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(Pinus taeda L.)

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Because of its wide range, its occurrence in pure stands, its abundance, and its versatility in use, loblolly pine (Pinus taeda) is the principal commercial species in the southeastern United States (fig. 1). It grows in the Coastal Plain and Piedmont from central Maryland and Delaware south to central Florida and west to eastern Texas (fig. 2) (72). It does not grow in the Mississippi River bottoms and is scarce in the deep, coarse sands of the lower Gulf Coastal Plain and sandhills of North and South Carolina.

HABITAT CONDITIONS

CLIMATIC

The climate of the loblolly pine range is humid, with long, hot summers and mild winters. Average annual rainfall varies from 40 to 60 inches per year; it is least in Maryland and Delaware and at the western end of the range in east Texas (124). Along the Gulf Coast it averages 60 inches. Summer is usually the wettest season and autumn the driest along the mid-Atlantic Coast. In the western portion of the range, rainfall is more uniformly distributed through the year, but summer droughts occur often enough to be a serious obstacle to natural regeneration and planting of the species.

The frost-free period lasts from 6 months in the North to 10 months in the South. July temperatures average over 75° F. and frequently exceed 100°; January temperatures average 36° to 63° and occasionally go down to -10° in the northern and western portions of the range.

The distribution of loblolly pine is associated with the average winter temperature, and the frequency and intensity of both winter and summer rainfall (57). During both winter and summer, the area within the range of loblolly pine has a greater number of days with rain and a greater frequency of effective amounts of rain (more than 0.50 inch) than the area immediately outside the range. The area inside also has a higher average temperature in winter. In spring and autumn, the weather inside and outside the range is more nearly the same. The main factor limiting northern extension of the species is probably temperature, but the western extension is probably limited by precipitation. Low air temperatures damage aerial portions, and low soil temperatures retard water absorption more in loblolly pine than in native northern species (65). Damage by snow and sleet, which is less frequent within the range, may also be a factor limiting the northern extension.



Figure 1.--Mature loblolly pine tree in the Crossett Experimental Forest, Crossett, Arkansas.

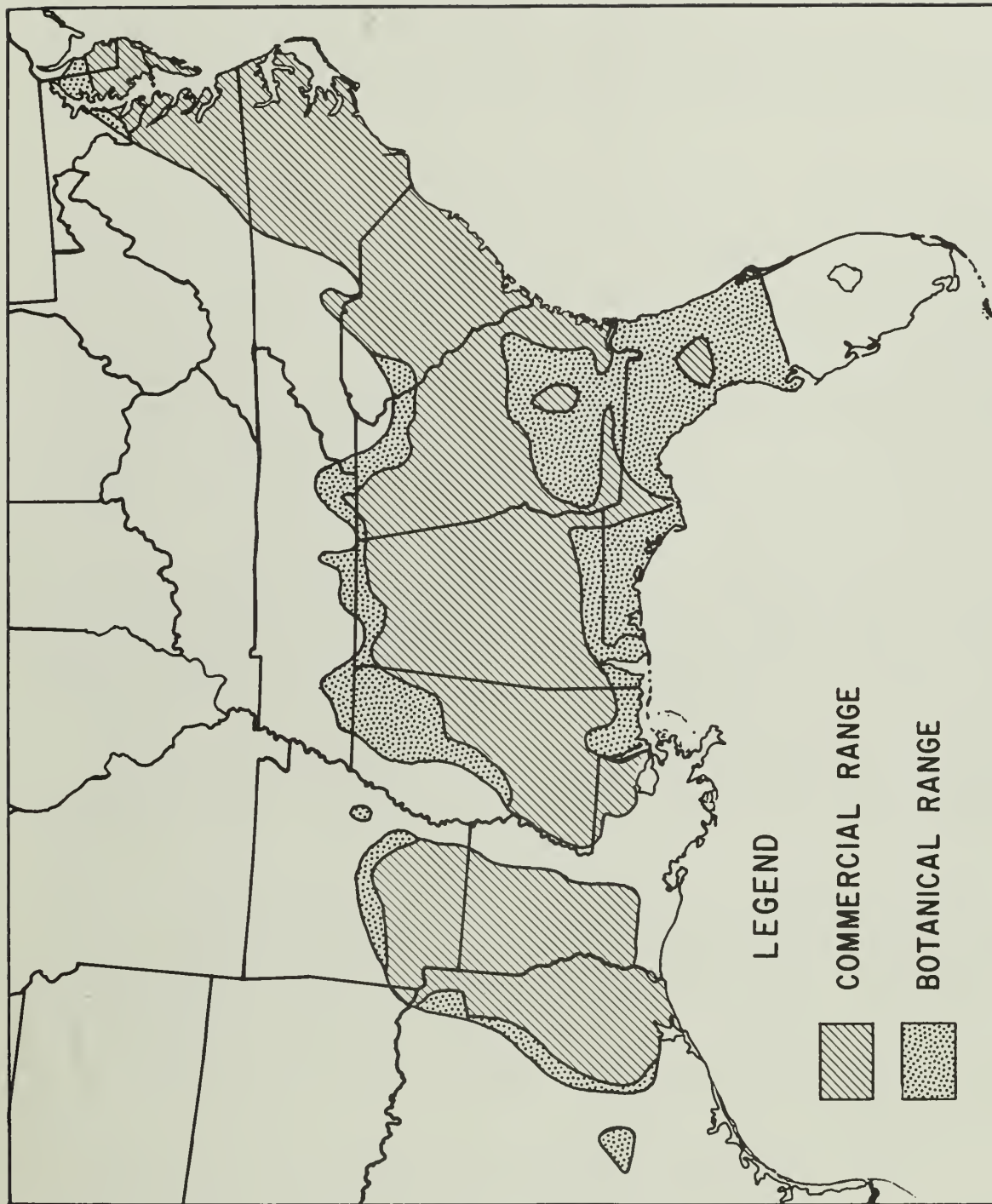


Figure 2. -- Botanical and commercial range of loblolly pine.

EDAPHIC

Loblolly pine occurs on a wide variety of soils, from the flat, poorly drained, ground-water podzols of the lower Coastal Plain to the old residual soils of the upper Piedmont. It grows best in soils with poor surface drainage, a deep surface layer, and a firm subsoil (48, 150).

