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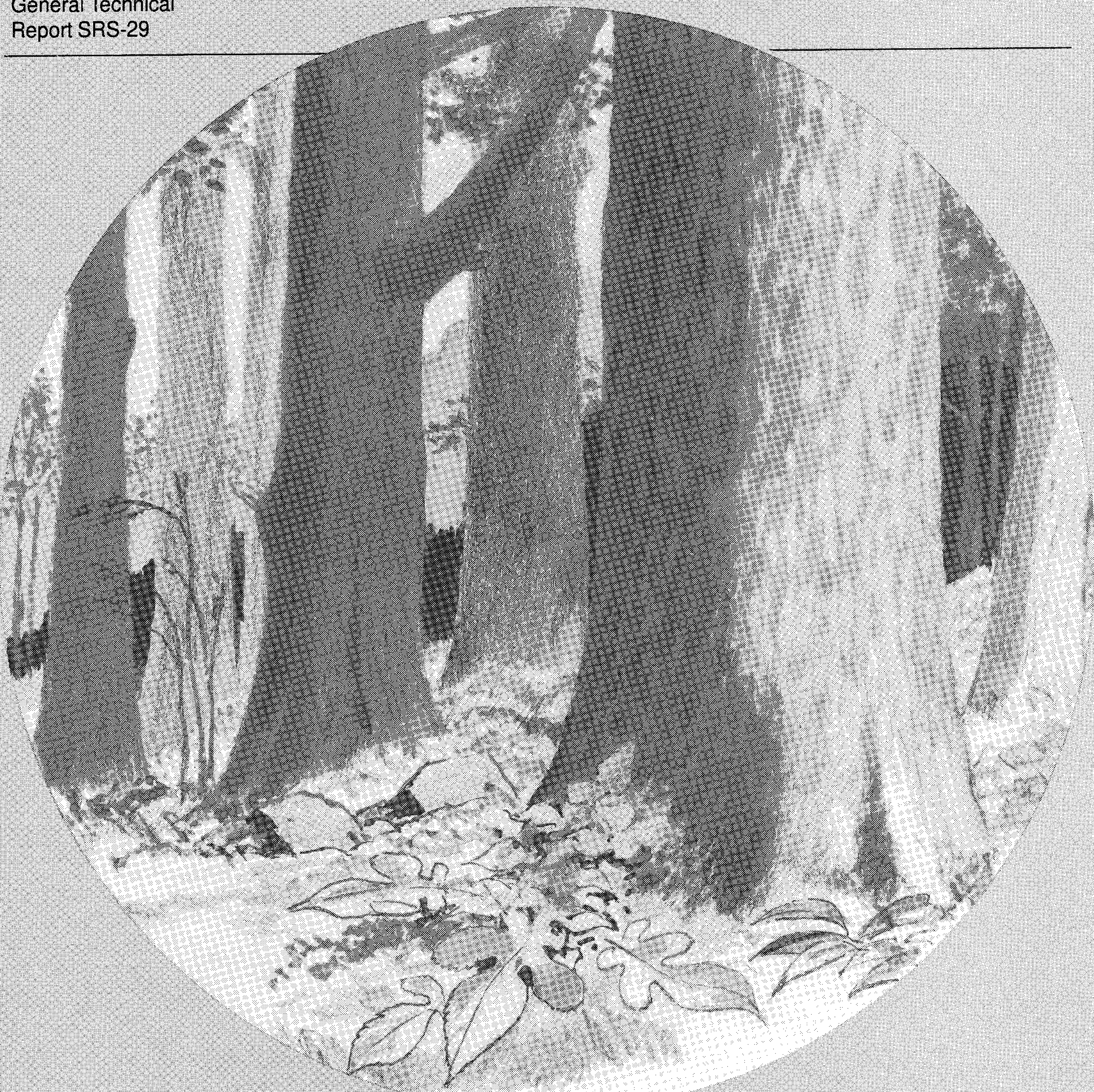
An Old-Growth Definition for Upland Longleaf and South Florida Slash Pine Forests, Woodlands, and Savannas

J. Larry Landers and William D. Boyer



A Section of the Old-Growth Definition Series

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Preface

Old growth is widely acknowledged today as an essential part of managed forests, particularly on public landa. However, this concept is relatively new, evolving since the 1970's when a grassroots movement in the Pacific Northwest began in eamest to define old growth. In response to changes in public attitude, the U.S. Department of Agricultnre, Forest Service began reevaluating its policy regarding old-growth forests in the 1980's. Iudeed, the ecological significance of old growth and its contribution to biodiversity were apparent. It was also evident that definitions were needed to adequately assess and manage the old-growth resource. However, definitions of old growth varied widely among scientists. To address this discrepancy and other old-growth issues, the National Old-Growth Task Group was formed in 1988. At the recommendation of this committee, old growth was officially recognized as a distinct resource by the Forest Service, greatly enhancing its status in forest management planning. The committee devised "The Generic Definition and Description of Old-Growth Forests" to serve as a basis for further work and to ensure uniformity among Forest Service Stations and Regions. Emphasis was placed on the quantification of old-growth attributes.

At the urging of the Chief of the Forest Service, al1 Forest Service Stations and Regions began developing old-growth defmitions for specific forest types. Because the Southem and Eastem Regions share many forest communities (together they encompass the entire Eastem United States), their efforts were combined, and a cooperative agreement was established with The Nature Conservancy for technical support. The resulting project represents the first large-scale effort to define old growth for al1 forests in the Eastem United States. This project helped briug the old-growth issue to public attention in the East.

Deíinitions will first be developed for broad forest types and based mainly on published information and so must be viewed accordingly. Refinements will be made by the Forest Service as new information becomes available. This document represents 1 of 35 forest types for which old-growth definitions will be drafted.

In preparing individual old-growth definitions, authors followed National Old-Growth Task Group guidelines, which differ from the standard General Technical Report format in two ways—the abstract (missing in this report) and the literature citations (listed in Southem Joumal of Applied Forestry style). Allowing for these deviations will ensure consistency across organizational and geographic boundaries.

