Longleaf Pine Vegetation of the Southern Atlantic and Eastern Gulf Coast Regions: A Preliminary Classification*

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ABSTRACT

Quantitative data on the composition of natural longleaf pine-dominated vegetation collected across the range of the species east of the Mississippi River are used to develop a preliminary, floristically-based, region-wide classification for use in conservation and preservation planning.

The strongest compositional gradients appear related to soil moisture. We recognize four major series of longleaf-dominated vegetation, primarily differentiated with respect to this gradient (xeric, subxeric, mesic, and seasonally wet). These series are divided into twenty-three communities, which correspond primarily to geographic position and physiographic province (the coastal plain and maritime fringe regions of the Atlantic and Gulf coasts respectively, the piedmont / uplands, and the fall-line sandhills).

The five communities that belong to the Xeric Longleaf Woodland series occur on coarse, well-drained sands. The six Subxeric Longleaf Woodland communities made up the majority of the longleaf-dominated landscape of presettlement times. The four Mesic Longleaf Woodland communities are remarkably rich in species, but are uncommon in the modern landscape because they are largely confined to soils well-suited for agriculture. The eight Seasonally-Wet Longleaf Woodland communities contain both shrubby flatwoods and grassy, floristically-rich savannas.

Despite a visual dominance by longleaf pine, wiregrass, and scrub oaks, the greater longleaf pine ecosystem of the southeastern United States contains some of the most diverse plant communities known from the temperate zone. Longleaf Savannas were regularly observed with over 40 species of plants per square meter, and Mesic Longleaf Woodlands were found with up to 140 species per 1000 m². Many of these species are largely confined to longleaf pine-dominated communities. These natural longleaf woodlands are being lost rapidly to a combination of land development and fire suppression.

^{*}Botanical nomenclature follows Kartesz (1994), except we follow Peet (1993) in recognizing that the plants traditionally treated as Aristida stricta should be divided into a northern (A. stricta) and a southern species (A. beyrichiana).

INTRODUCTION

Three centuries ago longleaf pine (*Pinus palustris*) dominated the coastal plain landscape of the southeastern United States. However, settlement of the region by Europeans dramatically altered the longleaf ecosystem (see Croker 1987, Frost 1993, Ware et al. 1993). As a consequence, much of the area once dominated by longleaf retains few, if any, longleaf trees.

Initially, longleaf pine was heavily exploited for tar, turpentine and rosin production. Most of the mature trees that survived were eventually cut for timber. Pine reproduction failed, primarily because of suppression of the fires that historically had controlled potential woody competitors, and because of the ubiquitous grazing of livestock, especially hogs which voraciously consumed young pines for their starchy taproots (Schwarz 1907, Hine 1925, Croker 1987, Lipscomb 1989, Frost 1993). Finally, because of the prevailing gentle topography, those areas with tillable soils were readily converted to agricultural production. In short, the combined impact of the naval stores industry, lumber extraction, grazing and agriculture has served to remove longleaf from much of its former range. This is particularly true in the northern portion of the longleaf range where the pines were exploited first. Today, longleaf is nearly absent from the Neuse River in central North Carolina northward, despite the fact that this species once dominated much of the coastal plain of northeastern North Carolina and southeastern Virginia (Fig. 1; Pinchot and Ashe 1897, Frost and Musselman 1987, Frost 1993).

Longleaf pine is not the only distinctive species of the once vast southeastern pinelands. The longleaf-dominated ecosystem also supports a great diversity of distinctive plant and animal species which today persist only in the small fragments of the original landscape that have managed to escape the bulk of the changes wrought by the growth of modern society. Not only has the exploitation of the longleaf resource per se been devastating to this diversity, but other, more subtle changes have had equally significant impacts. The most important of these has been the elimination of chronic fire. More recently, mechanical damage to the understory of longleaf stands by pinestraw raking and mechanized timber removal has begun to significantly reduce populations of many of the native species of the longleaf ecosystem.

Longleaf pine absolutely depends on frequent

fire for stand maintenance and reproduction. Before fire suppression, regular, low-intensity surface fires kept the pine woodlands open and relatively free of undergrowth. The presence of abundant grass, especially wiregrass (Aristida stricta in the north, A. beyrichiana in the south; see Fig. 1) and bluestem grasses (Andropogon spp., Schizachyrium spp.) provided a ready source of spatially continuous fuel which helped fire spread throughout the pine woodlands (Christensen 1988, Noss 1989, Stout and Marion 1993). Without fire, longleaf stands develop a thick undergrowth of broadleaved species under which pine regeneration is impossible. In addition, fuel levels can build to the point that fire is catastrophic when it eventually does occur. In the absence of fire, longleaf vegetation declines in species diversity owing to decreased light and increased litter depth. Preservation of longleaf-dominated woodlands is not sufficient for preservation of the longleaf ecosystem and its attendant biodiversity. Because the longleaf ecosystem is fire-maintained, only those few sites that have continued to experience chronic fire retain a strong resemblance to the natural longleaf systems of the Southeast.

Examples of natural longleaf vegetation containing both old-growth trees and an understory unaltered by fire suppression are almost nonexistent. Fortunately, fire has continued to be a tool for land management in many longleaf areas with the result that examples of second-growth stands with the understory vegetation still intact can be found, particularly on public lands such as national and state forests, gamelands, and military bases. While over 70% of the remaining longleaf vegetation is in private ownership, fire suppression is more pervasive in these generally smaller holdings. Over the total original natural range of longleaf, less than 3% of the natural upland vegetation remains in a seminatural, fire-maintained condition (Frost 1993). Further, this residual fraction is not really representative of the original vegetation in that the soils most conducive to agriculture were largely cleared of their natural vegetation well over a century ago (Pinchot and Ashe 1897, Mohr 1901, Harper 1906, Frost 1993) with the consequence that the remaining fragments persist primarily on atypically wet or dry sites.

Longleaf vegetation, while widespread, has been remarkably little studied (Noss 1988, Schafale and Weakley 1990, Stout and Marion 1993). Documentation of compositional variation can be found in the scientific literature for small portions of this system over limited ranges of soil conditions (e.g., Bozeman 1971, Kologiski 1977, Taggart 1990, 1994).

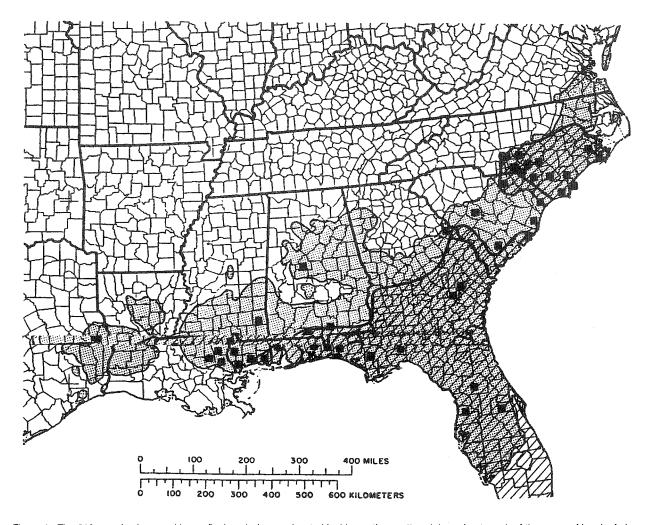


Figure 1. The 216 sample sites used in our final analysis were located in 44 counties scattered throughout much of the range of longleaf pine (*Pinus palustris*) east of the Mississippi River. The range of longleaf pine is indicated by stipples (after Little 1971 and Frost 1993) and the range of wiregrass (*Aristida stricta* and *A. beyrichiana*) by diagonal shading (after Peet 1993).

However, most of the longleaf region has not been subjected to rigorous ecological study. For some regions it is now too late; for example, we can hardly begin to describe the original longleaf vegetation of northeastern North Carolina and southeastern Virginia as virtually nothing is left to study (but see Frost and Musselman 1987, Frost 1993). Further, while descriptive treatments have been published for various portions of the longleaf region (e.g., Harper 1906, Pessin 1933), there have been no attempts to quantitatively document the floristic and structural variation in this ecosystem at a scale larger than a few counties.

If a significant fraction of the biotic diversity of the longleaf pine ecosystem is to be preserved, we need to act rapidly. A critical early step in this process is documentation of the variation in the longleaf pine ecosystem so that we will know what needs to be preserved. Toward this end, the Natural Heritage Programs in many of the southeastern states, in collaboration with The Nature Conservancy, have developed classifications of natural communities, including those dominated by longleaf pine. Our goal in this paper is to combine information from these qualitative state classifications with quantitative data collected by several independent researchers, to create a preliminary classification of the natural longleaf-dominated vegetation east of the Mississippi River. (Longleaf-dominated communities west of the Mississippi are described by Bridges and Orzell 1989 and Harcombe et al. 1993).

METHODS

Approach

Vegetation classification typically is a process of successive approximation. As our knowledge base increases, we can produce better descriptions and classifications, which in turn motivate new observations, which allow still better descriptions and classifications. Several cycles of this process generally are required before the major patterns of variation in a widely distributed vegetation type, such as the longleaf-dominated vegetation of the southeastern United States, can be understood. Our somewhat informal method of classification recognizes the importance of this successive approximation approach. We further recognize that our classification is only a preliminary effort, and will certainly require revision as additional information becomes available.

Our approach to classification of longleaf vegetation involved several steps. The first step was creation of an initial classification of longleaf pine communities based on existing vegetation classifications and other descriptive information. This classification was developed by DJA as part of the creation of a "Southeastern United States Ecological Community Classification" for use by The Nature Conservancy in protection of biodiversity at the community level (Allard 1990). The second step was to collect quantitative data on community composition from across the range of longleaf to help refine and validate the initial classification. Simultaneously, quantitative data were collected by the North Carolina Vegetation Survey (see Acknowledgments) from longleaf vegetation in the North Carolina fall-line sandhills as part of an independent project to validate and refine the North Carolina community classification of Schafale and Weakley (1990). These two datasets were supplemented with quantitative data from five other studies of longleaf-dominated vegetation to produce a dataset which included nearly 250 samples (Appendix I). In each case the botanical nomenclature was revised to conform to Kartesz (1994). In the third step, these data were subjected to various forms of multivariate analysis to refine the initial classification and to allow better characterization of the component communities.

The Southeastern Ecological Community Classification, from which our initial classification was developed, was constructed primarily from the Natural Heritage Program classifications of the twelve southeastern states. Community attributes used to create the classification included physiog-

nomy, plant species composition, geographic distribution, and important environmental factors such as moisture and soil texture. Quantitative data collection in longleaf communities was initiated prior to creation of the initial classification, which allowed some field experience gained during that activity to influence the form of the classification. Published literature on longleaf communities was also used, but to a lesser degree. The initial classification included 15 community types that spanned nearly all the major natural communities in which longleaf pine dominates the canopy or shares dominance with other species.

Both the initial classification and our subsequent preliminary classification were designed with the intent that protection of several high-quality examples of each of the communities, selected to represent the range of variation within each type, should be sufficient to protect and preserve much of the biota of the greater longleaf-dominated ecosystem. This approach, when combined with both additional efforts to protect rare plant species that occur in longleaf communities, and management of large, longleaf - dominated landscapes to sustain ecological processes such as fire, should provide an effective strategy for protection of the longleaf pine ecosystem and its biodiversity.

Vegetation data

We sought quantitative data on the species composition of longleaf pine vegetation from throughout the range of the species east of the Mississippi River. All stand data selected for inclusion in the study included a complete list of the vascular plant species in each sample plot, plus a measure of species importance that could be transformed to approximate a ten-point cover/ abundance scale. (Cover refers to the percentage of ground surface that would be covered by the leaf area projection of a particular species.) We included only stands that had not been subjected to an extended period of fire suppression. After stands known to be degraded by fire suppression or pinestraw raking were excluded, along with some examples of types that were over-represented, the final dataset included data from seven sources and contained 216 longleaf pine stands representing 44 counties spread across all states within the range of longleaf pine east of the Mississippi River, except Virginia (Fig. 1). Virginia was excluded because the only known extant example of longleaf vegetation in Virginia has been strongly modified by fire suppression and logging (see Frost and Musselman 1987). Details of the datasets employed are summarized in Appendix I.

Our standard cover/abundance scale is that developed by the North Carolina Vegetation Survey to provide maximum ease of interconversion with other widely-used scales: 1 = trace, 2 = <1% cover, 3 = 1-2%, 4 = 2-5%, 5 = 5-10%, 6 = 10-25%, 7 = 25-50%, 8 = 50-75%, 9 = 75-95%, 10 = >95% cover. For each of the seven datasets used, cover values were transformed to approximate this scale.

Multivariate analysis

Ordination methods frequently are used to arrange vegetation samples in an abstract, multidimensional space in such a fashion that samples with similar species composition (and, therefore, similar underlying environmental control) are located near each other, while dissimilar samples are located far apart. This allows identification and visualization of the dominant trends in composition. In an ideal, perfectly orderly world, the various axes of the multidimensional space would be interpretable in terms of environmental variables responsible for the vegetation pattern observed. In practice, only the first one or two axes are usually interpretable, while the meaning of the remaining variation is obscured by interactions and changing importances of the critical factors with respect to the first few axes extracted.

To simplify interpretation of complex, multidimensional datasets, a strategy of progressive fragmentation (Peet 1980) can be employed. Here, the first one or two axes are examined and interpreted. Interpretation is based on knowledge of the sites, and environmental data where they are available. Then, a portion the dataset that is seen in the first ordination to be readily interpretable in terms of some sort of environmental extreme is removed from the dataset so as to reduce its influence in the subsequent ordinations. In this fashion, the dataset can be progressively simplified, and more subtle and deeply buried patterns can be exposed and interpreted.

We employed a strategy of progressive fragmentation using Detrended Correspondence Analysis as an ordination technique (CANOCO 3.1; Hill and Gauch 1980, ter Braak 1987, see Peet et al. 1988). We also used a numerical classification produced using two-way indicator species analysis (TWINSPAN; Hill 1979) to help refine the divisions in the dataset and to characterize the resulting clusters. At each step, tentative community types were recognized in the ordinations, with the first approximation based on the initial classification developed from the Nature Conservancy classifi-

cation (Allard 1990). As groups of stands were recognized, those stands near the edges of groups or that did not fit well were reexamined to see if they might better fit into another community type.

