

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

**Robert K. Peet**

Department of Biology, CB#3280, University of North Carolina, Chapel Hill, NC 27599-3280

**Dorothy J. Allard**

The Nature Conservancy, Southeast Regional Office, Box 2267, Chapel Hill, NC 27515

## 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 m<sup>2</sup>. 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 semi-natural, 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).

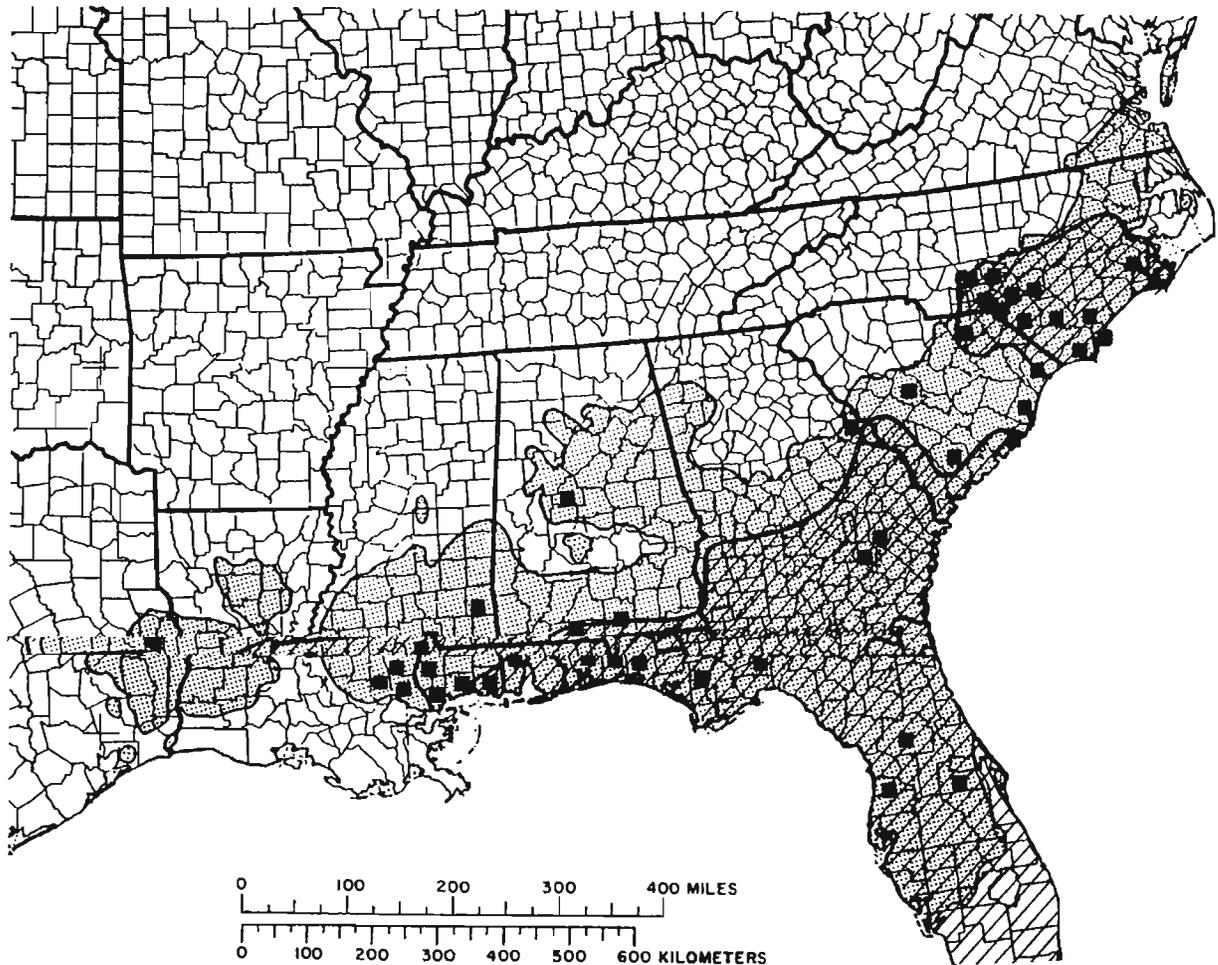


Figure 1. The 216 sample sites used in our final analysis were located in 44 counties scattered throughout much of the range of longleaf pine (*Pinus palustris*) east of the Mississippi River. The range of longleaf pine is indicated by stipples (after Little 1971 and Frost 1993) and the range of wiregrass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

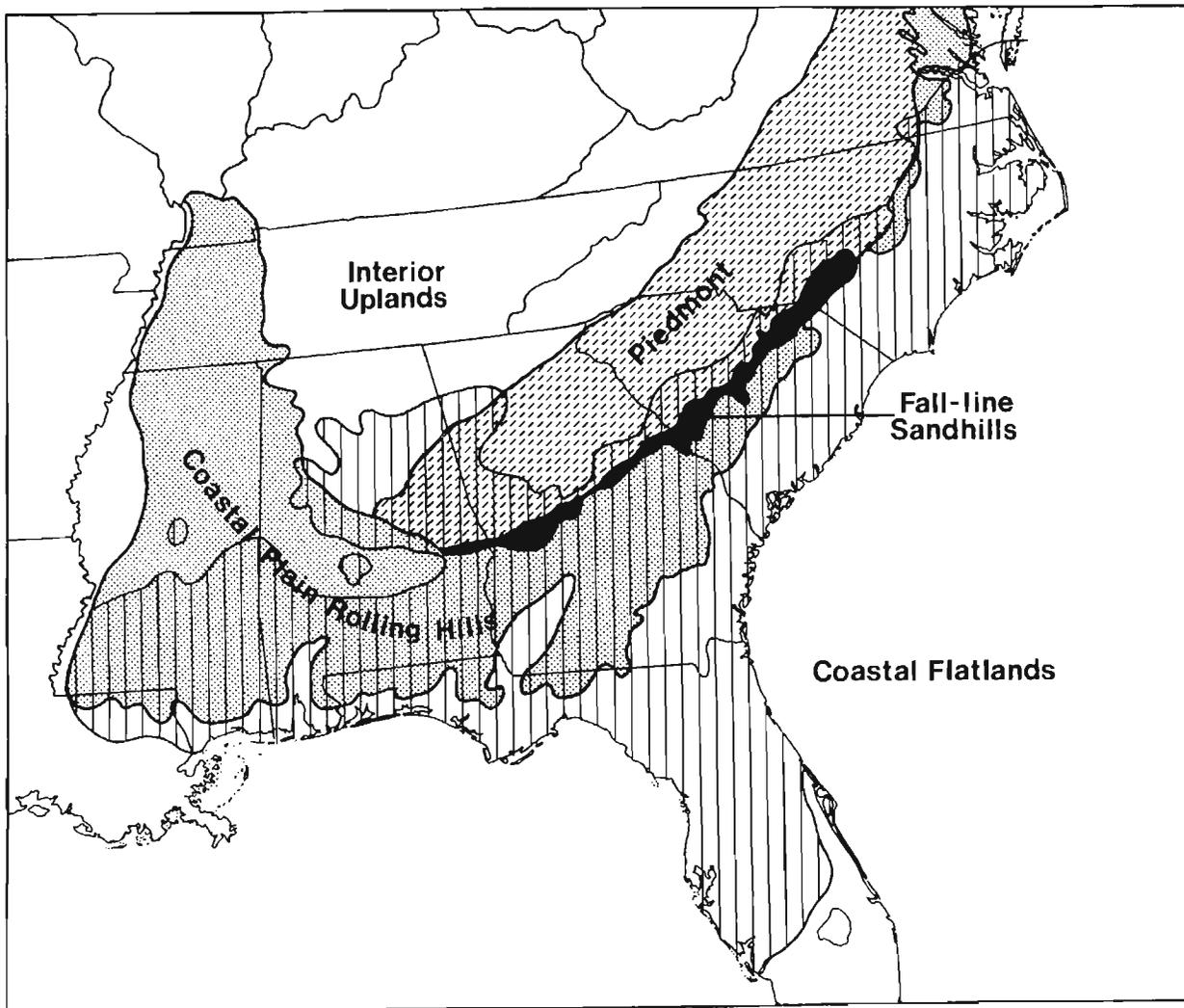


Figure 2. Longleaf pine (vertical lines) is distributed across several physiographic provinces, each with relatively distinct, longleaf-dominated communities (longleaf distribution after Little 1971 and Frost 1993; physiographic provinces modified from Hammond 1964 and Hodgkins 1965).

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, well-drained, 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 fall-line 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.

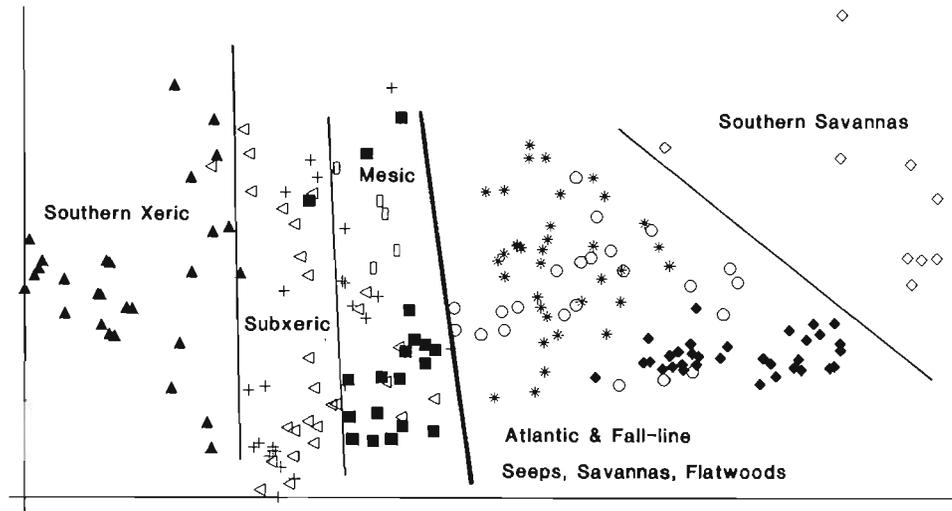


Figure 3. Ordination 1 contains all samples used in the final analysis. The first axis corresponds primarily to a moisture gradient with Xeric Longleaf Woodlands on the left, and moist savannas and flatwoods on the right. Among the moist sites, the Southern Longleaf Savannas ( $\diamond$ ) are most distinctive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

