A stand of 200-year-old longleaf pine growing in the red hills area north of Tallahassee, Florida.

Bartram (Van Doren 1928) described a typical longleaf dominated stand as he traveled through the lower coastal plain in 1773:

> *"Now the pine forests opened to view. We left the magnificent savanna and its delightful groves, passing through a level, open, airy pine forest, the stately trees scatteringly planted by nature, arising straight and erect from the green carpet, embellished with various grasses and flowering plants; … we joyfully entered the borders of the level pine forest and savannas which continued for many miles, never out of sight of little lakes or ponds, environed with illumined meadows, the clear waters sparkling through the tall pines."*

THE *Longleaf Pine* ECOSYSTEM OF THE SOUTH

Kenneth W Outcalt

Abstract

Longleaf pine (*Pinus palustris* P. Mill. [Pinaceae]) was once the most prevalent pine type in the southern US. Stands of longleaf were also habitat for a vast array of plant species. Decades of timber harvest followed by conversion to agriculture, urban development, or to other pine species, have reduced longleaf dominated areas to less than 5% of its original range. My paper discusses the habitat and history of this once vast resource, outlining its key role as an integral part of native plant communities. I also focus on the more recent recognition of the ecological importance of longleaf pine ecosystems. This appreciation, along with advances in technology and additional information, are combining to reverse the long-term trend and should help ensure that longleaf communities remain as a viable and valuable part of the South's heritage.

KEYWORDS: restoration, wiregrass, fire, bluestem

NOMENCLATURE: (plants and animals) ITIS (1998); (fungi) Tainter and Baker (1996)

Longleaf pine (*Pinus palustris* P. Mill. [Pinaceae]) is synonymous with Southern forests. It once dominated 24.3 million ha (60 million ac) in the southeast (Figure 1), stretching from southeastern Virginia, south to central Florida, and west into eastern Texas (Stout and Marion 1993). It was a co-dominant along with loblolly (*Pinus taeda* L. [Pinaceae]) and shortleaf (*Pinus echinata* P. Mill. [Pinaceae]) pine and hardwoods on an additional 14.6 million ha (36 million ac) in a band along the northern portion of its range (Frost 1993).

My objective is to give a better appreciation for longleaf pine and its role as a native plant in many of the communities of the South. This is done by highlighting the importance of the longleaf pine, which was the key tree species in a complex of fire-dependent ecosystems long native to the southeastern US (Figure 2). It was found on a variety of sites from wet coastal flatwoods to dry mountain ridges where it formed the canopy over highly diverse ground cover communities. An understanding of the decline of longleaf systems is conveyed through a brief history of the use of this once vast resource. The recent interest in increasing longleaf pine area and techniques and incentives to do so are discussed.

Habitat

Longleaf pine was native to a wide range of ecosystems. Along the Atlantic and Gulf coastal plain, it was the dominant tree on wet flatwoods and savannas. It also dominated higher, droughty sand deposits such as the fall line sandhills, where the Piedmont meets the upper coastal plain; the central ridge of Florida and rolling sandhills of lower Mississippi; as well as central Louisiana and east Texas (Stout and Marion 1993). Longleaf pine even extended onto the mountain slopes and ridges of Alabama and northwest Georgia, where it was found growing at elevations up to 600 m (1970 ft)(Boyer 1990).

The flatwoods sites of native longleaf are primarily sandy deposits that formed in shallow seas (Stout and Marion 1993). Because of abundant rainfall and slow surface drainage, flatwoods sites are seasonally wet with water at or above the surface at least part of the year; usually during the dormant season, from December to February. However, during the spring and early summer dry period, these sandy sites can become quite