Such soils are common in the lower Coastal Plain and in the flood plains of the larger rivers. Prominent examples are the Coxville and Bladen series; with deep surface layers these soils have a site index for loblolly of 90 to 95 feet (48). In the same category is the Elkton series: poorly drained, very plastic soils which have an average site index of 95 feet. Most productive are the river bottom or terrace soils, notably the Roanoke series in the east and the Ocklockonee in the west; these are fairly heavy soils that have site indices of over 100 feet (24, 48). In the Coastal Plain, the productivity of soils decreases with improvement in surface drainage. The presence of a hardpan within the root profile, as in the Leon series, drastically reduces the productivity. Deep, excessively drained sands are also very low in site quality (24) unless the water table lies within reach of the tree roots; with high water tables sands may have site indices of 90 to 100 feet.

In the inland and Piedmont regions, where surface drainage is well-developed, the physical characteristics of the soil, rather than drainage, determine the availability of moisture, and uneroded soils with a deep surface layer and a friable subsoil are best (36). Common in this category are soils of the Durham, Georgeville, Appling, Cecil, Davidson, and Lloyd series, which have site indices of 80 to 100 feet when not eroded. The least productive are eroded soils with a very plastic subsoil. Iredell, Orange, and Whitestore (red phase) series fall in this group; they are practically worthless when the A horizon is gone, with site indices of less than 40 feet.

PHYSIOGRAPHIC

The range of loblolly pine extends over two main physiographic regions, the Coastal Plain and the Piedmont. The Coastal Plain is generally very flat near the coast but becomes rolling and even sharply hilly in the inland reaches with elevations ranging up to 1,000 feet in Georgia. Topography in the Piedmont is more rolling than in the Coastal Plain, with highly developed drainage patterns and generally heavier soils. Elevations range up to 1,500 feet. In northern Alabama and Georgia, loblolly pine grows at elevations up to and over 2,000 feet.

The rougher topography of the Piedmont results in greater variations in site than in the Coastal Plain. Loblolly pine site indices generally increase from ridge tops to bottoms but this variation seems to be related to soil differences rather than to slope position or steepness (35). Soil features that determine site quality, such as surface soil thickness and subsoil consistency, are loosely correlated with topography, but past land use, differences in soil parent material, and other factors also affect soil profile development and cause variations in site quality independent of topography.

Because of plentiful rainfall, rolling topography, and soil physical characteristics, the upland soils of the Piedmont and many sections of the upper Coastal Plain are subject to moderate to severe sheet and gully erosion when exposed and unprotected. The loss of surface layers in the past has undoubtedly contributed to the prevailing poor site quality of upland soils in the region (39).

BIOTIC

Pure loblolly pine stands are widespread throughout the range where moisture is comparatively plentiful (fig. 3). In general, the main associate is sweetgum (Liquidambar styraciflua), but on well-drained sites shortleaf pine (Pinus echinata), southern red oak (Quercus falcata), post oak (Quercus stellata), and blackjack oak (Quercus marilandica) are frequently found with it. On poorly drained sites black tupelo (Nyssa sylvatica), water oak (Quercus nigra), yellow-poplar (Liriodendron tulipifera), and pond pine (Pinus serotina), and in the far south slash pine (Pinus elliottii) and laurel oak (Quercus laurifolia), usually occur in loblolly pine stands (113).

In east Texas, southern Arkansas, Louisiana, and to a lesser extent in other states, mixtures of loblolly pine and shortleaf pine occur, with shortleaf pine predominating on the drier ridges and loblolly pine on the wetter sites. Commonly associated with these species are sweetgum, black tupelo, hickories (Carya spp.), southern red oak, scarlet oak (Quercus coccinea), black oak (Quercus velutina), white oak (Quercus alba), post oak, and minor species.

Loblolly pine also grows in mixtures with hardwoods throughout its range. On wet sites sweetbay (Magnolia virginiana), redbay (Persea borbonia), black tupelo, swamp tupelo (Nyssa sylvatica var. biflora), and sweetgum are prominent in the hardwood component; water oak, laurel oak, willow oak (Quercus phellos), red maple (Acer rubrum), white ash (Fraxinus americana), green ash (Fraxinus pennsylvanica), and American elm (Ulmus americana) are frequently present. On drier sites southern red oak, white oak, northern red oak (Quercus rubra), hickories, common persimmon (Diospyros virginiana), and scarlet oak are the most common hardwoods, and shortleaf and longleaf pine (Pinus palustris) are frequent associates.

In the Piedmont, and in the Coastal Plain of northern Virginia and Maryland, loblolly pine also occurs with Virginia pine (Pinus virginiana). In northern Mississippi, Alabama, and in Tennessee it is a minor associate in the eastern redcedar-hardwood type. On moist sites, loblolly is found in the longleaf pine type, the longleaf pine-slash pine type, and in the slash pine-hardwood type. In the flood plains of major rivers it is a minor associate in the swamp chestnut oak-cherrybark oak type. On moist lower slopes in the Atlantic Coastal Plain it is an important element in the sweetgum-yellow-poplar type. In bays, ponds, swamps, and marshes of the Coastal Plain it is a common associate in the pond pine type, the cabbage palmetto-slash pine type, and in the sweetbay-swamp tupelo-red maple type (113).



Figure 3.---Pure, even-aged stand of loblolly pine 50 years old, near Crossett, Arkansas.

Because of the wide range of sites and the numerous types in which loblolly occurs, a great variety of lesser vegetation may be found in association with it and a list of even the most common would be quite lengthy. Worthy of mention are waxmyrtle (Myrica cerifera), pepperbush (Clethra alnifolia), gallberry (Ilex glabra), viburnums (Viburnum spp.), and a great variety of ericaceous shrubs.

In the natural state, mycorrhizae usually occur on loblolly pine. Infection by several species of fungi causes proliferation of the short roots, characterized by repeated dichotomous branching. This proliferation and the accompanying mantles of fungal hyphae greatly increase the absorbing surface, and conifers in infertile soil without mycorrhizae are very low in mineral content compared to those with mycorrhizae. Mycorrhizae apparently can also supply carbohydrates from the soil, although they seem primarily dependent on those in the plant (148). They also supply nitrogen compounds, and may be able to supply vitamins. Among the fungi capable of producing mycorrhizae in loblolly pine, the following have been identified (42, 55): Boletus granulatus, Boletus exinus, Boletus brevipes, Boletus chromapes, Boletus subluteus, Boletinus pictus, Cantharellus cibarius, Cenococcum graniforme, Russula lepida, and Amanita muscaria.