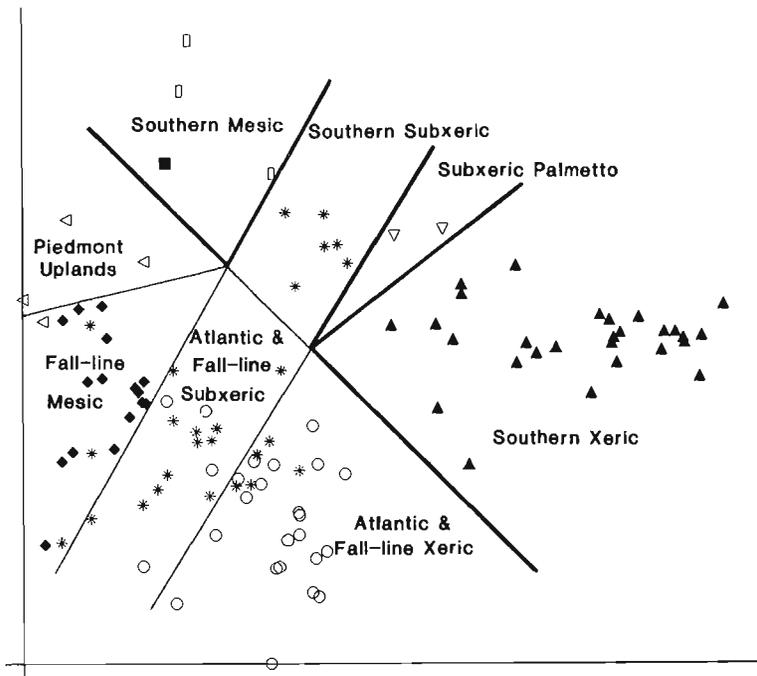


Figure 4. Ordination 2 was constructed using only sites from the dry half of the dataset (as defined by the bold line in Figure 3). A moisture gradient runs from the Xeric Longleaf Woodland sites on coarse quartz sands in the lower right ( $\blacktriangle$  = Southern;  $\circ$  = Fall-line and Atlantic), through Subxeric Longleaf Woodlands ( $*$ ,  $\triangle$ ) to moister sites on finer-textured, more fertile soils in the upper left ( $\square$  = Southern Mesic;  $\blacklozenge$  = and Fall-line Mesic;  $\triangleleft$  = 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 ( $\blacksquare$ ) from the Georgia piedmont occurs among the Southern Mesic Longleaf samples.

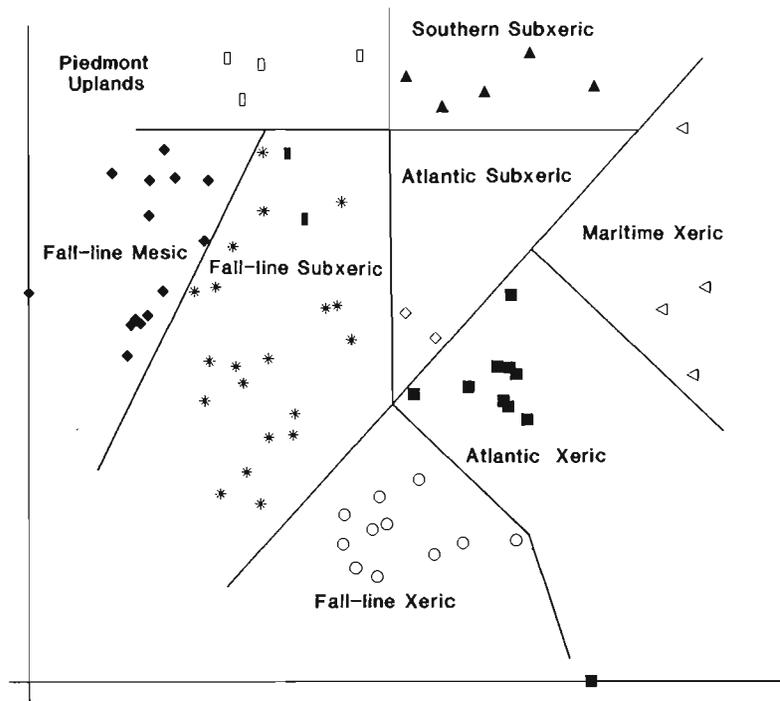


Figure 5. Ordination 3 resulted after reordinating the dry site dataset after removal of the Southern Xeric Longleaf, Subxeric Longleaf-Palmetto, and Southern Mesic Longleaf sites (defined by the bold lines in Figure 4) and the single Serpentine Subxeric Longleaf sample. A moisture gradient runs from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

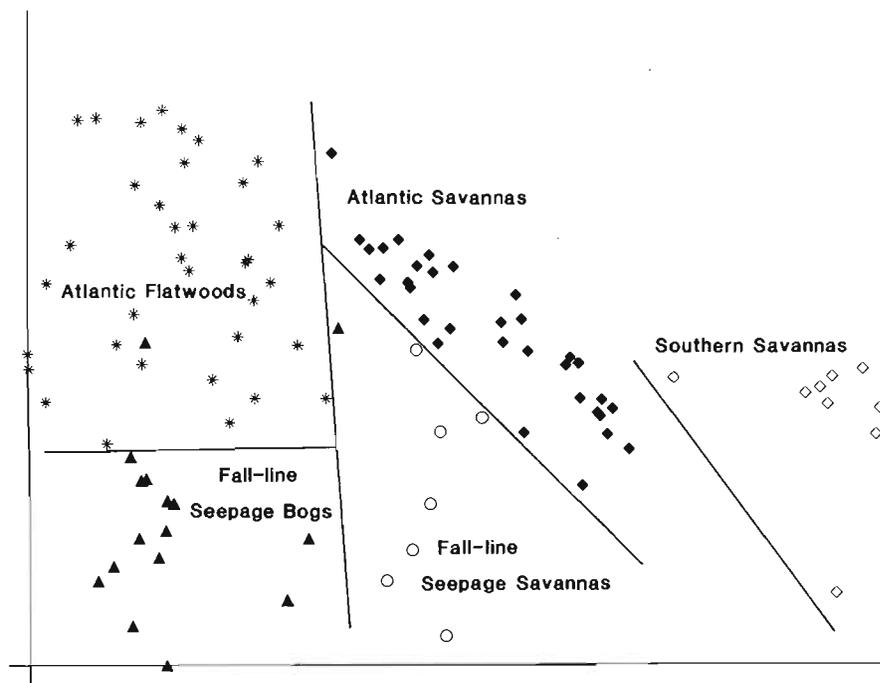


Figure 6. Ordination 5 illustrates the patterns of similarity among the Seasonally-wet Longleaf Woodlands. The more poorly-drained, nutrient-deficient Longleaf Savanna sites occur in the lower right (◊ = Southern; ♦ = Atlantic), while the somewhat more nutrient-rich, better-drained Longleaf Flatwood 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*, *Cnidocolus 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*, *Cnidocolus stimulosus*, *Schizachyrium scoparium*, *Euphorbia ipecacuanhae*, *Asclepias humistrata*, *Ionactis linariifolius*, *Aster tortifolius*, *Aureolaria pectinata*, and *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*, *Cnidocolus 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 subcaulis*, *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*, *Cnidocolus stimulosus*, *Euphorbia ipecacuanhae*, *Asclepias humistrata*, *Bulbostylis capillaris*, and *Dichantheium 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 ground-layer 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 sparseness 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 trifoliolate 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 pied-

mont 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 iron-cemented 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*), black-jack 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 Woodland (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*, *Cnidioscolus 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*, *Cnidioscolus 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. elliotii*, *Diospyros virginiana*, *Ilex vomitoria*, *Hypericum hypericoides*, *Aristida beyrichiana*, *Aster tortifolius*, *Baptisia lanceolata*, *Dichanthelium ovale*, *Galactia regularis*, *Rhynchosia reniformis*, *Lespedeza repens*, *Pteridium aquilinum*, *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. elliotii*, *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*, *Cnidioscolus 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 (*Gaylussacia* 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 post oak (*Q. margarettæ*), and pale hickory (*Carya pallida*). Fort Bragg, Hoke County, North Carolina.

*Aronia arbutifolia*, *Asplenium platyneuron*, *Pityopsis graminifolia*, *Aristida stricta*, *Gelsemium sempervirens*, and *Pyxidantha barbulate*.

