ECOLOGY OF SHORTLEAF PINE

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ABSTRACT

Shortleaf pine (Pinus echinata Mill.) occupies the broadest natural range of all the southern pines, and is found across a diverse range of geography, soils, topography, and habitats. Individual shortleaf trees achieve their best development on deep, well-drained soils of the Upper Coastal Plain, but shortleaf pine communities are most prominent in the Ouachita Highlands of the West Gulf Region. Two major ecological issues confront shortleaf pine -- the susceptibility of shortleaf pine stands to depredations of acid deposition, and the ecological tradeoffs underlying the planting of loblolly pine (P. taeda L.) on shortleaf pine sites which are north of loblolly's natural range.

OVERVIEW

Shortleaf pine (Pinus echinata Mill.) is the most widely distributed of all of the major southern pines, growing in 22 states over more than 440,000 square miles (Lawson and Kitchens 1983). Yet, it is also perhaps the most maligned of the southern pines as well. Reasons for this silvicultural disrespect center upon its slow growth rate, the difficulty in obtaining regeneration (both naturally and artificially), and its susceptibility to certain pathogens such as littleleaf disease (Phytophthora cinnamomi Rands). It is no wonder that some foresters look upon the species as little more than a resinous weed occupying sites better utilized for one of the 'real' southern pines.

However, undue concern over these limitations may mask the inherent silvicultural potential of shortleaf pine. Stem and crown form are generally better than in the other southern pines, and the species is a good pruner (Dorman 1976). It is unusually free from serious diseases, and is particularly resistant to fusiform rust (Cronartium fusiforme Hedg. & Hunt) (Hepting 1971). It is generally less susceptible to the adverse effects of ice, snow, and cold temperatures than any of the other major southern pines. Opportunities for genetic improvement in shortleaf pine include breeding for enhanced volume production, drought resistance, or the incorporation of desirable traits such as fusiform resistance in hybridization work with other southern pines (Dorman 1976).

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Taxonomically, shortleaf pine is in the subgenus *Pinus*, section *Pinus*, and subsection *Australes*, which also includes longleaf (*P. palustris* Mill.), loblolly (*P. taeda* L.), spruce (*P. glabra* Walt.), pitch (*P. rigida* Mill.), pond (*P. serotina* Michx.), table-mountain (*P. pungens* Lamb.), slash (*P. elliottii* Engelm.), Caribbean (*P. caribaea* Morelet), West Indian (*P. occidentalis* Sw.), and Cuban (*P. cubensis* Griseb.) pines. The other common southern pines, Virginia pine (*P. virginiana* Mill.) and sand pine (*P. clausa* (Chapm.) Vasey ex. Sarg.), are in the subsection *Contortae* (Little and Critchfield 1969).

A thorough literature review of shortleaf pine has been published by Haney (1962). Silvics of the species have been described by Fowells (1965) and updated by Lawson and Kitchens (1986); the genetics of the species have been reviewed by Dorman (1976). Silvicultural systems common to shortleaf pine have been described by Walker and Wiant (1966), and Lawson and Kitchens (1983).

NATURAL RANGE

Geography

Shortleaf pine occupies the broadest and most geologically varied habitats of any of the pines in the southeastern United States (Critchfield and Little 1966). Comparing its natural range to the physiography of the region (Fenneman 1946, USDI 1970), shortleaf pine is found in all of the states of the Atlantic Coastal Plain from southwest Connecticut and southeast New York to east Texas and southeast Oklahoma. In the Appalachian Highlands, the species is found in the Piedmont, the Blue Ridge, the Valley and Ridge, and the Appalachian Plateaus from isolated populations in Pennsylvania southwestward to northern Mississippi. Its range skirts the southern edge of the Interior Low Plateaus of the Interior Plains Division in Kentucky, Tennessee, and northern Alabama. However, shortleaf pine achieves its best community development generally west of the Mississippi River in the Ouachita and Ozark Highlands, extending from the isolated population in southwest Illinois, through Missouri and Arkansas, and into eastern Oklahoma.

Climate

Climate varies widely across the natural range of shortleaf pine. The southeastern United States is characterized by warm and humid summers, mild winters, and abundant rainfall. However, within the range of shortleaf pine, wide variations exist in temperature and rainfall (Wahlenberg and Ostrom 1956).