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Introduction

Longleaf pine (*Pinus palustris* Mill.) and South Florida slash pine (*P. elliottii var densa* Little & Dorman) ecosystems are distinguished by open, multiaged forests, woodlands, or savannas, sometimes referred to as the "pine barrens." Longleaf pine once occupied the largest area dominated by a single-tree species (Chapman 1932, Frost 1993) in North America. Although longleaf is a very intolerant pioneer species, it was ecologically persistent rather than successional or transitional (Platt et al. 1988), and maintained itself in place for thousands of years. The southeastem pine belt is noted for the high frequency of thunderstorms that generated the most chronic fire regime of any forest region in North America. The traits of these two pine species and associated native grasses played a key role in the facilitation of fire, an environmnental agent essential to the competitive success of these trees and the maintenance of their remarkably diverse, fue-dependent ecosystems. The old-growth setting for both longleaf and South Florida slash pine, which resembles longleaf within its limited range, is best characterized as a rich ensemble of grasses and other herbaceous vegetation topped only by pines of variable ages and densities.

This document describes probable old-growth conditions for upland longleaf and South Florida slash pine forests, woodlands, and savannas based on currently available information. Forests, woodlands, and savannas as defined here follow a standard terminology (Ford-Robertson and Winters 1983). A forest is an ecosystem characterized by a more or less dense and extensive tree cover; a woodland is a plant community in which trees are present but form an open canopy with intervening areas occupied by lower vegetation, commonly grasses; and a savanna (tree savanna) is generally a grassland with a scattering of trees and shrubs. The definitions are based on general appearance of the land rather than on numbers of trees or tree basal area per unit of area.

Description of Upland Longleaf and South Florida Slash Pine Forests, Woodlands, and Savannas

Range

The combined ranges of longleaf and South Florida slash pine (fig. 1) once extended across most of the southeastem Coastal Plain and southem reaches of the adjacent Piedmont, Blue Ridge, and Valley and Ridge physiographic provinces (Fenneman 1938). Longleaf pine-dominated communities ranged from southeastem Virginia through most of Florida and into eastem Texas (Critchfield and Little 1966, Frost 1993). South Florida slash pine occurs exclusively in central and southem Florida where it is considered the ecological equivalent of longleaf pine (Mohr 1897).

soils

Three soil orders are of major importance in this pine region (U.S. Department of Agriculture 1969). Ultisols are the principal order over much of the Deep South outside of peninsular Florida. Ultisols most commonly associated with longleaf are the Typic and Plinthic Paleudults. Deep, sandy Entisols, which are primarily Quartzipsamments, range from about 10 feet [3 meters (m)] above sea leve1 in Florida up to 600 feet (183 m) in Georgia and the Carolinas; they form the sandhills of the Carolinas, Georgia, and northwestem Florida and the sand ridges in the central highlands of Florida.

Surface soils are typically acidic and low in organic matter, nitrogen, calcium, and phosphorus (Wahlenberg 1946). On the Coastal Plain, these pines grow in sandy (and some loamy or clayey) surface soils on well-drained rolling or sloping sites, across dry to xeric hills or ridges, and on rises within moist flatwoods. In many areas they gradually incline to boggy flatwoods or wetland depressions. Lower soil horizons vary from almost pure sand to clays. Within mountain provinces, longleaf occupies thin, stony soils on dry ridges and slopes with south-to-southwest exposures. The South Florida slash pine is commonly found on thin soils over lime rocklands.