Our analysis and results are presented as a series of four two-dimensional ordination diagrams (Figs. 3-6). Symbols are used in these figures to indicate the final community type assignments of the vegetation samples. These diagrams show stands arranged in ordination space, so the axes are directly interpretable only in terms of species composition. Nonetheless, correlations with environmental variables exist and are described in the text. Further, the diagrams can be used to examine the relationships among the recognized community types and the degree to which the types differ from each other.

PHYSIOGRAPHY OF THE LONGLEAF PINE REGION

Although longleaf pine dominated the primeval vegetation of much of the Southeast, the area where it occurred was far from homogeneous. The natural range of longleaf covers nearly all the southeastern coastal plain and spills over onto the adjacent piedmont and interior uplands. Within the coastal plain, the species ranges from southeast Virginia south to central Florida and west to Texas, a large region that exhibits considerable variation in both geology and topography (Fig. 2).

The coastal plain is a region of marine sediments, in many cases extensively reworked by wave action. Because the coastal plain varies in topographic relief, it is convenient to recognize both a region of coastal flatlands where local relief is less than 35 m and over 80% of the land surface is at most gently sloping, and a region of rolling hills (see Fig. 2). This physiographic division follows Hammond (1964), but also approximates the divisions recognized by Hodgkins (1965; Flatlands Coastal Plain and Undulating Coastal Plain) and by Hodgkins et al. (1979; Middle Coastal Plain and Hilly Coastal Plain).

Coastal flatlands are best developed along the Atlantic coastal plain, but a narrow band of low relief continues along the Gulf coast. Marine transgressions across this flat landscape have left their marks in ways that strongly influence vegetation composition. Much of this flat outer coastal plain can be visualized as consisting of a series of old barrier dunes composed of coarse, siliceous sands, behind which are old embayment areas with soils

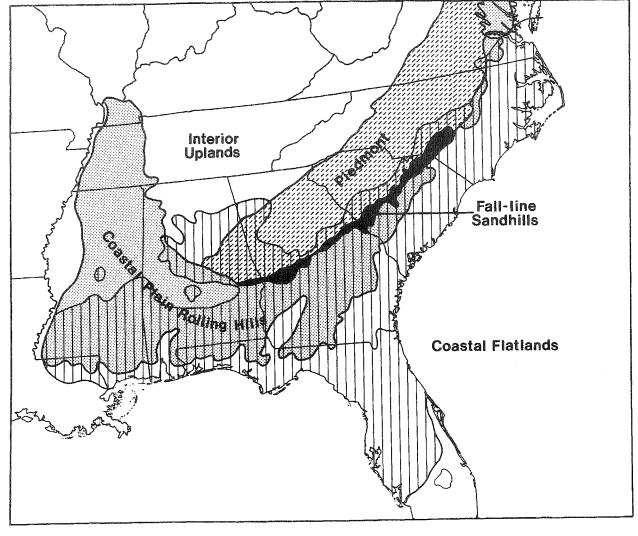


Figure 2. Longleaf pine (vertical lines) is distributed across several physiographic provinces, each with relatively distinct, longleaf-dominated communities (longleaf distribution after Little 1971 and Frost 1993; physiographic provinces modified from Hammond 1964 and Hodgkins 1965).

that are much finer and often dominated by fine clayey sands. Soils derived from the barrier dune systems tend to be extremely dry due to the rapid percolation of water, whereas the soils of the embayment regions tend to be seasonally saturated because the clay content of the soil and low relief make for poor drainage (DuBar et al. 1974, Daniels et al. 1984, Soller and Mills 1991).

Inland from the flatlands of the more recent marine terraces, the coastal plain is typically a region of low, rolling hills, often with loamy soils (Fig. 2). Farther inland the landforms are older and the topography is more hilly. A distinctive region of clay hills occurs in Alabama and Mississippi (Hodgkins 1965, Hodgkins et al. 1979), which extends a little into Georgia (Harper 1930). A similar but smaller area has also been recognized in South Carolina (Myers et al. 1986). The more pronounced topographic relief of the rolling inner

coastal plain allows better drainage with the consequence that seasonally wet sites are less common, mostly of local occurrence, and associated with near-surface impermeable and often indurated soil horizons.

Along the inner-most portion of the coastal plain from central North Carolina around to the eastern edge of Alabama are found the fall-line sandhills. This mass of primarily Cretaceous-age sandy sediments, in some places capped with Miocene dunes, is apparently the product of erosion of high mountains that once stood where today there remain only the low hills of the piedmont. Erosion of these piedmont hills has been so complete that the elevations of the sandhills now sometimes exceed those of the adjacent piedmont, erosion having been less intense because in the sandhills water drains readily into the sandy soil rather than running off the surface. These coarse

sands also cause the prevailing sandhill soils to be highly permeable and consequently very droughty for plant growth. However, embedded in these old marine deltaic sands are frequent clay lenses that locally inhibit drainage such that seeps occur where the lenses outcrop (see Sohl and Owens 1991).

Inland from the sandhills, north and west of the fall-line, is the piedmont region where marine sediments are replaced primarily by clay soils derived from weathering of ancient igneous and metamorphic rocks. Most of these areas have been above sea level since well before the start of the Tertiary, with the consequent that the soils are highly weathered and infertile, and the drainage systems are well developed. Farther west are the interior uplands of the Blue Ridge and the Ridge and Valley Provinces, again with ancient soils.

The longleaf vegetation of the coastal plain is well known to vary with soil drainage from xeric sandhill sites with coarse sandy soils to floristically rich savannas and flatwoods of poorly drained flatlands (Mohr 1901, Harper 1914b, Wells 1932, Braun 1950, Wharton 1978, Christensen 1988). This well-documented pattern led us to expect soil moisture to be a critical factor controlling composition of longleaf vegetation. We also anticipated that composition would vary in an interpretable manner between physiographic regions owing to differences in climate, soil texture and soil fertility.

VEGETATION PATTERNS

Regional gradients

Ordination of the complete dataset (Fig. 3) revealed a strong primary axis corresponding to soil moisture. Less pronounced sorting by latitude occurs along the second axes. This result led us to partition the dataset almost exactly in the middle of the ordination (bold line in Fig. 3), the break separating those sites that appeared to have seasonally-saturated soils from those with better-drained soils.

Stands from the dry half of the dataset were reordinated (Fig. 4). Again, a strong moisture gradient is evident with the extremely xeric sites of coarse, well-drained sands concentrated in the lower right and the mesic, more fertile sites with finer-textured soils clustered in the upper left. A middle range of moisture conditions occurs between the xeric and mesic sites, corresponding well to the samples we initially characterized as subxeric. Orthogonal to the moisture axis is a latitudinal gradient, which sepa-

rates almost perfectly samples from the Gulf Coast states (upper right) from the Carolina coastal plain and fall-line sandhill samples (lower left). Our few sites outside the coastal plain segregated at the far upper left with the mesic coastal plain sites. In our nomenclature, we designate the coastal plain of the Gulf states (AL, FL, GA, LA, MS), including the Atlantic coastal plain of Georgia, as "Southern", the coastal plain of the Carolinas (NC, SC) as "Atlantic", and the fall-line sandhills (AL, GA, NC, SC) as "Fall-line". The Atlantic region primarily falls within the coastal flatlands, but the southern segregate includes both the coastal flatlands of Georgia and Florida and the rolling hills of the Gulf coastal plain.

The xeric sandhill samples from western Florida segregated perfectly in the second ordination (Fig. 4) and these are designated as Southern Xeric Longleaf Woodland. The three mesic sites from the Gulf coastal plain also segregate well (Southern Mesic Longleaf Woodland), as do two samples from an unusual Gulf Coast type dominated by saw palmetto (Subxeric Longleaf - Saw Palmetto Woodland; see Pessin 1933, Allen 1956). All the other likely groups still exhibit some overlap in their membership. The three distinct groups (within bold lines in Fig. 4) were removed from the ordination, along with the single but distinctive sample from serpentine soils of the Georgia piedmont (Serpentine Subxeric Longleaf Woodland).

The final dry-site ordination (Fig. 5) shows very little overlap of the final recognized clusters. The predominant gradients are again related to moisture and geography, but soil texture and nutrients also appear important. Xeric, welldrained, infertile quartz sands are in the lower right while the clayey piedmont and upland sites (Piedmont/Upland Longleaf Woodland) segregate in the upper left, with the silty, mesic sites (Fall-line Mesic Longleaf Woodland) on the far left. Subxeric sites between the two extremes of the soil texture gradient, sorted along an orthogonal gradient corresponding to geographic location (Fall-line, Atlantic and Southern Subxeric Longleaf Woodland). The final gradient is a geographic one of proximity to the coast. The fallline sandhill samples occur at one extreme and the maritime fringe at the other, with the regular coastal plain samples in between. This is particularly apparent among the more xeric samples where we recognize three types (Fall-line, Atlantic and Atlantic Maritime Xeric Longleaf Woodland).

The first two axes of the wet-site ordination (Fig. 6) together separate the flatwood sites (upper left) characterized by somewhat shrubby understory vegetation and soils somewhat less sterile and clayey than those of the herb-dominated savanna sites. The "Southern," "Atlantic" and "Fall-line" Longleaf Savanna Woodlands segregate into three groups, reinforcing the significant differentiation with geographic position.

The four vegetation series and twenty-three vegetation types extracted based on the above analysis are listed in Table 1. In the following sections, generalized descriptions and discussions are provided for each series. At the end of the discussion of each series we provide summary sections that list the dominant (high cover and high frequency) and most abundant (numerous individuals and high constancy, i.e. high between-stand frequency) species for each community type.

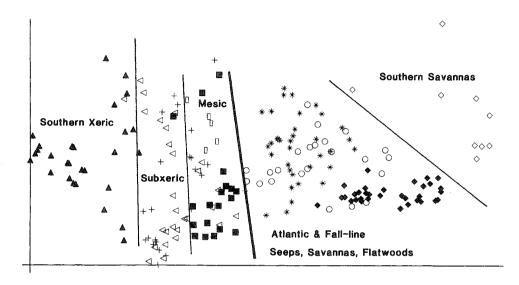


Figure 3. Ordination 1 contains all samples used in the final analysis. The first axis corresponds primarily to a moisture gradient with Xeric Longleaf Woodlands on the left, and moist savannas and flatwoods on the right. Among the moist sites, the Southern Longleaf Savannas (>) are most distinctive and extreme, but Atlantic Longleaf Savannas (>) separate from the Fall-line Longleaf Seepage Savannas (O) and Atlantic Longleaf Flatwoods (*). While Southern Xeric Longleaf Woodlands (A) are well separated, the Atlantic (+) and Fall-line Xeric Longleaf Woodlands (+) are inter-mixed with the Subxeric Longleaf Woodlands (-). Piedmont/Upland Subxeric Longleaf Woodlands (-) are mixed with the Mesic Longleaf Woodlands (-).

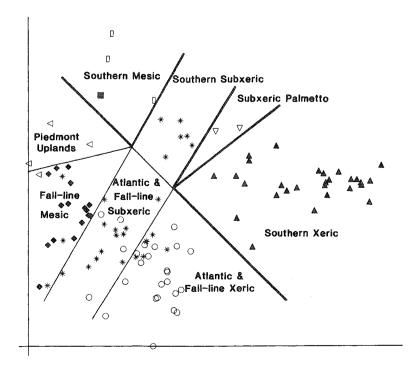


Figure 4. Ordination 2 was constructed using only sites from the dry half of the dataset (as defined by the bold line in Figure 3). A moisture gradient runs from the Xeric Longleaf Woodland sites on coarse quartz sands in the lower right (A= Southern; O= Fall-line and Atlantic), through Subxeric Longleaf Woodlands (*,) to moister sites on finer-textured, more fertile soils in the upper left (□ = Southern Mesic: ♦= and Fall-line Mesic: = Piedmont/Uplands Subxeric). Perpendicular to this gradient is a geographic gradient with virtually all the Atlantic and Fall-line sites in the lower left and all the Southern sites in the upper right. A single sample of Serpentine Subxeric Longleaf Woodland () from the Georgia piedmont occurs among the Southern Mesic Longleaf samples.

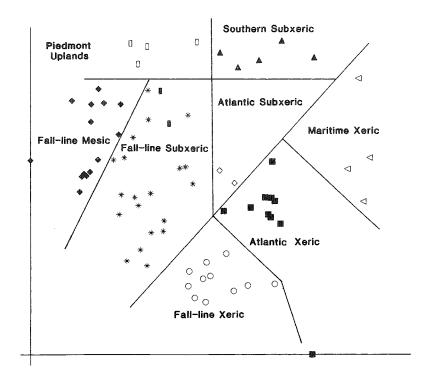


Figure 5. Ordination 3 resulted after reordinating the dry site dataset after removal of the Southern Xeric Longleaf, Subxeric Longleaf-Palmetto, and Southern Mesic Longleaf sites (defined by the bold lines in Figure 4) and the single Serpentine Subxeric Longleaf sample. A moisture gradient runs from the Xeric Longleaf Woodland sites in the lower right (O = Fall-line; = Atlantic; = Atlantic Maritime) to the Fall-line Mesic (*) and Piedmont/Upland (I) sites in the upper left. The perpendicular gradient is principally geographic with Fall-line Slope (I) and Subxeric sites (*) in the lower left and Southern (A) and Atlantic Subxeric sites (S) in the upper right. At this point the various Xeric and Subxeric types are distinct and separate from the Mesic sites.

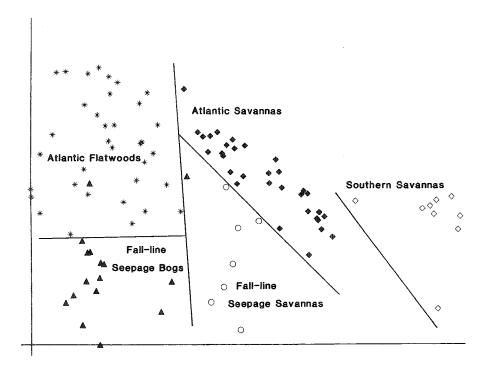


Figure 6. Ordination 5 illustrates the patterns of similarity among the Seasonally-wet Longleaf Woodlands. The more poorly-drained, nutrient-deficient Longleaf Savanna sites occur in the lower right (= Southern; • = Atlantic), while the somewhat more nutrient-rich, better-drained Longleaf Flatwood sites (*) occupy the upper left. The diagonal axis is largely one of distance from the coast with the fall-line sites at the bottom of the diagram (= Seepage Bogs;) = Seepage Savannas).