#### **Serpentine Subseric 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 m<sup>2</sup>, 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, north-facing 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 ordnance 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*, *Cnidioscolus 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 (Clewelly 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 m<sup>2</sup> samples from the North Carolina fall-line sandhills have in excess of 90 species. Thus, at both 1 m<sup>2</sup> and 100 m<sup>2</sup> 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 tricolorodes*, *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., wet-mesic 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 caroliniana*, *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., *Dichantheium* 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*, *Bigelovia 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 caroliniana*, *Linum media*, *Lophiola aurea*, *Lycopodiella alopecuroides*, *L. appressa*, *Dichantheium 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 crux-andreae*, *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. elliotii*, *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 elliotii*, *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 m<sup>2</sup> ranging up to 140, the largest values yet reported for the temperate Western Hemisphere. Samples of 100 m<sup>2</sup> 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 m<sup>2</sup> from Atlantic Longleaf Savannas (NC), Southern Longleaf Savannas (MS), and Fall-line 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 × 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 × 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<sup>2</sup> 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 x 50 m (0.1 ha), with percent cover recorded for all shrub and herb species in each of 25 0.5 x 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 m<sup>2</sup> 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 m<sup>2</sup> 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 x 20 m (200 m<sup>2</sup>) 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 Woodland	Atlantic Maritime LL Woodland	Fall-line Subseric LL Woodland	Atlantic Subseric LL Woodland	Southern Subseric LL Woodland	Subseric Saw Palmetto Woodland	Piedmont/Upland LL Woodland	Serpentine Subseric 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
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 FILICAILIS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	.	.	.
AGALINIS PURPUREA	.	.	.	.	0.050	.	.	.	.	.	.	0.071	.	.	0.057	0.265	.	.
AGERATINA AROMATICA	.	.	0.074	.	0.250	.	.	.	.	.	.	0.357	0.333	.	.	.	.	.
ALETTRIS AUREA	.	.	.	.	.	.	.	.	.	.	.	.	0.667	0.111	.	0.088	0.143	.
ALETTRIS FARINOSA	.	.	.	.	0.050	.	.	.	.	.	.	0.500	0.333	.	0.260	0.647	0.571	0.125
ALETTRIS LUTEA	.	.	.	.	.	.	0.200	.	.	.	.	.	.	0.556	.	.	.	.
ANDROPOGON GERARDII	.	.	.	.	.	.	.	.	.	.	.	0.071	0.667	0.111	.	.	.	0.125
ANDROPOGON GLOMERATUS GLAUCCOPSIS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	.	.	.
ANDROPOGON MOHRII	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	.	.	.	.
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	.	.	.	.
ANDROPOGON VIRGINICUS	.	.	0.111	0.750	0.200	.	0.600	.	0.250	.	.	0.143	.	0.778	0.229	.	.	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	.	.	.	.
ARISTIDA PURPURASCENS PURPURASCENS	.	.	0.037	.	0.050	.	.	1.000	.	1.000	.	.	.	.	.	.	.	0.125
ARISTIDA PURPURASCENS VAR. VIRGATA	.	.	0.037	.	.	.	0.400	.	.	.	.	0.143	0.667	0.778	0.114	0.234	.	.
ARISTIDA STRICTA	1.000	1.000	.	1.000	1.000	0.500	.	.	.	.	1.000	1.000	0.667	0.778	0.829	0.824	0.571	0.875
ARISTOLLOCHIA SERPENTARIA	.	.	0.037	.	0.050	.	0.600	.	.	1.000	.	.	0.333	.	.	.	.	.
ARCHIA ARBUTIFOLIA	.	.	.	0.250	0.050	.	.	.	.	.	.	0.143	0.333	0.333	0.657	0.412	0.571	0.750
ARUNDINARIA GIGANTEA	0.091	.	.	0.250	.	.	.	.	.	.	.	0.071	.	.	0.314	0.353	0.429	0.438
ASCLEPIAS AMPLEXICAULIS	0.091	.	0.037	.	0.300	.	.	.	.	.	.	0.143	0.333	.	.	.	.	.
ASCLEPIAS HUMISTRATA	0.364	0.200	0.185	0.250	0.050	.	0.200	0.500	.	.	.	.	.	.	.	.	.	.
ASCLEPIAS TUBEROSA	.	.	.	.	0.050	.	.	.	.	.	.	0.071	.	.	.	.	.	0.063
ASTER ADNATUS	.	.	0.037	.	0.050	.	0.200	0.500	.	.	.	.	1.000	0.111	.	.	.	.
ASTER CONCOLOR	.	.	0.236	.	0.350	.	.	.	.	.	.	0.786	0.333	.	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	.	.	.	.	.	0.500	0.200	0.500	.	.	.	.	0.333	.	.	.	.	.
ASTER PALUDOSUS	.	.	.	.	.	.	.	.	.	.	.	.	0.333	.	0.057	0.353	0.143	0.063
ASTER PATENS	.	.	.	.	.	.	0.200	.	0.250	.	.	.	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 Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
ASTER PATERINUS	.	.	.	.	0.400	.	.	.	0.250	.	0.500	0.643	.	.	0.029	0.029	.	0.063
ASTER SERICEUS	.	.	.	.	.	.	.	.	.	.	.	.	0.667	.	.	.	.	.
ASTER SOLIDAGINEUS	0.182	.	.	.	0.150	.	.	.	.	.	0.500	0.571	.	.	0.143	0.029	0.286	0.313
ASTER SURCULOSUS	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.	0.029	.	.	.
ASTER TORTIFOLIUS	0.364	0.900	0.148	.	0.500	1.000	1.000	1.000	0.500	.	.	0.786	0.667	.	0.171	0.235	0.143	0.250
ASTER WALTERI	.	.	.	.	0.500	0.500	.	.	.	.	.	1.000	.	.	0.371	0.412	0.429	0.250
AUREOLARIA PECTINATA	0.636	0.100	0.037	.	0.250	.	.	.	0.250	.	.	.	.	.	.	.	.	.
BALDWINIA UNIFLORA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	0.086	0.059	.	.
BAPTISIA ALBA	.	.	.	.	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.
BAPTISIA CALYCOSA VILLOSA	.	.	0.444	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
BAPTISIA CINEREA	0.909	.	.	.	0.700	.	.	.	.	.	.	0.643	.	.	0.029	0.069	.	0.125
BAPTISIA LANCEOLATA	.	.	0.074	.	.	.	0.800	.	.	.	.	.	.	.	.	.	.	.
BAPTISIA TINCTORIA	0.182	.	.	.	0.200	.	.	.	.	.	0.143	.	.	.	0.057	0.029	.	0.125
BARTONIA VIRGINICA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	0.176	.	.	.
BIGELOWIA NUDATA	.	.	.	.	.	.	.	.	.	.	.	.	.	1.000	0.143	0.624	0.571	.
BOLTONIA DIFFUSA	.	.	.	.	.	.	.	.	.	.	.	.	0.667	0.222	.	.	.	.
BULBOSTYLIS CAPILLARIS	0.091	.	0.074	0.250	.	.	.	0.500	.	.	.	.	.	.	.	.	.	0.063
BULBOSTYLIS CLYMATIFOLIA	0.182	.	0.148	.	0.060	0.500	.	.	.	.	.	.	.	.	.	.	.	.
CALAMANTHA COCCINEA	.	.	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.	.	.
CALAMANTHA GEORGIANA	.	.	.	.	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.
CALLICARPA AMERICANA	.	.	.	.	.	.	0.400	0.500	.	.	.	.	.	.	.	.	.	.
CALLISIA GRAMINEA	0.273	.	.	0.500	0.300	.	.	.	.	.	.	0.214	.	.	.	.	.	.
CALOPOGON PALLIDUS & BARBATUS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.333	.	0.882	0.286	.
CALOPOGON TUBEROSUS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.571	0.125
CARPHEPHORUS BELLIDIFOLIUS	1.000	0.600	.	0.250	0.750	.	.	.	0.250	.	0.500	0.500	.	.	0.114	.	0.143	0.125
CARPHEPHORUS ODORATISSIMUS	.	0.300	0.037	.	.	.	0.600	0.500	0.250	.	.	.	0.333	.	0.543	.	.	.
CARPHEPHORUS PANICULATUS	.	0.100	.	.	.	.	.	.	.	.	.	0.071	.	.	0.429	0.706	.	0.063
CARPHEPHORUS PSEUDOLIATRIS	.	.	.	.	.	.	.	.	.	.	.	.	1.000	.	.	.	.	.
CARPHEPHORUS TOMENTOSUS	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.314	0.500	.	0.063
CARYA ALBA	.	.	.	.	0.100	0.500	.	.	.	.	.	0.357	1.000	.	.	.	.	.
CARYA PALLIDA	0.182	.	.	.	0.060	.	.	.	0.500	.	.	0.560	.	.	.	.	.	0.063
CEANOETHUS AMERICANUS	.	.	0.074	.	0.330	.	0.200	.	.	.	.	0.214	0.667	.	0.029	.	.	0.053
CENTELLA ASIATICA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	0.086	0.147	0.286	0.053
CENTROSEMA VIRGINIANUM	.	.	0.037	.	.	0.500	.	.	.	1.000	.	.	0.667	.	0.029	0.029	.	.
CHAMAECRISTA FASCICULATA	.	.	0.630	.	.	1.000	0.200	.	.	.	.	.	.	.	0.029	.	.	.
CHAMAECRISTA NICTITANS	.	.	.	.	0.100	.	.	1.000	.	.	0.500	0.429	1.000	.	0.143	.	.	0.063
CHAPTALIA TOMENTOSA	.	.	.	.	.	.	.	.	.	.	.	.	1.000	.	0.057	0.382	0.714	.
CHASMANTHUM LAXUM	.	.	.	.	.	.	0.200	.	.	.	.	0.071	.	.	0.057	.	.	0.063
CHRYSOPSIS GOSSYPINA	0.455	.	0.556	.	0.350	.	.	0.500	.	.	.	.	.	.	.	.	.	.