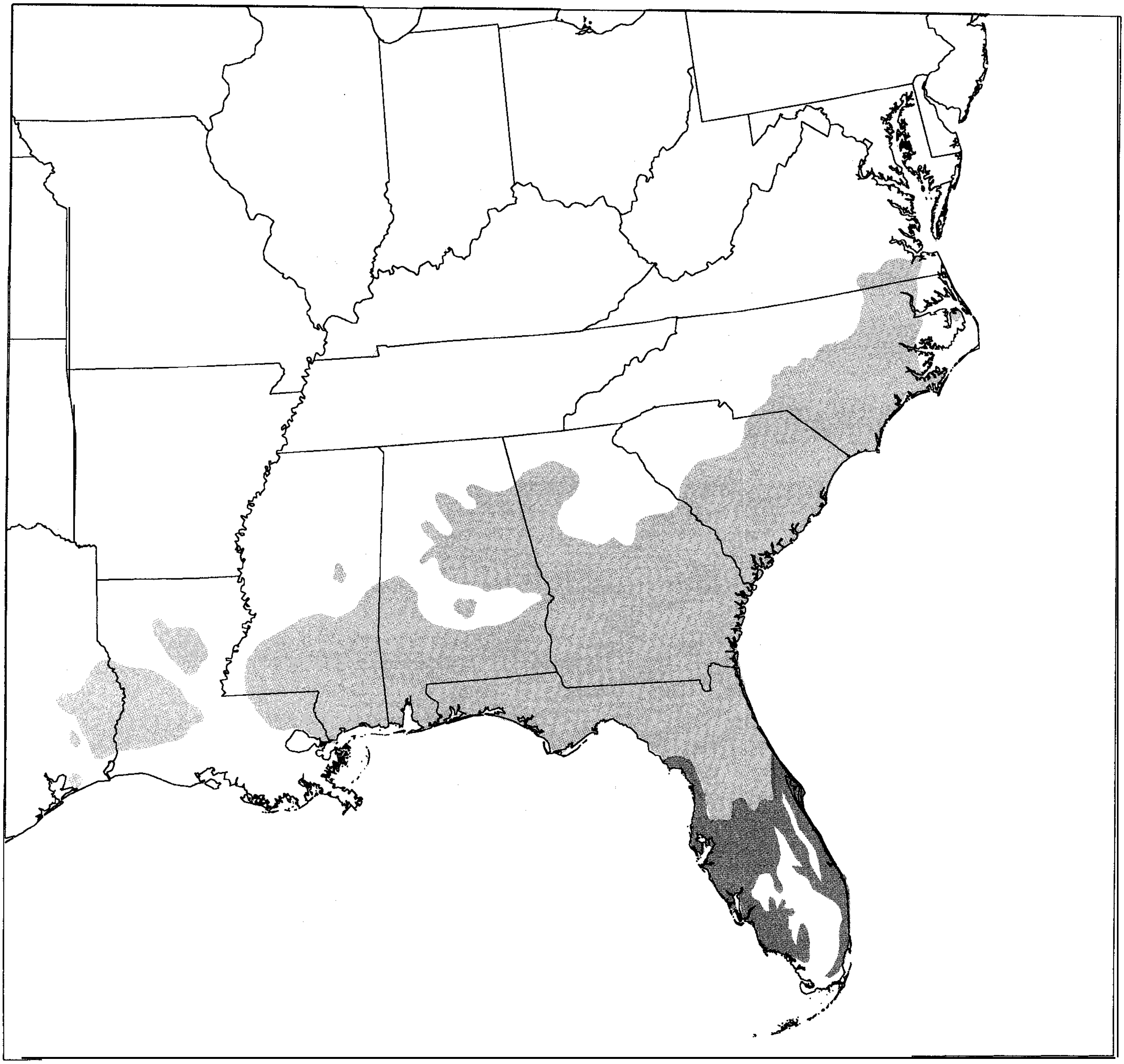

Figure 1—**Geographic ranges** of longleaf pine (light **gray) and** South Florida slash pine **(dark** gmy) **(Critchfield** and Little 1966).

Trees

Dominant longleaf or South Florida slash pines typically occur in ahnost pure stands, often with patchy to open canopies. Clusters of deciduous scrub oaks-turkey oak (*Quercus laevis* Walt.) and/or bluejack oak (*Q. incana* Bart.) on xeric or subxeric sands, post oak (*Q. margaretta* Ashe) on loamy sands, and blackjack oak (*Q. marilandica* Muench.) on clayey soils-sometimes occur. Some evergreen oaks, e.g., sand live oak (*Q. geminata* Small), may be significant natural associates of longleaf pine in coastal scrub woods. They are more tolerant of fire than other hardwoods. Some can grow into the midstory despite biennial, dormant-season fires (Boyer 1993).

Evergreen oak scrub or sand pine [*P. clausa* (Chapm. ex Engehn.) Vasey ex Sarg.]-evergreen oak scrub communities in some partially fue-protected areas may invade open pine communities where the fire regimes have been disrupted. Similarly, an abundance of mesic hardwoods growing with longleaf suggests an extended period of fire exclusion, overcuttmg, or soil disruption (Wahlenberg 1946). A mixture of both longleaf and slash pine, a recognized forest type, may also be a transition commuuity reflecting a long-term change in fire intervals. Some early observations have suggested that mixtures of longleaf, loblolly (*P. taeda* L.), and shortleaf (*P. echinata* Mill.) occurred with various mesic hardwoods on some hilly sites (Frost 1993); but few natural mixtures have been documented. Some associations were probably similar to those of southwestem Georgia where longleaf pine, oak, and hickory (*Carya* spp.) occurred at a ratio of 9 1: 1 :0.5 at the time of European settlement (1733-1832) (Plummer 1975). Other communities with a large hardwood component in the overstory and midstory are probably in transition from pine to late-successional, mixed-hardwood forest. Longleaf pine cannot succeed itself under these conditions, and the transition will be complete when the last of the residual pines die.

South Florida slash pine, also a fire-tolerant species, is often the sole canopy tree in woodlands and savannas, except in southcentral Florida where it overlaps with longleaf. On some high-quality sites, low densities of cabbage pahn [*Sabal palmetto* (Walt.) Lodd. ex Schult. & Schult.], which also tolerates frequent surface fires (Wade et al. 1980), and occasionally oaks, e.g., *Q. nigru* L., *Q. virginiana* Mill., may be considered natural associates. In rockland habitats, numerous broad-leaved subtropical trees, including exotics, have invaded South Florida slash pine sites. These trees have made native overstory associations difficult to determine.

Understory Vegetation

Both longleaf and South Florida slash pine ecosystems are named for the dominant and often exclusive canopy tree. Fires that maintained these forests over the millennia also supported fue-dependent plant communities on the forest floor. The broad geogmphic range of longleaf pine includes wide variations in the physical environment based on physiography, climate, soils, and topographic position. Many different understory plant community types developed in response to changing physical environments. The most distinctive changes within a locale are related to soil-moisture gradients. Twenty-three plant community types have been identified in longleaf forests, woodlands, and savannas east of the Mississippi River (Peet and Allard 1993). Further research will surely reveal many more. Similarly, a number of understory plant communities have been recognized in West Gulf longleaf ecosystems (Harcombe et al. 1993).

Although the ground cover beneath longleaf pine contains hundreds of herbs and low shrubs, dominant plants normally are the pyrogenic grasses, important to maintaining these fire-dependent communities-including the overstory pine. Wiregrass (*Aristida stricta* or *A. beyrichiana*) is of major importance, particularly east of South-central Alabama and the westem edge of the Florida Panhandle; bluestem grasses, e.g., *Schizachyrium tenerum, S. scoparius*, dominate most other areas (Wright and Bailey 1982). Abundant wiregrass is indicative of virgin sites because severe soil disturbance, such as plowing or intensive mechanical site preparation, will eliminate this species (Clewell 1989). Certain bluestems characterize most other locations. There is a similar relationship between South Florida slash pine and these same genera of grasses, along with scattered shrub patches (Snyder 1986). Today, mantles of saw pahnetto (*Serenoa repens*) are commonly found with South Florida slash pine (Gunderson and Loope 1982), but this shrub has so proliferated that its historic range is unknown.

Disturbance Regimes

The natural fire frequency needed to maintain longleaf pine ecosystems on upland sites is estimated to be 2 to 4 years (Landers et al. 1990). Fire intervals of 3 to 10 years have been estimated for longleaf in Coastal Plain sandhills where edaphic factors reduce the rate of fuel accumulation, topographic position, or both, limits fire entry (Wharton 1978, Clewell 1986) in the species' "transition" region and in other partially fire-protected areas (Ware et al. 1993). Before the natural systems were disrupted, fire-dependent

South Florida slash pine communities were similarly maintained by regularly recurring surface fires at 2- to 7-year intervals (Harper 1927, Wade et al. 1980, Gunderson and Loope 1982, Snyder 1986).