Xeric Longleaf Pine Woodlands

The five communities that comprise the Xeric Longleaf Woodlands all occur on deep, coarse, excessively drained sands. These sites typically occur on summits and shoulders of rises. The more extreme xeric sites are associated with dune systems such as occur on the east sides of Carolina bays (i.e., northeast of the primary axis of the depression) and along northeastern sides of large rivers that flow into the Atlantic (e.g., Altamaha, Cape Fear, Pee Dee, Savannah; see Bozeman 1971, Christensen 1979, 1988). In addition, remnant old barrier island systems scattered across the outer coastal plain (Dubar et al. 1974) typically support Xeric Longleaf Woodlands.

Longleaf pine is widely scattered in the xeric communities, and, owing to the extreme edaphic conditions, may not regenerate readily after cutting or extended fire suppression. Only on the outermost coastal plain of Georgia does longleaf cease to be the dominant species of the dry sand ridges (Bozeman 1971). Typically, there is a broad-leaved, deciduous subcanopy with turkey oak (*Quercus laevis*) virtually ubiquitous and persimmon (*Diospyros virginiana*) as a common associate. On somewhat finer-textured soils, bluejack oak (*Q. incana*) also can be important. In addition, scat-

tered shrubs (typically *Myrica cerifera*, *Gaylussacia dumosa* and *Vaccinium spp.*), and a sparse to moderate cover of herbs and grasses can be expected throughout. The grass layer of Xeric Longleaf Woodlands usually is dominated by wiregrass (*Aristida stricta* north of the Congaree-Cooper River system of SC, *A. beyrichiana* to the south), though these species are largely absent from central South Carolina and from much of the Gulf coastal region (see Fig. 1; Peet 1993). Bare sand typically is present at the soil surface, and species richness tends to be low.

Fall-line Xeric Longleaf Woodland can be found anywhere in the uplands of the fall-line sandhills where soils originate from coarse, well-drained sands (Christensen 1988, Stout and Marion 1993). The Atlantic and Southern Xeric Longleaf Woodlands can occur throughout the Atlantic and Gulf coastal plains respectively, though coarse sands are more frequent close to the coast and along northeast sides of major rivers (see Bozeman 1971). Along the Gulf Coast flats there is a general soil-texture gradient such that the more western sites have siltier, less sandy soils. As a consequence, Southern Xeric Longleaf Woodlands are more common and better developed in Florida than in coastal Mississippi or Louisiana.

Table 1. Longleaf pine Community Series and Types recognized in this study. Additional, undescribed communities for which preliminary information suggests recognition will likely be necessary when sufficient data are available are listed in parentheses immediately after the community within which they are currently included.

Xeric Longleaf Pine Woodland Series

Fall-line Xeric Longleaf Woodland Atlantic Xeric Longleaf Woodland Southern Xeric Longleaf Woodland Atlantic Maritime Longleaf Woodland Gulf Maritime Longleaf Woodland

Subxeric Longleaf Pine Woodland Series

Fall-line Subxeric Longleaf Woodland
Atlantic Subxeric Longleaf Woodland
Southern Subxeric Longleaf Woodland
(Southern Clayhill Subxeric Longleaf Woodland)
(Longleaf-Sand Pine Woodland)
(Florida Subxeric Longleaf Woodland)
Subxeric Longleaf Saw Palmetto Woodland
Piedmont/Upland Subxeric Longleaf Woodland
(Upland Subxeric Longleaf Woodland)
(Piedmont Subxeric Longleaf Woodland)
(Fall-line Clayhill Subxeric Longleaf Woodland)
Serpentine Subxeric Longleaf Woodland)

Mesic Longleaf Pine Woodland Series

Fall-line Mesic Longleaf Woodland Fall-line Slope Mesic Longleaf Woodland Atlantic Mesic Longleaf Woodland Southern Mesic Longleaf Woodland (Coosa Mesic Longleaf Woodland)

Seasonally-Wet Longleaf Pine Woodland Series

Fall-line Longleaf Seepage Savanna Fall-line Longleaf Seepage Bog Atlantic Longleaf Savanna Southern Longleaf Savanna Southern Longleaf Seepage Savanna Atlantic Longleaf Flatwood Southern Longleaf Flatwood Piedmont Longleaf Flatwood

Vegetation immediately adjacent to both the Atlantic and Gulf coasts experiences less extreme climatic conditions, with the consequence that most sites support closed forest. However, a distinctive Maritime Longleaf Woodland can develop on barrier islands and other near-coastal dunes where deep, coarse sands occur. Unfortunately, we have quantitative data only from southern North Carolina. Scattered barrier island longleaf populations occur from northern North Carolina near Nags Head south to at least Cumberland Island, Georgia (Hillestad et al. 1975, Wentworth et al. 1992). The Longleaf Woodland communities sampled along the North Carolina coastal fringe contain significant amounts of sand live oak and sand laurel oak (Quercus geminata, Q. hemisphaerica), whereas Clewell (1971) reports sand live oak to co-occur with myrtle oak (Q. myrtifolia) near the Apalachicola National Forest, Florida. Personal observations of this community type near Santa Rosa on the Florida Gulf coast suggest a quite different community from the Atlantic type; saw palmetto (Serenoa repens), false rosemary (Conradina canescens), and gallberry (*Ilex glabra*) share dominance in the shrub layer, together with such species as American olive (Osmanthus americanus), gopher apple (Licania michauxii), shiny blueberry (Vaccinium myrsinites) and numerous herbs. Further information can be found in Harper (1914b) and Wolfe et al. (1988). Although we have no quantitative data from this type as it is represented in Florida and the adjacent Gulf Coast states, our preliminary information suggests that both an Atlantic and a Gulf Maritime Longleaf Woodland should be recognized.

As with virtually all longleaf communities, fire is required in Xeric Longleaf Woodlands for regeneration of many of the component species, and for suppression of broadleaved understory tree species, particularly turkey oak (*Quercus laevis*). Although frequent, low-intensity surface fires once were common in this community, the low fuel load would have restricted the frequency and intensity of fire relative to other longleaf types (see Christensen 1988, Frost 1993, Stout and Marion 1993).

Fall-line Xeric Longleaf Woodland. Dominant species include Pinus palustris, Quercus laevis, and Aristida stricta. Other common species are Gaylussacia dumosa, Stipulicida setacea, Cnidoscolus stimulosus, Minuartia caroliniana, Euphorbia ipecacuanhae, Asclepias humistrata, Aureolaria pectinata, Bulbostylis capillaris, Carphephorus bellidifolius, Chrysopsis gossypina, and Pityopsis graminifolia.

Atlantic Xeric Longleaf Woodland (Figs. 7, 8). Dominant species include *Pinus palustris, Quercus incana, Q. laevis,* and *Aristida stricta*. Other common species are *Gaylussacia dumosa, Vaccinium tenellum, Cnidoscolus stimulosus, Schizachyrium scoparium, Euphorbia ipecacuanhae, Asclepias humistrata, Ionactis linariifolius, Aster. tortifolius, Aureolaria pectinata, and <i>Pityopsis graminifolia*. The driest sites often contain *Selaginella arenicola, Minuartia caroliniana* and *Stipulicida setacea*.

Southern Xeric Longleaf Woodland. Dominant species include Pinus palustris, Quercus laevis, Q. incana, Sporobolus junceus, and Licania michauxii. Other common species are Diospyros virginiana, Serenoa repens, Aristida beyrichiana, Cnidoscolus stimulosus, Eriogonum tomentosum, Pityopsis graminifolia, Yucca filamentosa, and Croton argyranthemus. Many species in this community, such as Ceanothus microphyllus, Asimina angustifolia and A. obovata, Baptisia lecontei, Berlandiera subacaulis, Aeschynomene viscidula, Rhynchosia cytisoides, Palafoxia integrifolia, Chapmannia floridana, Matalea pubiflora, Phoebanthus grandiflorus, Liatris chapmanii, and Andropogon floridanus do not occur in the mid-Atlantic states. While these species are never abundant in the Southern Xeric Longleaf Woodland, their presence makes it floristically quite different from the Atlantic type.

Atlantic Maritime Longleaf Woodland. Dominant species include Pinus palustris, Quercus geminata, Q. hemisphaerica, Myrica cerifera, Persea borbonia, Sassafras albidum, Ilex opaca, and Aristida stricta. Other common species are Quercus laevis, Q. incana, Osmanthus americanus, Gaylussacia dumosa, Vaccinium arboreum, V. tenellum, Smilax auriculata, Andropogon virginicus, Stipulicida setacea, Cnidoscolus stimulosus, Euphorbia ipecacuanhae, Asclepias humistrata, Bulbostylis capillaris, and Dichanthelium consanguineum.

Gulf Maritime Longleaf Woodland. Quantitative data are not available (see Harper 1914b, Clewell 1971, Wolfe et al. 1988).

Subxeric Longleaf Pine Woodlands

Subxeric Longleaf Woodlands, particularly the Atlantic and Southern Subxeric Longleaf Woodlands, dominated the presettlement landscape of most of the southeastern coastal plain (see Ware et al. 1993). They occurred on most well-drained upland sites, except for the extreme coarse sands occupied by the Xeric Longleaf Woodlands. The soils underlying these sites, while generally infertile and containing a significant amount of sand, typically

have a greater content of silt and clay than do those of the Xeric Longleaf Woodlands, a pattern recognized early on by Wells and Shunk (1931). Throughout the coastal plain and the fall-line sandhills, the general aspect of Subxeric Longleaf Woodlands is one of widely spaced pines with a sparse, broad-leaved deciduous understory and a continuous, well-developed ground layer containing a lush and diverse assemblage of grasses and forbs. The few remnants we have been able to sample have contained a large number of legume species.

The differences between the Atlantic and Southern Subxeric Longleaf Woodlands can be seen most readily in the ranges of the dominant species. In the more northern type, the dominant grass is the Carolina wiregrass (*Aristida stricta*), whereas in the Southern examples the dominant grass is predominantly the southern wiregrass (*A. beyrichiana*). Low blueberry species typically are abundant in both types, but *Vaccinium crassifolium* is essentially restricted to the northern variant, while *V. myrsinites* barely enters South Carolina.

The broad-leaved understory generally is comprised of scattered shrubby oaks, often including bluejack, turkey and sand post oak (*Quercus incana*, *Q. laevis*, *Q. margarettiae*) on the sandier sites, post oak (*Quercus stellata*) on the clay hills of the interior Gulf coastal plain, and blackjack (*Q. marilandica*) throughout where the clay content is particularly high. Persimmon (*Diospyros virginiana*) is also common. From Jackson County, Mississippi eastward, wiregrass (*Aristida beyrichiana*, then *A. stricta*) dominates much of the grassy herb layer,

though in the westernmost portion of its range wiregrass is largely restricted to the coastal tier of counties. Those subxeric sites remaining for study are predominantly on coarse-textured soils, the siltier soils of the inner coastal plain having long ago been converted to agriculture (except for limited areas of Alabama, Mississippi and Louisiana). The original vegetation of such fine-textured soils perhaps will remain forever unknown. However, the greater abundance of bluestems (Andropogon spp., Schizachyrium scoparium, and S. tenerum in the South) on the small patches on loamy soils that remain suggests that these grasses rather than wiregrass may well have been the original groundlayer dominants (Frost, Walker and Peet 1986). West of the range of wiregrass in Mississippi and Louisiana, and most of central Alabama, bluestems remain the most abundant grasses of the subxeric pinelands (see Grelen and Duvall 1966), as is the case in central South Carolina, between the ranges of the two wiregrasses.

Regional vegetation descriptions (e.g., Harper 1906, 1943, Myers 1990, Schafale and Weakley 1990) often contrast two forms of what we call Subxeric Longleaf Woodlands, corresponding to whether the underlying soil is predominantly sand or clay. Soil texture doubtless is important for explaining compositional variation in these woodlands, though the overriding importance of latitude and moisture largely mask the importance of texture in the ordination analysis we present. A separate analysis of just the Fall-line Subxeric Woodlands revealed a strong gradient in soil texture with the siltier soils having greater herb diversity, and the clayhills having a less well developed understory than the sandhills.

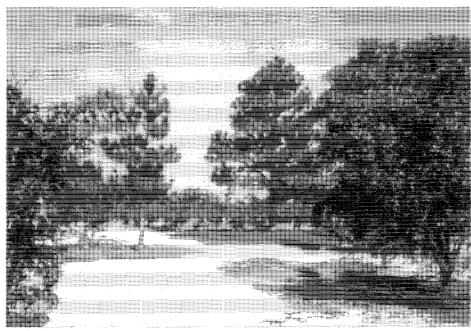


Figure 7. Atlantic Xeric Longleaf Woodland. The xeric extreme of longleaf vegetation on the Atlantic coastal plain is found on the eolian dune sands along the northeast sides of Carolina bays and major rivers. Salters Lake, Bladen County, North Carolina.

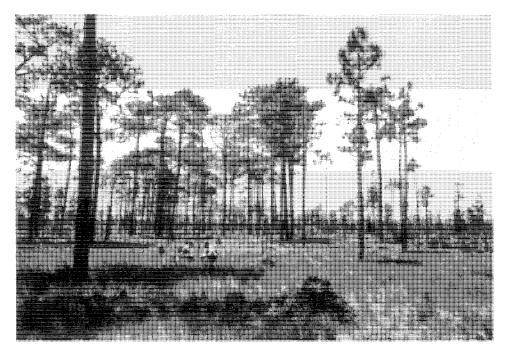


Figure 8. Atlantic Xeric Longleaf Woodland. This old-growth stand of longleaf is typical of xeric sites in the spareness of its wiregrass (Aristida stricta) and the presence of turkey oak (Quercus laevis). Croatan National Forest, Carteret County, North Carolina

Although longleaf and wiregrass dominate the visual aspect of the Subxeric Longleaf Woodlands, the herb layer can be impressively rich in species. Any inexperienced botanist attempting to catalog the important forb species seems destined to become lost in a confusing, though fascinating, collection of trifoliate legumes and Asteraceous basal rosettes. Like other longleaf communities, the Subxeric Longleaf Woodlands are fire-adapted, with frequent, low-intensity, growing-season fires required to control understory hardwoods. In the absence of fire, oaks and other hardwoods quickly assume dominance with the consequence that most of the understory herbs of the open pinelands are lost, as is the bulk of the wiregrass and virtually all longleaf regeneration.