Sample size	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subseric LL Woodland	Atlantic Subseric LL Woodland	Southern Subseric LL Woodland	Subseric Saw Palmetto Woodland	Piedmont Upland LL Woodland	Serpentine Subseric 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
CHRYSOOPSIS MARIANA	.	.	.	.	0.100	.	0.200	.	0.250	1.000	.	0.429	1.000	0.111	0.086	0.392	0.143	.
CIRSIIUM HORRIDULUM	.	.	.	.	.	0.500	.	.	.	.	.	.	0.667	.	.	.	.	.
CIRSIIUM REPANDUM	0.818	0.100	.	.	0.750	.	.	.	.	.	.	0.571	.	.	.	.	.	0.063
CLEISTES DIVARICATA	.	.	.	.	.	.	.	.	.	.	.	0.071	.	.	0.029	0.118	0.143	0.663
CLETHRA ALNIFOLIA	.	.	.	0.250	0.150	.	.	.	0.250	.	0.500	.	.	.	0.143	.	0.429	0.875
CLITORIA MARIANA	.	.	.	.	0.250	0.500	0.500	0.500	.	.	.	0.357	.	.	.	.	.	0.125
CNIDOSCOLLIS STRIATULOSUS	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	.	.	.	0.650	1.000	0.200	.	0.250	.	.	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	0.691	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	.	.	.	.	.	.	.	.	.	.	.
CYTENNUM AROMATICUM	.	.	.	.	.	.	0.200	.	.	.	.	.	.	.	.	.	.	.
CYPERUS PILUKENETII	.	.	.	.	.	1.000	.	0.500	.	.	.	.	.	.	.	.	.	.
CYRILLA RACEMIFLORA	.	.	.	.	.	.	.	.	.	.	.	0.071	0.333	1.000	0.029	0.529	0.857	0.250
DALEA PINNATA	0.162	.	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	.	.	.	.	.
DESMODIUM LINEATUM	0.091	.	.	.	0.150	0.500	.	.	.	.	.	0.714	1.000	0.111	0.057	0.029	.	0.063
DESMODIUM MARILANDICUM	.	.	.	.	0.150	0.500	.	.	.	.	.	0.143	0.333	.	0.029	.	.	.
DESMODIUM OBUSUM	.	.	.	.	0.050	.	.	0.500	.	.	.	0.071	0.333	.	0.029	.	.	.
DESMODIUM PANICULATUM	0.162	.	.	.	0.050	0.500	0.200	.	0.250	.	.	0.071	0.667	.	.	.	.	.
DESMODIUM STRICTUM	0.162	.	0.037	.	0.200	.	.	1.000	.	.	.	0.071	0.333	.	.	.	0.143	0.063
DESMODIUM TENUIFOLIUM	.	0.100	.	.	.	.	.	.	.	.	.	0.214	.	0.111	0.257	0.176	0.286	0.125
DICHANTHELIUM ACICULARE	.	.	0.148	.	0.100	1.000	0.600	1.000	.	.	.	0.357	1.000	0.333	0.114	.	.	0.063
DICHANTHELIUM CONMULATUM	.	.	.	.	0.350	.	.	.	0.250	1.000	.	0.571	.	.	.	.	.	0.125
DICHANTHELIUM CONSANGUINEUM	.	0.100	.	0.750	0.050	.	.	.	.	.	.	.	.	0.111	0.229	0.629	0.143	.
DICHANTHELIUM DICHOTOMUM DICHOTOMUM	.	.	.	.	.	.	0.200	0.500	0.250	1.000	.	0.143	.	.	.	.	0.143	0.250
DICHANTHELIUM DICHOTOMUM ENSIFOLIUM	.	.	.	.	.	.	.	.	0.250	.	.	0.214	0.667	0.778	0.114	0.706	0.857	0.313
DICHANTHELIUM DICHOTOMUM TENUE	.	.	.	.	0.100	.	.	.	.	.	.	0.357	.	0.333	0.143	.	.	0.250
DICHANTHELIUM LONGILIGULATUM	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	.	.	.	.
DICHANTHELIUM OLIGOSANTHES	.	.	.	.	0.150	.	0.200	.	.	.	.	0.143	.	.	.	.	.	0.063
DICHANTHELIUM OVALE	0.273	0.100	0.148	.	0.650	1.000	1.000	.	0.250	.	.	0.929	1.000	.	.	0.147	0.143	0.375
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	Atlantic Maritime LL Woodland	Fall-line Subxeric LL Woodland	Atlantic Subxeric LL Woodland	Southern Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
DICHANTHELIUM STRIGOSUM LEUCOBLEPHARIS	.	.	.	.	.	0.500	.	.	.	.	.	0.071	0.667	.	0.257	0.382	0.429	0.063
DICHANTHELIUM STRIGOSUM STRIGOSUM	.	.	.	.	.	.	.	.	.	.	.	0.071	.	0.444	0.057	.	.	0.188
DIONAEA MUSCIPULA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.588	.	0.063
DIOSPYROS VIRGINIANA	0.727	0.300	0.815	0.500	0.550	1.000	1.000	.	0.500	.	1.000	0.929	1.000	0.111	0.257	.	.	0.438
DROSER A BREVIFOLIA	.	.	.	.	.	.	.	.	.	.	.	0.071	.	0.111	.	0.029	0.143	0.063
DROSER A CAPILLARIS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	0.057	0.500	0.714	0.063
DYSCHORISTE OBLONGIFOLIA	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.	.	.	.	.
ELEPHANTOPUS ELATUS	.	.	0.074	.	.	.	0.200	1.000	.	.	.	.	0.333	.	.	.	.	.
ELEPHANTOPUS NUDATUS	.	.	.	.	.	.	0.400	.	.	.	.	0.286	.	.	0.066	0.118	.	0.250
ELEPHANTOPUS TOMENTOSUS	.	.	.	.	.	.	0.200	.	0.250	.	.	0.214	0.667	.	.	.	.	0.053
ERIGAEA REPENS	0.364	.	.	.	0.500	.	.	.	.	.	1.000	0.143	.	.	.	.	.	0.063
ERIGERON STRIGOSUS	.	.	.	.	0.200	0.500	.	.	.	1.000	.	0.071	0.333	.	.	.	.	0.063
ERIGERON VERNUS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	0.057	0.853	0.714	0.063
ERIOCAULON COMPRESSUM	.	.	.	.	.	.	.	.	.	.	.	.	.	0.667	.	.	.	.
ERIOCAULON DECANGULARE	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	.	0.205	0.143	.
ERIOGONUM TOMENTOSUM	.	.	0.852	.	.	.	0.400	.	.	.	.	.	.	.	.	.	.	.
ERYNGIUM INTEGRIFOLIUM	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	0.029	0.500	0.571	.
ERYNGIUM YUCCIFOLIUM	.	.	.	.	.	.	0.200	.	.	.	.	0.071	0.333	0.111	.	0.059	.	.
EUPATORIUM ALBUM	.	0.100	.	.	0.450	.	0.600	.	.	.	.	0.714	1.000	.	.	0.029	.	0.125
EUPATORIUM COMPOSITIFOLIUM	0.182	.	0.037	.	0.060	1.000	0.200	.	.	.	.	0.214	.	.	0.029	.	0.143	0.125
EUPATORIUM GLAUDESCENS	0.182	.	.	.	0.150	.	.	.	.	.	.	0.071	.	.	.	.	.	0.063
EUPATORIUM LEUCOLEPIS	0.091	.	.	.	.	.	.	.	.	.	.	0.143	.	0.556	0.314	0.794	0.714	0.188
EUPATORIUM MOHRII	0.091	.	.	.	0.050	.	.	.	.	.	.	0.500	.	.	0.057	.	0.143	0.375
EUPATORIUM PILOSUM	.	.	.	.	0.150	.	.	.	.	.	.	0.571	.	.	0.286	.	0.714	0.500
EUPATORIUM ROTUNDFOLIUM	0.091	.	.	.	0.150	.	0.200	.	0.250	.	.	0.857	1.000	0.111	0.400	0.618	0.857	0.875
EUPATORIUM SEMISERRATUM	.	.	.	.	.	0.500	.	0.500	.	.	.	0.667	0.111	.	.	.	.	.
EUPHORBIA COROLLATA	.	0.100	0.037	0.250	0.300	0.500	0.200	0.500	0.250	1.000	.	0.143	1.000	.	.	.	.	0.063
EUPHORBIA CURTISII	0.364	.	0.222	.	0.400	.	.	.	0.250	.	.	0.786	.	.	.	0.205	.	0.375
EUPHORBIA EXSERTA	.	.	.	.	0.150	.	.	.	.	.	.	0.571	.	.	.	.	0.143	.
EUPHORBIA FLORIDANA	.	.	0.667	.	.	.	0.600	.	.	.	.	.	.	.	.	.	.	.
EUPHORBIA IPECACUANHAE	1.000	0.500	.	0.500	0.650	.	0.400	.	.	.	.	0.214	.	.	.	.	.	.
EUTHAMIA TENUFOLIA	.	.	.	.	.	1.000	.	.	.	.	.	.	.	0.111	0.171	0.059	.	0.063
GALACTIA ERECTA	0.091	.	0.259	.	0.200	.	0.400	.	.	.	.	0.571	0.667	.	.	.	.	0.063
GALACTIA REGULARIS	0.636	0.300	0.593	.	0.450	1.000	0.800	0.500	.	.	0.500	0.286	0.333	.	0.029	.	0.143	0.125
GALACTIA VOLLUBILIS	.	.	0.037	.	.	0.500	0.200	.	.	.	.	0.071	0.667	.	.	.	.	.
GALAX URCEOLATA	.	.	.	.	.	.	.	.	.	.	0.500	.	.	.	.	.	.	.
GALIUM HISPIDULUM	.	.	.	.	0.050	.	.	.	.	.	.	.	.	.	.	.	.	.
GALIUM PILOSUM	0.091	.	0.148	.	0.400	.	0.600	.	.	.	.	0.571	0.667	.	.	.	.	0.053
GAMOCOAETA PURPUREA	0.091	.	.	.	0.050	.	.	.	.	.	.	0.143	.	.	0.029	.	.	.