Far-ranging lightning fires were common until forest fragmentation became widespread and forest fue-suppression policies were established (Robbins and Myers 1992). Komarek (1964) found that about 93 percent of lightning ignitions in northern Florida occurred from late May to early August. Most lightning fires occurred in May and June, although thunderstorms were most frequent in July and August. For south Florida, Snyder (1986) detected similar seasonal wildfire pattems.

Catastrophic events other than lightning fires occur within normal tire regimes-blowdowns, intense fires following prolonged droughts, and subsequent beetle attacks-that can variously impact pine forests (Schwarz 1907, Platt and Rathbun 1993). Widespread droughts of 5 or more years occur about every 22 years and altemate with periods of abundant rainfall (Plummer et al. 1980). Most of this region will experience tropical storms every one or two decades (Neumann et al. 1987, Hooper et al. 1990); one or two hurricanes are likely to make landfall every year. Tomados and microbursts are also common throughout most of the South.

Crosswalk with Society of American Foresters Forest Cover Types (Eyre 1980)

70—longleaf pine

7 1-longleaf pine-scrub oak

83-longleaf pine-slash pine

ll l-South Florida slash pine

Physiographic Provinces (after Fenneman 1938)

- Coastal Plain (al1 sections)
- Piedmont (upland section)
- Blue Ridge (southem section)
- Valley and Ridge (southem section)

Old-Growth Conditions

Today only a few old-growth longleaf and South Florida slash pine communities remain, and these fragments may not be large enough or ecologically cohesive enough to be self-sustaining over the long term. Only sketches of old-growth conditions can be assembled from reported observations, old photographs, and the few studies of surviving relicts. Al1 of these information sources were used to characterize old-growth attributes over the ranges of forests, woodlands, and savannas that were once dominated by these two species. Old-growth characteristics are summarized in table 1 along with the source cited.

Living Tree Component

F. Harper (1942) and M. Van Doren (1940) described sparse longleaf woodlands or savannas on the wettest and driest sites, and woodlands or forests of large, dense pines on intermediate sites. F. Harper (1942) noted short, large diameter pines on xeric sands in Florida; and in a savarma he estimated 20 to 100 yards (18 to 9 1 m) between pines, or about 0.2 to 3.9 trees per acre [0.5 to 9.5 per hectare (ha)]. Along a fa11 line sand ridge in Georgia, Muir (19 16) also noted wide spacing of longleaf pines 20 to 30 inches [5 1 to 76 centimeters (cm)] in diameter but only 60 to 70 feet (18 to 2 1 m) tall. Spacing in some virgin longleaf woodlands of southem Georgia was 30 to 50 feet (9.1 to 15.2 m) (Harper 1922-23), i.e., about 6 to 15 large trees per acre (15 to 37 per ha). Some areas in eastem Texas contained 9 to 60 old-growth longleaf trees per acre (22 to 148 per ha). They were 100 to 350 years old (Chapman 1909).

Schwarz (1907) summarized measurements from six virgin longleaf stands, one each in Alabama and Mississippi and four in Louisiana. These were selected as "typical examples of the character of growth of the main body of virgin longleaf pine." Overall, the stands averaged 100 (range 52 to 167) trees per acre [averaged 248 (range 128 to 4 12) trees per ha] distributed overall in diameter at breast height (d.b.h.) classes from 2 to 34 inches (5 to 86 cm). Stand density (basal area) averaged a relatively dense 109 square feet per acre (25 m^2 per ha), with a range from 68 to 146 square feet per acre (16 to 34 m^2 per ha) and a mean canopy cover of 62 percent (range 50 to 80 percent). Virgin stands were not necessarily old growth. One of Schwarz's six stands had three-fourths of al1 stems in the 8- to 12-inch (20- to 30-cm) d.b.h. classes, and nothing above the 18-inch (46-cm) class. Another had 82 percent of al1 stems in the 10-inch (25-cm) and smaller d.b.h. classes, with the largest munber in the 6-inch (15-cm) class. However, this stand also had four trees per acre (10 per ha) ranging from 20 to 28 inches (5 1 to 7 1 cm) in d.b.h. The larger trees would seem to have been older relicts among which a younger stand had grown. Noting that pine-population structure does not maintain its uniformity over more than a few hundred acres, often changing abruptly within 50 acres (20 ha), Schwarz characterized virgin forest as ". . . frequent transitions in the

Table 1 (English units)—Standardized table of old-growth attributes for upland longleaf and South Florida slash pine forests, woodlands, and savannas

Quantifiable attribute	Value Range	Value Mean	Number of stands[a]	References
Pine stand density (no./acre)				
—trees ≥4 in. d.b.h.	0.2-100	40	40	Harper 1942 Chapman 1905 Chapman 1909 Doren et al. 1993 Gunderson and Loope 1982 Harper 1922-23 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
Pine stand basal area (ft^2/acre)				
—trees ≥4 in. d.b.h.	0.2-110	35	38	Harper 1942 Chapman 1905 Chapman 1909 Doren et al. 1993 Gunderson and Loope 1982 Harper 1922-23 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
Age of large trees (yrs)[b]				
—longleaf pine	100-350	—	—	Chapman 1905 Chapman 1909 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
-South Florida slash pine	100-300	—	—	Doren et al. 1993
Number of 4-m size classes				
—longleaf trees ≥2 in. d.b.h.	5-8	7	7	Chapman 1905 Schwarz 1907
D.b.h. largest trees (in.)				
—longleaf pine	19-32	23	33	Chapman 1909 Meldahl et al. 1995 Muir 1916 Platt et al. 1988 Schwarz 1907
-South Florida slash pine	8-12	10	1	Doren et al. 1993

Table 1 (English units)—Standardized table of old-growth attributes for upland longleaf and South Florida slash pine forests, woodlands, and savannas (continued)

Quantifiable attribute	Value		Number of stands[a]	References
	Range	Mean		
Standing snags (no./acre)				
—longleaf pine	0.1-7.0	2.7	8	Harper 1942 Engstrom, personal communication[c] Meldahl et al. 1995 Schwarz 1907
-South Florida slash pine	3.0-5.8	3.9	1	Doren et al. 1993
Downed logs-longleaf pine				
—trees 23 in. (ft^3/acre)	—	183	1	Landers, unpublished data[d]
—trees ≥10 in. d.b.h. (no./acre)	0.4-4.5	2.3	1	Hermann 1993
No. of canopy layers	l-2	—	—	—
Percent canopy in gaps	20-80	50	8	Harper 1942 Platt, personal communication[e] Schwarz 1907

[a] Number of stands may not equal the number of citations.