Mean annual precipitation varies from 40 inches along the western and northern edges of the natural range to 64 inches along parts of the Gulf Coast. Variation is between 40 and 48 inches through the northeastern half of its range, and from 48 to 56 inches in most of the southwestern half (USDI 1970). Annual snowfall is also quite variable, ranging from virtually none in the southernmost part of the range to as much as 80 or more inches in the Appalachian Highlands.

Temperatures are similarly variable. Over shortleaf's range, average annual temperatures vary from 45°F. to 75°F. The 50°F. average annual temperature isotherm approximately parallels the northern limits of the natural range (Lawson and Kitchens 1983).

The interrelationship between temperature and precipitation is probably ecologically significant with respect to shortleaf pine. In the northeastern part of its range, temperature varies considerably with the seasons, but rainfall is more or less uniformly distributed throughout the year. Conversely, in the southwestern part of its range, temperatures are warmer and less variable, whereas precipitation occurs primarily during the winter and spring months; in summers, when annual temperatures are at their peak, precipitation is sporadic. Patterns such as these not only define shortleaf's physiological environment, but also undoubtedly affect shortleaf's ability to compete with other species.

Soils and topography

As might be expected from its extensive range, shortleaf pine occupies a wide variety of soils (USDI 1970). It occurs most commonly on soils with prominent clay textures in the surface or, especially, subsurface horizons rather than on sandy soils. Across the Coastal Plain, it is found primarily on Paleudults. These soils are generally moist, with low levels of subsurface organic matter and a thick horizon of clay accumulation without appreciable weatherable minerals. In the Piedmont, it is typically found on Hapludults which are characterized by a thin subsurface horizon of clay accumulation and/or a subsurface horizon having appreciable weatherable minerals. In the Appalachian Highlands, soils are generally Dystrochrepts which are moist, low in exchangeable bases, and have no free subsurface carbonates. Other soils in this subdivision which support shortleaf include scattered Fragiudalfs, Hapludalfs, and Paleudalfs characterized by subsurface clay horizons.

Individual shortleaf pine trees attain their best development on deep, well-drained sandy loam soils in the uplands of the Coastal Plain (Lawson and Kitchens 1983). Within narrower geographic subdivisions, shortleaf pine has been reported to attain its optimal development on deep soils in the Ozark Highlands of Arkansas and Missouri (Graney and Ferguson 1972) and southern Illinois (Gilmore 1963), and on deep soils of the Piedmont from North Carolina to Alabama, Georgia, and Virginia (Coile 1952, Coile and Schumacher 1953, Della-Bianca and Olson 1961, Kormanik 1966, Georgia Ike and Huppuch 1968.

Unfortunately for shortleaf enthusiasts, other species also exhibit high growth rates on such sites. Toward the southern part of its range, loblolly pine reaches its best development on similar soils (Baker and Balmer 1983), and tends to predominate in mixed stands by virtue of its superior growth rate. In the upland areas, shortleaf pine occupies deep soils only temporarily, maintaining dominance over the succeeding oak-hickory climax type (White 1980a).

Topographic factors associated with soil depth have also been reported as being significantly related to the development of shortleaf pine. In the Ozark Highlands, site quality increased as slopes went from convex to concave, as aspect was increasingly oriented from the south and southwest to the north and northeast, and as latitude generally decreased (Graney and Ferguson 1971, 1972). Similar trends were noted in the Georgia Piedmont, where site quality for shortleaf pine increased with decreasing elevation, lower slope position, and increasing orientation to the north and northeast aspects (Ike and Huppuch 1968).

Plant community associates

The recent reclassification of forest cover types (Eyre 1980) places shortleaf pine as a major component of three forest types -- the shortleaf pine type (#75), the loblolly pine-shortleaf pine type (#80), and the shortleaf pine-oak type (#76). Shortleaf pine is a varyingly minor component in 15 other cover types (Eyre 1980, Lawson and Kitchens 1986), typically in association with loblolly, longleaf, pitch, Virginia, and occasionally eastern white (P. strobus L.) pines, as well as the many species of more xerophytic oaks throughout the Appalachian region. Shortleaf is undoubtedly occasionally present in association with other species as well. This cosmopolitan occurrence is not surprising in light of its broad range and varied habitat.

