Longleaf pine (*Pinus palustris*), whose species name means "of the marsh," has been locally referred to as longstraw, yellow, southern yellow, swamp, hard or heart, pitch, and Georgia pine. In presettlement times, this premier timber and naval stores tree grew in extensive pure stands throughout the Atlantic and Gulf Coastal Plains. At one time the longleaf pine forest may have occupied as much as 24 million ha (60 million acres), although by 1985 less than 1.6 million ha (4 million acres) remained.

**Habitat**

**Native Range**

The natural range of longleaf pine (fig. 1) includes most of the Atlantic and Gulf Coastal Plains from southeastern Virginia to eastern Texas and south through the northern two-thirds of peninsular Florida. The species also grows in the Piedmont, Ridge and Valley, and Mountain Provinces of Alabama and northwest Georgia.

**Figure 1**—The native range of longleaf pine.
Climate

Longleaf pine grows in warm, wet temperate climates characterized by hot summers and mild winters. Annual mean temperatures range from 16° to 23° C (60° to 74° F) and annual precipitation from 1090 to 1750 mm (43 to 69 in), the least being 1090 to 1270 mm (43 to 50 in) in the Carolinas and Texas and the greatest along the Gulf Coast of Alabama, Mississippi, and extreme west Florida. A distinct summer rainfall peak occurs along the Atlantic Coast, being most pronounced in Florida. A secondary rainfall peak in March becomes pronounced along the Gulf Coast. Fall is the driest season of the year, although droughts during the growing season are not unusual.

Soils and Topography

Longleaf pine is native to a wide variety of sites ranging from wet, poorly drained flatwoods to dry, rocky mountain ridges. Elevations range from barely above sea level near the beaches on the lower Coastal Plain up to about 600 m (1,970 ft) in the mountains of Alabama. Most of the longleaf pine forests are found on the Atlantic and Gulf Coastal plains at elevations below 200 m (660 ft). Here the soils are largely derived from marine sediments and range from deep, coarse, excessively drained sands to poorly drained clays. For the most part, surface soils are sandy, acid, low in organic matter, and relatively infertile. In the Mountain Province, soils are derived largely from granite, quartzite, schist, phyllite, and slate, while in the Ridge and Valley Province, soils are derived mostly from sandstone, shale, limestone, and dolomite.

Within the natural range of longleaf pine, three soil orders are of major importance. Ultisols are the dominant order and cover most of the southeastern United States outside of peninsular Florida. Ultisols most commonly associated with longleaf pine are the Typic Paleudults and Plinthic Paleudults. The other two soil orders are Entisols and Spodosols. Deep, sandy Entisols, primarily Quartzipsamments, range from about 3 m (10 ft) above sea level in Florida up to about 185 m (600 ft) in Georgia and the Carolinas. Entisols have not developed diagnostic horizons. They make up the Sandhills of the Carolinas, Georgia, and northwest Florida and the sand ridges in the central Highlands of peninsular Florida. Spodosols, particularly Aquods, are typical of the flatwoods of the lower Coastal Plain in Florida. They are wet, sandy soils with a fluctuating water table that is at or near the surface during rainy seasons.

Associated Forest Cover

The principal longleaf cover types are Longleaf Pine (Society of American Foresters Type 70), Longleaf Pine-Scrub Oak (Type 71), and Longleaf Pine-Slash Pine (Type 83) (2). Longleaf pine is also a minor component of 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).

Longleaf pine develops in close association with periodic surface fires. The vegetation associated with longleaf pine reflects the frequency and severity of burning. In the past, frequent fires resulted in open, parklike stands of longleaf with few other woody plants and a ground cover dominated by grasses. Ground cover in longleaf pine in the Coastal Plains can be separated into two general regions, with the division in the central part of south Alabama and northwest Florida. To the west, bluestem (Andropogon spp.) and panicum (Panicum spp.) grasses predominate; to the east, wiregrass (pineland thrееəw, Aristida stricta) is most common.

