., 2023). These properties yield timber while providing world-class hunting opportunities; indeed, the Stoddard-Neel method, which balances aesthetics valued for hunting with supplemental income from periodic timber harvests, was developed to accommodate the multiple land use objectives of recreational properties (Moser et al., 2002). Beyond hunting, longleaf pine ecosystems provide excellent outlets for bird watching, botanizing, and hiking.

OTHER (ADDITIONAL CONSIDERATIONS)

Due to its water conservation traits and characteristic open woodland structure, interest in managing longleaf pine to restore streamflow and mitigate water scarcity has increased. In Georgia, Qi

et al. (2021) found that restoring longleaf pine woodlands would increase water yield by 5 percent, with up to 74 percent higher streamflow during low flow compared to the existing closed canopy forest. Watershed services are increasingly sought after in longleaf pine restoration projects for their positive impacts on public water supplies (Sellers et al., 2021).

URBAN FORESTRY

Urban Range and Abundance

Longleaf pine is not viewed as an urban tree and its occurrence depends on site legacy. For instance, in Gainesville, Florida, longleaf pine represented 0.6 percent of the total tree population (Andreu et al., 2017). In comparison, loblolly and slash pine were the two most populous species (17 percent and 11 percent of the estimated 7.2 million trees, respectively). Similarly, Hutchens (2023) observed that only 12 168 ha (30,068 acres) (2.4 percent) of Florida's longleaf pine cover area occurs in developed landscapes.

Forests in Cities

REPRODUCTION AND EARLY GROWTH

No research has been reported describing longleaf pine reproduction and early growth in cities.

SAPLING STAGES TO MATURITY

Urbanization affects longleaf pine ecosystems in multiple ways and is a significant threat to their sustainability (Costanza et al., 2015). Threats include deforestation and fragmentation, parcellation, fire suppression, and site degradation. Deforestation can occur when a site is cut over through harvesting or cleared for agriculture or housing development. Costanza et al. (2015) projected that urbanization in combination with fire suppression will result in the loss of more than 30 000 ha (74,100 acres) of longleaf pine by 2099. Fragmentation, on the other hand, divides existing forest cover into small, isolated patches. Hutchens (2023) modeled the effect of urbanization on longleaf pine stands and observed increasing fragmentation with urbanization. Fragmented forest patches are more vulnerable to biophysical stressors such as invasive species, insect outbreaks, and an increase in edge habitat than large-contiguous forest cover (Fahrig, 2003). For example, Gilliam (2020) reported that crape-myrtle (*Lagerstroemia indica*), a nonnative species planted in ornamental beds, has invaded longleaf pine natural areas on the University of West Florida campus.

Urbanization results in a more divided landscape. Parcellation is the process of dividing large, singularly owned landholdings into small landholdings with multiple owners. The transition from large to small ownerships can increase the overall cost of forest management (Vorhees, 2015). The expansion of the wildland-urban interface is one of the primary drivers of deforestation, fragmentation, and parcellation in the southeastern United States (Zipperer, 2002).

A major consequence of urbanization is its direct and indirect effects on fire (Costanza et al., 2015). In an urbanizing landscape, such as the wildland-urban interface, using prescribed fire can be prohibited because of the closeness of urban structures and the effect of smoke (Brockway et al., 2006;

Costanza et al., 2013). Although mechanical clearing can reduce hardwood invasions, it is costly to implement. Therefore, over time, longleaf pine sites adjacent to urban cover can degrade because of the lack of fire to suppress hardwood encroachment (Gilliam, 2023). The expansion of human population centers indirectly affects prescribed fire through the creation of smoke-sensitive areas and by increasing pressure on land management to prevent potential escapes.

In urban and urbanizing landscapes, longleaf pine ecosystems shift from an open canopy with savanna characteristics to a closed canopy with a dense midstory. Mature longleaf pine may remain on the landscape; however, natural regeneration is generally absent and understory degradation often occurs through fire exclusion and encroachment of nearby nonnative species (Gilliam et al., 2020).

Trees in Planted Urban Landscapes

SAPLING STAGES TO MATURITY

Although the occurrence of longleaf pine in cities is limited, it is well suited for the urban environment. Longleaf pine is resilient to high temperatures, altered moisture regimes, and susceptibility to beetles compared to other southern pines (Costanza et al., 2015). Additionally, longleaf pine provides a unique aesthetic appearance.

In general, longleaf pine is not planted in urban landscapes (Gilman et al., 2018), but remnant individuals, preserved during construction, do occur on golf courses as well as residential, institutional and commercial sites. Though longleaf pine is prized for its open habit, trees produce considerable amounts of needles, sap, branches, and large cones. Roots can also crack asphalt when growing beneath the surface. Because of this debris and root damage, trees are not planted near parking lots, streets, and other paved surfaces (Gilman et al., 2018).

Because of its grass stage, longleaf pine is planted in ornamental beds to provide a different texture and structure from planted grasses. However, these seedlings will eventually exit the grass stage, which alters the configuration of the bed and may pose a problem for nearby buildings. Longleaf pine establishes best on acidic soils. However, because of the high pH of irrigation water, longleaf pine is prone to chlorosis if these beds are continually irrigated (Gilman et al., 2018).

Urban Goods and Services

In urban areas, goods and services shift toward aesthetics and wildlife sightings. Longleaf pine is a tall, stately tree with unique bark and an open, spreading canopy. Additionally, longleaf pine provides wildlife habitat with its seed production and shelter. Consequently, longleaf pine trees offer ample opportunities for wildlife viewing, especially birds. Longleaf pine also provides patchy shade, but it is less valued as a shade tree compared to many deciduous species. Remnant longleaf pine patches in public parks also provide opportunities to educate the public about the importance of prescribed fire in fire-dependent communities.

KNOWLEDGE GAPS

While knowledge of longleaf pine has expanded tremendously over the past three decades, there remain several important unanswered questions.

- From a genetics standpoint, research is needed to develop cost-effective genome-wide markers for routine genotyping. Such markers would (1) facilitate genome-informed seed source selection for climate matching to planting sites; (2) ensure that adequate levels of genetic diversity are included in seed production areas, seed source collections, and nursery crops; and (3) provide tree breeders with molecular tools to improve the accuracy of selection for traits of economic and ecological importance.
- Unanswered questions continue to hamper artificial regeneration efforts. For example, little is known about how fall-planted longleaf pine will perform on old-field sites. Questions also surround the efficacy of planting containerized seedlings high on sites with little potential for soil movement. Little can be definitively said about whether planted trees will approximate the ecological function of natural regenerated trees as they age. Similarly, little research has focused on whether herbicide site preparation tank mixes can be tailored to retain components of the understory while still promoting longleaf pine establishment.
- In terms of natural regeneration, consensus has yet to be reached on the optimal gap size for regenerating longleaf pine. Moreover, research describing the effects of variable retention harvesting or gap expansion on longleaf pine regeneration is currently lacking. Myriad questions also exist surrounding the causal factors of longleaf pine mortality in fire. In general, silvicultural studies in the Mountain and Piedmont ecoregions are lacking compared to the Coastal Plain and Sandhills. Studies examining mixed-conifer dynamics are also needed to account for loblolly pine encroachment on former longleaf pine sites.
- From an ecological perspective, studies examining southern pine performance under a common structure are needed to evaluate the importance of species identity in woodland restoration. Further research is also needed to understand the mechanisms underpinning longleaf pine drought tolerance. Little is also currently known about how old-growth longleaf pine stands will respond to varying climatic conditions.

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