Few of the animals that live within the range of loblolly pine are associated with it by a closer tie than the accident of location. Probably the most noteworthy is the red-cockaded woodpecker (Dryobates borealis) (115). This bird invariably digs its nesting cavity in a living pine tree with red heart (Fomes pini). When the cavity is finished, the bird pecks the bark all around the entrance hole, causing a heavy flow of pitch. The surface around the entrance hole thus becomes very sticky, presumably keeping out intruders. Among other birds frequently found in pine forests in the South are the brown-headed nuthatch (Sitta pusilla), the pine-woods sparrow (Peucaea aestivalis aestivalis), the southern pine finch (Peucaea aestivalis bachmani), the pine warbler (Dendroica vigorsii), and the prairie warbler (Dendroica discolor) (115).

Four-footed animals are scarce in full stands, but after clear cutting, rodent populations increase rapidly. White-footed mice and red mice (Peromyscus spp.), harvest mice (Reithrodontomys humulis), pine mice (Microtus pennsylvanicus), cottonrats (Sigmodon hispidus), and short-tailed shrews (Blarina brevicauda) are common in cutover areas in eastern North Carolina (121). Gray squirrels (Sciurus carolinensis) are fond of pine seed and begin to shell out cones in late summer, as soon as the seeds are well filled.



LIFE HISTORY OF THE SPECIES

SEEDING HABITS

Flowering and fruiting. -- The development of loblolly pine seed requires nearly three growing seasons from the time of flower bud initiation. Flower buds are formed during midsummer, some time after the middle of June, but do not become visible until early autumn. Staminate flower buds can be seen in the South Atlantic Coastal Plain during October as small knobs around the base of vegetative buds. Later, some vegetative buds develop pointed swellings near the apex, which are pistillate flower buds. These flower buds grow rapidly in late winter and for a short time before flowering the staminate buds are very prominent.

Vegetative growth begins about March 1 in the Gulf States and about 6 weeks later near the North Carolina-Virginia boundary (44). Flowers mature and pollen cast begins about 10 days later (131). The staminate flowers are long, yellow catkins, and the pistillate flowers are small, pink or red strobili. Pollination lasts 7 to 10 days. Staminate flowers usually are the most plentiful and are borne all over the crown, while pistillate flowers tend to be concentrated in the upper portions of the crown. On the same tree, staminate flowers tend to mature before pistillate flowers (128). Thus, pollination depends largely on pollen from neighboring trees and may be inhibited if trees shed pollen at different times or are too far apart. In general, pine pollen is not carried in effective quantities farther than 300 feet, and most falls much closer to the source (146).

Within the pistillate strobili the growing pollen tubes do not reach the embryo sac to fertilize the egg cells until late the following spring. By that time, the strobili have become conelets one-half to three-fourths of an inch long. Growth of cones and seed is rapid during the second season, after fertilization occurs.

Cones mature and seed ripens usually during the early part of October. Time of seed ripening does not appear to vary greatly with latitude (44). Individual cones may contain from less than 20 to more than 200 seeds, sound and defective (131).^{1/} The percentage sound may vary from about 15 percent up to nearly 100 percent. In southeastern Virginia, the average number of sound seeds per cone varied from 30 in stands averaging only 1 cone per tree up to 110 in stands averaging 150 cones per tree.^{2/} The over-all average was 57 sound seeds per cone.

The seeds vary in size from 16,000 to 25,000 per pound and average 18,400 per pound (126).

^{1/} Records of the Tidewater Forest Research Center, Franklin, Virginia, 1952.

^{2/} Wenger, K. F. Seed tree stimulation study. 1951. (Report on file, Southeast. Forest Expt. Sta.)

Seed production. -- Individual loblolly pine trees occasionally produce cones and viable seed at less than 10 years of age. Pistillate flowers have been observed on 5-year-old trees, staminate flowers on 6-year-old trees (106), and viable seed have been obtained from 9-year-old trees (132). But appreciable quantities of seed are not produced until much later. Seed production of dominant and codominant trees in undisturbed, even-aged stands increases gradually until the trees are 30 to 50 years old and 12 inches or more in diameter (99). It then increases rapidly until the full potential is attained. However, the viability of seed from young trees just beginning to bear is as high as that of seed from older trees (131).

Although loblolly pine stands are capable of heavy seed production to advanced ages, seed crops fluctuate widely from negligible amounts in some years to nearly a million seeds per acre in other years. Seed crops of a 70-year-old stand in North Carolina Piedmont varied from 18,000 to nearly 300,000 seed per acre during 13 years from 1936 to 1948 (101). Seed production tends to be better in the coastal portions than in the inland portions of the loblolly pine range (128), and annual seed crops of one 95-year-old and two 145-year-old stands in northeastern North Carolina ranged from 50,000 to 832,000 seed per acre from 1947 to 1954. A partially cut 35- to 45-year-old stand in coastal South Carolina produced 1.4 million seeds per acre in 1955, which is apparently the greatest seedfall recorded in loblolly pine up to that year (77).

The annual fluctuations in seed crops depend mainly on weather and the physiological status of the trees at the time of flower bud formation. In the three stands in northeastern North Carolina, the size of seed crop was positively correlated with the May-to-July rainfall of 2 years earlier and negatively correlated with the size of the seed crop 2 years earlier (142).

Although conditions may favor a heavy set of flower buds, many agencies may reduce or destroy the cone crop before maturity. Flowers may be destroyed by subfreezing temperatures, heavy rain, hail, or strong winds, or rainy weather may inhibit or prevent pollination. Drought may retard development, and insects damage both cones and seed.