With a reduction in fire occurrence, hardwoods and other pines encroach on the longleaf forest. Within the range of slash pine (Pinuselliottii), this species becomes increasingly important, leading to the cover type Longleaf Pine-Slash Pine. Elsewhere loblolly and shortleaf pines (P. taeda and P. echinata) as well as hardwoods gradually replace the longleaf, eventually resulting in Loblolly Pine-Hardwood (Type 82) or occasionally Loblolly Pine-Shortleaf Pine (Type 80). On poor, dry sandhills and mountain ridges, scrub hardwoods invade the understory creating forest cover type Longleaf Pine-Scrub Oak and finally Southern Scrub Oak (Type 72) as the pine disappears (12).

Hardwoods most closely associated with longleaf pine on mesic Coastal Plain sites include southern red, blackjack, and water oaks (Quercus falcata, Q. marilandica, and Q. nigra); flowering dogwood (Cornus florida); blackgum (Nyssa sylvatica); sweetgum (Liquidambar styraciflua); persimmon (Diospyros virginiana); and sassafras (Sassafras albidum). The more common shrubs include gallberry (Rex glabra), yaupon (I. vomitoria), southern bayberry (Myrica cerifera), shining sumac (Rhus copallina), blueberry (Vaccinium spp.), huckleberry (Gaylussacia spp.), and blackberry (Rubus spp.). On xeric sandhill sites, the most common associates are turkey, bluejack, blackjack, sand post, and dwarf live oaks (Quercus laevis, Q. incana, Q. marilandica, Q. stellata var. margaretta, and Q. minima). On the dry clay hills and mountains of Alabama, blackjack, post (Q. stel-
and southern red oaks, and mockernut hickory (Carya tomentosa) are found with longleaf pine. On low, wet flatwood sites near the coast, the most conspicuous understory plants are gallberry and saw-palmetto (Serenoa repens). Other common understory plants in low, wet Longleaf Pine or Longleaf Pine—Slash Pine types are sweetbay (Magnolia virginiana), swamp cyrilla (Cyrilla racemiflora), large gallberry (Ilex coriacea), buckwheat-tree (Cliftonia monophylla), blueberries, and blackberries.

**Life History**

**Reproduction and Early Growth**

Flowering and Fruiting-Like all species in the pine family, longleaf pine is monoecious. The strobili of longleaf pine, both male (catkins) and female (conelets), are initiated during the growing season before buds emerge. Catkins may begin forming in July, while conelets are formed during a relatively short period of time in August. The number of flowers produced is apparently related to weather conditions during the year of initiation. A wet spring and early summer followed by a dry period in late summer promotes conelet production (27). Catkin production, however, is favored by abundant rainfall throughout the growing season. Female strobili are borne most frequently in the upper crown, and male strobili predominate in the lower crown (26). Late summer rainfall depresses conelet initiation, probably because vigorous exposed shoots in the middle and upper crown continue to grow. In the lower crown, where most catkins are borne, shoots stop growing earlier than they do in the upper crown.

Since rainfall patterns associated with catkin initiation differ from those favoring conelets, large crops of male and female flowers do not necessarily coincide. Ten years of observation did not show any correlation between size of conelet and pollen crops in longleaf pine.

Variable but usually heavy annual losses of longleaf pine conelets can be expected; observed losses have ranged from 65 to 100 percent (2,24,30). Several agents, alone or in combination, may be responsible. The more important appear to be insects, bad weather, and insufficient pollen. Over 15 years at one location, cone production was related to pollen density, to the point of a sufficiency of pollen (2). Further increases in pollen density had little effect. In some cases, nearly all the losses have been attributed to insects (24), while in others the more common causes of conelet losses were not responsible (30). Most conelet losses seem to occur in the spring, at about the time of pollination, although substantial losses may also occur in the summer (24). Most of the spontaneous conelet abortions in longleaf pine may result from excess ethylene production by foliage and shoots. A foliar spray with antiethylene compounds soon after anthesis has reduced conelet abortion by half, doubling seed yields (18).