A particularly distinct form of longleaf vegetation found on well-drained sandy flatlands along the Gulf Coast is the Subxeric Longleaf - Saw Palmetto Woodland. Identified by Pessin in 1933 as Xerophytic Coniferous Forest, and also recognized by Allen (1956), this little-known community of the coastal flatlands from southeast Mississippi east to southeast Georgia and south into central Florida is distinctive in appearance because of an almost continuous cover of saw palmetto (*Serenoa repens*), punctuated with scarlet balm (*Calamintha coccinea*) and a scattering of other herb and shrub species. The best examples known to the authors are located in the DeSoto National Forest in Mississippi.

The original range of longleaf-dominated vegetation extended beyond the coastal plain onto the generally drier and clayier soils of the lower piedmont and southern-most portions of the interior uplands (see Fig. 2). Except for central Alabama, longleaf habitats probably were always relatively uncommon on these upland sites, and little remains of this Piedmont/Upland Longleaf Woodland because of the longer history of fire suppression in the piedmont and mountain regions. As a consequence, much of the original diversity of this type has been lost, and much of what remains is degraded. We have lumped these various upland types together, fully aware that further differentiation probably will be required if additional data ever become available. Some indication of their original diversity can be found in Mohr's (1901) and Harper's (1943) summaries of the forests of Alabama, in which they discuss the longleaf forests of both the piedmont and the interior uplands.

Central Alabama has always contained the most extensive examples of the Piedmont/Upland Longleaf Woodland (see Mohr 1901, Harper 1943, Golden 1979). Indeed, in Alabama longleaf originally extended to an elevation of greater than 600 meters.

A few piedmont populations also remain in the Uwharrie Mountains of the North Carolina (see Schafale and Weakley 1990, Frost 1993). We recognize as closely related the vegetation of sheltered rocky slopes of the coastal plain where the flora shows close affinities with the clayier soils of the piedmont. Typically, such slopes occur where ironcemented sandstones formed over impermeable clay layers and now are evident at the surface due to erosion of the overlying sands. This community

has moderately spaced pines in the canopy, with a scattered understory of oaks, a variable shrub layer, and a sparse to moderate herb layer. Typical understory associates include black gum (Nyssa sylvatica), sparkleberry (Vaccinium arboreum), blackjack oak (Quercus marilandica) and mountain laurel (Kalmia latifolia). Some examples are patchy, containing small, grassy openings dominated by bluestems (Andropogon spp.) in the middle of open forest. The region of upper Clay Hills of Alabama (sensu Hodgkins 1965), and sometimes the clay hills in the Carolina Fall-line Hills (Fenneman 1938), appears quite distinct from the rest of the Subxeric Longleaf Woodlood (see Mohr 1901, Beckett and Golden 1982) and is perhaps worthy of recognition as a separate type. However, for the lack of quantitative data, we tentatively include these sites with the Piedmont/Upland Longleaf Woodlands.

At Burke Mountain in Columbia County, Georgia, a particularly unusual vegetation type has developed over serpentine rock, which we designate as Serpentine Subxeric Longleaf Woodland. The naturally droughty conditions of the soils associated with serpentine (Whittaker 1954) probably account for the occurrence of longleaf there (and pine in general on eastern North American serpentine). Given that most serpentine soils support unusual, often disjunct plant species, it is not surprising that the Burke Mountain sample stands out as different from all our other longleaf samples. We expect that similar vegetation occurred on those few other sites with serpentine-like substrate, but we know of no other extant examples within the range of longleaf.

Our vegetation samples from peninsular Florida are extremely restricted and insufficient for construction of even a preliminary classification. Nonetheless, published compositional data make clear that what is commonly known as "high pine" in north-central Florida is similar to our Southern Subxeric Longleaf Woodland (e.g., Sellards et al. 1915, Laessle 1942, Myers 1990, Stout and Marion 1993). What is less clear is whether there is sufficient longleaf - sand pine transition to justify recognition of this as a separate community. Similarly, the infrequently described scrubby flatwoods (see Laessle 1942, Abrahamson and Hartnett 1990, Stout and Marion 1993) also may occasionally be dominated by longleaf, but the information available to us currently is insufficient to justify recognition of a longleaf-dominated form of this community.

Fall-line Subxeric Longleaf Woodland (Figs. 9, 10). Dominant species include *Pinus palustris*, *Quercus laevis*, *Q. marilandica*, *Diospyros virginiana*,

Rhus copallinum, Aristida stricta, Andropogon spp., Schizachyrium spp., Pityopsis graminifolia, Solidago odora, and Toxicodendron pubescens. Other common species are Quercus incana, Q. margarettiae, Gaylussacia dumosa, Vaccinium tenellum, Liatris spp., Ionactis linariifolius, Baptisia cinerea, Carphephorus bellidifolius, Cirsium repandum, Cnidoscolus stimulosus, Coreopsis major, Dichanthelium ovale, Silphium compositum, Smilax glauca, and Tephrosia virginiana.

Atlantic Subxeric Longleaf Woodland. Dominant species include Pinus palustris, Quercus laevis, Q. margarettiae, Q. incana, Q. marilandica, Vaccinium arboreum, Vaccinium fuscatum, Gaylussacia dumosa, Rhus copallinum, Diospyros virginiana, Aristida stricta, Schizachyrium scoparium, and Andropogon ternarius. Other common species are Ionactis linariifolius, Hedyotis procumbens, Pityopsis graminifolia, Rhynchosia reniformis, Rhynchospora grayi, Solidago odora, Lechea spp., Stillingia sylvatica, Stylisma patens, Cnidoscolus stimulosus, Desmodium spp., Lespedeza spp., Mimosa quadrivalvis, Tephrosia spp., and Pteridium aquilinum, although not all of these species are found throughout the range of the community.

Southern Subxeric Longleaf Woodland Dominant species include Pinus palustris, Quercus laevis, Q. margarettiae, Q. incana, Q. marilandica, Q. falcata, Q. pumila, Vaccinium arboreum, V. elliottii, Diospyros virginiana, Ilex vomitoria, Hypericum hypericoides, Aristida beyrichiana, Aster tortifolius, Baptisia lanceolata, Dichanthelium ovale, Galactia regularis, Rhynchosia reniformis, Lespedeza repens, Pteridium aquilinium, Smilax bona-nox, Stylisma patens, and Gelsemium sempervirens. Other common species are Vaccinium fuscatum, Ionactis linariifolius, Hedyotis procumbens, Pityopsis graminifolia, Gymnopogon ambiguus, Rhynchospora grayi, Solidago odora, Lechea paniculatum, Desmodium ciliare, Mimosa quadrivalvis, and Tephrosia virginiana.

Subxeric Longleaf - Saw Palmetto Woodland. The dominant species in the two Mississippi sites are Pinus palustris, Quercus laevis, Q. incana, Q. marilandica, Cornus florida, Serenoa repens, Ilex vomitoria, Vaccinium fuscatum, V. elliottii, V. stamineum, Calamintha coccinea, Smilax pumila, Schizachyrium scoparium, Galactia regularis, Pityopsis graminifolia, Rhynchosia cytisoides, and Cyperus retrofractus. Other common species are Aristida purpurascens, Ionactis linariifolius, Chamaecrista nictitans, Cnidoscolus stimulosus, Dalea pinnata, Desmodium strictum, Elephantopus elatus, Gaura filipes, Hedyotis procumbens, Hypericum hypericoides, Lechea spp., Opuntia humifusa, Dichanthelium



Figure 9. Fall-line Subxeric Longleaf Woodland. Frequently burned Subxeric Longleaf Woodlands typically have a well-developed sward of wiregrass (Aristida stricta), punctuated with scattered small oaks (here turkey and bluejack oak; Quercus laevis, Q. incana), huckleberries (Gavlussacia spp.) and bracken fern (*Pteridium aquilinum*). Numerous herbaceous species can be found growing between the wiregrass clumps. Sandhills Gamelands, Scotland County, North Carolina.

aciculare, Quercus falcata, Sassafras albidum, Scleria spp., Stylisma patens, Tephrosia chrysophylla, and Toxicodendron pubescens.

Piedmont/Upland Subxeric Longleaf Woodland. Dominant species and other common species vary significantly across the geographic range of the community. An occurrence on the Oakmulgee District of the Talladega National Forest in Alabama is dominated by Pinus palustris, Nyssa sylvatica, Vaccinium arboreum, Kalmia latifolia, Pteridium aquilinum, and Tephrosia virginiana. Other common species include Aster tortifolius, Andropogon spp., Smilax glauca, and Gelsemium

sempervirens. In the Uwharrie National Forest in the North Carolina piedmont, dominant species include Pinus palustris, Quercus marilandica, Nyssa sylvatica, Oxydendrum arboreum, Pinus virginiana, Pinus echinata, Quercus prinus, Vaccinium tenellum, Andropogon spp. and Schizachyrium spp. Other common species are Diospyros virginiana, Pteridium aquilinum, Dichanthelium spp., Pityopsis graminifolia, Tephrosia virginiana, and Solidago odora. At Sugarloaf Mountain Recreational Area, Sandhills National Wildlife Refuge, South Carolina, dominant species include Pinus palustris, Pinus virginiana, Kalmia latifolia, Vaccinium arboreum, and Vaccinium crassifolium. Other common species are



Figure 10. Fall-line Subxeric Longleaf Woodland. Subxeric sites with significant quantities of silt or clay in the soil often support a well-developed deciduous subcanopy, here including turkey oak (Quercus laevis), sand postoak (Q. margaretta), and pale hickory (Carya pallida). Fort Bragg, Hoke County, North Carolina.

Aronia arbutifolia, Asplenium platyneuron, Pityopsis graminifolia, Aristida stricta, Gelsemium sempervirens, and Pyxidanthera barbulata.

Serpentine Subxeric Longleaf Woodland. Dominant species include Pinus palustris, P. echinata, Quercus marilandica, Schizachyrium scoparium, and Calamintha georgiana. Other common species are Baptisia alba, Chrysopsis mariana, Centrosema virginianum, and Gelsemium sempervirens.

Mesic Longleaf Pine Woodlands

Mesic Longleaf Woodlands generally differ from other longleaf communities in that they occur on moderately well-drained, often rolling uplands, but have relatively fertile, fine-textured, usually loamy soils. Many of the examples sampled in the fall-line sandhills occurred on alluvial terraces. While appropriate upland soils exist in the fall-line region, virtually all of these sites have been cleared for agriculture, or have been fire suppressed sufficiently long that the natural understory long ago disappeared. We did not succeed in finding data from any Atlantic coastal plain examples (Atlantic Mesic Longleaf Woodland), though appropriate soils are relatively common and we have recently seen two extant sites in Robeson County, NC. Most of these areas already had been converted to agriculture two centuries ago. The few remaining areas are mostly fire suppressed because they are isolated pockets in an agricultural mosaic. The best and most numerous remaining examples of Mesic Longleaf Woodland occur in the rolling hills of the Gulf coastal plain and are classified here as Southern Mesic Longleaf Woodland. Finer-textured, loamy soils are more abundant in this region, and the conversion to agriculture did not start as early or proceed as quickly as on the Atlantic coastal plain (Frost 1993).

Mesic Longleaf Woodlands that have continued to experience frequent fires are generally dominated by sufficiently dense canopy pines that the individual trees are nearly in contact with each other. Favorable growing conditions certainly would cause this vegetation, in the absence of fire, to quickly succeed to deciduous forest (see Veno 1976). The understory typically is lush, sometimes bordering on rank, with abundant herb species mixed among the bluestem grasses (*Schizachyrium spp.* and *Andropogon spp.*) and wiregrass (*Aristida stricta*, *A. beyrichiana*). Particularly striking is the species-richness, and especially the legume-richness, of the herb layer. With species counts rang-

ing between 100 and 140 vascular plant species per 1000 m², these communities appear richer in species at this scale than any other communities known from temperate North America (Peet et al. 1990).

We examined two samples of Mesic Longleaf Woodland from the Carolina fall-line sandhills that appear strikingly different from the other mesic samples. These occurred on cool, steep, somewhat north-facing slopes in the buffer zone surrounding the Fort Bragg, NC artillery range where hot summer fires have been a regular occurrence for many decades. Particularly unusual is the occurrence of such mountain zone species as mountain laurel (Kalmia latifolia) and galax (Galax urceolata) beneath a relatively open canopy of longleaf with a few scattered blackjack oak (Quercus marilandica). We know of no other place where steep, cool, northfacing slopes retain an open, fire-maintained vegetation (though Kalmia latifolia occurs with some regularity on the sandhill variant of the Piedmont/ Uplands Longleaf Woodland described earlier). Certainly this type was never common, and would have been among the first to be lost with a decline in fire frequency. We only tentatively recognize the Slope Mesic Longleaf Woodland as a natural vegetation type since it may be largely an artifact resulting from exceptionally high fire frequency.

Longleaf-dominated communities once occurred in the Coosa Valley at the southern end of the Ridge and Valley Province in Cherokee and Etowah counties, Alabama, and Floyd County, Georgia (Mohr 1897, Harper 1943, Wharton 1978). While these communities are known only from historic accounts, mesic, valley-bottom stands of longleaf probably were at one time abundant. However, most of the lands likely to have contained this community were inundated by construction of the Weiss Reservoir, while all other occurrences of the community apparently have been destroyed by agriculture or development (Wharton 1978). If an example of the mesic longleaf forests of the Coosa Valley were to be found, a new community type might well need to be recognized.

Fall-line Mesic Longleaf Woodland (Fig. 11). Dominant species include Pinus palustris, Quercus marilandica, Q. laevis, Q. margarettiae, Diospyros virginiana, Rhus copallinum, Gaylussacia dumosa, Vaccinium tenellum, Schizachyrium scoparium, Aristida stricta, Ionactis linariifolius, Aster walteriana, Eupatorium rotundifolium, Iris verna, Lespedeza repens, Pityopsis graminifolia, Solidago odora, Tephrosia virginiana, Toxicodendron pubescens, and Pteridium



Figure 11. Fall-line Mesic Longleaf Woodland. Mesic Longleaf Woodlands are relatively rare today because suppression of fire results in quick succession to dominance by shrubs and broad-leaved trees. Some of the best remaining examples are found on military bases in and adjacent to artillery ranges where hot summer fires are assured, and unexploded ordinance provides protection from development. McPherson Danger Area, Fort Bragg, Hoke County, North Carolina.

aquilinum. Other common species include Aster concolor, A. tortifolius, Desmodium lineatum, Eupatorium album, Euphorbia curtisii, Lespedeza capitata, Smilax glauca, Stylosanthes biflora, and many more.