Cone damage varies from year to year, usually amounting to 10 to 40 percent but may often be more or less in any given locality (63). Cone losses on individual seed trees in southeastern Virginia, caused mainly by insects, varied from 2 to 100 percent in one year and from 4 to 71 percent in the following year. Losses were greater in small crops than in large crops, and trees that sustained heavy losses in one year also had heavy losses in the next year. Most of the insect damage probably is caused by the larvae of a small moth, Dioryctria amatella (63), but cone beetles, mainly Conophthorus taedae, may also cause appreciable losses (40). Another small moth, Laspeyresia toreuta, destroys a small proportion of the individual seeds without otherwise damaging the cones (63). Insect damage tends to be higher in older stands and on better sites.

The quality of seed also varies from year to year with the size of the seed crop. In both the Piedmont and Coastal Plain of North Carolina viability ranged, on the average, from a little more than 40 percent in light crops to nearly 80 percent in heavy crops (101, 143). In individual stands, viability as low as 25 percent occurred.

Individual dominant and codominant trees in undisturbed stands may bear as many as 500 cones but most trees bear less than 100 cones. Intermediate and suppressed trees may never produce good crops. Fruitfulness apparently is hereditary to some degree, and cone crops of individual trees are closely related to past fruitfulness (45, 52, 99, 137). Cone crops are also proportional to diameter at breast height, and crown volume and crown density have been found to affect size of cone crops (53).

In the Atlantic Coastal States, cone and seed production of individual dominant and codominant trees released from competition and of stands partially cut increased 2- to 10-fold three growing seasons later (46, 99, 119, 137). Trees of larger diameter and greater past fruitfulness produced much larger crops after release than smaller or less fruitful trees. As many as 1,500 cones may develop on some trees after release but most trees bear less than 500 cones. The response to release is greater when it coincides with good seed years; in partially cut stands it seems to be proportional to the intensity of cutting. It usually persists for several succeeding crops but eventually subsides (46, 137).

The cone crop in the third succeeding fall is larger if the release cutting is done before late spring. In the South Atlantic Coastal Plain the critical period is some time during late June or July--release during or after that period is not reflected in cone crop until the fourth succeeding year. The reduction in transpiration accompanying the removal of competing trees, which is probably equal to several inches of rain, may be the primary cause of the increase in cone crops following release (142).

Seed dissemination. --Seedfall usually begins during the early part of October and does not vary greatly with latitude (44). It reaches a peak very quickly and then declines. By January 1, 80 to 90 percent of the seed has fallen, although some continues to fall until late spring. Seedfall is hastened by dry, warm, windy weather and retarded by cool, wet weather (59). Viability of the seed is highest at the peak of the seedfall. Seed falling later is progressively lower in viability until the end of seedfall in the spring.

Although loblolly pine seed is entirely wind-disseminated, and was apparently carried 2.5 miles from the source in one case (104), it is usually not dispersed in effective quantities more than 300 feet. In strip cuttings in North Carolina, 67 percent of the seed fell within 100 feet and 85 percent fell within 200 feet of the windward uncut strip (101). In old fields, where seed dispersal was less restricted, the number of seedlings established fell below 1,000 per acre at 330 feet from the seed source, and beyond 462 feet was less than 500 per acre (83).

VEGETATIVE PROPAGATION

When 1- to 3-year-old seedlings of loblolly pine are decapitated or injured, they sprout readily from buds formed in the axils of primary needles (116, 117). ^{3/} Older seedlings and trees do not sprout. Rooting ability is similarly confined to young seedlings. Nearly half of the cuttings from 1-year-old seedlings rooted, but only 6 percent rooted from 2-year-old seedlings, and none rooted from 3-year-old seedlings (49). Rooting by air-layering has been somewhat more successful. Six of ten 2½-year-old seedlings developed roots in air-layers in one test (152), and good results were obtained with 3- and 5-year-old seedlings in another (20). In the latter test, results were poorer with older trees but air-layers even from 60-year-old trees developed a few roots. ✓

Loblolly pine has been successfully grafted by several methods. In very limited tests, one-half or more soft-tissue grafts were successful (151). These included loblolly scions on loblolly and shortleaf stocks and shortleaf and slash scions on loblolly stocks. Side grafts of loblolly on loblolly were completely successful when made in April and somewhat less successful when made in February and March (31). Wedge grafts were least successful.

SEEDLING DEVELOPMENT

Establishment. -- Birds and rodents probably eat appreciable amounts of seed between seedfall and germination, but apparently not enough to hinder natural regeneration (143) except in poor seed years. Bob-white quail (Colinus virginianus) in eastern Maryland have been found to eat pine seed in preference to wild and cultivated leguminous seed (145). However, as many as 89 percent of sound seeds may fail to germinate (100, 126). Further losses occur because of limited moisture related to seedbed conditions and the failure of the radicle of germinating seeds to penetrate hard soil surfaces and deep litter (51, 100).

Moisture remains the most important factor in survival throughout the first growing season. The greatest mortality occurs shortly after germination (47) and tends to be higher in lighter soils. Droughts after midsummer, when soil moisture is already quite low, may also cause heavy mortality, particularly where competing vegetation is abundant. A study in Arkansas showed that most new seedlings established on third-year and older seedbeds had disappeared by the following year (86), probably because of competition from hardwood brush.

Losses from these various causes are reflected in the large number of sound seeds needed to establish a seedling, even on the best seedbed. In northeastern North Carolina, the number of sound seeds needed to establish 1 seedling on fresh seedbeds averaged 9 on exposed mineral soil, 15 on burned soil surfaces, and 40 on undisturbed litter and logging slash (118). A similar effect of seedbed condition on seedling establishment was observed in southeastern Arkansas (51). Thus, much larger amounts of seed are required for

^{3/} Little, S. Official correspondence, Southeast. Forest Expt. Sta. 1957.

satisfactory reproduction on undisturbed litter than on mineral soil. Favorable seedbed conditions disappear rapidly, and about four times as many seeds are needed on second-year as on first-year seedbeds to establish one seedling (86, 120, 141). By the third year, initially favorable seedbeds have become nearly as unfavorable as undisturbed litter.

Natural regeneration of loblolly pine thus depends on adequate amounts of seed in the first year after logging or seedbed preparation (120). In small ownerships adequate seed can often be obtained by postponing harvest cutting until after seedfall. The seed-tree method gives the greatest control of the seed supply through variations in the numbers of seed trees (140), but adequate seed can also be obtained from seed strips. Seed is usually more plentiful in stands managed by the selection method because of the large number of seed-bearing trees and the stimulation of seed production by repeated cutting.