Catkin buds normally emerge in November, then remain dormant for about a month before growth resumes. Conelet buds emerge in January or February. The rate of development of both conelets and catkins thereafter is almost entirely dependent on ambient temperature. Catkins are purple from the time they emerge from the buds until they shed their pollen. Upon emerging from the bud, conelets are red until they are pollinated, after which they gradually fade to a yellowish green. Most mature catkins range from 3 to 5 cm (1.2 to 2.0 in) in length.

The average date of peak pollen shed and conelet receptivity may range from late February in the southern part of longleaf pine's range to early April toward the northern limits. Most locations may experience flowering dates close to these extremes. The date of peak pollen shed and conelet receptivity coincides on individual longleaf pine trees but can vary considerably among trees in a stand. Some trees are consistently early and others late in time of flowering, although the differences vary from year to year, depending on air temperatures before and during the flowering period (5). Over 22 years of observation, the time required for shedding 80 percent of all pollen in a longleaf pine stand ranged from 5 to 21 days and averaged 13 (5).

Pollination takes place in the late winter or spring, but fertilization does not occur until the following spring. At this time conelets are growing rapidly, increasing in length from about 2.5 cm (1 in) in February to about 18 cm (7 in) by May or June (16). Mature cones range in length from 10 to 25 cm (4 to 10 in). Cones reach maturity between mid-September and mid-October of their second year. Cones, as they become ripe, change color from green to dull brown, although cones may be ripe before the color change (26). The specific gravity of ripe cones ranges from 0.80 to 0.89. Ripeness can be tested by flotation in SAE 20 motor oil; ripe cones will float but those not yet ripe will sink (26).

**Seed Production and Dissemination—Tree size, crown class, stand density, site quality, and, most important, genetic predisposition, all affect cone production by an individual tree. The best cone producers are dominant, open grown trees with large crowns, 38 cm (15 in) or more in d.b.h., with a past record of good cone production (11). Trees 38 to 48 cm (15 to 19 in) in d.b.h. have produced an average
of 65 cones annually compared to 15 cones by trees from 25 to 33 cm (10 to 13 in) in d.b.h. The number of sound seeds per cone varies widely and is related to size of seed crop in a particular year. In good seed years there may be about 50 seeds per cone, in average years 35, and in poor years 15 (10).

Seed production per hectare reaches a peak at stand densities between 6.9 and 9.2 m²/ha (30 to 40 ft²/acre) of basal area, assuming that the stand is comprised of dominant-codominant trees of cone bearing size (3). A shelterwood stand with a basal area of 6.9 m²/ha (30 ft²/acre) produces three times as many cones per unit area as a stand of scattered seed trees averaging 2.3 m²/ha (10 ft²/acre) in good seed years (11).

Throughout its range, longleaf pine in shelterwood stands produces seed crops adequate for natural regeneration, about 2,500 cones per hectare (1,000/acre), on the average of once every 4 to 5 years (11). However, everything else being equal, good cone crops are more frequent in some parts of the longleaf pine range than in others, so the general average may be meaningless at a given location. The production of female strobili is much less variable from place-to-place than is the production of mature cones, indicating that geographic differences in cone production are due more to conelet and cone losses than failure to produce conelets in the first place (7).

When a shelterwood stand is created by cutting back a stand of substantially higher density, increased cone production resulting from release does not occur until the end of the third growing season after cutting (9). Release that occurs after conelet initiation has no effect on that crop, other than initiating seedlings are susceptible to damage or loss before seedfall, either mechanically or by burning. The accumulated material must be removed before seedfall, either mechanically or by burning. Burning within a year of seedfall normally provides an adequate seedbed. Lack of seedbed preparation can result in a regeneration failure.