Fall-line Slope Mesic Longleaf Woodland. Dominant species include Pinus palustris, Quercus marilandica, Diospyros virginiana, Nyssa sylvatica, Kalmia latifolia, Gaylussacia dumosa, G. frondosa, Lyonia mariana, Vaccinium tenellum, Epigaea repens, Aristida stricta, Schizachyrium scoparium, and Smilax rotundifolia. Other common species include Oxydendrum arboreum, Carphephorus bellidifolius, Gentiana autumnalis, Hypericum hypericoides, Pityopsis graminifolia, and Myrica cerifera.

Atlantic Mesic Longleaf Woodland. No quantitative data are available yet. However, the dominant species probably include Pinus palustris, Quercus stellata, Q.falcata, Quercus nigra, Liquidambar styraciflua, various shrubs, Aristida stricta, Schizachyrium scoparium, and Pteridium aquilinum. Other common species are probably Quercus incana, Quercus margarettiae, Q. marilandica, Q. pumila, Carya pallida, C. alba, Ilex glabra, Gaylussacia frondosa, G. dumosa, Lyonia mariana, Persea palustris, Gymnopogon brevifolius, Anthaenantia villosa, Dalea pinnata, Euphorbia corollata, Eupatorium rotundifolium, and Solidago odora.

Southern Mesic Longleaf Woodland (Fig. 12). Dominant species include Pinus palustris, Quercus marilandica, Quercus falcata, Q. incana, Q. margarettiae, Diospyros virginiana, Vaccinium

fuscatum, Gaylussacia dumosa, Ilex glabra, Schizachyrium scoparium, S. tenerum, Andropogon gerardii, Andropogon ternarius, Aristida purpurascens var. virgata, and Pteridium aquilinum. Aristida beyrichiana may dominate within its range. Other common species include Aletris aurea, Polygala nana, Eupatorium rotundifolium, E. semiserratum, Onosmodium virginianum, Gymnopogon ambiguus, G. brevifolius, Cnidoscolus stimulosus, Paspalum setaceum, Dichanthelium spp., Stylosanthes biflora, Desmodium lineatum, Aster tortifolius, Pityopsis graminifolia, Euphorbia corollata, Tragia urens, Stillingia sylvatica, Rhynchosia reniformis, Croton argyranthemus, Carphephorus odoratissimus, Helianthus angustifolius, Hieracium gronovii, Hypericum hypericoides, and H. stans, among many others.

Seasonally-Wet Longleaf Pine Woodlands

Poorly to moderately drained pinelands are common on the coastal flatlands of the southeast and are typically dominated by longleaf pine, though slash pine (*Pinus elliottii*) will often share or assume dominance on wetter sites from southern South Carolina south and across the Gulf states, and pond pine (*P. serotina*) will assume dominance in the wettest sites, usually those with organic soils, from Virginia to western Florida. In much of Florida and southeast Georgia, slash pine replaces longleaf completely on the wettest sites, thus limiting the range of communities that we might re-



Figure 12. Southern Mesic Longleaf Woodland. Mesic Longleaf Woodlands occur over relatively fine-textured soils and can support an extraordinarily species-rich herb layer. Wade Tract, Thomas County, Georgia.

fer to as longleaf types in that region (Clewell 1971, Gano 1917, Monk 1968). Westward along the Gulf coast in Alabama, Mississippi and Louisiana, slash pine was originally more narrowly distributed, occurring primarily on the edges of drainages with the flatwood and savanna lands almost exclusively dominated by longleaf (Penfound and Watkins 1937).

The vegetation of seasonally wet flatlands is called variously savanna or flatwoods. Within the ecological literature, the term "savanna" is used to describe a multiplicity of vegetation types, either lacking trees or containing widely spaced trees over a well-developed grassland. In the Southeast, the term normally is used in the narrower sense of open, graminoid-dominated and largely shrub-free pine woodland on seasonally-wet, oligotrophic soils. Accordingly, in this treatment we use savanna to refer to seasonally-wet pinelands with widely spaced trees on mineral soil with graminoid-dominated groundlayers, few shrubs and often an exceptionally species-rich herbaceous layer. Flatwoods contrast with savannas in that shrubs typically share dominance with the graminoids, or even surpass them, although shrub density and size will vary with fire history.

Species counts of 40 or more per square meter have been recorded for a number of savannas in the fall-line sandhills, the coastal flatlands of North Carolina, and the lower coastal plain of Mississippi. A few 100 m² samples from the North Carolina fall-line sandhills have in excess of 90 species. Thus, at both 1 m² and 100 m² scales, the southeastern sa-

vannas contain some of the most species-rich communities known from temperate North America.

Longleaf Savanna vegetation is most extensively developed on the flat terraces of the outer coastal plain, but originally occurred throughout the coastal plain portion of the range of longleaf pine where drainage was restricted and fire was frequent. Nonetheless, extensive areas of savanna appear to have been most frequent in Southeast North Carolina, and then from the Apalachicola region west along the Gulf Coast to Louisiana. Both regions have a number of endemic savanna species. For example, in the Carolina center one finds such endemics as Dionaea muscipula, Gentiana autumnalis, Lysimachia asperulaefolia, L. loomisii, Solidago pulchra, S. verna, Tofieldia glabra, and the two dominant grasses Aristida stricta and Sporobolus sp. nov. (aff. teretifolius; personal communication, A. Weakley). Endemics to the Gulf center include several species each of Aster, Pinguicula, Sarracenia, and Xyris and numerous others. A significant number of species have disjunct ranges with occurrences in the Carolina center and again in the Florida panhandle and westward (e.g., Helianthus heterophyllus, Lilium iridollae, Parnassia caroliniana, Pleea tenuifolia, Polygala hookeri, Rhynchospora breviseta, R. chapmanii, R. oligantha, Thalictrum cooleyi).

This break in the distribution of savanna species is largely responsible for the compositional differences observed in our analysis which led us to distinguish separate Atlantic (Carolina and north Georgia) and Southern Longleaf Savanna commu-

nities. Both centers appear to have distinctive infertile flatland soils composed of fine clayey sands that are largely absent in between. Our limited number of samples from the Georgia and southern South Carolina coastal plain makes it difficult to know whether the phytogeographical break is strongest in central South Carolina as described for the Subxeric types and corresponding to the break between the ranges of the two wiregrass species, or in Georgia corresponding to several of the disjunctions listed in the previous paragraph. Our choice of a central Georgia break must remain provisional until further data are available.

Savanna soils always are oligotrophic and seasonally saturated. Where a hardpan or other impermeable soil layer is present, soil conditions may be particularly xeric during drought periods. Although the texture of savanna soils can vary from relatively sandy to predominantly clay, the best developed and most floristically rich savannas are invariably on finer-textured, poorly drained, soils (Walker and Peet 1983, Frost, Walker and Peet 1986, Christensen 1988, Taggart 1990). Although several authors recognize different forms of savannas associated with clay and sand soils (e.g., Woodwell 1956, Taggart 1990, 1994), the sandier sites with seasonally wet soils generally clustered with flatwoods in our analysis.

The wealth of showy herbaceous species of the Longleaf Savannas has attracted considerable floristic attention, with the result that these now relatively rare communities are among the best known of the original longleaf community types (e.g., Kologiski 1977, Folkerts 1982, Walker and Peet 1983, Norquist 1984, Taggart 1994). Nestled among the dominant grasses (Andropogon spp., Aristida stricta and beyrichiana, Ctenium aromaticum, Muhlenbergia capillaris tricopodes, Sporobolus spp.) are numerous basal-rosette composites (e.g., Balduina, Bigelowia, Carphephorus, Coreopsis, Helianthus, Solidago), small sedges (e.g., Fimbristylis, Rhynchospora, Scleria), insectivorous plants (e.g., Drosera, Dionaea, Pinguicula, Sarracenia, Utricularia), orchids (e.g., Calopogon, Cleistes, Platanthera, Pogonia, Spiranthes) and lilies (e.g., Aletris, Lilium, Tofieldia, Zigadenus). Legumes are conspicuously absent from most savannas, a phenomenon noted by Gano (1917) and Wells and Shunk (1931) and Taggart (1990, 1994). The absence is made all the more notable by the wealth of legumes found in the mesic and subxeric community types, which is consistent with Walker's (1985) and Taggart's (1990) reports of increased legume abundance on savannas that are better drained.

The fall-line sandhills and the coastal plain rolling hills generally do not have the extensive flat lands with impeded drainage necessary to support true savanna. However, impermeable clay layers are frequent in these regions and, where these layers approach the surface, seeps develop and the resulting wet mineral soils support Longleaf Seepage Savannas, provided fire has been sufficiently frequent to keep out shrubs. These usually are similar to true coastal plain savannas in their species composition. Fall-line Longleaf Seepage Savanna is best known from the Carolinas (e.g., Wells and Shunk 1931), but a couple of examples have been reported from as far west as the fall-line sandhills of Alabama (Harper 1922). The similar Southern Longleaf Seepage Savanna can be found in the coastal plain rolling hills of the Gulf states, but we lack quantitative data for these sites. Bridges and Orzell (1989) have described such communities for the longleaf region west of the Mississippi River, but descriptions are lacking for this community as it occurs farther east, though some mention can be found in a number of more general works (e.g., Eleuterius 1968, Folkerts 1982, Harper 1906, 1914a, Plummer 1963). Where fall-line seepages develop on sandier soils, often with more shrubs, we recognize a separate community, the Fall-line Longleaf Seepage Bog. This community might be viewed as the fall-line analog of the flatwoods of the outer coastal plain.

Like "savanna", the term "flatwood" has a multiplicity of meanings and is often applied to rather dry sites with abundant shrubs. We use the term more narrowly to refer to moist sites between Mesic Longleaf Woodlands and Longleaf Savannas where shrubs are moderately abundant (i.e., wetmesic longleaf woodlands). These seasonally wet sites of low topographic relief differ from savannas in that the canopy is denser, shrubs and understory trees are frequent, and the soil is somewhat more fertile and often sandier. Soils are often saturated during the winter and droughty during the growing season. Longleaf Flatwoods occur throughout the range of longleaf pine in the Atlantic and Gulf coastal plains from North Carolina to Texas. The relative abundance of shrubs on flatwood sites is little understood, though a somewhat higher fertility and better drainage than found in savannas is probably important (see Christensen 1988, Stout and Marion 1993).

In addition to pines, hardwoods such as black gum (*Nyssa biflora*), sweetgum (*Liquidambar sylvatica*) and water oak (*Quercus nigra*) occur in flatwoods and can form a subcanopy. The shrub layer usually is well developed and dominated by

the same species that typically dominate bay forests, such as sweet bay (Magnolia virginiana), red bay (Persea palustris) gallberry (Ilex glabra), and titi (Cyrilla racemiflora). Southward, running oaks (Quercus minima, Q. pumila) often are dominant species in the shrub layer of drier flatwoods. However, from central South Carolina southward, the characteristic species is saw palmetto (Serenoa repens) which can at times form a solid understory canopy. Understory herbs are much less abundant than in the savannas because of the denser tree canopy and increased competition from the shrub layer. Nonetheless, wiregrass and other plants of both Longleaf Savanna and Mesic Longleaf Woodland are frequent.

A type of longleaf vegetation occurs (or once occurred) in the eastern portions of the piedmont, from North Carolina to Alabama (See Pinchot and Ashe 1897) with a species composition that places it in the flatwood type. This Piedmont Longleaf Flatwood currently is known only from highly degraded remnants in North Carolina that have been subjected to logging and fire suppression. The community occurs on poorly drained upland flats that are themselves unusual in the piedmont. Little information is available on the original composition of this community. Remnant stands do support wiregrass (Aristida stricta) and creeping blueberry (Vaccinium crassifolium), but most of the other original ground layer species are now gone (see Schafale and Weakley 1990).

Atlantic Longleaf Savanna (Fig. 13). Dominant species include Pinus palustris, P. serotina, Aristida stricta, Andropogon spp., Ctenium aromaticum, Rhynchospora plumosa, Muhlenbergia

capillaris tricopodes and Sporobolus sp. nov. (aff. teretifolius). Other common species include Platanthera spp., Cleistes divaricata, Calopogon pallida, C. tuberosus, Dionaea muscipula, Drosera capillaris, Pinguicula spp., Utricularia spp., Rhynchospora spp., Fimbristylis spadacea, Lachnanthes caroliana, Lachnocaulon anceps, Xyris ambigua, X. caroliniana, Dichromena latifolia, Rhexia alifanus, R. petiolata, R. lutea, Eriocaulon compressum, Liatris spp., Carphephorus paniculatus, C. tomentosus, Coreopsis linifolia, Hypoxis spp., Dichanthelium spp., Agalinis spp., Andropogon mohrii, Eryngium integrifolium, Eupatorium leucolepis, E. rotundifolium, Lycopodiella caroliniana, Osmunda cinnamomea, O. regalis, Polygala spp., Sabatia spp., and Zigadenus glaberrimus. Bridges and Orzell (1989) and Taggart (1990) discuss geographic differences in species composition of longleaf savannas.

Southern Longleaf Savanna (Fig. 14). The most abundant species include *Pinus palustris*, *P. elliottii*, *Bigelowia nudata*, *Carphephorus pseudoliatris*, *Chaptalia tomentosa*, *Coreopsis linifolia*, *Ctenium aromaticum*, *Helianthus heterophyllus*, *Ilex glabra*, *Lobelia brevifolia*, *Rhexia alifanus*, *Rhynchospora plumosa*, *R. oligantha*, *Scleria reticularis*, and *Xyris ambigua*.

Southern Longleaf Seepage Savanna. Quantitative data are lacking for this community. However, limited personal observation suggests that common species of seepage savannas in southwestern Mississippi include Andropogon spp., Anthaenantia rufa, Aristida purpurascens virgata, Cacalia ovata, Calopogon pallidus, C. tuberosus, Coreopsis linifolia, Chaptalia tomentosa, Ctenium aromaticum, Eragrostis refracta, Eriocaulon compressum, E. dectangulare, Helianthus heterophyllus,

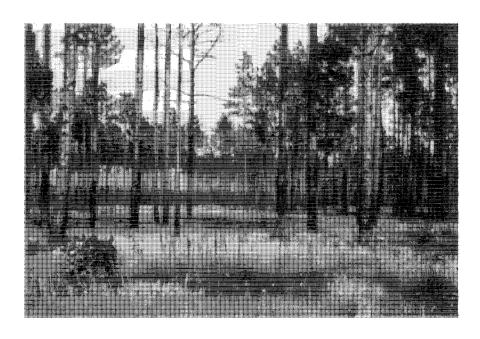


Figure 13. Atlantic Longleaf Savanna. Southeastern coastal plain flatlands with fine-textured, seasonally-saturated soils contain among the highest small-scale species densities known from the Western Hemisphere. Where fire is frequent, the average species number can exceed 40 per square meter. Green Swamp, Brunswick County, North Carolina.