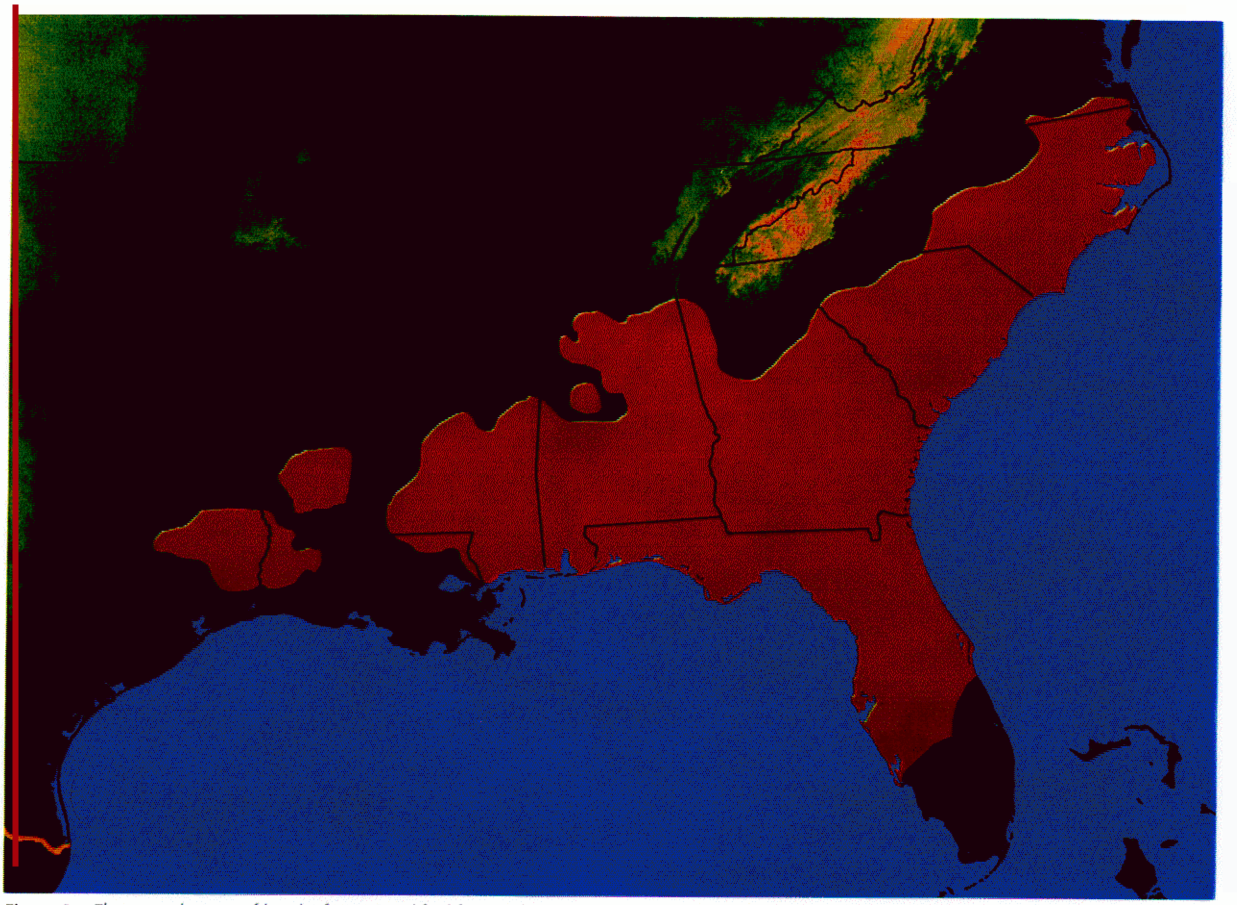

Figure 1 • The natural range of longleaf pine (modified from Little 1971).

droughry. Longleaf pine is able to tolerate such fluctuations and once formed pure stands across most of rhe coastal plain (Ware and others 1973). Much of the former longleaf occurred on sandhills where deposits of coarse sands with hilly topography were quite droughty. Mountain longleaf forests also occupied droughry, but rocky sires. The species also tended to be more prevalent on the drier south- and west-facing slopes.

Although able to dominate poor sandy and rocky sites, longleaf also occurred on better soils. Embedded in the coastal plain, especially on the inner and higher terraces, are deposits of finer-sized clay and silt that developed soils that are less droughty and more fertile. Hills with clay parent material, such as the Red Hills area of southern Georgia, also had extensive longleaf forests. Other upland sites with better soils were found from North Carolina to Texas. These were the most productive longleaf sites, producing the best growth and largest trees.

History

The history of longleaf pine ii intertwined with the history of European settlement of the South. Naval stores, which began with the first settlements in Virginia (Frost 1993), were so called because the pine tar produced was first used extensively for wooden sailing ships to seal cracks and preserve ropes and sails. From Virginia, the naval stores industry moved into North Carolina then expanded south and west, eventually to the limits of the longleaf range in east Texas. Many acres of longleaf were destroyed because wildfires would readily ignite the pitch soaked boles left after a naval stores operation. Lumbering also began with the first European settlements; trees were cut with axes to build log structures (Croker 1987). The boom years of southern lumbering were 1880 to 1920 when the great forests of longleaf pine were cleared from the Carolinas to Georgia and Florida, across Alabama and Mississippi, into Louisiana and finally Texas. In 1896, logging yielded 8.6 million m^3 (3.7 billion board feet) of longleaf pine timber (Mohr 1896). Production reached its peak in 1907, when 30.6 million m^3 (13 billion board feet) were cut (Wahlenberg 1746). By 1930, nearly all old-growth longleaf had been harvested.

It seemed that longleaf pine, a tree so well adapted to the southern region and covering such vast areas would surely replace itself on harvested areas, but it usually did not. Mohr (1888) concluded that rhe prospect of maintaining longleaf forests seemed hopeless. Although smaller and poor quality trees that were capable ofproducing seed were left on most areas (Wahlenberg 1946). many sites did nor regenerate

see **Longleaf Pine** on page 47

Longleaf Pine *from page* 44

to longleaf pine. Along the Atlantic coastal plain of rhe Carolinas, the more competitive loblolly pine captured many sites following harvest of longleaf pine. On other flatwoods areas further south, slash pine (*Pinus elliottii* Engelm. [Pinaceae]) replaced longleaf, while hardwoods and shortleaf pine became dominant on many of the upland areas of the interior. The longleaf pine's irregular seed production-it has good seed years only every 5 y or more (Boyer 1990)—made re-establishment uncertain. In some areas a good seed crop may occur only once every 20 y. Also, because seeds are large, a number of insects, rodents, and birds ear them (Wahlenberg 1946). With such long intervals between seed crops and seed predation, it is not surprising that other more prolific seed producing pines became dominant on many sites.