Germination of longleaf pine seed is epigeal (26). Newly germinated seedlings have virtually no aboveground hypocotyl, and the cotyledons are close to the ground line. The primary needles appear after germination and the secondary needles about 2 months later. The epicotyl, or stem above the cotyledons, does not elongate rapidly as in most other pines. Even in the nursery, seedlings are virtually stemless after one growing season (16). This stemless condition is one of the unique characteristics of longleaf pine. It is referred to as a grass stage and may last 2 to many years, depending on growth conditions. During this time, longleaf pine is most susceptible to its major disease, the brown-spot needle blight, Scirrhia acicola (11).

While in the grass stage, seedlings develop extensive root systems. Growth can be followed by observing the increase in root-collar diameter. When it approaches 2.5 cm (1 in), active height growth is imminent. Grass-stage seedlings, once they reach 0.8 cm (0.3 in) in root-collar diameter, are highly resistant to fire, even during the growing season. Seedlings in early height growth, up to a height of about 0.6 to 0.9 m (2 to 3 ft), become susceptible to damage by fire. Once beyond this stage, longleaf pines are again fire resistant.

Competition and brown-spot needle blight have great impact on the rate of seedling development and together largely determine the duration of the grass stage. Longleaf seedlings can be easily established and usually survive for years under an overstory of parent pines. Growth, however, is very slow. Seedlings respond promptly with an increased rate of growth when released from overstory competition.

Growth rate varies widely among individuals in a natural seedling stand, and vigorous fast-growing seedlings express dominance early. The rapid breakup of a seedling stand into a wide range of size classes reduces the risk of stand stagnation (fig. 2). About 10 percent of a natural seedling stand shows resistance to the brown-spot disease, and this gives
them a growth advantage that persists for many years. At age 24, trees that had little or no brown-spot infection averaged 2.4 m (8 ft) taller than trees that had 30 percent or more of their foliage destroyed by the disease as seedlings

A low level of competition permits early initiation of height growth. One longleaf pine plantation on a prepared site had nearly 60 percent of the trees in active height growth by the end of the second growing season, and over 90 percent by the end of the third. Early initiation of height growth circumvented a brown-spot problem as the disease did not have time to build up to serious proportions.

Vegetative Reproduction-Longleaf pine seedlings, if top killed, can sprout from the root collar. Sprouting ability decreases sharply when seedlings begin height growth. In one study, almost 40 percent of seedlings cut off at the ground line during grass stage had living sprouts a year later. Only 14 percent of seedlings up to 1.37 m (4.5 ft) in height so treated developed sprouts, however, and those larger than this did not sprout at all (14). Longleaf is not as easy to reproduce asexually as some of the other southern pines. Cuttings can be rooted but the process is difficult. Air-layering has met with limited success. Grafting has proven to be a reliable technique, and this is now the most common method of establishing seed orchards (28).

Sapling and Pole Stages to Maturity

Growth and Yield-Longleaf pine is a high quality timber tree, well suited to a whole range of products—poles, piling, posts, sawlogs, plywood, pulpwood, and naval stores. Longleaf naturally prunes itself well. Most stems are well formed, straight, and largely free of branches. The species almost always has higher stemwood specific gravities and produces more dry wood per unit volume than either loblolly or slash pine (28). Intense exploitation since colonial days, plus lack of planned regeneration, contributed to the decline of longleaf pine forests that continues to this day. Once height growth has begun, the species can grow as well as the other major southern pines on many sites originally occupied by longleaf, and often exceeds them in growth.

The critical element in the growth of longleaf pine stands is the duration of the grass stage. About 70 percent of the variation among plantations in the form of height-over-age curves was related to the condition of the planting site: early height growth on unprepared cutover sites was much slower than on old fields and mechanically prepared cutover sites (6).

Reduction of competing ground cover in grass stage seedling stands can have a large impact on growth and future volume yields. One study (25) observed the effects of a single aerial application of 2,4,5-T to stands of 1-year-old longleaf seedlings. Twenty years later, treated stands had significantly greater tree diameter (10 percent), height (17 percent), and total volume per unit area (32 percent) than adjacent untreated stands, although there was no difference in the number of trees per unit area. Treated stands averaged 83.5 m³/ha (1,193 ft³/acre) total inside-bark (i.b.) volume, compared to 63.2 m³/ha (904 ft³/acre) for untreated stands.