Figure 14. Southern Longleaf Savanna. A wealth of herbaceous species including numerous orchids and insectivorous plants can be found in coastal plain pine savannas. Pitcher plants (*Sarracenia alata*) and sundews (*Drosera tracyi*) dominate in the foreground on this Gulf Coast savanna. Sandhill Crane National Wildlife Refuge, Jackson County, Mississippi.

Lachnanthes caroliana, Linum media, Lophiola aurea, Lycopodiella alopecuroides, L. appressa, Dichanthelium dichotomum ensifolium, Polygala lutea, Rhexia alifanus, R. petiolata, Rhynchospora ciliaris, R. chapmanii, Sarracenia alata, S. psittacina, Xyris ambigua, X. baldwiniana, X. caroliniana, X. difformis, and Zigadenus glaberrimus.

Fall-line Longleaf Seepage Savanna. The most abundant species include Pinus palustris, P. serotina, Ilex glabra, Aristida stricta, Aster dumosus, Ctenium aromaticum, Drosera capillaris, Erigeron vernus, Eupatorium rotundifolium, Lachnocaulon anceps, Osmunda cinnamomea, Pycnanthemum flexuosum, and Rhexia alifanus. Other common species are Chaptalia tomentosa, Coreopsis linifolia, Eupatorium leucolepis, E. pilosum, Hypericum cruxandreae, Viburnum nudum, and Viola primulifolia.

Fall-line Longleaf Seepage Bog. Dominant species include Pinus palustris, P. serotina, Clethra alnifolia, Lyonia lucida, Cyrilla racemiflora, Aronia arbutifolia, Ilex glabra, Arundinaria gigantea, Pteridium aquilinum, Vaccinium crassifolium, and Aristida stricta. Other common species are Gaylussacia frondosa, Symplocos tinctoria, Ilex opaca, Vaccinium stamineum, Acer rubrum, Toxicodendron vernix, Magnolia virginiana, Persea palustris, Osmunda cinnamomea, and Woodwardia virginica.

Atlantic Longleaf Flatwood. Dominant species include *Pinus palustris*, *P. elliottii*, *P. serotina*, *Ilex glabra*, *Serenoa repens*, *Quercus pumila*, *Ilex coriacea*, *Myrica cerifera*, and *Aristida stricta*, although not all of these species occur throughout the range. For instance, *Serenoa repens* occurs only as far north as

South Carolina, and *Quercus pumila* is largely absent from North Carolina. In addition, *Aristida stricta* does not occur south of northern South Carolina. Other common species of Wet Longleaf Pine Flatwoods include *Vaccinium crassifolium*, *Gaylussacia frondosa*, *Carphephorus odoratissimus*, *Kalmia angustifolia*, *Lyonia mariana*, *Myrica cerifera*, *Cyrilla racemiflora*, *Pteridium aquilinum*, *Smilax spp.*, and *Rhynchospora spp.*

Southern Longleaf Flatwood. Dominant species include Pinus palustris, Pinus elliottii, Myrica cerifera, Ilex glabra, Serenoa repens, and Aristida beyrichiana. Other common species are Pinus serotina, Kalmia hirsuta, Vaccinium myrsinites, Lyonia lucida, and Sabal palmetto (Wharton 1978, Abrahamson and Hartnett, 1990). Much variation in species composition exists within this type.

Piedmont Longleaf Flatwood. Dominant species in remnant occurrences include Pinus palustris, Pinus taeda, Acer rubrum, Liquidambar styraciflua, Gaylussacia frondosa, Lyonia mariana, Vaccinium fuscatum, Ilex glabra, Vaccinium crassifolium, Panicum virgatum, Chasmanthium laxum, and Aristida stricta. Many species have coastal plain affinities. Other common species include Quercus marilandica, Q. stellata, Nyssa sylvatica, Andropogon glomeratus, Eupatorium spp., Osmunda cinnamomea, Solidago odora, Rhynchospora spp., and Pityopsis graminifolia (Schafale and Weakley 1990).

DISCUSSION AND CONCLUSIONS

Although the once extensive Southeastern

longleaf pine woodlands may appear to the casual observer as a rather homogeneous expanse of longleaf pine, wire grass and scrub oak, this is decidedly not the case. We have documented considerable compositional variation which we have summarized using 23 communities; we also anticipate a future need to recognize additional vegetation types. The longleaf communities we recognize are largely separated along gradients corresponding to soil moisture, soil texture, and geographic region.

An equally important and little recognized aspect of the remarkable diversity of longleaf ecosystems is found in the numbers of species present in individual samples. We report Mesic Longleaf Woodlands with numbers of vascular plant species per 1000 m² ranging up to 140, the largest values yet reported for the temperate Western Hemisphere. Samples of 100 m² with species counts over 90 collected from Fall-line Longleaf Seepage Savannas also represent a new record for temperate North America. Finally, counts of more than 40 species per m² from Atlantic Longleaf Savannas (NC), Southern Longleaf Savannas (MS), and Fallline Longleaf Seepage Savannas (NC) exceed all other values yet reported for the Western Hemisphere. Many of these species are restricted to the longleaf pine ecosystem.

The remarkable diversity of the greater longleaf ecosystem is being lost rapidly, both through active habitat destruction and through neglect. Much habitat is being destroyed through development or conversion for greater economic yield. Simultaneously, much of what remains is being lost through fire suppression, which quickly leads to loss of many of the numerous species that inhabit the longleaf communities. If even a substantial fraction of the diversity of the greater longleaf ecosystem is to be preserved, action must be taken quickly to both preserve and manage the best remaining examples of each of the longleaf communities.

ACKNOWLEDGMENTS

For permission to use unpublished data we thank William Boyer, Cecil Frost, Cary Norquist, James Snyder, John Taggart, and the members of the North Carolina Vegetation Survey (Cecil Frost, Michael Schafale, Alan Weakley, Thomas Wentworth, Peter White, and RKP). Earlier versions of the manuscript benefited from the helpful comments of William Boyer, Cecil Frost, Jeff

Glitzenstein, Cary Norquist, Rebecca Reed, John Taggart, and Thomas Wentworth.

APPENDIX 1. DATA SOURCES

North Carolina Vegetation Survey data. We used data from 69 plots sampled during June, 1989 and 1990 in the fall-line sandhills of North Carolina. The fundamental sampling unit was a 10 x 10 m module wherein the percent cover for each vascular plant species was recorded using the ten-point scale described in the methods section. Typically, a sample plot consisted of a block of 4 contiguous modules, plus cover values of all additional species encountered in a full 2x5 block of 10 modules, or 0.1 ha plot. Occasional plots were smaller, the smallest containing only a single 10 x 10 m module. In addition, we used data from four maritime fringe longleaf pine communities collected as part of a comprehensive study of barrier island maritime forests in May 1988 (see Wentworth et al. 1992). The methods employed were identical to those used in the fall-line sandhills study.

Nature Conservancy data. Data were collected from 47 plots between April 1989 and November 1990 in a study explicitly designed to provide information for refining the initial Nature Conservancy classification. This study was coordinated through the Southeast Regional Office of The Nature Conservancy by DJA and involved ecologists from the regional and state offices of the Nature Conservancy and the state Natural Heritage Programs. In this study longleaf-dominated communities were sampled in all states within the species' range except for Virginia, although time constraints did not allow all longleaf-dominated community types in the initial classification to be included.

Permanent 20×50 m (0.1 ha) plots were established in relatively undisturbed longleaf pine communities. Emphasis was placed on sampling sites over the mesic to xeric portion of the moisture gradient because fewer published data were available for these sites. As in the North Carolina Vegetation Survey study, quantitative data were collected from four contiguous 100 m^2 modules in each plot. Cover class was recorded for each plant species in each module using the same 10-point scale, and species presence was noted for the remainder of a full 0.1 ha plot.

Frost data. Four plots from an unpublished data set collected by Cecil Frost as part of his doctoral dissertation research were used in this analysis. These data were from relatively undisturbed

areas of the Croatan National Forest in the outer coastal plain of central North Carolina. Plots were 20×50 m (0.1 ha), with percent cover recorded for all shrub and herb species in each of $25 \cdot 0.5 \times 2$ m subplots. Tree diameters were recorded and subsequently converted to cover using regression models developed from the North Carolina Vegetation Survey data.

Taggart data. As part of his doctoral research, John Taggart (1990, 1994) collected data from seasonally-wet coastal plain savannas located between the Congaree-Cooper river system in South Carolina and the Neuse River in North Carolina. We include the 40 of his plots that contained longleaf pine. Sites were minimally disturbed; while past ditching and lumbering were allowed, soil disturbance and prolonged fire suppression were not. Tree diameters were measured in a 0.1 ha circular plot, shrub cover values were recorded using a 6-level scale in a 0.01 ha circular plot at the center of the tree plot, and frequency and cover of herbs were recorded in 19 1 m² plots inside the shrub plot.

Forest Service data. In a study of Florida panhandle sandhills vegetation, H.E. Grelen and others from the U.S. Forest Service collected data from 50 stands. Of these, we used data from a represen-

tative set of 20 of the 40 stands that contained longleaf pine. In each stand ten quadrats were sampled for herbaceous data, while woody species were recorded from 30 quadrats. Data originally were recorded by 5 abundance classes which we converted to match our ten-point scale.

Norquist Data. Cary Norquist collected data from seven relatively undisturbed coastal savannas in southern Mississippi as part of her masters research (1984). Although Norquist did not record information on the sparse tree stratum, she did report that longleaf and slash pine (*Pinus palustris*, *P. elliottii*) were the only important trees on any of her plots and were likely the original dominant species (presently, the sites are dominated primarily by sparsely planted slash pine). Twenty 0.25 m² quadrats were sampled at each savanna site, with presence recorded for each quadrat.

Snyder data. James Snyder collected extensive data on the vegetation of the Croatan National Forest on the outer coastal plain of central North Carolina as part of his masters research (1978, 1980). We used those 26 plots in his dataset that contained longleaf pine. Plots were $10 \times 20 \text{ m}$ (200 m²) in size. Snyder recorded cover of each plant species using a seven-point scale which we transformed to conform to our ten-point scale.

APPENDIX 2: COMMUNITY COMPOSITION

This table contains the frequencies of species that occurred in the samples included in our analysis. The number of samples included is shown at the top of each column. Only species that had a frequency of at least .50 in one community, or that occurred in at least 4 communities, are included. The full table, including all rare species, is available from the authors upon request. Nomenclature follows Kartesz (1994).

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodiand	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodiand	Fall-line Mesic LL Stope Woodland	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Fail-line Seepage Savanna	Fall-line LL Seepage Bog	
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16	
ACALYPHA GRACILENS							0.200			1.000			0.333						
ACER RUBRUM					0.050				0.250			0.286	0.333	0.111	0.429	0.206	0.429	0.688	
AGALINIS FILICAULIS														0.556					
AGALINIS PURPUREA					0.050							0.071			0.057	0.265			
AGERATINA AROMATICA			0.074		0.250							0.357	0.333						
ALETRIS AUREA													0.667	0.111		0.088	0.143		
ALETRIS FARINOSA					0.050							0.500	0.333		0.200	0.647	0.571	0.125	
ALETRIS LUTEA							0.200							0.556					
ANDROPOGON GERARDII												0.071	0.667	0.111				0.125	
ANDROPOGON GLOMERATUS GLAUCOPSIS													•	0.556					
ANDROPOGON MOHRII											•			0.778	,		0.574	0.500	
ANDROPOGON SP.	0.727	0.400			0.800	1.000	0.200	0.500	0.250			0.857		0.556	0.429	1.000	0.571	0.563	
ANDROPOGON TERNARIUS			0.185				0.400	0.500			•		0.667	0.222	,		,	0.075	
ANDROPOGON VIRGINICUS			0.111	0.750	0.200		0.600	•	0.250		•	0.143		0.778	0.229	. 0.000	•	0.375	
ANTHAENANTIA VILLOSA			0.037		0.050		0.400			•	•		0.667		0.029	0.059	•		
ARISTIDA BEYRICHIANA			0.444				0.800		0.250				•	0.333		•		0.125	
ARISTIDA PURPURASCENS PURPURASCENS			0.037		0.050			1.000		1.000		0.143	0.667	0.778	0.114	0.294			
ARISTIDA PURPURASCENS VAR. VIRGATA ARISTIDA STRICTA			0.037		1.000	0.500	0.400	•	•		1.060	1.000		0.710	0.829	0.824	0.571	0.875	
ARISTOLOCHIA SERPENTARIA	1.000	1.000	0.007	1.000	0.050	0.000	0.600	,		1.000	1.000	1.000	0.333	•	0.023	0.024		0.013	
ARIONIA ARBUTIFOLIA		•	0.037	0.250	0.050	•	0.000			1.000	•	0.143	0.333	0.333	0.657	0.412	0.571	0.750	
ARUNDINARIA GIGANTEA	0.091	•	•	0.250		•	•	•			•	0.071		0.000	0.314	0.353	0.429	0.438	
ANONDINAMA GIDANTEA ASCLEPIAS AMPLEXICAULIS	0.091	•	0.037		0.300	•		•	•	•	•	0.143	0.333		0.017	0.000	0.140	y. 130	
ASCLEPIAS HUMISTRATA	0.364	0.200	0.185	0.250	0.050		0.200	0.500		•	,	0.140			•				
ASCLEPIAS TUBEROSA	0.004	0.200			0.050		0.200	0.000	•		•	0.071						0.063	
ASTER ADNATUS	•	•	0.037	•	0.050	•	0.200	0.500	•	,	•	0.071	1.000	0.111				,	
ASTER CONCOLOR	•		0.007		0.350	•			•	•		0.786	0.333	V.111	0.086	0.029	0.143		
ASTER DUMOSUS			0.037	•	0.050	•			0.250	•	•	0.643	1.000	0.667	0.286	0.471	0.857	0.188	
ASTER LATERIFLORUS	•	•	0.001		0.000	0.500	0.200	0.590	0.200				0.333		0.200				
ASTER PALUDOSUS	,			•	•	0.000		0.000	•	•	•		0.333		0.057	0.353	0.143	0.063	
ASTER PATENS	•					•	0.200	•	0.250		•	•	1.000		0.001	0.000		4.5.5	
NULLITALLIN		•	•	•	•		0.200		0.200			•	1.000				•	•	