Even where prc-existing longleaf seedlings survived logging operations, they often did not survive heavy feeding by feral hogs (Schwarz 1907). The settler's free-ranging and feral hogs not only consumed the large longleaf seeds, but, even worse, they would root out young seedlings to get at the starch filled longleaf roots. Many acres of potential longleaf pine forest were thereby lost. The destructive potential was demonstrated by early fencing studies, which showed that only 20 seedlings per ha (8 per ac) survived in unfenced areas, while fenced sires contained over 14,826 seedlings per ha (6000 per ac) (Mattoon 1922).

Harvest of second-growth stands began in earnest in the late 1940s. Because planted longleaf pine seedlings had very poor survival and perceived slow early growth because of the grass stage, it was seldom selected for reforestation. Therefore, many second-growth longleaf stands were clear-cut, mechanically site prepared, and converted to plantations of loblolly or slash pine. On some private lands, owners made no effort to reforest harvested sires. Many such sires were captured by loblolly or slash pine also, from seedlings in place or seed dispersed from adjoining uncut trees. Old fields also were planted with loblolly or slash pine, or were colonized by these more aggressive pines following abandonment.

As a result of cumulative impacts wrought by 3 centuries of land use, longleaf pine, once one of the most prevalent forest types in the South, has declined dramatically. By 1900, logging, naval stores, and agriculture had reduced the area dominated by longleaf pine by more than half (Frost 1993)(Figure 3). By 1935, the original longleaf forest had been cut; only scattered fragments remained. Second-growth longleaf stands occupied one-third of the species' original range (Wahlenberg 1946). Conversion to other species and loss to urban expansion continued to reduce the longleaf area through 1985 (Kelly and Bechtold 1990). Over the next decade, longleaf pine was reduced to less than 5% of its original area (Outcalt and Sheffield 1996).

Fire and Community Composition

Key to the success of longleaf pine is its adaptation to fire. Longleaf pine ecosystems arc fire-shaped and fire-mainrained. Before landscape fragmentation, natural fire occurred every 2 to 8 y across the species' range (Christensen 1981; Abrahamson and Hartnett 1990; Ware and others 1993). Lightning is a frequent occurrence across the South and historically was the ignition source for fires that shaped the vegetation of the region (Komarek 1964; Robins and Myers 1992). Native Americans augmented those effects by using fire to manage vegetation.

Longleaf pine dominated much of rhe South because it was better able to tolerate fire than irs competitors. Longleaf has evolved the seedling grass stage, where root growth is favored and the rop remains a tuft of needles. A higher moisture content in the spreading needle arrangement of grass stage seedlings rends to cool flames, furnishing protection for the central bud during fast-moving surface fires. After a fire, seedlings can quickly grow new needles from the unharmed central meristem. Because there is no stem, there is very little exposure of cambium that would be susceptible to damage in a thin barked young seedling. When sufficient root reserves have accumulated, seedlings achieve a height of 1 to 2 m (3.2 to 6.6 ft) in a few yews. Such rapid growth puts the terminal bud beyond the reach of most surface fires.

Adaptation to fire is evident throughout the life of longleaf pine. The bark is relatively thick and protects the cambium from lethal hearing by surface fires (Wahlenberg 1946). It tends to naturally prune, thus providing a clear bole between rhe crown and surface fuels. This prevents fires from traveling easily into crowns where damage would be more severe. Longleaf also favors regeneration in open areas, rather than under parent trees (Brockway and Outcalt 1998); keeping ladder fuels away from crowns of adult trees.

Longleaf pine has a competitive advantage over other southern pines like slash and loblolly, as well as hardwoods because it is able to tolerate frequent surface fires. Borh loblolly and slash pine are capable of growing on many sites historically dominated by longleaf and produce more seeds on a more regular basis. Thus, they can out compete longleaf by flooding areas with faster growing seedlings. However, loblolly and slash pine seedlings are thin-barked and quite susceptible to fire-caused mortality. Longleaf pine usually dominated sites where fire was frequent. With longer fire-rerun, intervals, slash and loblolly pine seedlings can grow large enough to survive surface fire. Therefore these species tended to be found on wetter areas where fires occurred at intervals of IO y or more. Slash pine was typically found along the margins of cypress strands and ponds (Abrahamson and Hartnett 1990), while loblolly most often occupied wetter riverside sites (Mohr 1896).

Variation in weather and topography and thus fire return, resulted in a transition zone of mixed pine species, especially along the northern Fringe of the longleaf range (Frost 1993). In this transition zone, relief is greater and thus aspect becomes more important. Pure stands of longleaf tended to occupy drier south facing slopes and ridges. More mesic sires were often a mixture of longleaf, loblolly, and shortleaf pine

Figure 2 • Longleaf pine and other flora after a spring burn in the Apalachicola National Forest in Florida.

along with hardwoods such as oak. Fire frequency was likely less in this more dissected northern portion of the longleaf range, which would favor mixed stands (Frost 1993).

Young hardwoods are also quite susceptible to top kill by fire; and frequent fires kept hardwood sprouts at low stature in longleaf stands (Komarek 1977; Landers and others 1990). Occasionally, random variation in fires or protective micro-site conditions allowed a hardwood stem to survive a few fires and become large enough to resist future surface fires (Rebertus and others 1993). Scattered hardwood trees occurred then, in the canopy or subcanopy of longleaf-dominated stands (Greenberg and Simons 1999). In the absence of fire, hardwoods were able to quickly emerge from the understory and form a dense midstory that could shade out herbaceous species and longleaf seedlings. Some have argued that longleaf not only needs fire for site domination, but that it actually perpetuates frequent surface fire through the production of long flammable needles, that as litterfall, promote the spread of frequent surface fire (Landers 1991).