Longleaf pine growth and yield predictions have been published for periodically thinned even-aged natural stands (15) and also for unthinned plantations in the west Gulf region (22). Predicted total volume (i.b.) yields for two common site index classes are given in table 1. The merchantable proportion of total volume ranges from 78 to 86 percent at age 20, to 97 to 98 percent at age 40. The peak in periodic annual increment is reached between ages 20 and 30.

The optimum stand density to maintain by periodic thinning varies by site and management goals. A rather broad range of stand densities, above a basal area of about 13.8 m²/ha (60 ft²/acre), produces near maximum periodic volume growth (13). Lower densities concentrate growth on fewer trees. Longleaf responds well to release provided by thinning if the released trees have crowns equal to at least one-third
Table 1-Predicted total volume yields inside bark for even-aged natural stands of *Pinus palustris*

<table>
<thead>
<tr>
<th>Stand age in years</th>
<th>Basal area</th>
<th>Site index at base age 50 years</th>
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<tr>
<td></td>
<td>21.3 m or 70 ft</td>
<td>24.4 m or 80 ft</td>
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<td></td>
<td>m²/ha</td>
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<td></td>
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<td>2,954</td>
</tr>
<tr>
<td>40</td>
<td>144</td>
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</tbody>
</table>

*Determined from ring counts taken at 1.2 m (4 ft), plus 7 years.

to one-half of total tree height. Small-crowned intermediate or suppressed trees do not respond promptly to release. Thinning should be from below to release well-formed dominant and codominant trees.

Present indications are that *Pinus palustris* plantations should produce volume growth similar to natural stands if other factors are equal. To the extent that plantations have had better competition control, with consequent acceleration of early growth, a particular volume yield should be reached at an earlier age in plantations than in natural stands.

**Rooting Habit-Longleaf pine** develop massive taproots that, in mature trees, may extend to a depth of 2.4 to 3.7 m (8 to 12 ft) or more. A hardpan can arrest downward growth of the taproot. If the hardpan is close to the surface, windfirmness of the tree is reduced. Longleaf pines develop extensive lateral root systems. Most lateral roots are within 0.3 m (1 ft), and nearly all within 0.6 m (2 ft), of the surface (29).

**Reaction to Competition-Longleaf** pine is intolerant of competition, whether for light or for moisture and nutrients. The species will grow best in the complete absence of all competition, including that from other members of the species. Fortunately, as noted earlier, young even-age Longleaf pine stands break up rapidly into a broad range of size classes, due to variability in duration of the grass stage. Stagnation is almost never a problem. However, even suppressed trees in a stand will slow the growth of dominant neighbors. Optimum stand density for development of crop trees needs to be maintained by periodic thinning. Given release from neighboring trees, dominant and codominant trees in an over-dense stand will respond promptly with increased diameter growth, as will some intermediate trees that retain crown ratios of 30 percent or more. Suppressed trees, while they may continue to live, rarely respond to release with improved growth.

**Damaging Agents-Longleaf** pine is less susceptible to most damaging agents than the other southern pines and is a relatively low risk species to manage. It is strongly resistant to fire, except as a small seedling of less than 0.8 cm (0.3 in) root collar diameter and in early height growth. It is also resistant to most pathogenic agents. The major disease is the brown-spot needle blight. This disease causes serious damage only to grass-stage seedlings. Continued severe defoliation by brown-spot suppresses and eventually destroys seedlings. Once rapid height growth begins, seedlings are no longer seriously afflicted. Seedlings growing in the open are most vulnerable, particularly if the groundcover is sparse; the disease usually does not seriously affect seedlings growing under a pine overstory. Other diseases occasionally of economic importance in local areas are pitch canker (*Fusarium moniliforme* var. *subglutinans*), annosus root rot (*Heterobasidion annosum*) in thinned plantations, cone rust (*Cronartium strobilinum*) near the coast, and also the condition known as dry face of turpentined trees. Fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) is rarely a problem for *longleaf* pine (20).