[b] Includes dominants and codominants in the upper canopy.

[c] Personal communication. [Date unknown]. R.T. Engstrom, Wildhfe Biologist, Tall Timbers Research Station, Route 1, Box 678, Tallahassee, FL 323 12.

[d] Landers, J.L. 1993. Data on longleafpine coarse wood debris in Hauss Park, Flomaton, AL: 183.2 ft^3/ac (12.8 m^3/ha) as determined by line-transect method. Unpublished data. On file with: Joseph W. Jones Ecological Research Center at Ichauway, Newton, GA 31770.

[e] Personal communication. 1993. W.J. Platt, Professor, Department of Plant Biology, Louisiana State University, Baton Rouge, LA 70803.

Table 1 (metric units)—Standardized table of old-growth attributes for upland longleaf and South Florida slash pine forests, woodlands, and savannas

Quantifiable attribute	Value Range	Value Mean	Number of stands[a]	References
Pine stand density (no./ha)				
—trees ≥10 cm d.b.h.	0.5-247	**99**	40	Harper 1942 Chapman 1905 Chapman 1909 Doren et al. 1993 Gunderson and Loope 1982 Harper 1922-23 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
Pine stand basal area (m^2/ha)				
—trees ≥10 cm d.b.h.	0.05-25.2	8.0	38	Harper 1942 Chapman 1905 Chapman 1909 Doren et al. 1993 Gunderson and Loope 1982 Harper 1922-23 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
Age of large trees (yrs)				
—longleaf pine	100–350	—	—	Chapman 1905 Chapman 1909 Meldahl et al. 1995 Platt et al. 1988 Schwarz 1907
-South Florida slash pine	100-300	—	—	Doren et al. 1993
Number of 1 O-cm size classes				
—longleaf trees ≥5 cm d.b.h.	5-8	7	7	Chapman 1905 Schwarz 1907
D.b.h. largest trees (cm)[b]				
—longleaf pine	48-82	**59**	33	Chapman 1909 Meldahl et al. 1995 Muir 1916 Platt et al. 1988 Schwarz 1907
-South Florida slash pine	20-3 1	25	1	Doren et al. 1993

Table 1 (metric units)—Standardized table of old-growth attributes for upland longleaf and South Florida slash pine forests, woodlands, and savannas (continued)

Quantifiable attribute	Value		Number of stands[a]	References
	Range	Mean		
Standing snags (no./ha)				
—longleaf pine	0.2-17.3	2.7	8	Harper 1942 Engstrom, personal communication[c] Meldahl et al. 1995 Schwarz 1907
-South Florida slash pine	7.4-14.3	3.9	1	Doren et al. 1993
Downed logs-longleaf pine				
—trees ≥8 cm (m^3/ha)	—	12.8	1	Landers, unpublished data[d]
—trees ≥25 cm d.b.h. (no./ha)	1-11	5.7	1	Hermann 1993
No. of canopy layers	1-2	—	—	—
Percent canopy in gaps	20-80	50	8	Harper 1942 Platt, personal communication' Schwarz 1907

[a] Number of stands may not equal the number of citations.

[b] Includes dominants and codominants in the upper canopy.

[c] Personal communication. [Date unknown]. R.T. Engstrom, Wildlife Biologist, Tall Timbas Research Station, Route 1, Box 678, Tallahassee, FL 32312.

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ages and in the density of growth, so that the effect is often that of a succession of large and small groves, either gradually merging into one another or changing abruptly from young and dense to mature and opener growth, orto a mixture of variable sizes and ages."

In an analysis of the Wade Tract, an old-growth longleaf pine preserve in southwestern Georgia, Platt et al. (1988) showed a rotated sigmoid diameter distribution representing many loosely aggregated age groups. Mature trees tended toward random dispersion; the authors estimated about ll longleaftrees per acre (27 per ha) 100 to 250 years old and 59 younger trees ≥ 1 inch (2.5 cm) in d.b.h. per acre (146 per ha). The tract included many small gaps, some with patches of pine regeneration of various ages and others remaining treeless for years. They concluded that natural longleaf stands are mrely stable, yet they persist as long as frequent fires can maintain openings until colonization.

An uncut, old-growth stand in south Alabama has been degraded due to absence of fire for over 45 years. As a result, no longleaf has been recruited, although other pines and hardwoods have invaded the stand (Meldahl et al. 1995). Longleaf pines were dominant with 128 stems per acre (3 16 per ha) and a basal area of 82 square feet per acre (19 m^2 per ha). Other trees constituted 1,0 18 stems per acre (2,5 15 stems per ha) and had a basal area of 44 square feet per acre (10 m^2 per ha). All trees > 15 inches (38 cm) in d.b.h. were longleaf pine. The older trees measured ranged from 140 to 210 years.

For an old-growth South Florida slash pine tract that had not been protected from wildfires (mostly from April to June), Doren et al. (1993) documented a similar population structure. Early narratives about old-growth South Florida slash pine suggest that there were open, uneven-aged savannas (Doren et al. 1993).

The approximate age at which old-growth features begin to appear is about one-half the maximum age of the predominant tree species (Maine Critical Areas Program 1983). Applying that guideline to average lifespan estimates for longleaf and South Florida slash pines (Landers 199 1) suggests that those conditions would appear at about ll 5 and 1 OO years, respectively. Longleaf can be considered fully mature and perhaps entering old-growth status when height growth ends, an age that will vary among individuals. However by 100 to 110 years, height growth has stopped in about one-half of observed longleaf pines.

Longleaf pine may live 500 years or longer, although lightning strikes, intense fire, and windthrow generally shorten its lifespan. Annual longleafattrition of about one canopy tree per 5 acres (2 ha) in mature, well-stocked stands (Boyer 1979) suggests that, in the absence of catastrophic events, the last tree in a cohort would die by age 500.