Another important component of the fuel matrix in longleaf stands were the grasses. While longleaf pine dominated the overstory of southern ecosystems, grasses dominated the understory. In the eastern portion of the longleaf range, wiregrass (*Aristida stricta* Michx. [Poaceae] and *Aristida beyrichiana* Trinius & Ruprecht [Poaceae]) was the major understory species (Figure 4). However, because it was not the dominant grass in all longleaf pine communities, wiregrass is not an essential component of the system. In the Gulf coastal region, little bluestem (*Schizachyrium scoparium* (Michx.) Nash [Poaceae]) was the dominant native grass (Frost 1993). Even within its major range, wiregrass was not always the dominant grass on all sites. A number of other grass species native to the area must have dominated some sites. I have

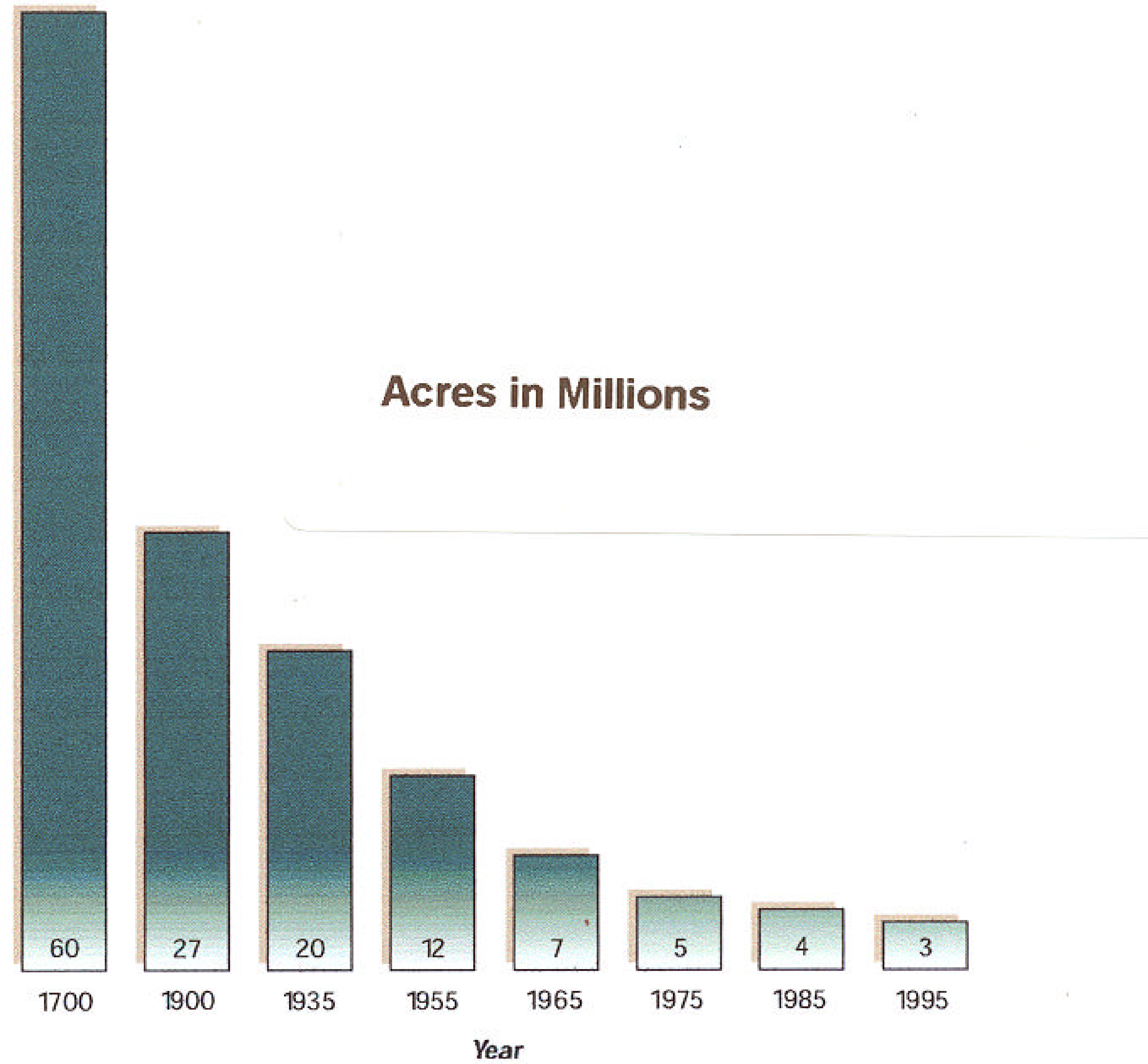

Figure 3 • *Change in forest area dominated by longleaf pine since European settlement. Based on data from Wahlenberg (1946), Kelly and Bechtold (1990), Frost (1993), Stout and Marion (1993), and Outcalt and Sheffield (1996).*

sampled a number of relatively undisturbed dry sandhills sites where wiregrass was a co-dominant with piney woods dropseed (*Sporobolus junceus* (Beauv.) Kunth [Poaceae]). I also have sampled flatwoods sites where Curtis' dropseed (*Sporobolus curtissii* (Vasey ex Beal) Small ex Scribn. [Poaceae]), a bunch grass with a growth form similar to wiregrass, dominated the understory.