Sample size	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 Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
GAYLUSSACIA DUMOSA	0.818	0.700	0.037	0.500	0.750	1.000	0.600	.	0.500	.	1.000	1.000	0.667	.	0.657	0.353	0.429	0.625
GAYLUSSACIA FRONDOSA	0.091	0.700	.	0.250	0.050	0.500	.	.	0.250	.	1.000	0.357	.	.	0.800	0.471	0.429	0.813
GELSEMIUM SEMPERVIRENS	.	0.100	0.111	0.500	0.050	.	1.000	0.500	0.250	1.000	.	0.286	0.333	.	0.343	.	.	0.125
GENTIANA AUTUMNALIS	.	.	.	.	0.200	.	.	.	.	.	0.500	0.429	.	.	0.086	.	.	0.313
GRATIOLA PILOSA	.	.	.	.	.	.	.	.	.	.	.	0.143	.	.	0.029	0.147	0.143	0.125
GYMNOPOGON AMBIGUUS	.	.	0.222	.	.	0.500	0.200	.	.	.	.	.	1.000	.	.	.	.	0.053
GYMNOPOGON BREVIFOLIUS	0.091	.	.	.	0.150	.	.	.	.	.	.	0.429	1.000	0.556	.	0.147	0.286	0.125
HELIANTHEMUM CANADENSE	0.091	.	.	.	.	0.500	0.400	.	.	.	.	0.143	.	.	.	.	.	.
HELIANTHUS ANGUSTIFOLIUS	.	.	0.037	.	.	.	.	.	.	.	.	.	0.333	0.222	.	0.206	0.429	.
HELIANTHUS ATRO-RUBENS	0.031	.	.	.	0.050	.	.	.	.	.	.	0.571	.	.	0.029	.	.	.
HELIANTHUS HETEROPHYLLUS	.	.	.	.	.	.	.	.	.	.	.	.	1.000	0.029	0.559	0.143	.	.
HIERACIUM GROSSUM	0.091	0.100	0.074	.	0.200	1.000	0.400	0.500	0.250	.	.	0.214	0.667	.	0.086	.	.	0.053
HIERACIUM X MARIANUM	0.091	.	.	.	0.400	.	.	.	.	.	0.500	0.500	.	.	.	.	.	0.125
HOUSTONIA LONGIFOLIA	.	.	.	.	.	.	.	.	.	1.000	.	0.071	.	.	.	.	.	.
HOUSTONIA PROCUMBENS	.	.	0.185	.	.	.	0.600	1.000	.	.	.	.	0.333	.	.	.	.	.
HYPERICUM CRUX-ANDRAE	.	.	.	.	.	.	0.200	.	.	.	.	0.071	1.000	0.222	0.257	0.235	0.857	0.375
HYPERICUM DENTICULATUM	.	.	.	.	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.
HYPERICUM GENTIANOIDES	0.273	.	0.111	.	.	.	0.200	.	.	1.000	.	0.071	.	.	.	.	.	0.053
HYPERICUM HYPERICOIDES	0.909	0.100	0.185	0.250	0.500	1.000	0.800	1.000	0.500	1.000	0.500	0.571	0.667	.	0.114	.	.	0.250
HYPOXIS HIRSUTA	.	.	.	.	.	.	.	.	0.250	1.000	.	0.143	.	0.333	.	.	.	.
HYPOXIS MGRANTHA	.	.	.	.	0.300	.	.	.	.	.	.	0.143	.	.	.	0.471	0.571	.
ILEX CORIACEA	.	.	.	.	.	.	.	.	.	.	.	0.143	0.333	.	0.286	0.029	.	0.250
ILEX GLABRA	.	0.200	0.037	0.250	0.100	.	0.800	0.500	.	.	.	0.357	0.333	0.889	0.914	0.794	0.857	0.625
ILEX OPACA	.	0.100	0.037	0.750	0.050	.	0.600	.	.	.	.	0.071	0.333	.	0.200	.	.	0.125
ILEX VOMITORIA	.	.	0.074	0.500	.	.	1.000	1.000	.	.	.	.	0.667	.	.	.	.	.
IGNACIUS LINARIFOLIUS	0.455	0.800	0.074	.	0.750	1.000	0.600	1.000	.	.	.	0.929	1.000	.	0.486	0.324	0.286	0.188
IRIS VERNA VERNA	0.273	.	.	.	0.500	.	.	.	0.250	.	.	0.857	.	.	0.457	0.235	0.286	0.563
JUNCUS BIFLORUS	.	.	.	.	0.050	.	.	.	.	.	.	0.071	.	.	0.029	.	.	0.053
KALMIA LATIFOLIA	.	.	.	.	.	.	.	.	0.250	.	1.000	.	.	.	.	.	.	.
LACHNANTHES CAROLINIANA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	0.057	0.176	.	.
LACHNOCAULON ANCEPS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.333	0.086	0.765	0.857	0.438
LECHEA MINOR	.	.	0.037	.	.	.	0.200	.	.	.	.	.	1.000	.	0.029	.	.	.
LECHEA SESSLIFLORA	.	.	0.630	.	.	.	.	1.000	.	.	.	.	.	.	.	.	.	.
LESPEDEZA ANGUSTIFOLIA	.	.	.	.	0.050	.	.	.	.	.	.	0.429	.	.	0.114	0.029	.	0.125
LESPEDEZA CAPITATA	0.091	.	.	.	0.250	.	.	.	.	.	.	0.714	0.667	0.111	0.314	0.265	0.429	0.250
LESPEDEZA HIRTA	.	0.100	0.074	.	0.200	.	0.200	.	.	.	.	.	0.333	.	0.029	.	.	0.053
LESPEDEZA INTERMEDIA	.	.	.	.	0.050	.	.	.	.	.	.	0.071	.	.	.	.	.	0.053
LESPEDEZA PROCUMBENS	0.091	.	0.037	.	0.050	.	0.200	.	.	.	.	.	.	.	.	.	.	.
LESPEDEZA REPENS	0.091	.	0.222	.	0.400	0.500	0.800	.	0.250	.	.	0.929	1.000	.	0.029	0.059	.	0.125

	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 Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
LESPEDEZA VIRGINICA	.	.	.	.	0.250	.	.	.	0.250	.	0.500	0.571	0.667	.	0.029	.	0.286	0.053
LIATRIS GRAMINIFOLIA	0.727	0.300	0.111	.	0.750	0.500	.	.	.	.	.	0.571	.	.	0.235	.	0.571	0.053
LIATRIS SPICATA	0.091	.	.	.	.	.	.	.	.	.	.	0.286	.	0.667	0.086	0.176	0.143	.
LIATRIS SQUARROSA	.	.	.	.	0.050	.	.	.	.	.	.	.	1.000	.	.	.	.	.
LIATRIS SQUARRULOSA	.	.	.	.	.	.	.	.	.	.	.	.	0.667	.	.	.	.	.
LICANIA MICHAUDII	.	.	0.852	.	.	.	0.400	0.500	.	.	.	.	.	.	.	.	.	.
LIQUIDAMBAR STYRACIFLUA	.	.	.	.	.	.	0.200	.	0.250	.	.	.	.	.	0.457	0.059	.	0.125
LOBELIA BREVIIFOLIA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.889	.	.	.	.
LOBELIA NUTTALLII	.	.	.	.	.	.	.	.	.	.	.	0.143	.	.	0.114	0.765	0.429	0.375
LOBELIA PUBERULA	.	.	.	.	.	.	.	.	.	.	.	.	1.000	0.111	.	.	.	.
LOPHICLA AUREA	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	.	.	.	.
LUDWIGIA HIRTIELLA	.	.	.	.	0.050	.	.	.	.	.	.	.	.	0.111	.	.	.	.
LUDWIGIA VIRGATA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.111	0.086	0.118	0.266	0.063
LYCOPODIELLA ALOPECUROIDES	.	.	.	.	.	.	.	.	.	.	.	0.071	.	0.111	0.029	0.471	0.429	.
LYCOPODIELLA CAROLINIANA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.111	.	0.324	0.143	0.188
LYONIA LIGUSTRINA	.	.	.	.	.	.	.	.	.	.	.	0.214	.	.	0.114	0.429	0.438	0.438
LYONIA MARIANA	.	0.100	.	0.250	0.400	0.500	.	.	0.250	.	1.000	0.571	.	0.457	0.118	0.266	0.688	
MAGNOLIA VIRGINIANA	.	.	.	0.250	0.050	.	.	0.500	.	.	.	0.286	.	.	0.486	0.353	0.266	0.250
MANFREDIA VIRGINICA	.	.	.	.	.	.	.	.	.	1.000	.	.	0.333	.	.	.	.	.
MARSHALLIA GRAMINIFOLIA	.	0.100	.	.	.	.	.	.	.	.	.	.	.	.	0.029	0.412	0.429	.
MARSHALLIA OBOVATA	0.091	.	.	.	0.100	.	.	.	.	.	.	0.286	.	.	.	.	0.143	.
MARSHALLIA RAMOSA	.	.	.	.	.	.	.	.	1.000	.	.	.	.	.	.	.	.	.
MIMOSA QUADRIVALVIS	.	.	0.519	.	0.200	.	0.400	.	.	.	.	0.357	0.667	.	.	.	.	0.063
MINJARTIA CAROLINIANA	0.727	.	0.185	.	0.050	.	.	.	.	.	.	.	.	.	.	.	.	0.063
MULLENBERGIA CAPILLARIS TRICHOPODES	.	.	0.074	.	.	.	0.200	.	.	.	.	0.071	.	0.778	0.676	0.429	0.125	0.125
MYRICA CERIFERA	.	0.800	0.037	1.000	0.050	1.000	.	0.500	.	.	0.500	.	1.000	0.444	0.829	0.735	0.143	0.063
MYRICA HETEROPHYLLA	.	.	.	.	.	.	.	.	.	.	.	0.143	.	.	0.343	0.441	0.571	0.563
NYSSA BIFLORA	.	0.100	.	.	.	.	.	.	.	.	.	.	.	0.111	0.114	0.176	.	0.250
NYSSA SYLVATICA	.	0.100	.	0.250	0.150	.	0.200	.	0.250	.	1.000	0.500	1.000	.	0.200	.	.	0.375
OENOTHERA FRUITICOSA	.	.	.	.	0.150	.	.	.	.	1.000	.	0.286	.	.	0.029	0.029	0.143	.
OPUNTIA HUMIFUSA	0.182	.	0.148	.	0.050	.	.	1.000	.	.	.	.	.	.	.	.	.	.
ORBEXILLUM PEDUNCULATUM PSORALICOIDES	0.091	.	.	.	0.150	.	.	.	.	.	.	0.429	.	.	.	0.147	0.286	0.313
OSMANTHUS AMERICANUS	.	.	.	0.750	.	.	0.200	0.500	.	.	.	.	0.333	.	.	.	.	.
OSMUNDA CINNAMOMEA	.	.	.	.	0.050	.	.	.	.	.	.	0.143	.	.	0.257	0.029	0.714	0.688
OXYDENDRUM ARBOREUM	.	.	.	.	0.100	.	.	.	0.250	.	0.500	0.071	.	.	.	.	.	0.125
OXYPOLIS FILIFORMIS	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	.	.	.	.
OXYPOLIS TERNATA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	0.059	0.429	0.125
PANICUM ANCEPS	.	.	.	.	.	0.500	0.400	.	.	.	.	.	1.000	0.222	0.029	.	.	.
PANICUM VIRGATUM	0.091	.	0.259	.	.	.	0.200	.	.	.	.	0.071	.	0.556	0.029	0.088	0.286	0.188
PASPALUM LAEVE	.	.	.	.	0.050	.	.	.	.	.	.	.	0.667	0.111	.	0.058	.	.