In medium- to well-stocked, even-aged longleaf pine stands, a steady state (growth and mortality in balance), which is another indicator of old-growth conditions, can be expected to begin at about age 120. Mortality will include normal attrition among canopy trees and self-thinning, which gradually eliminates suppressed trees. Depending on initial stocking density and the absence of any catastrophic event, the steady-state condition may last up to 200 years before mortality increasingly exceeds growth and the stand begins to break up. Formerly suppressed trees or established regeneration may fill gaps created by the death of old residuals.

At the estimated minimum old-growth age of ll 5 years, longleaf should begin to display some of the features typical of old-growth conditions--large boles, contorted and flat-topped crowns with a few massive primary branches, decay within some live trees, near cessation of height growth, resin core formation, and resinous large woody debris (Chapman 1905, Chapman 1909, Platt et al. 1988). Similar features have been observed in old-growth South Florida slash pines (Doren et al. 1993), and the age of some old-growth stands has been estimated at nearly 200 years (Mohr 1897) although some stands may reach up to 300 years (Doren et al. 1993).

A number of pines that are well over a century old would favor wildlife species whose diet includes pine seeds or who use large boles for nesting or foraging. A scientific summit on requirements of the endangered red-cockaded woodpecker set a target age of 100 to 250+ years for longleaf to provide suitable nesting habitat (Southeast Negotiation Network 1990). Considering the important old-growth structural features and the sensitive ecosystem elements associated with its structure, a minimum age of 115 years seems an appropriate target for the dominant pine component of an old-growth longleaf stand.

Sizes of pines in the older age classes are variable because diameter is strongly influenced by stand density and height by site quality. Age, as well as the present and former competitive position in the stand, also affects both diameter and height of individual trees. At age 115 years, Schwarz' (1907) longleaf diameter growth curves derived for each tree in a ½-acre (0.2-ha) old-growth stand show a range from about 8 to 25 inches (20 to 64 cm) (scaled from curves) and average about 16.8 inches (42.7 cm) in d.b.h. When these measurements were made, the largest tree was 2 10 years old, the smallest was 120 years old. The d.b.h. of the oldest cohort alone ranged from 24 to 32 inches (61 to 8 1 cm). At age 115, the d.b.h. of the oldest cohort ranged from 17 to 25 inches (43 to 64 cm). Continuing competition from older trees in the stand slowed long-term diameter growth of the younger trees. Pine timber 2.20 inches (5 1 cm) in d.b.h. appears to be necessary to sustain the red-cockaded woodpecker in the long term (Hamel et al. 1982). Most trees reaching old-growth status should be near this size or larger.

Dead Tree Component

Snag density, of course, varies with overstory cover, as well as with disturbarme. Mature, dominant trees are most often killed by lightning (Komarek 1968, Platt et al. 1988) and occasionally by intense fire in the growing season, e.g., late summer (Chapman 1957, Boyer 1990). In turn, canopy trees often die in clumps. Schwarz (1907) recorded a mean of six dead or dying trees per acre (range 0 to 12) [mean of 15 dead or dying trees per ha (range 0 to 30)], representing mortality over an undetermined number of years. The snags were mostly small poles but included an average of at least 0.5 large pines per acre (1.2 per ha). Despite a strong taproot and dense wood, hunicane-forte winds can destroy pine canopy trees in patches to huge tracts (Schwarz 1907, Wahlenberg 1946, Bengtson et al. 1993, Platt and Rathbun 1993).

The size of snags associated with old growth is difficult to surmise because of the great variance in tree size within old age classes and the variable effects of disturbance. However, lightning tends to select the largest trees. The minimum requirements of characteristic wildlife species are usable indicators of snag size. Of 11 snag-dependent birds in an old-growth longleaf census by R.T. Engstrom,[1] the smallest species require trees ≥ 6 inches (15 cm) in d.b.h., and one of the largest (pileated woodpecker) requires snags ≥ 20 inches (51cm) (Hamel et al. 1982).

Snags can stand for many years but are prone to lightning strikes and susceptible to fires. Accumulated bark and fallen branches at the snag base serve as important fuel sources (Platt et al. 1988). Most early writers described easy travel through pinewoods, but Cabeza de Vaca (1542) noted severe obstructions due to many downed, lightning-killed trees in some areas of Florida.

Light accumulation of woody debris is normal in old-growth stands in the South because resin-soaked logs bum readily and wood decays rapidly. The soil is likely to include fine charcoal and decaying organic matter from surface deposits and stump or root charmels. Research is needed to determine the influence of wood debris on soil characteristics, storage or flow of nutrients and energy, and facilitation of decomposers and heterotrophs.

Other

Interactions between fire and downed logs influence plant community dynamics. During a tire, areas immediately downwind of logs may become fire shadows where newly established pine seedhngs may survive (Schwarz 1907). Burning piles of surface debris often kills all vegetation, leading to colonization-by including new plants and pine regeneration. Pine often responds with accelerated growth (the ashbed effect), which also may trigger local changes in soil chemistry and biota. These processes, coupled with the effects of fossorial and herbivorous animals, help support an unusually diverse ground flora (Hermann 1993). In the northeast Florida-southwest Georgia arca, Small(1923) recorded about 250 plant species in the longleaf-scrub oak forests; the nearby Wade Tract supports more than 360 species (Tal1 Timbers Research Station herbarium list). Longleaf pine ecosystems contain the greatest diversity of plant life ever found in a temperate zone (Peet and Allard 1993), often with over 40 species per square meter and as many as 140 species per 1000 m^2. Of the 191 rare vascular plant taxa associated with wiregrass in the Southeastern United States, 122 are considered endangered or threatened (Hardin and White 1989).

Pits and mounds associated with windthrown trees usually do not persist because stumps are bumed and frequent rains have a leveling effect. Nonetheless, soil that erodes into old pita, burrows, and stump caverns may be important in maintaining heterogeneous substrates.

Important fungal diseases, such as brownspot needle blight and root rot, are mitigated by fire. Multiple interactions have been identified among pine trees, fungí, and key animal species. The relationship between red heart decay in living, old pines and the red-cockaded woodpecker, which excavates cavities in decaying boles (Walters 199 1), is well known. This bird's selection of red heart trees that have been suppressed and later released (Conner and O'Halloran 1987) suggests that dominance-class diversity may be another attribute of old growth. This certainly seemed to be the case in the stand examined by Schwarz (1907). Weigl et al. (1989) noted a three-way relationship among longleaf pine,

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its mycorrhizae, and the southem fox squirrel, which eats longleaf seeds and disperses mycorrhizae spores.