The leaves of these grasses typically arch outward from the center of the bunch and overlap with adjoining individuals. Wiregrass leaves are short-lived; 85% die within 12 mo of formation (Parrott 1967). Dead wiregrass leaves remain attached to the plant (Landers 1991) and decay quite slowly (Christensen 1993). Living and dead wiregrass leaves intercept the shed needles of overstory pines, causing an accumulation of dead biomass in a very flammable configuration. These fuels reach a peak of 6160 to 7840 kg/ha (5495 to 6993 lb/ac) in 3 to 4 y (Parrott 1967). Lightning-caused fires can spread quickly through this fine-fuel matrix (Abrahamson and Hartnett 1990). Wiregrass therefore tended to shorten the fire-return interval, which favored longleaf pine domination.

Grass- and pine needle-fueled fires also control brown spot needle blight (*Mycospaerella dearnessii* Barr [Loculoascomycetes]), which can severely limit growth and survival of longleaf seedlings (Boyer 1975). In addition, most biomass is below ground, 60% to 80% for wiregrass (Parrott 1967), where high root turnover adds significant amounts of organic matter to the soil. Thus, a wiregrass understory maintains a better soil environment by improving soil structure and water- and nutrient-holding capacity (Snedaker and Lugo 1972).

Although longleaf dominated the overstory and grasses the understory, these communities contained many other plant species. Common woody associates in the flatwoods were saw palmetto (*Serenoa repens* (Bartr.) Small [Arecaceae]), gallberry (*Ilex glabra* (L.) Gray [Aquifoliaceae]), wax myrtle (*Morella cerifera* (L.) Small [Myricaceae]), and runner oaks (*Quercus* minima (Sarg.) Small & Q. *pumila* Walt. [Fagaceae]) (Peer and Allard 1993). Composites were often the dominant forbs. Other common herbaceous species included meadow beauty (*Rhexia* L. spp. [Melastomataceae]), beakrush (*Rhynchospora* Vahl spp. [Cyperaceae]), and yellow-eyed grass (*Xyris* L. spp. [Xyridaceae]). Wet savannas contained a mix of herbaceous species, including insectivorous pitcherplants (*Sarracenia* L. spp. [Sarraceniaceae]) and sundews (*Drosera* L. spp. [Droseraceae]), numerous orchids, and showy, flowered composites like sunflowers (*Helianthus* L. spp. [Asteraceae]). Upland longleaf stands had a very lush undersrory that contained many herbaceous species, including a number of composites and legumes (Peet and Allard 1993). Common woody species were blackjack oak (*Quercus marilandica* Muenchh. [Fagaceae]), sand-pax oak (*Quercus margarettae* Ashe [Fagaceae]), and persimmon (*Diospyros virginiana* L. [Ebenaceae]). On sandhills sires, turkey oak (*Quercus laevis* Walt. [Fagaceae]) is such a common woody associate of longleaf pine that many have referred to it as the longleaf-turkey oak association (Scour and Marion 1993). Other common woody associates include bluejack oak (*Quercus incana* Bartr. [Fagaceae]), persimmon, dwarf huckleberry (*Gaylussacia dumosa* (Andr.) Torr. & Gray [Ericaceae]), and blueberries (*Vaccinium* L. spp. [Ericaceae]). The undersrory on these dry sites often can appear to be a sea of grass, especially where wiregrass is dominant. However, many other species grow among the grass clumps in these communities. Common herbs include beggar lice (*Desmodium* Dew. spp. [Fabaceae]) and several members of the Asteraceae: deer tongue (*Carphephorus* Cass. spp.), dog fennel (*Eupatorium* L. spp.), grass-leaved gold aster (*Pityopsis graminifolia* (Michx.) Nutt.), gold aster (*Chrysopsis gossypina* (Michx.) Ell.), asters (*Aster* L. spp.), and blazing stars (*Liatris* Gaertn. ex Schreb. spp.). Woody associates in mountain longleaf communities included blackjack oak and shortleaf pine (Harper 1905). Herbaceous species were mostly the same as occurred on dry sandhills sires, including grass-leaved gold aster, sweet goldenrod (*Solidago odora* Ait. [Asteraceae]), bracken fern (*Pteridium aquilinum* (L.) Kuhn [Dennstaedtiaceae]), and sunflowers. In the mountain longleaf stands in northern Alabama, Mohr (1901) noted a number of legume species including beggar lice, bush clover (*Lespedeza* Michx. spp. [Fabaceae]), and goat rue (*Tephrosia virginiana* (L.) Pers. [Fabaceae]).

Although some herbaceous species were found on most sites of similar nature across the longleaf range, there was a lot of variation in the understory community. Thus, even though it is commonly referred to as the longleaf ecosystem, it is nor uniform. Peer and Allard (1993) divided the longleaf ecosystem into 4 major units (xeric, subxeric, mesic, and seasonally wet) based on soil moisture. They further divided these classes into 23 communities on the basis of geographic location and physiagraphic province. Each extremely diverse community has its own characteristic plant species. The diversity of ground cover plants per unit area makes longleaf pine ecosystems among the most species-rich plant communities outside the Tropics. Peer and Allard (1993) reported finding as many as 140 species of vascular plants in a 1000 m^2 (10,772 ft^2) area and in many longleaf communities, equally impressive counts of more than 40 species in a m^2 (10.8 ft^2). Many of these species are restricted to or arc found principally in longleaf habitats. Hardin and White (1989) listed at least 191 taxa of vascular plants that are endemic to or exist largely in longleaf communities. Walker (1993) reported 96 plant species as local endemics associated with longleaf pine ecosystems.