Ecological implications

In summary, researchers have implicated site quality for shortleaf pine with soil moisture. Individual shortleaf pine trees attain their physiologically optimal development on deep soils in advantageous topographic positions, most notably in the Upper Coastal Plain. On these sites shortleaf is typically outcompeted by faster-growing associates such as loblolly pine. But through a variety of poorly-understood traits, shortleaf is not completely excluded from such sites; it persists as a minor component of varying importance in natural mixed stands.

As sites become increasingly thin-soiled, oriented to more extreme topographic exposures, and subject to increasingly harsh climatic conditions, site quality for shortleaf pine decreases. Yet, the ecological importance of shortleaf pine in plant communities increases. Reasons for this might include shortleaf's larger root system or its lower demand for soil nutrients (Zak 1961), or its greater tolerance of site disturbances such as fire (Bramlett 1980, White 1980b), than its common associates. In the absence of disturbance, or on better sites, hardwood species (particularly the longer-lived oaks) will eventually outcompete shortleaf. But in the presence of either natural or human disturbance, the succession to hardwoods will be arrested, and shortleaf will be more likely to successfully reestablish itself.

In the Ouachita and Ozark Highlands, ecological conditions are so unfavorable for loblolly pine that it reaches the northerly limits of its natural range in the lower foothills of the southern part of the Ouachita Plateau. Further, particularly on poorer sites, the competitive abilities of hardwood species are limited by unfavorable physiographic and edaphic conditions and by disturbances such as drought and fire. Perhaps not coincidentally, shortleaf pine as a forest type reaches its most extensive development in this region, occurring in pure stands over the largest areas, and having the highest stand volumes, of any region throughout its natural range (Fowells 1965, Sternitzke and Nelson 1970).

A hypothesis regarding the prominence of shortleaf pine in the Ouachitas can be drawn from these considerations. To the south, shortleaf's dominance is limited by superior competitive associates, most notably loblolly pine. To the north, it is limited by climatic, physiographic, and ecological conditions in which species such as the oaks and interior pines are able to gain competitive advantage. Shortleaf is generally the most successful overstory species in those areas where climate and physiography limit the other southern pines, and where instability of moisture and nutrient supply conspire against its oak-hickory associates from the northeast. The region where these factors allow shortleaf to most prominently express its species individuality is in the Ouachita Highlands.

LIFE HISTORY

Reproduction

Shortleaf pine is monoecious, with male and female flowers borne on the same tree. Trees begin to produce seed at about age 20, though earlier fruiting has been reported (Fowells 1965). Some seed is produced every year, and three-year cycles of seed production are commonly reported

(Yocom and Lawson 1977). One can expect good seed crops every 3 to 6 years in the southwestern range of the species, and every three to ten years in the northeastern range (Lawson and Kitchens 1983).

Flowering in shortleaf pine occurs from March to April, cones ripen from October to November, and seedfall occurs fairly quickly upon ripening (USDA 1974). The earlier phenologies occur in the southern part of its natural range. Hybridization with other pines, particularly loblolly pine, is thought to occur rather extensively (Bilan 1966, Hare and Switzer 1969), although many putative hybrids are thought to more closely resemble shortleaf than loblolly pine. Some workers have suggested that if hybridization is occurring, it is via the introgression of loblolly genes into shortleaf populations rather than vice versa (Bhat and Hicks 1976). The most obvious trait promoting reproductive isolation of shortleaf pine from loblolly pine is non-synchronous flowering (Cotton et al. 1975).

Shortleaf has smaller cones and seed, and fewer seed per cone, relative to other southern pines. Data indicate approximately 35 pounds of cones per bushel, and seed ranging from 2 to 3 pounds per 100 pounds of cones; these values are roughly the same as for loblolly (USDA 1974). A bushel of shortleaf cones produces from 0.4-1.1 lb of seed per bushel, compared to from 0.6-1.3 lb for loblolly. In a pound of shortleaf seed, one can expect between 32,100 and 72,900 seeds, whereas loblolly will have 12,300-26,400 seed per lb (USDA 1974). Shortleaf seed have germinative energies of between 81 and 88 percent, germinative capacity of 90 percent, and viability in cold storage of up to 35 years (USDA 1974).

Establishment and early growth

Autumn dissemination results in stratification of the seed during the winter months. Germination then commences in early spring (Fowells 1965) and, like other pines, is most assured when the seed is on exposed mineral soil. Establishment is best if a small amount of overstory shade is present to prevent seedling dessication, particularly on exposed sites (Lawson 1979).