·Frequent tires inhibit soil microfauna and some insectivorous small mammals that burrow underground (Heyward and Tissot 1936). By contrast, fires favor larger herbivorous burrowers like gopher tortoises, pocket gophers, and severa1 small rodents.

Wildlife diversity depends on a variety of habitat features often formed by interacting disturbances. For example, at least 145 vertebrate species have been identified on the Wade Tract. Important habitat components include large, old pines and snags; younger age classes of pine; patchy forest and groundcover; diverse ground flora; oak patches; open air spaces; bare soil patches; fallen coarse woody debris; and root-soil mounds tipped up by tree falls (Landers et al. 1990) (see footnote 1). The red-cockaded woodpecker plays a key role in that its cavities are used by many other birds and mammals. R.T. Engstrom (see footnote 1) recorded the woodpecker among 22 bird species that frequent the longleaf forest and are more abundant or found exclusively in old growth. The long-term survival of the Coastal Plain fox squirrel may also depend on mature to old-growth longleaf (Kantola and Humphrey 1990). The gopher tortoise is a primary grazer on xeric sites, and its burrows are used by at least 60 vertebrate and 302 invertebrate species (Jackson 1989). The oak toad is also associated with the native, grassy groundcover; and the flatwoods salamander depends on large woody debris within grassy flatwoods (Mount 1975).

Forest Dynamics and Ecosystem Function

Functional and persistent old-growth longleaf pine ecosystems depend on repeated fires to prevent hardwood domination, including Sres during the growing season, which can slow or prevent recruitment of several fire-resistant hardwoods into the midstory. Fire effects vary with environmental gradients established by topography, soils, and moisture levels. Sites intermediate in elevation and moisture tend to burn more often and more completely, but less intensely, than either higher, xeric sites or lower, hydric sites. Characteristic of the longleaf pines are mosaics of longleaf pine-scrub oaks on sandhills grading to ahnost pure longleaf pine on more mesic sites. Similar fire-maintained associations that also span a range of sites from xeric to hydric constitute habitats of South Florida slash pine.

Among the unique features of longleaf and South Florida slash pine communities are the intricate relationships between biological diversity and disturbance. Southeastem pine uplands persisted for millennia under a regime of frequent, widespread fires in a region of abundant rainfall. In such a humid environment, community persistence was probably reinforced by selection for both fire tolerance and longevity in key species of pines, some oaks, and grasses (Christensen 1981, Clewell 1986, Platt et al. 1988, Landers 199 1, Rebertus et al. 1993). The tire-tolerant grasses and overstory with multiaged pine populations may be one of the defining characteristics of old growth. This system's persistence is consistent with the concept of a true "climax," but only if lightning (an ignition source) is considered as integral to climate, which determines the climax type (Chapman 1932).

Fire plays an essential ecological role by clearing seedbeds and recycling nutrients. Fire early in the growing season promotes height growth in "grass stage" seedlings of longleaf and South Florida slash pine, as well as wiregrass seed production. It also synchronizes the flowering of many herbaceous plants. Frequent fire tends to screen out broad-leaved woody vegetation and favor a rich assortment of plant life on the forest floor, including nitrogen-fixing legumes (mostly perennials), low shrubs, and free-living soil organisms.

Replacement of volatilized nutrients soon after a bum contributes to a dynamic soil-nutrient equilibrium, as do the nutrient- and water-absorbing functions of bunch grasses (Clewell1986). Frequently burned pinelands have a humus layer generated by grass roots that is less acidic with more macronutrients available than that of unburned sites (Wahlenberg 1946). Burning vegetation releases varying quantities of nutrients into the atmosphere. It generally increases the incorporation of phosphorus, potassium, magnesium, calcium, nitrogen, and organic matter into mineral soil, although short-term, fire-induced changes in the proportion of elements will vary (Heyward and Bamette 1934, Christensen 1977, Hough 198 1, McKee 1982, Richter et al. 1982, Gilliam 1988, Binkley et al. 1992). Long-term research in Coastal Plain forests suggests that frequent burning mobilizes calcium in the forest floor, retards soil weathering processes, and maintains nutrient balances that favor pine productivity (McKee 1982). Additional research should center upon variation in nutrient flux, transformation, and availability relative to geomorphic setting and fire regime.

Conservation and Management

Human alteration of pine forests, woodlands, and savannas probably date back nearly 12,000 years. Historical records suggest that Native Americans increased the fire frequency in many areas, but they bumed in various seasons, adding to rather than completely displacing natural fire regimes (Robbins and Myers 1992, Frost 1993). Vast pinelands with intact groundcover persisting through the era attest that Indian agriculture did not greatly disrupt upland pine sites, probably because of low site fertility.

By 1920, European settlement had brought agriculture, livestock grazing, logging, and a nearly total loss of old-growth forests (Frost 1993). A 95-percent reduction in fire activity over the last 50 years (Simard and Main 1987), due mainly to forest fire exclusion policies set in the 1920's, has also accelerated the loss of fire-dependent ecosystems.

Longleaf pine, which was the dominant or principal tree species on an estimated 92.5 million acres (37.5 million ha) (Frost 1993), had dwindled to an estimated 3.8 million acres (1.5 million ha) by 1985 (Kelly and Bechtold 1990). Since then, its decline continued to about 3.2 million acres (1.3 million ha) by 1990 and to < 3 million acres (1.2 million ha) by 1995 (Landers et al. 1995, Outcalt and Sheffield 1996) or about 3 percent of the its presettlement area. Trees < 60 years old are few, and most of the remaining second growth is 80 to 100 years old. However, < 2 percent of the Southeast land area now contains longleaf pine, compared to 59 percent when settlement began (Frost 1993). Much of the rest has been degraded by the absence of recurrent tire.