Not surprisingly, there are a number of animal species that depend on the longleaf ecosystem far much of their habitat, including the red-cockaded woodpecker (*Picoides borealis* Vieillot) and the gopher tortoise (*Gopherus polyphemus* Daudin). The tortoise is especially critical because its burrows provide homes for many secondary users from snakes to insects (Speake 1981; Jackson and Milstrey 1989). The longleaf-grass systems also are vital to the maintenance of a number of embedded ecosystems that occur across the South (Landers and others 1990). Many of these communities require periodic fire to maintain structure and health (Kirkman and others 1998). Fire begins in the longleaf-grass type and then spreads into adjoining habitats such as seepage slopes, canebrakes, treeless savannas, and sand pine scrub. Without periodic fire, these communities, like the longleaf systems, change in ways that make them less suitable to the plants and animals that have evolved with fire.

Longleaf Importance

Because of continued losses, habitat reduction became a cause for concern among natural resource and conservation organizations in the South. Longleaf pine communities are extraordinarily diverse and because they once covered such a large area, many plants and animals adapted to rhe habitat they provided. There is also growing evidence that ranges of certain amphibians and reptiles coincide with the longleaf ecosystem (Guyer and Bailey 1993). About 10% of all arthropods found in longleaf ecosystems are endemics (Folkerts and others 1993). It has become apparent that if the decline continues there will be many more endangered and threatened species needing special management. A growing realization of the importance of the longleaf forest type has fostered committed efforts to restore and manage these ecosystems (see Kush 1998, 1999).

Habitat protection is only 1 reason for the growing interest in longleaf pine. Early on, some industrial owners recognized the potential of longleaf pine (Croker 1987). Its many advantages have been well documented by Landers and others (1995), including the ability to produce as much or more fiber than other southern pines on dry, sandy sites (Outcalt 1993). Longleaf pine is less susceptible than other southern pines to damage and mortality from insects, like bark beetles, and diseases such as fusiform rust (*Cronartium quercuum* (Berk.) Miyabe: Shirai f. sp. *Fusiforme* Burds. et Snow [Melampsoraceae]). It also is very versatile, producing high-value products like poles and peeler logs. Poles are the highest value wood product taken from southern timberlands, and longleaf stands can yield from 30% to 80% poles (Boyer and White 1990). Longleaf forests also produce pine straw, which has borh wholesale and retail landscaping markers (Williston and others 1990).

Even some private landowners who hold only small parcels of land are considering longleaf pine when choosing a species for their sites. Improved techniques for growing, handling, and planting longleaf seedlings are nor just raising survival rates to levels comparable to other pines; they also are decreasing rime seedlings are in the grass stage, thereby increasing growth rates (Barnett and others 1990). Longleaf also can be managed using the shelterwood (Boyer and White 1990) or the all-aged selection systems Of harvest and regeneration (Farrar and Boyer 1991) as well as the even-aged clear-cut system.

Assistance programs, which pay a portion of the cost of planting trees, are available that encourage landowners to reforest sites. In North Carolina, the cost share rate, that is the payment the landowner gets per acre, is higher for longleaf pine to offset the higher cost of seedlings. Recent changes in the US Department of Agriculture (USDA) Conservation Reserve Program also encourage landowners to plant longleaf on areas enrolled in the program by designating longleaf plantings as priority areas. Areas that would be planted to longleaf are given preference for enrollment. Thr Natural Resource and Conservation Service, a branch of USDA that handles enrollment, recently announced that over 41,310 ha (102,000 ac) of cropland in the South will be planted with longleaf pine.

Planting longleaf pine will nor ensure re-establishment of the longleaf ecosystem, because the diversity exists in the understory community. However, even old field plantings furnish some of the functions of a complete system. Also, such sires serve as areas demonstrating the benefits of longleaf pine. This should encourage others to plant or naturally regenerare longleaf following harvest, thereby conserving intact longleaf habitat where it does exist. This would reverse a long-term trend of converting to other species following harvest. The flow of information from organizations like the Longleaf Alliance (for example, Franklin 1997) is also increasing awareness and helping bolster the visibility of longleaf pine, which may encourage landowners to choose longleaf pine for their sites.

Because the habitat is good for white-railed deer (*Odocoileus virginianus* Zimmermann) and bobwhite quail (*Colinus virginianus* L.), longleaf pine forests can also produce income from hunting leases. Larger, private landowners have long recognized and valued such opportunities. Many hectares of the longleaf type exist because of the hunting provided in addition to timber production. This is only one aspect of the longleaf tradition in southern culture. Many longtime southerners remember longleaf pine from an earlier era. Even though much of the region was converted to other pines,

Figure 4 • Longleaf pine with a flowering wiregrass understory on a sandhills site in the Ocala National Forest in Florida.

home sites and cities still contain longleaf pine trees from the original or second growth forest. Old longleaf can be seen in neighborhoods from Wilmington, North Carolina, to Valdosta, Georgia, to Gulfparr, Mississippi, and in most other southern cities and towns as well as around older rural home sites.