Where the bulk of a well-stocked stand is cut, tractor logging exposes mineral soil on about 50 percent of the logged area, which is usually sufficient for satisfactory regeneration in good seed years (118). In mediocre seed years, however, or with less effective logging methods, additional site preparation is essential. Scarification with a bush-and-bog diskharrow or burning before or after logging have been successful (23, 30, 73) and will usually compensate for the lower seed supply in mediocre seed years. Periodic winter fires throughout the rotation, with the last fire just before the harvest, or several annual summer fires before the harvest, have also been tested with considerable success (76, 105). The effects of site preparation on the amount of hardwood brush persist for several years, so that a greater percentage of established seedlings become dominant (75, 143).

In poor seed years, the number of seed trees needed becomes prohibitively large, even with intensive seedbed preparation, unless the seed trees are selected and released from competition 3 to 5 years before the harvest cut. In the South Atlantic Coastal Plain, released trees produce enough seed for adequate regeneration even in poor seed years (140). Since heavy cone crops are evident a year before maturity (119) and are usually followed by a poor crop 2 years later, poor seed years apparently can be predicted far enough in advance so that trees can be released in time to supply increased amounts of seed in the poor year (142).

Early growth. -- The resumption of growth in the spring is mainly a response to rising air temperature but is also influenced by soil temperature (64).^{4/} It usually occurs before the date of the last killing frost (66), in late March or early April in the northerly portions and about a month earlier in the southerly portions of the range. Twenty percent or more of the year's height growth occurs each month from April to August and is usually at least 80 percent complete by July 1 in all parts of the range (66, 103, 144). Vigorous seedlings make several surges of height growth, normally three, during a growing season; the first is the longest and the last is usually very short (138).

^{4/} Hahn, V. W. The effect of soil and air temperatures on the resumption of growth of tree seedlings in the spring. 1942. (Unpublished Master's thesis, Duke University, Department of Botany.)

Best growth occurs when night temperatures are 12° to 13° C. lower than day temperatures (70). Thus, slowing of height growth in midsummer may be due in part to high night temperatures. High night temperatures may also be an important factor in the generally slower growth of loblolly pine along the Gulf Coast. Height growth ends in late summer, before air temperatures become unfavorable and apparently in response to shorter periods of daylight (64). Foliage is usually retained till the end of the second growing season, although it may be cast earlier if infected by the needle-blight fungi, chiefly Lophoderium pinastri and Hypoderma lethale (9, 11).

Roots of loblolly pine grow at all times of the year (103, 123). Most root growth occurs in spring (April and May), and in late summer and early fall; least root growth occurs in winter and midsummer. Growth in winter is limited by low temperatures, none having been observed at less than 53° F. (123). Growth in summer is limited by low soil moisture and high temperatures. Optimum temperature is 77° F. and root growth ceases between 86° and 95° (103).

During the first 5 to 10 years, height growth of vigorous loblolly pine seedlings follows a rising trend, and may average 2.5 feet per year (12, 127, 138). Under favorable conditions, seedlings may reach 2 feet in height in the first year but the average first-year height is about 4 inches (102). In North Carolina, first-year seedling heights varied with soil surface conditions; the tallest 10 percent of seedlings present exceeded 11 inches in severely burned areas, 7 inches on bare soil or disturbed litter, and 5 inches in undisturbed litter, slash piles, and lightly burned spots. The better growth in severely burned areas was still evident at 5 years (138). Light shade apparently is beneficial in the first year (8); thereafter it is not.

In the Coastal Plain of North Carolina, seedlings grew faster in sandy loams with friable subsoils than in silt loams with plastic subsoils (139). Seedlings on the better soils also had larger crowns. In a study of potted seedlings, growth was least in sand and best in a silty clay (136). Loosening of the soil by disking apparently aids height growth during the early years (139).

Height growth of loblolly pine seedlings is inversely related to the stocking of larger trees within a 30-foot radius and directly related to level of shade (12, 29). In Arkansas, heights of 5-year-old seedlings ranged from 0.8 foot under a full canopy to 10.0 feet in large openings (127).^{5/} In 8- to 15-foot openings, seedlings were 2.6 feet tall in 5 years; this rate of growth was judged to be adequate for survival, but in smaller openings growth was less. In Georgia, the average seedling was 0.7 foot shorter for every 10-foot lower shade level (12). If the over-topping trees are hardwoods, seedling growth is still less--in Arkansas seedlings were 0.14 foot shorter for every 10 percent increase in the basal area of hardwood cover.^{5/} Seedlings growing beneath larger hardwood trees invariably die if they are not released. In a

^{5/} Wahlenberg, W. G. Effect of overwood on survival and development of loblolly pine seedlings in southern Arkansas. 1946. (South. Forest Expt. Sta. office report.)

study in Louisiana, no seedling established under hardwood shade survived for more than 19 years, and the average period of survival was 5.27 years (29). Seedlings that grow less than 6 inches annually in height probably will not survive (29, 127, 138).

Low-level competition from hardwood shrubs and sprouts reduces height growth and is often fatal to loblolly pine seedlings. Approximately 80 percent of overtopped 3-year-old and older seedlings and 15 to 40 percent of seedlings with side competition do not survive (109, 138). Height growth and crown expansion of hardwood sprouts is rapid during the first 3 years and much slower thereafter (13, 138). Consequently, seedlings that are not overtopped at 3 years or later have a good chance of outgrowing the competing hardwoods.

These variations in seedling growth are responses mainly to differences in light and soil moisture caused by competing hardwoods. The maximum rate of photosynthesis is greater in hardwoods than in loblolly pine, and the hardwoods reach their maximum rate at one-third or less of full sunlight (61, 68). Pine reaches its maximum rate at that light intensity only in the first year, because the primary needles are so arranged that they shade each other very little (8). But the arrangement of secondary needles on older seedlings results in much mutual shading (67) and photosynthesis proceeds in proportion to light intensity, reaching the maximum rate only in full sunlight (61, 68). Low light intensity also reduces photosynthesis through its effect on water absorption. Pine root systems are smaller than hardwood root systems under full light but the difference becomes much greater under partial light (34, 61, 62, 136). Thus, absorption is retarded under partial light, even when soil moisture is ample, and moisture stress in the seedlings is increased, which reduces the photosynthetic rate. When soil moisture is also low, the moisture stress in the seedlings is still greater. Thus, photosynthesis is reduced more rapidly in pine than in hardwoods by decreasing soil moisture (7, 59).