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodiand	Serpentine Subxeric LL Woodland	Fall-line Mesic LL Slope Woodland	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
ASTER PATERNUS ASTER SERICEUS ASTER SOUDAGMEUS ASTER SURCULOSUS ASTER TORTIFOLIUS ASTER WALTERI	0.182 0.364	0.900	0.148		0.400 0.150 0.500 0.500	1,000 1,000 0,500	1.000	1.000	0.250 . 0.500		0.500 0.500	0.643 0.571 0.786 1.000	0.667 0.667		0.029 0.143 0.029 0.171 0.371	0.029 0.629 0.235 0.412	0.286 0.143 0.429	0.063 0.313 0.250
AUREOLARIA PECTIAATA BALDURIA UNIFLORA BAPTISIA ALBA BAPTISIA CALYCOSA VILLOSA BAPTISIA CONCRETA BAPTISIA LANCEOLATA	0.636 0.909	0.100	0.037 0.444 0.074		0.250 0.700		0.890	· · · · · ·	0.250	1.000	· · · · · · ·	0.643	•	0.778	0.986 0.029	0.059 0.059	· · · · · · · ·	0.125
BAPTISIA TINCTORIA BARTONIA VIRGINICA BIGELONIA NUDATA BOLITONIA DIFFUSA BULBOSTYLIS CAPILLARIS BULBOSTYLIS CAZILLARIS	0.182 0.091 0.182	·	0.074 0.148	0.250	0.200 0.050	0.500		0.500			· · · · · ·	0.143	0.667	0.556 1.000 0.222	0.057 0.143	0.029 0.176 0.824	0.571	0.125 0.063
CALAMNTHA COCCINEA CALAMNTHA GEORGIANA CALLICARPA AMERICANA CALLISIA GRAMNEA CALLISIA GRAMNEA CALOPOGON PALLIDUS & BARBATUS	0.702			0.500	0.300		0.400	1.000 0.500	· · · ·	1.000	· · · ·	0.214	0.667	0.333		0.882	0.266	
CALOPOGON TUBEROSUS CARPHEPHORUS BELLIDIFOLIUS CARPHEPHORUS ODORATISSIMUS CARPHEPHORUS PANICULATUS CARPHEPHORUS PSEUDOLIATRIS	1.000	0.600 0.300 0.100	0.037	0,250	0.750		0.600	0.500	0.250 0.250		0.500	0.500 0.071	0.333	1.000	0.114 0.543 0.429	0.706	0.571 0.143	0.125 0.125 0.063
CARPHEPHORUS TOMENTOSUS CARYA ALBA CARYA PALLIDA CEANOTHUS AMERICANUS CENTELLA ASIATICA	0.182		0.074		0.100 0.050 0.300	0.500	0.200		0.500			0.357 0.500 0.214	1.000 0.667	0.778	0.314	0.500 0.029 0.147	0.296	0.063 0.063 0.063 0.063
CENTROSEMA VIRGINIANUM CHAMAECRISTA FASCICULATA CHAMAECRISTA NICTITIANS CHAPITALIA TOMENTOSA CHASMANTHIUM LAXUM CHRYSOPSIS GOSSYPINA	0.455		0.037 0.630 0.556		0.100 0.350	0.500 1.000	0.200 0.200	1.000 0.500		1,000	0.500	0.429 0.071	0.667 1.000	1.000	0.029 0.029 0.143 0.057 0.057	0.029 0.382	0.714	0.063 0.063

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodian	Subxeric Saw Palmetto Woodlan	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodlan	Fall-line Mesic LL Slope Woodlar	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic Ll. Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
CHRYSOPSIS MARIANA					0.100		0.200		0.250	1.000		0.429	1.000	0.111	0.086	0.382	0.143	
CIRSIUM HORRIDULUM						0.500					,		0.667					
CIRSIUM REPANDUM	0.818	0.100			0.750							0.571						0.063
CLEISTES DIVARICATA	*											0.071			0.029	0.118	0.143	0.063
CLETHRA ALNIFOLIA				0.250	0.150				0.250		0.500	0.286			0.143		0.429	0.875
CLITORIA MARIANA					0.250	0.500		0.500				0.357						0.125
CNIDOSCOLUS STIMULOSUS	1.000	0.900	0.481	0.500	0.650	0.500	0.400	1.000				0.071	0.667		0.029			
COREOPSIS LINIFOLIA												0.071		1.000	0.029	0.794	0.714	0.188
COREOPSIS MAJOR	0.091				0.600	1.000	0.200		0.250		4.	0.357	0.333		0.029			0.313
COREOPSIS VERTICILLATA					0.050				0.250		0.50	0.429			0.029		0.143	
CORNUS FLORIDA			0.037		0.100		0.600	1.000	0.250			0.286	0.667					0.063
CRATAEGUS UNIFLORA	0.091		0.370		0.100		0.400					0.214						
CROTALARIA PURSHII			0.148		0.050	1.000						0.500	0.667		0.029	0.147		
CROTALARIA ROTUNDIFOLIA			0.222	•	•	0.500		0.500					0.333					
CROTALARIA SAGITTALIS											•		0.667					•
CROTON ARGYRANTHEMUS			0.852				0.400										0.057	
CTENIUM AROMATICUM		•	•	•			0.200					0.071	0.333	1.000	0.029	0.529	0.857	0.250
CYPERUS PLUKENETII	4					1.000		0.500										
CYRILLA RACEMIFLORA												0.071		0.111	0.200	0.147	*	0.250
DALEA PINNATA	0.182		0.444		0.100	0.500		1.000										
DANTHONIA SERICEA		•			0.250							0.643			0.029		0.286	0.063
DESMODIUM CILIARE				,	0.150	0.500	0.200		0.250			0.500	0.333				•	
DESMODIUM LAEVIGATUM	0.091				0.050		0.200					0.214	0.333				*	0.000
Desmodium Lineatum	0.091			,	0.150	0.500						0.714	1.000	0.111	0.057	0.029	*	0.063
DESMODUM MARILANDICUM				•	0.150	0.500						0.143	0.333		0.029	•	*	
DESMODRUM OBTUSUM					0.050			0.500			•	0.071	0.333		0.029		*	
DESMODIUM PANICULATUM	0.182				0.050	0.500	0.200		0.250			0.071	0.667				0.440	
DESMODIUM STRICTUM	0.182		0.037		0.200			1.000				0.071	0.333			0.470	0.143	0.063 0.125
DESMODRUM TENUFOLIUM		0.100									•	0.214	4 000	0.111	0.257	0.176	0.286	0.125
DICHANTHELIUM ACICULARE			0.148	•	0.100	1.000	0.600	1.000	. 050			0.357	1.000	0.333	0.114		•	0.003
DICHANTHELIUM COMMUTATUM	•		• *		0.350	,		•	0.250	1.000	•	0.571		. 0.444	0.000	0.000	0.640	0.125
DICHANTHELIUM CONSANGUINEUM		0.100		0.750	0.050		. 0.000	0.500	. 0.00			0.140		0.111	0.229	0.029	0.143	0.250
DICHANTHELIUM DICHOTOMUM DICHOTOMUM	•				•		0.200	0.500	0.250	1.000		0.143	0.007	0.770	A 44.4	0.700	0.143	0.230
DICHANTHELIUM DICHOTOMUM ENSIFOLIUM				•		•			0.250		•	0.214	0.667	0.778	0.114	0.706	0.857	0.250
DICHANTHELIUM DICHOTOMUM TENUE					0.100							0.357		0.333	0.143		•	U.20U
DICHANTHELIUM LONGRUGULATUM	•		•	•	. 0.450		0.000					0.149	•	0.778				0.063
DICHANTHELIUM OLIGOSANTHES DICHANTHELIUM OVALE	0.070	0.100	0.110		0.150		0.200	•	0.050			0.143	1.000			0.147	0.142	0.063
	0.273	0.100	0.148		0.650	1.000	1.000	•	0.250			0.929	1.000		A 44.4	0.147	0.143	0.373
DICHANTHELIUM SABULORUM		0.200	0.037	•		*	•					0.071			0.114			
DICHANTHELIUM SPHAEROCARPON	•				•	•				•	•	•	0.667	•				

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Allantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Paimetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fall-line Mesic LL Slope Woodland	Fall-line Mesic L. Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
DICHANTHELIUM STRIGOSUM LEUCOBLEPHARIS DICHANTHELIUM STRIGOSUM STRIGOSUM DICNAEA MUSCIPULA DICSPYROS VIRGINAMA DROSERA BREVIFOLIA DROSERA CAPILLARIS DYSCHORISTE OBLONGIFOLIA ELEPHANTOPUS ELATUS ELEPHANTOPUS TOMENTOSUS ELEPHANTOPUS TOMENTOSUS EPIGAEA REPENS ERIGERON STRIGOSUS ERIGERON VERNUS ERICCAULON COMPRESSUM ERICCAULON DECANGULARE ERICGOZUM TOMENTOSUM ERNOGUM INTEGRIFOLIUM ELPATORIUM COMPOSTIFOLIUM EUPATORIUM ALBUM EUPATORIUM COMPOSTIFOLIUM EUPATORIUM MOHRII EUPATORIUM MOHRII EUPATORIUM PUCSUM EUPATORIUM PUCSUM EUPATORIUM PUCSUM EUPATORIUM PUCSUM EUPATORIUM SEMISERRATUM EUPATORIUM SEMISERRATUM EUPATORIUM SEMISERRATUM EUPHORBIA COROLLATA EUPHORBIA COROLLATA EUPHORBIA PECACUANHAE	0.727 	0.300	0.815 0.074 0.852 0.037 0.037 0.222	0.500	0.950 0.950 0.950 0.200 0.200 0.450 0.050 0.150 0.150 0.150 0.150 0.150 0.150	2 0.500 1.000 1.000 0.500 1.000 1.000 1.000 1.000 1.000 1.000	0.400 0.400 0.200 0.400 0.200 0.200 0.600 0.200 0.200 0.200 0.200 0.200 0.200 0.200	2	0.500 0.500 0.250 0.250 0.250 0.250	1.000	2 	0.071 0.071 0.071 0.929 0.071 0.286 0.214 0.143 0.071 0.714 0.071 0.144 0.071 0.143 0.500 0.571 0.857 0.143 0.786 0.571	0.667 1.000 0.333 0.667 0.333 1.000 1.000 0.667 1.000	0.444 0.111 0.111 0.778 0.556 0.667 0.778 0.556 0.111 0.111 0.556 0.111 0.111 0.111	0.257 0.057 0.257 0.057 0.096 0.057 0.029 0.029 0.029 0.029 0.314 0.057 0.286 0.400	0.382 	0.429 0.143 0.714 0.714 0.714 0.143 0.714 0.143 0.714 0.143 0.714 0.857	0.963 0.188 0.063 0.433 0.063 0.063 0.063 0.063 0.063 0.063 0.125
COLHARIA I ENUTUDIA GALACTIA ERECITA GALACTIA PEGULARIS GALACTIA VOLUBILIS GALAX URCEOLATA GALIUM HISPRULUM GALIUM PILOSUM GAMOCHAETA PURPUREA	0.636 0.636 0.091	0.300	0.259 0.593 0.037 0.148		0.250 0.450 0.050 0.460 0.050	1.000 0.500	0.400 0.800 0.200 	0.500			0.500 0.500 0.500	0.571 0.286 0.071 0.571 0.143	0.667 0.333 0.667 0.667		0.029		0.143	0.063 0.125

	Fall-line Xeric L.L Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fall-line Mesic LL Slope Woodland	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Falkline Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
GAYLUSSACIA DUMOSA GAYLUSSACIA PRONDOSA GELSEMIUM SEMPERVIRENS GENTIAMA AUTUMNALIS GRATIOLA PLOSA GYMNOPOGOM AMBIGIUUS GYMNOPOGOM AMBIGIUUS GYMNOPOGOM AMBIGIUUS GYMNOPOGOM BREVIPOLIUS HELIANTHUS ANGUSTIFOLIUS HELIANTHUS ARTORUBENS HELIANTHUS ARTORUBENS HELIANTHUS HETEROPHYLIUS HIERACIUM GRONOVII HIERACIUM X MARIANUM HOUSTONIA LONGIPOLIA HOUSTONIA LONGIPOLIA HOUSTONIA LONGIPOLIA HYPERICUM CRUX-ANDREAE HYPERICUM GENTIANOIDES HYPOXIS HIRSTUR HYPOXIS HIRSTUR HYPOXIS INISTUR HYPOXIS INISTUR HOYOCALICA LEX COMACEA ILEX (OMTORIA IONACTIS LINARIIFOLIUS IRIS VERNA VERNA JUNCUS BIFLORUS KALMA LATIFOLIA LACHNOCALICAN ANCEPS LECHEA MINOR	0.818 0.991 0.991 0.091 0.091 0.091 0.091 0.091 0.091 0.273 0.909 0.273 0.909 0.455 0.273	0.760 0.760 0.700 0.100 0.190 0.100 0.100	28 0.037 0.111 0.222 0.037 0.185 0.111 0.185 0.037 0.037 0.074 0.074 0.037	4 0.590 0.260 0.500 0.250 0.750 0.500 	20 0.750 0.050 0.050 0.200 0.150 0.200 0.400 0.400 0.500 0.300 0.100 0.050 0.750 0.500 0.050 0.500 0.500 0.500 0.500	2 1.000 0.500 0.500 0.500 1.000 1.000 1.000 1.000	5 0.600 1.000 0.200 0.400 0.400 0.200 0.800	2 	0.500 0.250 0.250 0.250 0.250 0.250 0.250 0.250 0.250	1.000 	2 1,000 1,000 0,500 0,500 0,500 1,000	14 1,000 0,357 0,286 0,429 0,143 . 0,429 0,143 . 0,571 . 0,214 0,500 0,071 . 0,071 0,571 0,143 0,143 0,143 0,357 0,071 . 0,929 0,857 0,071	0.667 	0.556 0.222 1.600° 0.222 0.333 0.889	0.657 0.890 0.343 0.066 0.029 0.029 0.029 0.029 0.026 0.0257 0.0114 0.200 0.466 0.914 0.200 0.466 0.457 0.029 0.029	0.353 0.471 0.147 0.206 0.559 0.235 0.471 0.029 0.794 0.324 0.235 0.471 0.029	2 0.429 0.429 0.429 0.143 0.286 0.143 0.155 0.157 0.15	0.625 0.813 0.125 0.313 0.125 0.063 0.125 0.063 0.125 0.063 0.125 0.063 0.125 0.063 0.125 0.063 0.250 0.250 0.625 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125 0.125
Lechea Sessiliflora Lespedeza angustipolia Lespedeza capitata Lespedeza hirta Lespedeza hirta Lespedeza nitermedia Lespedeza procumbens Lespedeza procumbens Lespedeza prenen	0.091 0.091 0.091 0.091	0.100	0.630 0.074 0.037 0.222		0.050 0.250 0.200 0.050 0.050 0.400	0.500	0.200 0.200 0.200 0.800	1.000				0.429 0.714 0.071	0.667 0.333 1.000	0.111 	0.114 0.314 0.029	0.029 0.265	0.429 	0.125 0.250 0.063 0.063