	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 Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
PASPALLUM PRAECOX	.	.	.	.	.	.	.	.	.	.	.	.	.	0.556	.	0.059	.	.
PASPALLUM SETACEUM	.	.	0.037	.	.	.	0.400	1.000	.	.	.	0.333	0.222	0.029	0.029	.	.	.
PENSTEMON AUSTRALIS	.	.	0.037	.	0.200	0.500	.	.	.	.	.	0.286	.	.	.	.	.	0.063
PERSEA BORBONIA	.	0.300	.	0.750	0.050	.	.	.	.	.	.	0.071	0.333	.	0.571	.	.	.
PERSEA PALUSTRIS	.	.	.	.	0.050	.	.	.	.	.	.	.	.	.	.	0.059	0.143	0.500
PINGICULA SPP.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.444	.	0.206	0.143	0.063
PINUS ECHINATA	.	.	.	.	0.050	.	.	.	0.500	1.000	.	.	0.333	.	.	.	.	0.063
PINUS PALUSTRIS	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PINUS SEROTINA	.	.	.	.	0.100	.	.	.	.	.	.	0.214	.	.	0.257	0.647	0.429	0.500
PINUS TAEDA	0.182	0.200	0.037	1.000	0.150	.	0.400	.	0.500	1.000	.	0.286	0.333	0.222	0.200	.	.	0.063
PITYOPSIS GRAMINIFOLIA	1.000	0.100	0.889	0.250	0.900	1.000	0.600	1.000	0.250	1.000	0.500	0.929	1.000	0.333	0.114	0.882	0.286	0.250
POLYGALA CRUCIATA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	.	0.382	.	.
POLYGALA LUTEA	.	.	.	.	.	.	.	.	0.250	.	.	.	.	.	0.371	0.912	0.571	0.375
POLYGALA MARIANA	.	.	.	.	.	.	.	.	.	.	0.500	.	.	.	0.029	.	.	.
POLYGALA NANA	.	.	.	.	.	.	0.600	.	.	.	.	.	0.667	.	.	.	.	.
POLYGALA POLYGAMA	0.091	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POLYGALA RAHOSA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.444	.	0.206	0.143	.
POLYGONELLA GRACILIS	.	.	0.704	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
POLYGONELLA POLYGAMA	0.091	.	0.037	0.500	.	0.500	.	.	.	.	.	0.071	.	.	.	.	.	.
POTENTILLA CANADENSIS	.	.	.	.	.	.	.	.	0.250	.	.	0.571	.	.	.	0.029	0.286	0.063
PRUNUS SEROTINA	.	.	0.037	.	0.600	0.500	0.600	.	0.250	.	0.500	0.429	1.000	.	.	.	.	0.188
PTERIDIUM AQUILINUM	.	0.400	0.407	0.250	0.400	0.500	0.800	.	0.500	.	0.500	0.857	0.333	.	0.657	0.647	0.571	0.813
PTEROCaulon VIRGATUM	.	.	0.148	0.250	.	1.000	.	.	.	.	.	.	.	.	0.171	0.118	.	.
PYCNANTHEMUM FLEXUOSUM	.	.	.	.	.	.	.	.	.	.	.	0.286	.	.	0.086	0.098	0.857	0.375
PYRIDANTHERA BARBULATA	0.091	.	.	.	0.100	.	.	.	.	.	0.500	.	.	.	0.114	.	.	0.125
QUERCUS FALCATA	.	0.300	.	.	0.150	0.500	0.800	1.000	0.250	.	.	0.071	1.000	.	0.057	.	.	.
QUERCUS GEMINATA	.	.	0.148	1.000	.	0.500	.	.	.	.	.	.	.	.	0.029	.	.	.
QUERCUS HEMISPHERICA	.	0.100	0.037	1.000	0.050	1.000	0.400	0.500	.	.	.	0.071	0.333	.	0.057	.	.	0.063
QUERCUS INCANA	0.909	1.000	0.815	0.750	0.600	1.000	0.800	1.000	.	.	.	0.571	0.667	.	0.143	.	.	0.188
QUERCUS LAEVIS	1.000	0.500	1.000	0.750	0.950	1.000	0.800	1.000	0.250	.	0.500	0.857	0.333	.	.	.	.	0.188
QUERCUS MARGARETTAE	0.273	0.300	0.556	0.250	0.700	1.000	0.800	1.000	0.250	.	.	0.929	0.333	.	0.057	.	.	0.250
QUERCUS MARILANDICA	.	.	.	.	0.900	.	0.400	.	0.500	1.000	1.000	.	.	0.111	0.114	0.059	0.143	0.438
QUERCUS NIGRA	.	0.100	.	.	0.100	.	0.200	.	.	.	.	0.143	1.000	.	0.200	.	.	0.063
QUERCUS PUMILA	.	.	.	.	.	.	0.600	.	.	.	.	.	.	.	0.057	0.029	.	.
QUERCUS STELLATA	.	0.100	.	.	0.050	.	0.200	.	0.500	.	.	0.286	0.667	.	0.066	.	.	.
RHEXIA ALIFANUS	.	.	.	.	.	.	0.200	.	.	.	.	0.571	0.667	1.000	0.543	0.941	0.657	0.938
RHEXIA MARIANA	.	.	.	.	.	.	.	.	.	.	0.071	0.333	0.222	0.057	0.118	.	.	0.313
RHEXIA PETIOLATA	.	.	.	.	.	.	.	.	.	.	0.071	.	.	.	0.086	0.471	0.429	0.313
RHOODENDRON ATLANTICUM	.	.	.	.	0.050	.	.	.	.	.	.	0.143	.	.	0.029	0.059	.	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 LL Woodland	Southern Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
RHUS COPALLINUM	0.182	0.100	0.074	.	0.800	1.000	0.400	0.500	0.500	1.000	0.500	0.929	1.000	.	0.314	.	0.429	0.438
RHYNCHOSIA CYTISOIDES	.	.	0.593	.	.	.	0.200	1.000	.	.	.	.	.	.	.	.	.	.
RHYNCHOSIA RENIFORMIS	0.273	0.100	0.333	.	0.400	1.000	0.800	0.500	.	.	.	0.214	1.000	.	.	.	.	.
RHYNCHOSIA TOMENTOSA	.	.	.	.	.	0.500	.	.	.	.	.	0.286	0.333	.	.	.	.	.
RHYNCHOSPOA BALDWINII	.	.	.	0.250	.	.	.	.	.	.	.	.	.	0.667	.	0.412	.	.
RHYNCHOSPOA BREVISETA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.500	0.143	.
RHYNCHOSPOA CHAPMANII	.	.	.	.	.	.	.	.	.	.	.	.	.	0.667	.	0.529	0.571	0.063
RHYNCHOSPOA CILIARIS	.	.	.	.	.	.	.	.	.	.	.	0.333	0.111	0.096	0.096	0.853	.	.
RHYNCHOSPOA FASCICULARIS	.	.	.	.	.	.	.	.	.	.	.	.	0.778	0.029	0.029	0.235	.	.
RHYNCHOSPOA GLOBULARIS	.	.	.	.	.	.	.	.	.	.	.	.	0.667	0.111	.	0.088	.	.
RHYNCHOSPOA GRAYI	0.636	.	0.222	.	0.150	.	0.400	0.500	.	.	.	0.357	0.333	.	.	.	0.143	.
RHYNCHOSPOA LATIFOLIA	.	.	.	.	0.050	.	.	.	.	.	.	.	.	0.556	.	0.059	0.143	.
RHYNCHOSPOA OLIGANTHA	.	.	.	.	.	.	.	.	.	.	.	.	0.889	0.029	.	.	.	.
RHYNCHOSPOA PLUMOSA	.	.	.	.	.	.	.	.	.	.	.	.	1.000	0.171	0.765	0.266	0.063	.
RHYNCHOSPOA RARIFLORA	0.091	.	.	.	.	.	.	.	.	.	.	.	.	0.556	0.029	0.266	.	.
RUBUS ARGUTUS	.	.	.	.	0.100	.	.	.	.	1.000	.	0.071	0.667	.	0.057	.	.	0.125
RUBUS CUNEIFOLIUS	.	.	.	.	.	0.500	.	.	0.250	.	.	0.071	.	.	.	.	.	.
RUBUS FLAGELLARIS	.	.	.	.	0.150	.	0.400	.	.	.	.	0.333	.	.	0.029	.	.	0.188
RUBUS TRIMALIS	.	.	.	.	.	.	0.400	.	.	.	.	0.071	.	.	0.057	0.059	.	0.653
RUDBECKIA HIRTA	.	.	.	.	.	.	.	.	.	.	.	.	0.567	.	.	.	.	.
SABATIA CAMPANULATA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.778	.	.	.	.
SARRACENIA ALATA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.667	.	.	.	.
SARRACENIA FLAVA	.	.	.	.	.	.	.	.	.	.	.	0.071	.	.	0.086	0.294	0.429	0.653
SARRACENIA PURPUREA	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.029	0.118	0.143	0.250
SASSAFRAS ALBIDUM	0.182	0.300	0.037	1.000	0.500	0.500	0.200	1.000	0.250	.	0.500	0.500	1.000	.	0.029	.	.	0.500
SCHIZACHYRIUM SCOPARIUM	0.273	0.600	0.074	0.250	0.300	.	0.200	1.000	.	1.000	1.000	0.214	1.000	0.667	0.314	.	0.143	0.188
SCHIZACHYRIUM TENERIUM	.	.	0.259	.	.	.	.	.	.	.	.	1.000	1.000	0.111	.	.	.	.
SCLERIA CILIATA	0.273	.	0.074	.	0.500	.	.	.	0.250	1.000	.	0.357	0.333	.	0.029	.	0.143	0.063
SCLERIA MINOR	.	.	.	.	.	.	.	.	.	.	.	0.071	.	.	0.086	0.412	0.266	0.063
SCLERIA PAUCIFLORA	0.091	.	.	.	.	.	.	.	.	.	.	0.214	0.333	0.778	0.086	0.529	0.571	0.125
SCLERIA RETICULARIS	.	.	.	.	0.050	.	.	.	.	.	.	.	.	0.889	.	0.059	0.143	.
SCLERIA TRIGLOMERATA	.	0.200	.	.	0.400	0.500	.	.	.	.	.	0.714	.	.	0.114	.	.	0.375
SERENOA REPENS	.	.	0.630	.	.	.	.	1.000	.	.	.	.	.	.	.	.	.	.
SEYMERIA CASSIOIDES	.	.	.	.	0.200	.	.	.	.	.	0.500	0.071	.	.	0.086	0.529	.	.
SILPHIUM COMPOSITUM	0.354	.	0.185	.	0.750	0.500	0.600	.	.	.	.	0.643	.	.	.	.	.	0.125
SISYRINCHIUM ALBIDUM	.	.	0.074	.	0.100	.	.	.	.	.	.	0.071	0.333	.	0.029	.	.	0.653
SISYRINCHIUM NASHII	0.182	.	0.259	1.000	0.100	.	.	.	.	.	.	0.143	.	.	.	.	0.143	0.125
SMILAX AURICULATA	.	.	0.259	1.000	.	.	0.400	.	.	.	.	.	0.333	.	.	.	.	.
SMILAX BONA-NOX	.	0.100	0.037	.	.	.	1.000	.	.	1.000	.	.	.	.	0.029	.	.	0.063