Since low light intensity and low soil moisture usually occur together under natural conditions, loblolly pine suffers much more than the hardwoods from competition. In the first year, moisture is evidently the more important factor; in a study in North Carolina, pine seedlings in their first year did not respond to increased light at low moisture levels (47). After the first year, light is the more important factor; loblolly pine seedlings in the shade do not develop root systems large enough to supply the moisture needed for survival. With ample light, root systems are larger and supply the water and nutrients needed for survival even with soil moisture as low as that within a stand (69, 95). However, either deficient light or deficient soil moisture will retard growth; if both are deficient the seedlings usually die (60).

Too much water may also be detrimental to seedling growth and survival, although loblolly pine can endure prolonged flooding of the roots better than pond pine, its wet-land associate. One test of various periods of flooding showed that at least 10 months of continuous flooding with standing water was needed to permanently injure roots of loblolly pine seedlings (58). Pond pine showed permanent injury by failure to make normal height growth during

periodic drying after 3 months of continuous flooding. Another test showed that loblolly pine could endure flooding for a 50-percent longer period than pond pine.^{6/}

Growth and survival of loblolly pine seedlings are also affected by insect and disease attacks. Repeated attacks by the Nantucket pine tip moth (Rhyacionia frustrana) reduce height growth and cause crooking and forking but usually do not cause mortality. The pales weevil (Hylobius pales) and its close relatives may kill planted seedlings in large numbers in recently cut or burned areas but have not been important in natural reproduction. The red-headed pine sawfly (Neodiprion lecontei) and the pine webworm (Tetralopha robustella) can cause mortality by defoliation and occasionally cause large losses in limited localities. In many localities west of the Mississippi the Texas leaf-cutting ant (Atta texana) is a serious pest on natural and planted seedlings, and control measures are necessary.

The most common disease is fusiform rust (Cronartium fusiforme). It causes lethal stem and branch cankers and has oak as an alternate host. The brown spot needle disease (Scirrhia acicola) is common in some areas and heavy infections probably check growth (10).

SAPLING STAGE TO MATURITY

Growth and yield. -- Pure, even-aged stands of loblolly pine vary greatly in growth and yield in response to differences in site quality. Individual trees in particularly favorable locations may attain diameters of 50 to 60 inches and heights of 150 feet at advanced ages (2). The largest recorded loblolly pine presently in existence is located in Dinwiddie County, Virginia, and is 63 inches d.b.h. and 128 feet tall (1); another in Hertford County, North Carolina, is 54 inches d.b.h. and 151 feet tall. The average tree is much smaller. Sizes attained by average trees in the dominant portion of well-stocked, unmanaged natural stands are shown in the tabulation below (125). Trees in managed stands would be considerably larger in d.b.h. at the same ages.

Age (Years)	Site Index 60 feet		Site Index 90 feet		Site Index 120 feet	
	D.b.h. (Inches)	Height (Feet)	D.b.h. (Inches)	Height (Feet)	D.b.h. (Inches)	Height (Feet)
20	4.6	32	6.9	48	8.5	64
30	6.6	45	9.6	67	11.9	89
40	8.1	54	11.7	81	14.6	108
50	9.4	60	13.6	90	16.8	120
60	10.4	64	15.0	96	18.6	128

^{6/} Gaiser, R. N. The growth of loblolly and pond pine seedlings under differing conditions of soil flooding. 1947. (Unpublished manuscript, Duke University, Department of Botany.)

Because of its economic importance and wide range, several yield and growth studies of well-stocked natural stands of loblolly pine have been made (2, 79, 85, 125). One of these sampled the entire range of the species and indicated a maximum mean annual growth rate of 1,300 board-feet per acre (Int. 1/8-inch) in trees 6.6 inches d.b.h. and larger at 45 years, the age of culmination of mean annual increment for stands of 120-foot site index (125). On 60-foot sites the maximum rate was 318 board-feet per acre per year. Data from permanent sample plots in the Atlantic Coastal States indicated a possible current annual growth rate of 1,500 to 2,000 board-feet per acre (Int. 1/4-inch) in trees 9.6 inches d.b.h. and larger on the very best sites at age 55. Yields at 60 years in trees 6.6 inches d.b.h. and larger range from 19,000 board-feet per acre (Int. 1/8-inch) in well-stocked stands of 60-foot site index up to 73,000 board-feet per acre in stands of 120-foot site index (125).

Mean annual cubic-foot growth in trees 1.6 inches d.b.h. and larger ranges from 76 cubic feet per acre at 35 years (culmination of MAI) on a 60-foot site to 204 cubic feet per acre on a 120-foot site (125). Cubic-foot yields at 60 years in well-stocked stands vary from 2,400 cubic feet per acre on the poorest sites to nearly 12,000 cubic feet per acre on the best sites (79).

Mean annual growth in standard cords in trees 3.6 inches d.b.h. and larger ranges from 0.88 cord per acre per year at 40 years in well-stocked stands of 60-foot site index up to 2.37 cords per acre per year at 35 years on 120-foot sites (128). Yields of well-stocked stands at 60 years range from 46 cords per acre on 60-foot sites to 121 cords per acre on 120-foot sites.

In addition to varying with age and site quality, volume growth is strongly related to stand density, increasing with density up to a maximum that is higher on good sites than on poor sites (80). The volume growth of thinned stands also varies with age, site quality, and residual stocking. Recent studies by the Southeastern Forest Experiment Station suggest that the growth of thinned and unthinned stands does not differ greatly after one thinning when age, site quality, and stocking are equal. Although information presently available is insufficient to compare yields of managed and unmanaged stands, stands maintained at their optimum density by thinning throughout the rotation will undoubtedly produce more wood because most moribund trees will be salvaged and the residual trees will grow faster.

Reaction to competition. -- Loblolly pine is classed as an intolerant species, of the same degree of tolerance as shortleaf pine and Virginia pine, less tolerant than the oaks, and more tolerant than slash pine and longleaf pine (3).