Many species of birds, mice, and squirrels feed on *longleaf* pine seeds, the latter often taking them from unripe cones. Several species of ants feed on germinating seeds and cotyledon seedlings. Cottontails as well as other predators can destroy newly established seedlings. Grass-stage seedlings are vulnerable to destruction by hogs, pales weevil (*Hyllobius pales*), and heavy livestock grazing. Pocket gophers cut seedlings off just below the ground surface.

Most seedling losses occur during the first year after establishment, untimely drought being the greatest single hazard. Logging of the overstory can destroy close to 50 percent of a seedling stand, although actual damage depends on type and season of logging, volume removed, and seedling size. Fire takes its toll of small, weak, or diseased seedlings. *Longleaf* pine can be damaged by ice storms but is less susceptible to ice damage than slash pine (19).

The southern pine beetle (*Dendroctonus frontalis*) does not seem to afflict the species severely. The black turpentine beetle (*Dendroctonus terebrans*) can
be a problem, especially on trees injured by turpentine logging, or fire. Perhaps the greatest single cause of mortality in longleaf stands of pole and sawlog size is lightning, which is often followed by infestation by bark beetles (Ips spp.). Windthrow from hurricanes or tornados can cause heavy losses locally. Long term observations throughout the longleaf region have shown an average annual mortality of 1 tree per hectare (0.4/acre) in mature longleaf pine stands (4).

Special Uses

Longleaf pine is used for a broad range of forest products. Even old lighted stumps (those having resin-soaked heartwood characteristic of old trees) are pulled out and the stumpwood destructively distilled for chemicals. Longleaf “pine straw” is in demand for use as a mulch, so fresh needle litter is sometimes collected, baled, and sold. The longleaf pine forest, if regularly burned, has a parklike appearance with an understory dominated by grasses and forbs (fig. 3); an excellent habitat for game, especially quail, and quail hunting has long been associated with this timber type. The understory produces a substantial amount of high quality forage for both cattle and deer (17,31). Mature longleaf stands also provide the most desirable habitat for the red-cockaded woodpecker.

Figure 3-Forty-five-year-old second-growth longleaf stand regularly burned. Note grass cover and scarcity of hardwoods and shrubs.

Genetics

Population Differences

Longleaf pine is a highly variable species, and a considerable proportion of this variation is genetic. Considering the economically important traits, longleaf pines have as much or more genetic variation than other southern pines.

Variation among individual trees is greater than that among stands or among geographically diverse seed sources (23,28). Nevertheless, the diversity of environments throughout the longleaf range has promoted the development of genetic variation among populations. According to rangewide provenance tests, trees from coastal areas usually outgrow those from inland areas at all but the coldest locations. Trees originating from the central Gulf Coast should be more productive than trees from other sources on most coastal plain longleaf sites from Georgia and north Florida west to east central Louisiana (28). Elsewhere, local seed sources may be safest to use until more information is available.

Hybrids

The major southern pines, as well as some minor species, are closely related and have overlapping ranges. Natural hybridization has contributed to genetic diversity among trees and populations. Natural hybridization is common between longleaf and loblolly pine, producing the Sonderegger pine (P. x sondereggeri H. H. Chapm.). This is the only named southern pine hybrid. Throughout much of the longleaf pine range, the flowering of longleaf and loblolly pines overlaps in most years so there is no phenological barrier to natural crossing. Natural hybridization between longleaf and slash pine is unlikely, based on differences between the species in dormancy and heat requirements for flowering (5).

Artificial crosses between longleaf pine and both loblolly and slash pines can be achieved easily. Crossovers between longleaf and shortleaf pine have not been found in nature but have been produced artificially. There are no reported successful crosses of longleaf pine with any other pine species (28).

Literature Cited