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fall-line Mesic LL Slope Woodland	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Attantic LL Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	- 4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
Satique size LESPEDEZA VIRGINICA LIATRIS GRAMMIFOLIA LIATRIS SPICATA LIATRIS SOLIARROLOSA LIATRIS SOLIARROLOSA LICANIA MICHAUXII LICUIDIAMBAR STYPACIFLUA LOBELIA BREVIFOLIA LOBELIA DELIA BREVIFOLIA LOBELIA PUBERULA LOPHICIA AUREA LUDWIGIA VIRGINIA LUDWIGIA VIRGINIA LYCOPODIELLA CAROLINIANA LYCOPODIELLA CAROLINIANA LYCOPODIELLA CAROLINIANA LYCOPODIELLA CAROLINIANA LYCOPA LIGUISTRINA LYCOPA LIGUISTRINA LYONA MARIANA MAGNOLIA VIRGINICA MARSHALLIA GRAMMIFOLIA MARSHALLIA GRAMMIFOLIA MARSHALLIA CAROLINIANA MUNICA GRAMMIFOLIA MARSHALLIA CAROLINIANA MUNICA CERIFERA MYRICA CERIFERA	11 0.727 0.091 0.091 0.091	0.300 0.100	28 0.1111 0.852 0.519 0.185 0.074 0.037	0.250 0.250 0.250 0.250	20 0.250 0.750 0.050 0.050 0.050 0.400 0.050 0.100 0.200 0.050 0.050	2 0.500 	5	2	4 0.250 0.250 0.250 0.250 	1.000	2 0.500	14 0.571 0.571 0.571 0.296 0.214 0.143 0.071 0.214 0.571 0.286 0.296 0.357 0.071	3 0.667 1.000 0.667 1.000 0.333 0.667 	9	35 0.029 0.096 0.457 0.114 0.066 0.029 0.114 0.457 0.496 0.029 0.029 	0.235 0.176 0.059 0.765 0.029 0.118 0.471 0.324 0.412 0.412 	2 0.286 0.571 0.143 0.429 0.286 0.286 0.286 0.429 0.143 0.429 0.143 0.429 0.143 0.429	16 0.063 0.063 0.125 0.063 0.063 0.063 0.063 0.063 0.063 0.063 0.250 0.063 0.063
NYSSA SYLVATICA CENOTHERA FRUTICOSA OPUNTIA HUMFUSA ORBEXILUM PEDLANCULATUM PSORALIOIDES CSMANTHUS AMERICANUS OSMUNDA CINAMOMEA OXYDENDRUM ARBOREUM OXYDEIUS FILIFORMIS	0.182 0.091	0.100	0.148	0.250 0.750	0.150 0.150 0.050 0.150 0.050 0.100		0.200 0.200	1.000 0.500	0.250 0.250	1.000	1.000 0.500	0.500 0.286 0.429 0.143 0.071	1,000 0,333		0.200 0.029 0.257	0.029 0.147 0.029	0.143 0.286 0.714	0.375
OXYPOLIS TERNATA PANICUM ANCEPS PANICUM VIRGATUM PASPALUM LAEVE	0.091	•	0.259	•	0.050	0.500	0.400 0.200		•		· · · ·	0.071	1.000 0.667	0.222 0.556 0.111	0.029 0.029	0.059 0.088 0.088	0.429 0.286	0.125 0.188

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fall-line Mesic LL Slope Woodland	Fall-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
PASPALUM PRAECOX PASPALUM SETACEUM PENSTEMON AUSTRALIS PERSEA BORBONIA PERSEA PALUSTRIS PINUS ECHINATA PINUS ECHINATA PINUS ECHINATA PINUS SEROTINA PINUS TAEDA PITYOPSIS GRAMINFOLIA POLYGALA CRUCIATA POLYGALA CRUCIATA POLYGALA AMARIANA POLYGALA HARRANA POLYGALA RANOSA POLYGONELLA GRACLIS POLYGONELLA GRACLIS POLYGONELLA POLYGAMA POLYGALA RANOSA POLYGONELLA POLYGAMA POLYGONELA POLYGAMA POLYGONELA POLYGAMA POLYGONELA POLYGAMA POLYGALA POLYGAMA POLYGONELA POLYG	11	10	0.037 0.037 0.037 0.037 0.037 0.889 0.704 0.037 0.407 0.148 0.037 0.815 1.000 0.556	4	20 0.260 0.050 0.050 0.050 1.000 0.160 0.150 0.900 0.100 0.400 0.400 0.150 0.050 0.050 0.050 0.050	2 0.500 1.000 1.000 0.500 0.500 0.500 0.500 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000 1.000	. 0.400	2	0.500 1.000 1.000 0.250 0.250 0.250 0.250 0.250 0.250 0.250 0.250 0.250 0.250 0.250	1	2 		0.333 0.333 1.000 0.333 1.000 0.333 1.000 0.667 0.333 0.333 0.667 0.333 0.333 0.667	0.556 0.222 0.444 1.000 0.222 0.333 0.778 0.444	0.029 0.571 1.000 0.257 0.200 0.114 0.029	0.059 0.029 0.059 0.206 1.000 0.647 0.882 0.382 0.912 0.029 0.029 0.029 0.029 0.0888 0.091 0.0888 0.091 0.0988 0.090 0.099 0.0099 0.0099 0.0099 0.0099 0.0099 0.0099 0.0099 0.0099 0.0099 0.0099	0.143 0.143 1.000 0.429 0.286 0.571 0.143 0.857	0.500 0.063 0.630 0.633 1.000 0.500 0.063 0.250
RHEXIA ALIFANUS RHEXIA MARIANA RHEXIA PETICLATA RHODODENDRON ATLANTICUM	•		*/ * * *		0.050	•	0.200 · ·	· · ·			•	0.571 0.071 0.071 0.143	0.667 0.333	1.000 0.222	0.543 0.057 0.086 0.029	0.941 0.118 0.471 0.059	0.857 0.429	0.938 0.313 0.313 0.250

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric L.L Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fal-line Mesic LL Stope Woodfand	Fall-line Mesic LL Woodland	Southern Mesic L.L. Woodland	Southern LL Savanna	Atlantic LL Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Fall-line L1. Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
RHUS COPALLINUM RHYNCHOSIA CYTISOIDES RHYNCHOSIA TENENORMS RHYNCHOSPORA TOMENTOSA RHYNCHOSPORA BALDWANII RHYNCHOSPORA BEVISETA RHYNCHOSPORA CHARMANII RHYNCHOSPORA CHARMANII RHYNCHOSPORA CHARMS RHYNCHOSPORA GLOBULARIS RHYNCHOSPORA GLOBULARIS RHYNCHOSPORA GLOBULARIS RHYNCHOSPORA BALTIFOLIA RHYNCHOSPORA LATIFOLIA RHYNCHOSPORA PLUMOSA RHYNCHOSPORA RUBUS ARGUTUS RUBUS CUNEIFOLIUS SABRIA CAMPANULATA SARRACENIA FLAVIA SARRACENIA SARRACENIA FLAVIA SARRACENIA FLAVIA SARRACENIA FLAVIA SARRACENI	0.182 	0.100 0.100	0.074 0.593 0.333 0.222 		0.800 0.490 0.150 0.050 0.150 0.150 0.500 0.300 0.300 0.490 0.490 0.750 0.190 0.190	1.000 1.000 0.500 	0.400 0.200 0.800 0.400 0.	0.500 1.000 0.500 0.560 1.000 1.000	0.500	1.000	0.500	0.929 0.2141 0.286 0.0357 0.071 0.071 0.071 0.0500 0.214 0.357 0.071 0.214 0.071 0.214 0.071 0.214 0.071	1.000 0.000 0.333 0.667 0.333 0.667 1.000 1.000 0.333 1.000 1.000 0.333 0.333 0.333	0.667 0.111 0.778 0.111 0.556 0.869 1.000 0.556 0.778 0.667 0.111 	0.314 	0.412 0.500 0.529 0.853 0.235 0.059 0.765 0.029 0.059 0.234 0.118	0.429 0.143 0.571 0.143 0.143 0.143 0.286 0.286 0.429 0.143 0.143 0.286 0.571 0.143	0.438
SMLAX AURICULATA SMLAX BONA-NOX	V.10£	0.100	0.259 0.037	1.660	0.100		0.400 1.000			1.000	•		0.333		0.029	•		0.063

	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subexeric LL Woodland	Subxeric Saw Palmetto Woodland	Peidmont/Upland LL Woodland	Serpentine Subxeric LL Woodland	Fail-line Mesic LL Slope Woodland	Fail-line Mesic LL Woodland	Southern Mesic LL Woodland	Southern LL Savanna	Atlantic LE Flatwood	Atlantic LL Savanna	Fall-line Seepage Savanna	Falt-line LL Seepage Bog
Sample size	11	10	28	4	20	2	5	2	4	1	2	14	3	9	35	33	2	16
SMILAX GLAUCA SMILAX PUMILA SMILAX SAMLII SOLIDAGO COORA SOLIDAGO RUGOSA SOLIDAGO STRICTA & PULCHRA SORGHASTRIJAN NUTANS SPORGEOLUS JJACEUS STILLINGIA SYLVATICA STIPULICIDA SETACEA STROPHOSTYLES UMBELLATA STYLISMA PATENS STYLOSANTHES BIFLORA SYMPLOCOS TINCTORIA TEPHROSIA CHRYSOPHYLLA TEPHROSIA CHRYSOPHYLLA TEPHROSIA FLORIDA TEPHROSIA FLORIDA TEPHROSIA SPICATA TEPHROSIA OROBRYCHOIDES TEPHROSIA SPICATA	0.364 0.182 1.000 0.818 0.182 0.455 0.0091 0.455	0.400	0.074 0.830 0.815 0.370 0.778 0.556 0.593 0.148 0.074 	0.250 	0.500 0.900 0.200 0.150 0.150 0.150 0.350 0.550 0.160 0.300 0.300 0.350 0.650 0.650 0.650 0.650 0.650 0.650 0.650 0.650	1,000 0,500 1,000 0,500 1,000 0,500 1,000 0,500 1,000 0,500	0.200 0.400 0.600 0.600 0.600 0.600 0.600 0.400 0.200 0.400 0.200 0.400 0.200 0.400 0.200 0.400	0.500 1.000 0.500 0.500 0.500 0.500 1.000 0.500 0.500 0.500 0.500	0.500	1.000	0.500 1.000 0.500	0.714 0.971 0.857 0.071 0.071 0.786 0.071 0.786 0.071 0.429 0.929 0.429 0.929 0.857 0.071 0.0429	1.000 333 0.667 0.657 1.000 0.667 0.657 0.333 1.000 0.667 0.667 0.667 0.667 0.667	0.111 0.333 0.1111 0.1111 	0.457 0.229 0.343 0.066 0.029 0.143 0.257 0.174 0.114 0.114 	0.029 0.059 0.082 0.029 0.294 0.029 0.294 0.029 0.029 0.029 0.706 0.029 0.029 0.706 0.029 0.706	0.286 0.571 0.571 0.286 0.143 0.143 0.429 	0.625 0.500 0.563 0.188 0.063 0.125 0.125 0.125 0.188 0.250 0.313 0.125 0.188
VACCINUM DARROWII VACCINUM ELIOTTII VACCINUM FORACSUM VACCINUM FUSCATUM VACCINUM FUSCATUM VACCINUM MYRSINTES VACCINUM TEMELLUM VERNONIA ACAULIS		0.100 0.100 0.600	0.111 0.037 0.296 0.148	0.250 	0.050 0.050 0.050 0.100 0.600	0.500 1.900	0.200 1.000 0.600 0.200 0.400	1.000 1.000 1.000 1.000	0.250 0.250 0.500 0.500 0.250 0.250	1.000 1.000	1.000	0.200 0.071 0.214 0.143 1.000 0.571	0.667 1.000 		0.743 0.436 0.029 0.800 0.057	0.018 0.029 0.029 0.059	0.429	0.563 0.375

Fall-line Seepage Savanna	2	-	-	0.714		٠	0.714	0.143	0.571		0.286	0.143
Atlantic LL Savanna	æ			0.28			0.353	0.118	0.912		0.176	0.088
Atlantic LL Flatwood	38			670.0	67070	990'0	0.057		0.543		6200	0.029
Southem LL Savanna	6						0.889	0.444	0.222		0.111	0.222
Southem Mesic LL Woodland	eo.		0.667	-	-	0.333			-			
Fall-line Mesic LL Woodland	4	0.214	0.571	0.143		0.429			0.143			
Fail-line Mesic LL Slope Woodland	2									-		
Serpentine Subxeric LL Woodland	-		£63		1000	1.000						
beidoont/J bnslqU\tombieq	4					0.500		-				
Subxeric Saw Palmetto Woodland	2				-					-		
Southern Subexeric LL Woodland	ĸ	0.400	0.400	-	-	0.600			-			
Atlantic Subxeric LL Woodland	2	1.000				0.500						
Fall-line Subxeric LL Woodland	93	0.500	0.450			0300		-		-	-	0.100
Atlantic Maritime LL Woodland	4	٠	٠			0.500						-
Southern Xeric LL Woodland	88	0.296		-	-	0.074				0.481		•
Atlantic Xeric LL Woodland	9	0.100				0100	-					
Fall-line Xeric LL Woodland	Ŧ.	0.364	0.273									

03.7 · 0.00 · 0.

VERNONIA ANGUSTIFOLA
VOLA PEDATA
VOLA PRALLICUIA
VOLA SAGITTATA
VITIS POTUNDIFOLIA
XYRIS MARBGUA
XYRIS BALDWINIANA
XYRIS CAROLLIANAV
XYRIS CAROLLIANAV
XYRIS CAROLLIANAV
ZOGADENUS GENESIS
ZIGADENUS GLABERRIAUS

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