The more tolerant hardwoods readily become established in the understory of loblolly pine stands, and on uplands throughout the range of loblolly pine the progress of plant succession is toward a hardwood, oak-hickory climax (94). The succession can be most clearly seen in old-field stands (fig. 4). Light-seeded and intolerant hardwood species, such as sweetgum, red maple, yellow-poplar, blackgum, and waxmyrtle are early invaders. Somewhat later the components of the climax, oaks and hickories, appear.



Figure 4.--Old-field stand of loblolly pine in the Kisatchie National Forest, Louisiana. The understory of small hardwoods has developed since the stand was established.

They increase in size and number as the pine stand matures (5, 94) and replace pines in the overstory as the stand disintegrates between 100 and 300 years of age. Cutting of the pine stand without provision for reestablishment hastens the process, which accounts for the increase in hardwood types throughout the loblolly pine range. Fires during the dormant season have little effect on the succession because the hardwoods sprout prolifically and vigorously, and even annual dormant-season fires do not reduce the hardwood crown area or number of stems (76). However, repeated fires at intervals of less than 10 years ultimately eliminate loblolly pine (30, 134). Crown fires destroy the entire stand, as may hot surface fires during the growing season (17), but pine readily becomes reestablished if a seed supply is available because the hardwoods are also killed back to the ground (93).

Because it is intolerant of shade, loblolly pine expresses dominance early, and crowns differentiate rapidly under competition on good sites. In dense stands on poor sites, expression of dominance and crown differentiation are much slower. The density of undisturbed stands approaches an equilibrium at a rate that probably varies with site quality (21). Well-stocked stands ranged from 118.7 square feet of basal area per acre for trees 4 inches in d.b.h. up to 175.4 square feet for trees 16 inches d.b.h. (114). In Arkansas, well-stocked stands tended toward a basal area of 155 square feet per acre (28).

Annual radial growth of loblolly pine is positively correlated with total rainfall from January to May and negatively correlated with temperature (33). It reaches a maximum early in the growing season (149), and is directly proportional to crown ratio (54, 71), crown length, and total height.^{7/} Volume growth, however, also depends on the length of the clear stem. In 26-year-old trees, cubic volume growth of the clear stem was greatest with a crown length that was 40 percent of total tree height (71).

Loblolly pine prunes itself readily at younger ages, before branches develop heartwood. The maximum contribution to main-stem growth is made by branches in the upper portion of the crown, 15 percent of tree height from the top (71). Below this point the contribution becomes progressively less, until branches halfway down the stem contribute nothing.

The increase in diameter growth after release is also directly related to crown ratio, but trees of large diameter respond less than trees of small diameter (26, 78). MacKinney (78) found that trees about 60 feet tall increased diameter growth more than shorter or taller trees after release. Thus, tall, slender trees with well-developed crowns, that is, codominants and better intermediates, respond best to release. Trees long suppressed also grow much faster in both height and diameter after release but may never attain the growth rate of trees that were never suppressed (26). Height growth

^{7/} Dubow, D. A. The relationship between crown and bole length and their ratios with diameter growth in young loblolly pine plantations. 1953. (Unpublished Master's thesis, North Carolina State College, School of Forestry.)

after release apparently depends mainly on age at release, while diameter growth depends on crown size and growing space. The capacity of loblolly pine to respond to release means that noncommercial removal of competing hardwoods is usually a profitable investment (15, 112).

Mortality in loblolly pine stands is caused mainly by competition (16, 111), but fire, wind, lightning, sleet, disease, and insects may cause substantial losses. Accidental fires may completely destroy stands, but more commonly reduce growth (4) and cause stump wounds that permit the entrance of decay fungi and insects and result in pitch soaking (50). Trees in repeatedly burned areas develop greater butt swell than unburned trees (27). Large, dominant trees are more vulnerable to wind damage than smaller trees (122), and trees with large cankers caused by the southern fusiform rust break more readily than sound trees (135). Although direct losses to lightning are small, averaging only 2 trees per 100 acres per year (122), lightning-struck trees often become centers of infestations by the southern pine beetle (*Dendroctonus frontalis*). Other injuries and drought conditions also favor this insect and it has killed large volumes of loblolly pine throughout the range. The engraver beetles (*Ips* spp.) and the black turpentine beetle (*Dendroctonus terebrans*) may also cause serious losses under the same circumstances (84). Sleet storms bend, break, and uproot many trees and may severely damage heavily stocked stands (82, 91), particularly those made up of slender, small-crowned trees. Loblolly pine beyond the sapling stage is seldom killed by disease, but fungi cause appreciable cull in older stands. Heart rot (*Fomes pini*), entering through branch stubs, and butt rot (*Polyporus schweinitzii*), entering through fire wounds, are the most important causes of such losses (56).

After heavy partial cutting in older stands of moderate or higher density, many residual trees die from causes directly related to logging and exposure. Intermediate and suppressed trees may succumb to the drastic change in environment (22, 74). Isolated dominants and codominants, as in seed-tree stands, die at the rate of about 1 percent of the number of trees per year, mainly from wind and lightning (32, 74, 122). Logging injuries and bark-beetle attack are important causes of death in the first few years after cutting; puddling of heavy, wet soils and attendant root damage have also caused substantial losses (81). Ice damage to residual trees is negatively correlated with live-crown ratio, small-crowned spindling saplings being most vulnerable (92).



SPECIAL FEATURES

In common with other hard pines, loblolly pine is highly resinous, although less so than slash pine and longleaf pine. The constitution of the oleoresin of loblolly pine is as follows (90):

Density	0.8570 ²²
Index of refraction	1.4675 ^{27.5}
Specific rotation, degrees	+ 20.2
Turpentine yield, percent	19
Turpentine composition, percent	85 d-alpha-pinene 12 1-beta-pinene

The specific gravity of green loblolly pine wood averages 0.47 and increases from the pith outward. The trend is mainly due to age of the tree at the time the annual ring is formed and partly due to decreasing width of rings (147). Specific gravity is greatest near the base of the tree and decreases with height; and it is greater in small-crowned than in large-crowned trees (97). It also increases as the percentage of summerwood increases.