Sample size	Fall-line Xeric LL Woodland	Atlantic Xeric LL Woodland	Southern Xeric LL Woodland	Atlantic Maritime LL Woodland	Fall-line Subseric LL Woodland	Atlantic Subseric LL Woodland	Southern Subseric LL Woodland	Subseric Saw Palmetto Woodland	Piedmont/Upland LL Woodland	Serpentine Subseric 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
SMILAX GLAUCA		0.400		0.250	0.600		0.200		0.500	1.000	0.500	0.714	1.000	0.111	0.457			0.625
SMILAX LAURIFOLIA								0.500						0.333	0.229	0.029	0.286	0.500
SMILAX PUBULA			0.074					1.000					0.333					
SMILAX ROTUNDIFOLIA					0.050						1.000	0.071	0.667		0.029			
SMILAX SMALLII							0.400						0.667					
SOLIDAGO ODORA	0.364		0.630		0.900	1.000	0.600	0.500	0.250		0.500	0.857	1.000	0.111	0.343	0.059	0.571	0.560
SOLIDAGO RUGOSA													0.667					
SOLIDAGO STRICTA & PULCHRA															0.086	0.882	0.571	
SORGHASTRUM NUTANS					0.200		0.200			1.000		0.429	0.333		0.029	0.029		0.168
SPOROBOLUS JUNCEUS	0.364		0.815		0.200			0.500		1.000		0.071	0.667					
STILLINGIA SYLVATICA	0.182		0.370		0.150		0.600											
STIPULICIDA SETACEA	1.000			0.250	0.150							0.071						0.063
STROPHOSTYLES UMBELLATA													0.667					
STYLISMA PATEHS	0.818	0.330	0.778	0.250	0.350	1.000	0.800	1.000				0.357	0.333					
STYLOCOON CARINEUS					0.050	0.500	0.200					0.071						
STYLOSANTHES BIFLORA	0.182		0.556		0.550	1.000	0.400	0.500		1.000		0.786	1.000		0.143	0.294	0.286	0.125
SYMPLOSIS TRICOLORIA					0.100	0.500		0.500	0.250			0.071			0.257	0.029		0.125
TEPHROSIA CHRYSOPHYLLA			0.593					1.000										
TEPHROSIA FLORIDA	0.455	0.200	0.148		0.300	1.000						0.429	1.000		0.057			0.188
TEPHROSIA HISPIDULA		0.100						0.500							0.200	0.294		
TEPHROSIA ONOBRYCHOIDES													0.667	0.111				
TEPHROSIA SPICATA					0.050							0.429	0.667		0.114		0.143	
TEPHROSIA VIRGINIANA	0.091	0.100	0.074		0.650	0.500	0.600		0.500		0.500	0.929	0.667		0.114	0.029	0.143	0.250
TOPFIELDIA RACEMOSA														0.222		0.706	0.429	
TOXICODENDRON PUBESCENS	0.455	0.100	0.074		0.800		0.400	1.000				0.857	1.000					0.313
TOXICODENDRON RADICANS		0.200		0.250			0.250					0.071			0.143			0.125
TOXICODENDRON VERNIX								0.500									0.286	0.188
TRAGIA URENS	0.636	0.400	0.222		0.350	1.000	0.800	0.500				0.643	0.333					0.125
UTRICULARIA SUBULATA														0.556		0.029	0.143	
VACCINIUM ARBOREUM	0.091	0.200	0.111	1.000	0.150	1.000	1.000	0.500	0.250			0.214	1.000					
VACCINIUM CRASSIFOLIUM		0.500		0.250	0.200						1.000	0.286			0.743	0.618	0.429	0.375
VACCINIUM DARROWII							0.200						0.667					
VACCINIUM ELLIOTTII			0.111				1.000	1.000	0.250	1.000		0.071	1.000					
VACCINIUM FORMOSUM									0.250			0.214						
VACCINIUM FUSCUM		0.100	0.037		0.050	0.500	0.600	1.000	0.500			0.143			0.486	0.029	0.429	0.563
VACCINIUM MYRSINITES			0.295		0.050		0.200											
VACCINIUM STAMINEUM	0.091	0.600	0.148	0.250	0.100	1.000	0.400	1.000	0.250	1.000			1.000		0.029			
VACCINIUM TENELLUM	0.091	0.800		0.750	0.600				0.250		1.000	1.000			0.800	0.059	0.429	0.625
VERNONIA ACAULIS									0.250	1.000		0.571			0.057	0.059		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 Subxeric LL Woodland	Subxeric Saw Palmetto Woodland	Piedmont/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
VERNONIA ANGUSTIFOLIA	0.354	0.100	0.296	.	0.500	1.000	0.400	.	.	.	.	0.214	.	.	.	.	.	0.125
VIOLA PEDATA	0.273	.	.	.	0.450	.	0.400	.	.	1.000	.	0.571	0.667	.	.	.	.	0.188
VIOLA PRINULIFOLIA	.	.	.	.	.	.	.	.	.	.	.	0.143	.	.	0.029	0.294	0.714	0.063
VIOLA SAGITTATA	.	.	.	.	.	.	.	.	.	1.000	.	.	.	.	0.029	.	.	.
VITIS ROTUNDFOLIA	.	0.100	0.074	0.500	0.300	0.500	0.600	.	0.500	1.000	.	0.429	0.333	.	0.086	.	.	0.250
XYRIS AUBIGLIA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.869	0.057	0.353	0.714	0.188
XYRIS BALDWINIANA	.	.	.	.	.	.	.	.	.	.	.	.	.	0.444	.	0.118	0.143	.
XYRIS CAROLINIANA	.	.	.	.	.	.	.	.	.	.	.	0.143	.	0.222	0.543	0.912	0.571	0.625
YUCCA FILAMENTOSA	.	.	0.481	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ZIGADENUS DENSUS	.	.	.	.	.	.	.	.	.	.	.	.	.	0.111	0.029	0.176	0.286	.
ZIGADENUS GLABERRIMUS	.	.	.	.	0.100	.	.	.	.	.	.	.	.	0.222	0.029	0.088	0.143	0.313

## LITERATURE CITED

- Abrahamson, W.G. and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. Pages 103-149 in *Ecosystems of Florida*. R.L. Myers and J.J. Ewel, eds. The University of Central Florida Press, Orlando.
- Allard, D.J. 1990. Southeastern United States ecological community classification. Interim report, Version 1.2. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC.
- Allen, R.M. 1956. Relation of saw-palmetto to longleaf pine reproduction on a dry site. *Ecology* 37:195-196.
- Beckett, S. and M.S. Golden. 1982. Forest vegetation and vascular flora of Reed Brake Research Natural Area, Alabama. *Castanea* 47:368-392.
- Bozeman, J.R. 1971. A sociologic and geographic study of the sand ridge vegetation of the coastal plain of Georgia. Ph.D. Dissertation, University of North Carolina, Chapel Hill, NC.
- Braun, E.L. 1950. *Deciduous forests of eastern North America*. Hafner, New York.
- Bridges, E.L. and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. *Natural Areas Journal* 9:246-263.
- Christensen, N.L. 1979. The xeric sandhill and savanna ecosystems of the southeastern Atlantic coastal plain. *Veröffentlichungen Geobotanischen Institutes, ETH, Stiftung Rübel, Zürich*. 68:246-262.
- Christensen, N.L. 1988. Vegetation of the southeastern coastal plain. Pages 317-363 in *North American Terrestrial Vegetation*. M.G. Barbour and W.D. Billings, eds. Cambridge University Press, Cambridge.
- Clewell, A.F. 1971. The vegetation of the Apalachicola National Forest: an ecological perspective. Contract 38-2249, Final Report. U.S. Forest Service, Atlanta, Georgia.
- Crocker, T.C. 1987. Longleaf pine: a history of man and a forest. U.S. Department of Agriculture, Forest Service, Forestry Report R8-FR7.
- Daniels, R.B., H.J. Kleiss, S.W. Buol, H.J. Byrd and J.A. Phillips. 1984. Soil systems in North Carolina. North Carolina Agricultural Research Service, Bulletin 467, Raleigh, NC
- DuBar, J.R., H.S. Johnson Jr., B.G. Thom and W.O. Hatchell. 1974. Neogene stratigraphy and morphology, south flank of the Cape Fear arch, North and South Carolina. Pages 139-173 in *Post-Miocene stratigraphy, Central and Southern Atlantic Coastal Plain*. R.Q. Oaks Jr. and J.R. DuBar, eds. Utah State University Press, Logan, UT.
- Eleutrius, L.N. 1968. Floristics and ecology of coastal bogs in Mississippi. Masters Thesis, University of Southern Mississippi, Hattiesburg, MS.
- Fenneman, N.M. 1938. *Physiography of Eastern United States*. McGraw-Hill, New York, NY.
- Folkerts, G.W. 1982. The Gulf Coast pitcher plant bogs. *American Scientist* 70:260-267.
- Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. In *The longleaf pine ecosystem: ecology, restoration and management*. This volume.
- Frost, C.C., and L.J. Musselman. 1987. History and vegetation of the Blackwater Ecologic Preserve. *Castanea* 52:16-46.
- Frost, C.C., J. Walker and R.K. Peet. 1986. Fire-dependent savannas and prairies of the Southeast: original extent, preservation status and management problems. Pages 348-357 in *Wilderness and natural areas in the Eastern United States*. D.L. Kulhavy and R.N. Conner, eds. Center for Applied Studies. Nacogdoches, TX.
- Gano, L. 1917. A study of physiographic ecology in northern Florida. *Botanical Gazette* 63:337-372.
- Golden, M.S. 1979. Forest vegetation of the lower Alabama piedmont. *Ecology* 60:770-782.
- Grelen, H.E. and V.L. Duvall. 1966. Common plants of longleaf pine - bluestem range. U.S. Department of Agriculture, Forest Service, Research Paper SO-23.
- Hammond, E.H. 1964. Classes of land surface form in the 48 states, U.S.A. *Annals of the Association of American Geographers* 54(1): map supplement.