Summary

Healthy longleaf pine ecosystems are aesthetically pleasing. The tall pines with clear boles for half or more of the total tree height are topped with a spreading crown of long needles, making the trees stately and picturesque. The profusion of flowers after growing season burns, followed by a waving sea-like cover of grasses, is also visually appealing. Managing and restoring longleaf pine systems is now recognized as appropriate for conserving species, generating economic returns, and creating pleasing visual landscapes. This realization, coupled with cultural ties and improved knowledge gained from research and adaptive management, along with better dissemination of information are leading to a concerted effort to maintain and restore longleaf pine communities. It is hoped this will reverse the long-term loss of the longleaf pine type. Thus, although longleaf pine will not be re-established on most of the areas it once occupied, it should remain as a viable habitat in the southern US.

Author Information

Kenneth W Outcalt
Research Ecologist
USDA Forest Service
Southern Research Station
320 Green Street
Athens, GA 30602
Outcalt_Kenneth/srs_athens@fs.fed.us

References

Abrahamson WG, Hartnett DC. 1990. Pine flatwoods and dry prairies. In: Myers RL, Ewel JJ, editors. Ecosystems of Florida. Orlando (FL): University of Central Florida Press. p 103–149.

Barnett JP, Lauer DK, Brissette JC. 1990. Regenerating longleaf pine with artificial methods. In: Farrar RM, editor. Proceedings of the symposium on the management of longleaf pine; 1989 Apr 4–6; Long Beach, MS. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. General Technical Report SO-75. p 72–93.

Boyer WD. 1975. Development of brown-spot infection in longleaf pine seedlings stands. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. Research Paper SO-108. 10 p.

Boyer WD. 1990. Longleaf pine. In: Burns RM, Honkala BH, technical coordinators. Silvics of North America. Volume 1, Conifers. Washington (DC): USDA Forest Service. Agriculture Handbook 654. p 405–412.

Boyer WD, White JB. 1990. Natural regeneration of longleaf pine. In: Farrar RM, editor. Proceedings of the symposium on the management of longleaf; 1989 Apr 4–6; Long Beach, MS. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. General Technical Report SO-75. p 94–113.

Brockway DG, Outcalt KW. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. Forest Ecology and Management 106:125–139.

Christensen NL. 1981. Fire regimes in southeastern ecosystems. In: Mooney HA, Bonnicksen TM, Christensen NL, Lotan JE, Reiners WA, technical coordinators. Proceedings, fire regimes and ecosystem properties; 1978 Dec 11–15; Honolulu, HI. Washington (DC): USDA Forest Service, Washington Office. General Technical Report WO-26. p 112–135.

Christensen NL. 1993. The effects of fire on nutrient cycles in longleaf pine ecosys- of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management. Tallahassee (FL): Tall Timbers Research Station 18:205–214.

Croker TC, Jr. 1987. Longleaf pine: a history of man and a forest. USDA Forest Service, Southern Region. Forestry Report R8-FR7. 37 p.

Farrar RM, Jr., Boyer WD. 1991. Managing longleaf pine under the selection system – promises and problems. In: Coleman SS, Neary DG, editors. Proceedings of sixth biennial southern silvicultural research conference; 1990 Oct 30–Nov 1. Memphis, TN. New Orleans (LA): USDA Forest Service, Southeastern Forest Experiment Station. General Technical Report SE-70. p 357–368.

Folkerts GW, Deyrup MA, Sisson DC. 1993. Arthropods associated with xeric longleaf pine habitats in the southeastern United States: a brief overview. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:159–192.

Franklin RM. 1997. Stewardship of longleaf pine forests: a guide for landowners. Andalusia (AL): Auburn University, Solon Dixon Forestry Education Center. Longleaf Alliance Report Number 2. 44 p.

Frost CC. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:17–44.

Greenberg CH, Simons RW. 1999. Age, composition, and stand structure of old-growth oak sites in the Florida high pine landscape: implications for ecosystem management and restoration. Natural Areas Journal 19:30–40.

Guyer C, Bailey MA. 1993. Amphibians and reptiles on longleaf pine communities. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:139–158.

Hardin ED, White DL. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Natural Areas Journal 9:234–245.

Harper RM. 1905. Some noteworthy stations for *Pinus palustris*. Torreya 5(4):55–60.

[ITIS] Integrated Taxonomic Information System. 1998. Biological names. Version 4.0 (on-line database). URL: http://www.itis.usda.gov/plantproj/itis/itis_query.html (updated 15 December 1998).

Jackson DR, Milstrey ER. 1989. The fauna of gopher tortoise burrows. In: Diemer JE, editor. Proceedings of the gopher tortoise relocation symposium. Tallahassee (FL): Florida Game and Fresh Water Fish Commission. p 86–98.

Kelly JF, Bechtold WA. 1990. The longleaf pine resource. In: Farrar RM, editor. Proceedings of the symposium on the management of longleaf pine; 1989 Apr 4–6; Long Beach, MS. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. General Technical Report SO-75. p 11–22.

Kirkman LK, Drew MB, West LT, Blood ER. 1998. Ecotone characterization between upland longleaf pine/wiregrass stands and seasonally-ponded isolated wetlands. Wetlands 18:346–364.

Komarek EV Sr. 1964. The natural history of lightning. Proceedings, third annual tall timbers fire ecology conference. 1964 Apr 9–10; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station. Tall Timbers Fire Ecology Conference 3:139–183.