Conservation of naturally regenerated longleaf pine is a challenge because two-thirds of the remaining acreage is privately owned (Outcalt and Sheffield 1996), and much private land is managed primarily for wood products. The first step needed in a comprehensive conservation plan is to inventory residual old growth, second growth that could become old growth, and areas with native ground flora on which pine could be restored. It would also be helpful to identify sites with relatively undisturbed soils on which native plant associations could be restored. Restoring and maintaining fire-dependent ecosystems as a significant part of southeastem landscapes would require regionwide cooperation.

Successful restoration and maintenance of old growth will generally require restoration of entire biological systems, along with disturbance processes on which these systems depend. A minimum for established plant communities would be initial rough-reduction burns during the dormant season, followed by a variable growing-season burn regime (Robbins and Myers 1992). Procedures to reintroduce native plants on cleared land, beginning with those species essential to ecosystem processes, e.g., carbon storage, fire ignition, plant dispersal systems, food webs, nutrient and energy cycling, and soil development, are needed.

Whether the pine species should be regarded primarily as even-aged or uneven-aged is an important question. It may be that lar-ge, even-aged stands were most common near the coasts, particularly in major hurricane zones. Descriptions suggest that, in many areas, mosaics of small, even-aged or multiaged units persisted because of fire and localized disturbances. In some areas, mosaics may also have resulted from the gradual breakup, through attrition, of even-aged stands established after a catastrophic event. Given the loss of these ecosystems, old-growth diversity should be recovered and maintained by developing a range of stand structures and sizes. There is growing evidence that the dynamic population structure of old-growth longleaf and South Florida slash pine ecosystems is contingent upon variation in the frequency, behavior, and effects of fires that occur at different seasons (Platt et al. 1988, Doren et al. 1993). There is also a pressing need for guidelines suitable for multiple-value forests. Research should focus on the amount of volume growth (perhaps 60 to 70 percent) that could be harvested periodically without jeopardizing the habitat of the flora and fauna indigenous to old-growth ecosystems. Equally challenging is the maintenance of understory plant communities through cycles of harvest and regeneration.

Methods of forest management that would simulate old-growth conditions have natural analogs. Some of these include frequent prescribed burning (especially in April to June); harvesting in patches and keyed to major masting events; partial cutting, such as single tree or group selection, seed-tree reserve, or irregular shelterwood with varying stand sizes; creating and maintaining a balanced distribution of age and size, or both, and dominance classes by taking advantage of or simulating natural disturbances; preparing seedbeds by buming only; establishing seedlings through natural regeneration or irregular plantings, if necessary; minimizing disruption of soil and groundcover vegetation; and leaving live cavity trees, snags, and downed logs. Low-intensity operations, e.g., hand planting, chainsaw felling, and logging with draft animals or small equipment, may be necessary to maintain ecological integrity within the context of timber production.

Great challenges to sustain both ecological systems and economic forestry operations in this region lie ahead.

Because so many forests have disappeared, the fate of pine ecosystems now depends on the extent of restoration. Solutions lie in developing networks of old-growth preserves combined with managed forests dedicated to integrating timber use and biodiversity, refmed stewardship schemes for each objective, and economic incentives for landowners to practice environmentally sensitive management.

The minimum area of such preserves will depend on the elements to be perpetuated and the context in which the area will be used. For example, the 206-acre (83-ha) Wade Tract is a relatively fertile site within several thousand acres of second growth with much intact groundcover (Platt et al. 1988). Prescribed fires maintain the natural plant community there during the growing season. On the other hand, the Wade Tract contains only three clusters of cavity trees used by the red-cockaded woodpecker, a species that requires old pines for nesting and extensive pine stands for foraging. Considering estimates for a breeding core of 3 10 to 390 pairs to sustain a viable population and a minimum territory of 200 acres (8 1 ha) per pair, the minimum area of acceptable habitat required may be 80,000 acres (32,374 ha) or more (Southeast Negotiation Network 1990). However, periodic genetic information may reduce the minimum size of a breeding core and the acreage required for a stable population (Walters 199 1).

Because of the uncertainty of area parameters, it may be useful to consider a minimum building block for stewardship of old growth within a younger forest. For example, 125 acres (5 1 ha) of old growth should generally encompass a mosaic of pine age classes, the minimum territory for a single red-cockaded woodpecker clan, the range for a breeding group of fox squirrels (Weigl et al. 1989), and space for many other animals and plants common to old growth. However, the critical area necessary for populations of most species and the importance of community interactions are not yet known. Viability of the ecosystem will likely increase with the size and number of old-growth reserves covering the principal sites and community types, shorter distances between reserves, and greater similarities in composition and structure among the reserves and the areas separating them. Long-term research will be needed to determine minimum areas required for long-term maintenance of complete old-growth systems.

Representative Old-Growth Stands

For the remaining old-growth areas, landowners have controlled access. Few sites have been frequently burned, so most tracts do not entirely represent natural community structure and composition. Fire must be reintroduced to restore plant communities, including natural pine regeneration. Ecological research and restoration, or both, and stewardship are being planned or implemented for all tracts listed below.

Longleaf Pine

- Boyd Tract-Weymouth Woods Sandhills Nature Preserve, Moore County, North Carolina
- Big Woods—Greenwood Plantation, Thomas County, Georgia
- Hauss Park-Flomaton, Escambia County, Alabama (Champion International Corp.)
- Patterson Tract-Okaloosa County, Florida (Eglin Air Force Base)
- Wade Tract-Thomas County, Georgia (Tall Timbers, Inc.)

South Florida Slash Pine

- Lostman's Pines-Everglades National Park, Florida
- Raccoon Point-Big Cypress National Preserve, Florida

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Upland longleaf pine forests, woodlands, and savannas once occupied most of the Atlantic and Gulf Coastal Plains from southeastem Virginia south through the northem two-thirds of Florida and west to east Texas, with extensions into the Piedmont and mountains of Alabama and northwest Georgia. South Florida slash pine is native to the southem half of peninsular Florida. The probable stmcture of and variability in old-growth forests, woodlands, and savannas of these two overlapping and fire-dependent ecosystems are described based on al1 available information. A number of old-growth attributes are listed for both species, including estimates of the variability that can be expected in these attributes.

Keywords: Longleaf pine, old growth, savannas, South Florida slash pine, Southeastem United States, woodlands.