Tracheid length varies greatly from tree to tree, suggesting that it is strongly dependent on hereditary factors as well as on environmental conditions (6). Tracheid length averages 4.3 millimeters and ranges from 1.5 up to 7.0 millimeters (14). It increases sharply from the pith outward during the first 10 years and at a slower rate beyond that point; it also increases from the base of the tree upwards to middle height and decreases above that level (6).

The angle made by the fibrils (strands of cellulose that make up the tracheids) with the main axis of the tracheid is related to longitudinal stability of lumber and tearing strength of both sulfite and sulfate pulp made from the wood (98). Large fibril angles are associated with much shrinkage along the grain and lesser tearing strength of the pulp. Fibril angles in loblolly pine vary from 2 to 51 degrees, decrease from the pith outward and from the base of the tree upwards, and are smaller in narrower annual rings. Closely spaced trees with small crowns have smaller fibril angles than widely spaced, large-crowned trees.

RACES AND HYBRIDS

Distinct races of loblolly pine have not been identified and described, but definite variations in survival, growth rate, disease resistance, drought hardiness, and cold hardiness associated with seed source have been observed. In tests at several locations in the Southern and Central States, seedlings from north Alabama seed had a higher survival rate at 2 years than seedlings from Maryland and Virginia seed, while no seedlings from North Carolina and South Carolina survived (41). In other widely scattered tests in the South, seed from North Carolina and South Carolina has given better results (130).

Seedlings from seed of six different sources planted in southern Illinois showed a significantly different rate of height growth in the first year for each seed source (88). In another study, Maryland seedlings planted at a number of places throughout the south grew less in height than those from other locations, but had exceptionally well-developed fibrous roots (130).

Near Bogalusa, Louisiana, trees from a local seed source were taller, larger in d.b.h., and greater in cubic-foot volume per acre at 22 years than trees from Texas, Georgia, and Arkansas seed sources (129). In South Africa, loblolly pine trees from southern seed sources in the United States were taller at 9 years than those from northern sources, except that seedlings from Onslow County, North Carolina, were taller for their latitude, and seedlings from the Kisatchie National Forest in Louisiana and from the Crossett Experimental Forest in Arkansas were shorter (108). At Athens, Georgia, and Jasper, Texas, the variation in height growth with latitude of seed source was much less pronounced than in South Africa, but the good performance of the North Carolina strain and the poor behavior of the Louisiana and Arkansas strains showed up again (129).

Eastern strains of loblolly have shown a higher susceptibility to fusiform rust infection than western strains. In the Bogalusa plantings, 37 percent of Georgia trees were infected, while infection of other strains ranged from 4 to 6 percent. In the Jasper and Athens plantings, eastern strains had a much higher incidence of rust than western strains, but northeastern strains, from Virginia and Maryland, had very few infections in either locality (129).

Cold resistance also varies with seed source. Seedlings of Virginia, Maryland, Tennessee, and Arkansas strains in nursery beds in southern Illinois were not damaged by subfreezing temperatures, but North Carolina seedlings sustained moderate damage, and South Carolina and Mississippi seedlings sustained moderate to severe damage (89). In Maryland, seedlings from local seed were not injured by cold, but those from more southerly sources were damaged, the southern-most strain--from Louisiana--being conspicuously injured (130).

Because of its well-known adaptability to a wide range of environmental conditions, loblolly pine has been planted in many places outside its range. It has been successfully grown in Australia, New Zealand, South Africa, and in the coastal region of Uruguay; in the United States it has been grown at Placerville, California, and in parts of Tennessee, southern Illinois, southern Indiana, western Kentucky, and southern New Jersey. In Pennsylvania and Massachusetts, seedlings are winter-killed; in Ohio and southern Indiana, needles commonly show cold injury (96). Cold also injures loblolly pine in the Ozarks (110).

In the "Lost Pines" area and at the western edge of its range in east Texas, where summer rainfall is often deficient, loblolly pine is apparently more drought hardy than it is farther east. In a test in east Texas, seedlings from that locality had consistently better survival than seedlings from Louisiana, North Carolina, and Florida (154). No differences in growth among the surviving seedlings were observed, however.

Variations in the behavior of individual trees have also been traced to hereditary factors. In South Carolina, seedlings from different mother trees differed significantly in height growth and survival (87).

One natural hybrid involving loblolly pine has been identified and named. This is the hybrid known as Sonderegger pine (Pinus x sondereggeri). It is common in Louisiana, and perhaps elsewhere, in longleaf stands near a source of loblolly pine pollen (25, 43). The seed apparently comes from longleaf pine trees; hence loblolly pine is probably the male parent. Many trees with characteristics intermediate between those of shortleaf and loblolly pine, which may be hybrids, have been found in east Texas (153) and may occur wherever these two species grow in mixture. Loblolly pine flowers before shortleaf pine but early conelets of shortleaf pine may become receptive while loblolly pine pollen is still being cast; or loblolly pine flowering may occasionally be retarded by cold weather so that loblolly pine conelets might still be receptive when shortleaf pine starts pollinating. Where loblolly and pond pine are closely associated, pines with intermediate characteristics between these two species are common.

Interspecific hybrids of loblolly pine are not difficult to obtain (43) and a number of successful hybrids have been produced by controlled pollination. Some successful hybrids that have been reported are as follows (18, 19, 38, 107, 133):

<u>Seed parent</u>	<u>Pollen parent</u>
Shortleaf	Loblolly
Slash	"
Pitch	"
Longleaf	"
Loblolly	Pitch
Shortleaf x loblolly	Loblolly
Loblolly	Shortleaf
"	Slash
Shortleaf x loblolly	Loblolly x slash
Loblolly x slash	Slash
Loblolly	Sonderegger
"	Shortleaf x loblolly
Shortleaf	Shortleaf x loblolly
Shortleaf x loblolly	Loblolly x slash
Shortleaf x slash	Sonderegger
Longleaf	Sonderegger

Seedlings from a cross between loblolly pine and South Florida slash pine (Pinus elliottii var. densa) are growing at Hamilton, Georgia, and at the Southern Institute of Forest Genetics near Gulfport, Mississippi.^{8/} Seedlings of pond x loblolly pine are growing at the Westvaco Experimental Forest, near Georgetown, South Carolina (37).

^{8/} Dorman, K. W. Official correspondence, Tidewater Forest Research Center, Franklin, Virginia. April 27, 1956.

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