Seedlings develop a characteristic J-shaped crook near the base at an early age, usually within 2 to 3 months of germination. Axillary buds form at this crook, and provide the tree with the rather unique ability to sprout in the event of mortality of the upper stem (Chapman 1942, Fowells 1965). This characteristic might contribute to the ability of shortleaf pine to maintain itself in mixture with loblolly pine on the deep, well-drained sandy loams of the upper Coastal Plain.

Shoots of the seedlings develop slowly, as the plant invests its photosynthetic production in development of its root system. Growth in the species is multinodal; most growth is completed by July, but shortleaf will respond to favorable late-season precipitation by resumption of height growth (Fowells 1965). Average annual growth rates of saplings have been reported as ranging from 1 to 3 feet (Lawson and Kitchens 1986).

Stand development

Shortleaf pine is intolerant of shade. Overstory competition generally inhibits the development of reproduction. However, the species will persist in exceedingly dense stands, and responds to release at older ages (Fowells 1965).

Because of its intolerance to shade and the ecology of disturbance, shortleaf pine most commonly develops in even-aged aggregations. The development of a hardwood stand beneath a shortleaf overstory frequently follows, although depends upon overstory density and absence of disturbances such as fire (White 1980a). While the species is infrequently managed to its biological capabilities, individual stems can attain sizes of 3 feet in diameter, 120 feet in height, and 150 years in age, with larger and older veterans reported (Harlow and Harrar 1969).

IMPLICATIONS FOR CONTEMPORARY RESEARCH

Within the realm of the ecology of shortleaf pine, the last decade has not been a fruitful period for promoting an enhanced understanding of the species. But society's pressure on the use of forests for non-timber resources will undoubtedly increase in the future, and these needs must be satisfied on an ever-decreasing forest land base. In the future, available forest land must be used efficiently, and in harmony with other uses. From this perspective, a new consideration of the ecology of shortleaf pine may be in order.

Areas of contemporary research which would undoubtedly be of value are those relating to both acid deposition and a further understanding of the ecological interrelationships between loblolly and shortleaf pine. These concerns can be effectively illustrated using the shortleaf forests of the Ouachita Mountains.

Acid deposition

Acid deposition encompasses two related phenomena, that of the deposition of wet precipitation (familiarly known as acid rain) and dry deposition, which includes aerosol and particulate deposition. It has been implicated in observations of forest decline both in Europe and the United States. Among the many hypotheses which attempt to explain the relationship between forest decline and acid deposition (Schutt and Cowling 1985), two have become the focus of international scientific inquiry.

The first hypothesis suggests that air pollution directly causes a decrease in net photosynthesis in the tree, which, in association with other secondary effects, results in the tree being afflicted with an overall debilitating syndrome (Schutt and Cowling 1985). The second hypothesis suggests that the problem is in the displacement of exchangeable bases by acids in the soil, resulting in both the loss of those cations by leaching and the increasing availability of aluminum in the soil as soil pH becomes increasingly acid. The aluminum then interferes with normal uptake of nutrients (Matzner and Ulrich 1985). In either case (or both, if concurrently occurring), the result is reduced tree vigor and, ultimately, mortality.

Large areas through the heart of the range of shortleaf pine are thought to be highly susceptible to acid deposition. The problem is expected to be particularly acute in those soils which are low in exchangeable bases and organic matter. Currently, Arkansas is thought to be at the fringe of the region affected by acid precipitation in North America. As such, it represents an opportunity to provide baseline ecological data on normal ecosystem processes in the absence of acid deposition. If acid deposition becomes more widespread and eventually encompasses Arkansas, then such baseline data will serve as an invaluable ecological benchmark for studying the effects of whatever forest decline which might result. In accordance with these ideas, researchers in Arkansas are initiating a long-term project to monitor conditions in this state, so as to better understand and document the potential ecological damage which will result as the West Gulf Region becomes increasingly exposed to acid deposition (Beasley 1986).

Competitive interrelationships of loblolly and shortleaf pine

The ecological interrelationships between loblolly and shortleaf pine are readily apparent in Arkansas. West of the Mississippi River bottomlands, loblolly pine is found in Louisiana, east Texas, and southern Arkansas (Critchfield and Little 1966). Shortleaf pine is also found in Louisiana and east Texas, but extends northward throughout western and northwestern Arkansas into eastern Oklahoma and southern Missouri (Critchfield and Little 1966).