Komarek EV Sr. 1977. Tall Timbers Research Station, a quest for ecological understand ing. Tallahassee (FL): Tall Timbers Research Station. Miscellaneous Publication 5. 140 p.

Kush JS, compiler. 1998. Proceedings of the longleaf pine ecosystem restoration symposium, presented at Society for Ecological Restoration ninth annual international conference; 1997 Nov 12–15; Ft Lauderdale, FL. Andalusia (AL): Auburn University, Solon Dixon Forestry Education Center. Longleaf Alliance Report Number 3. 87 p.

Kush JS, compiler. 1999. Longleaf pine: a forward look, proceedings of the second Longleaf Alliance conference; 1998 Nov 17–19; Charleston, SC. Andalusia (AL): Auburn University, Solon Dixon Forestry Education Center. Longleaf Alliance Report Number 4. 196 p.

Landers JL. 1991. Disturbance influences on pine traits in the southeastern United States. In: Hermann SH, editor. Proceedings of the 17th Tall Timbers fire ecology conference. High intensity fire in wildlands, management challenges and options; 1989 May 18–21; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 17:61–98.

Landers JL, Van Lear DH, Boyer WD. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry 93(11):39–44.

Landers JL, Byrd NA, Komarek R. 1990. A holistic approach to managing longleaf pine communities. In: Farrar RM, editor. Proceedings of the symposium on the management of longleaf pine; 1989 Apr 4–6; Long Beach, MS. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. General Technical Report SO-75. p 135–169.

ittle EL Jr. 1971. Atlas of United States Trees. Volume 1, Conifers and important hardwoods. Washington (DC): USDA Forest Service. Miscellaneous Publication Number 1146. p 65E.

Aattoon WR. 1922. Longleaf pine. Washington (DC): USDA. Bulletin Number 1061. 50 p.

Aohr CT. 1888. The long-leaved pine. Garden and Forest 1:261–262.

Aohr CT. 1896. The timber pines of the southern United States. Washington (DC): USDA Division of Forestry. Bulletin Number 13. 176 p.

Aohr CT. 1901. Plantlife of Alabama. Germany: Veriag Von J. Cramer.

Dutcalt KW. 1993. Southern pines performance on sandhills sites in Georgia and South Carolina. Southern Journal of Applied Forestry 17:100–102.

Dutcalt KW, Sheffield RM. 1996. The longleaf pine forest: trends and current conditions. Asheville (NC): USDA Forest Service, Southern Research Station. Resource Bulletin SRS-9. 23 p.

'arrott RT. 1967. A study of wiregrass (*Aristida stricta* Michx.) with particular reference to fire [MSc thesis]. Durham (NC): Duke University. 137 p.

'eet RK, Allard DJ. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf coast regions: a preliminary classification. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:45–82.

:ebertus AJ, Williamson GB, Platt WJ. 1993. The impact of temporal variation fire regime on savanna oaks and pines. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:215–226.

:obins LE, Myers RL. 1992. Seasonal effects of prescribed burning in Florida: a review. Tallahassee (FL): Tall Timbers Research Station. Miscellaneous Publication Number 8. 96 p.

ichwarz GF. 1907. The longleaf pine in virgin forest: a silvical study. New York (NY): John Wiley & Sons. 135 p.

inedaker SC, Lugo AE, editors. 1972. Ecology of the Ocala National Forest. Atlanta (GA): USDA Forest Service, Southern Region. 211 p.

Speake SW. 1981. The gopher tortoise burrow community. In: Proceedings of Gopher Tortoise Council. p 44–47.

Stout I J, Marion WR. 1993. Pine flatwoods and xeric pine forest of the Southern (lower) Coastal Plain. In: Martin WH, Boyce SG, Echternacht AC, editors. Biodiversity of the southeastern United States, lowland terrestrial communities. New York (NY): John Wiley & Sons. p 373–446.

Tainter FH, Baker FA. 1996. Principles of forest pathology. New York (NY): John Wiley and Sons Inc. 805 p.

Van Doren M. 1928. Travels of William Bartram. New York (NY): Dover Publications. p 186–187.

Wahlenberg WG. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Washington (DC): CL Pack Forestry Foundation and USDA Forest Service. 429 p.

Walker JL. 1993. Rare vascular plant taxa associated with the longleaf pine ecosystem. In: Hermann SH, editor. Proceedings of the 18th Tall Timbers fire ecology conference. The longleaf pine ecosystem: ecology, restoration and management.; 1991 May 30–Jun 2; Tallahassee, FL. Tallahassee (FL): Tall Timbers Research Station 18:105–126.

Ware S, Frost CC, Doerr PD. 1993. Southern mixed hardwood forest: the former longleaf pine forest. In: Martin WH, Boyce SG, Echternacht AC, editors. Biodiversity of the southeastern United States, lowland terrestrial communities. New York (NY): John Wiley & Sons. p 447–493.

Williston HL, Guthrie JG, Hood CA. 1990. Managing and harvesting longleaf pine for specialty products. In: Farrar RM, editor. Proceedings of the symposium on the management of longleaf pine; 1989 Apr 4–6; Long Beach, MS. New Orleans (LA): USDA Forest Service, Southern Forest Experiment Station. General Technical Report SO-75. p 209–214.