Westward migration of these species is most likely limited by some fundamental climatic factor, as evidenced by the approximately congruent demarcation of the range of the two pines in east Texas. Most prominent is an increasingly xeric environment, which exerts an effect on both growth and reproduction. Factors affecting growth include increased competition from more drought-tolerant species such as post oak (Quercus stellata Wangenh.); factors affecting reproduction include smaller and increasingly rare seed crops, and an increasingly dry and hostile environment for seedling establishment and survival (Bilan and Stransky 1966, Schneider and Stransky 1966, Eneim and Watterston 1970).

The environmental factors limiting northern expansion of the two species are more complex. The northern boundary of the natural range of loblolly is a sharp demarcation across central Arkansas; shortleaf extends into Missouri. The reason for the difference is not clear. Critical factors might include temperature (Hocker 1956, Yates and Cullom 1973), cold-related damage (Meade 1951, Shoulders 1952, Boggess and McMillan 1954, Shepard 1975, Shepard 1978, Burton 1981), soils and surface geology (Yates and Cullom 1973), soil moisture (Phares and Rogers 1968, Graney and Ferguson 1971, Shoulders and Tiarks 1980), and actual transpiration (Manogaran 1975).

These ecological speculations relate directly to a major silvicultural issue in Arkansas -- the practice of planting loblolly pine in areas which are at the limit or to the north of its natural range. In plantation comparisons through age 20, loblolly has been reported to outgrow shortleaf in southwest Arkansas (Meade 1969), the Arkansas Ozarks (Meade 1951), east Texas (Chandler et al. 1943), northern Mississippi (Williston 1958, 1972), western Tennessee (Williston 1959, 1972), and southern Illinois (Gilmore and Gregory 1974). Improved strains of loblolly pine show the potential for gains of 8 feet in site index and as much as 25 percent in volume over local sources of loblolly in southern Arkansas (Grigsby 1973, 1977, Wells and Lambeth 1983). Thus, it is likely that planting improved strains of loblolly pine in areas to the north of its range will continue, though with increasing effort to delineate exactly which sites have a high potential for risk (Lambeth et al. 1984).

Why, then, does the natural range of loblolly stop where it does? Ecologically, some natural barrier may act as an impediment to either growth or reproduction. A growth impediment would be the rare disturbance severe enough to kill loblolly, but not shortleaf, over broad areas. Extensive drought or heavy ice storms might be appropriate examples of this. Such disturbances would, in the long run, require an assessment of risk in corporate management strategies. By way of example, loblolly plantations established north of its range have not all been successful. In newly-established plantations subject to severe drought, widespread seedling mortality can result (Lambeth et al. 1984). Older plantations are also subject to mortality, as has been reported when mild-climate seed sources planted in an area subject to severe climatic conditions undergo a sudden stressful climatic event, such as extended drought (Wells and Lambeth 1983, Wells and Rink 1984, Wells 1985). As a result, the use of local seed sources on sites subject to environmental stress is becoming an increasingly accepted recommendation (Long 1980, Wells 1983).

Alternatively, a reproduction impediment would be a disturbance which causes failures in either seed production or seedling establishment. Drought may affect quality and viability of seed produced, as appears to be the case in east Texas (Bilan and Stransky 1966). Cold damage to newly-emerged female strobili has been noted in shortleaf pine (Campbell 1955, Schoenike 1955); similar damage could occur to loblolly pine strobili, which are known to flower earlier than shortleaf (Dorman and Barber 1956). Heavy rains during pollen release may wash pollen from the air, resulting in smaller crops of seed (Schoenike 1955, Boyer 1966). If impediments such as these are the major limitation for the northerly natural dissemination of loblolly pine, then planting the species to the north of its natural range, and thus circumventing the impediment, might be successfully accomplished.

Conclusion

Work on the ecological characterization of shortleaf pine in the past decade has been minimal, reflecting the gradually declining interest in management of the species. However, opportunities currently exist which might allow the next decade of ecological research to be more fruitful. Baseline ecological studies of shortleaf pine stands will quantify the long-term effects of acid deposition, and will be of international scientific interest. The ecological interrelationships of loblolly and shortleaf pine, especially on shortleaf pine sites directly to the north of loblolly's natural range, have important implications for contemporary forestry. Research such as this may help foresters to better understand shortleaf pine, and will go a long way to enhance the professional respect in which foresters hold the species.

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