- Harcombe, P.A., J.S. Glitzenstein, R.G. Knox, S.L. Orzell, and E.L. Bridges. 1993. Western Gulf coastal plain communities. In *The longleaf pine ecosystem: ecology, restoration and management*. This volume.
- Harper, R.M. 1906. A phytogeographical sketch of the Altamaha Grit Region of the coastal plain of Georgia. *New York Academy of Science* 7:1-415.
- Harper, R.M. 1914a. A superficial study of the pine-barren vegetation of Mississippi. *Bulletin Torrey Botanical Club* 41:551-567.
- Harper, R.M. 1914b. Geology and vegetation of North Florida. *Florida Geological Survey. Sixth Annual Report* 163-451.
- Harper, R.M. 1922. Some pine-barren bogs in central Alabama. *Torrey* 22:57-61.
- Harper, R.M. 1930. The natural resources of Georgia. School of Commerce, Bureau of Business Research, Study No. 2, *Bulletin of the University of Georgia* 30(3):105.
- Harper, R.M. 1943. Forests of Alabama. *Alabama Geological Survey Monograph* 10. Alabama Geological Survey, University of Alabama. University, AL.
- Hill, M.O. 1979. TWINSPAN - A FORTRAN Program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University. Ithaca, NY.
- Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47-58.
- Hillestad, H.O., J.R. Bozeman, A.S. Johnson, C.W. Berisford and J.I. Richardson. 1975. The ecology of Cumberland Island National Seashore, Camden County, Georgia. Technical Report Series 75-5, Georgia Marine Science Center, Skidaway Island.
- Hine, W.R.B. 1925. Hogs, fire, and disease versus longleaf pine. *Southern Lumberman* 119(1544):45-46.
- Hodgkins, E.J. 1965. Southeastern forest habitat regions based on physiography. Agricultural Experiment Station, Auburn University, Forestry Department Series, No. 2. Auburn, AL.
- Hodgkins, E.J. M.S. Golden and W.F. Miller. 1979. Forest habitat regions and types on a photomorphic-physiographic basis: A guide to forest site classification in Alabama - Mississippi. Southern Coop Series 210., Alabama Agricultural Experiment Station, Auburn, Alabama.
- Kartesz, J.T. 1994. Synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Second edition. Timber Press, Portland, OR.
- Kologiski, R.L. 1977. The phytosociology of the Green Swamp, North Carolina. North Carolina Agricultural Experiment Station, Technical Bulletin 250. Raleigh, NC.
- Laessle, A.M. 1942. Plant communities of the Welaka area. University of Florida Publications in Biological Science Series 4:1-143.
- Lipscomb, D.J. 1989. Impacts of feral hogs on longleaf pine regeneration. *Southern Journal of Applied Forestry* 13:177-181.
- Little, E.L. Jr. 1971. Atlas of United States trees. Volume 1, Conifers and important hardwoods. U.S. Department of Agriculture, Forest Service, Miscellaneous Publication 1146.
- Mohr, C. 1897. Timber pines of the southern United States. U.S. Department of Agriculture, Division of Forestry. Bulletin 13.
- Mohr, C. 1901. Plant life of Alabama. Contributions U.S. National Herbarium 6.
- Monk, C.D. 1968. Successional and environmental relationships of the forest vegetation of north-central Florida. *American Midland Naturalist* 79:441-457.
- Myers, R.K., R. Zahner and S.M. Jones. 1986. Forest habitat regions of South Carolina from LANDSAT imagery. Clemson University, Department of Forestry Research Series No. 42.
- Myers, R.L. 1990. Scrub and high pine. Pages 150-193 in *Ecosystems of Florida*. R.L. Myers and J.J. Ewel, eds. University of Central Florida Press, Orlando, FL.
- Norquist, H.C. 1984. A comparative study of the soils and vegetation of savannas in Mississippi. Masters Thesis, Mississippi State University, Mississippi State, MS.

- Noss, R.F. 1988. The longleaf landscape of the Southeast: Almost gone and almost forgotten. *Endangered Species Update* 5(5):1-8.
- Noss, R.F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal* 9:211-213
- Peet, R.K. 1980. Ordination as a tool for analyzing complex data sets. *Vegetatio* 42:171-174.
- Peet, R.K. 1993. A taxonomic study of *Aristida stricta* and *A. beyrichiana*. *Rhodora* 95:25-37.
- Peet, R.K., R.G. Knox, R.B. Allen and J.S. Case. 1988. Putting things in order: the advantages of detrended correspondence analysis. *American Naturalist* 131:924-934.
- Peet, R.K., E. van der Maarel, E. Rosen, J., Willems, C. Norquist and J. Walker. 1990. Mechanisms of coexistence in species-rich grassland. *Bulletin, Ecological Society of America* 71:283.
- Penfound, W.T. and A.J. Watkins. 1937. Phytosociological studies in the pinelands of southeastern Louisiana. *American Midland Naturalist* 18:661-682.
- Pessin, L.J. 1933. Forest associations in the uplands of the Lower Gulf Coastal Plain (longleaf pine belt). *Ecology* 14:1-14.
- Pinchot, G. and W.W. Ashe. 1897. Timber trees and forests of North Carolina. *Bulletin No. 6*, North Carolina Geological Survey. Raleigh, NC.
- Plummer, G.L. 1963. Soils of the pitcher plant habitats in the Georgia coastal plain. *Ecology* 44:727-734.
- Schafale, M.P. and A.S. Weakley. 1990. Classification of the natural communities of North Carolina. Third approximation. North Carolina Natural Heritage Program. Raleigh, NC.
- Schwarz, G.F. 1907. Longleaf pine in virgin forest: a silvicultural study. John Wiley & Sons, New York, NY.
- Sellards, E.H., R.M. Harper, C.N. Mooney, W.J. Latimer, H. Gunter and E. Gunter. 1915. The natural resources of an area in Central Florida. Florida State Geological Survey, Annual Report 7:117-188.
- Snyder, J.R. 1978. Analysis of vegetation in the Croatan National Forest, North Carolina. M.A. Thesis. University of North Carolina. Chapel Hill, NC.
- Snyder, J.R. 1980. Analysis of coastal plain vegetation, Croatan National Forest, North Carolina. *Veröffentlichungen Geobotanischen Institutes, ETH, Stiftung Rübel, Zürich*. 69:40-113.
- Sohl, N.F. and J.P. Owens. 1991. Cretaceous stratigraphy of the Carolina coastal plain. Pages 191-220 in *The geology of the Carolinas*. J.W. Horton and V.A. Zullo, eds. University of Tennessee Press, Knoxville, TN.
- Soller, D.R. and H.H. Mills. 1991. Surficial geology and geomorphology. Pages 290-308 in *The geology of the Carolinas*. J.W. Horton and V.A. Zullo, eds. University of Tennessee Press, Knoxville, TN.
- Stout, I.J. and W.R. Marion. 1993. Pine flatwoods and xeric pine forests of the Southern (lower) coastal plain. Pages 373-446 in W.H. Martin, S.G. Boyce and A.C. Echternacht, eds. *Biodiversity of the Southeastern United States: Lowland terrestrial communities*. John Wiley and Sons, New York, NY.
- Taggart, J.B. 1990. Inventory, classification, and preservation of coastal plain savannas in the Carolinas. Ph.D. Dissertation. University of North Carolina. Chapel Hill, NC.
- Taggart, J.B. 1994. Ordination as an aid in determining priorities for plant community protection. *Biological Conservation* 68:135-141.
- ter Braak, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69:69-77.
- Veno, P.A. 1976. Successional relationships of five Florida plant communities. *Ecology* 57:498-508.
- Walker, J. 1985. Species diversity and production in pine-wiregrass savannas of the Green Swamp, North Carolina. Ph.D. Dissertation, University of North Carolina, Chapel Hill, NC.
- Walker, J. and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163-179.

- Ware, S., C. Frost and P.D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages 447-493 in W.H. Martin, S.G. Boyce and A.C. Echternacht, eds. *Biodiversity of the Southeastern United States: Lowland terrestrial communities*. John Wiley and Sons, New York, NY.
- Wells, B.W. 1932. *The natural gardens of North Carolina*. University of North Carolina Press, Chapel Hill, NC.
- Wells, B.W. and I.V. Shunk. 1931. The vegetation and habitat factors of the coarser sands of the North Carolina coastal plain: An ecological study. *Ecological Monographs* 1:466-520.
- Wentworth, T.R., M.P. Schafale, A.S. Weakley, R.K. Peet, P.S. White and C.C. Frost. 1992. A preliminary classification of North Carolina barrier island forests. Pages 31-46 In *Barrier island ecology of the Mid-Atlantic coast: a symposium*. C.A. Cole and K. Turner, eds. U.S. National Park Service, Technical Report NSP/SERCAHA/NRTR-93/04, Washington, DC.
- Wharton, C.H. 1978. *The natural environments of Georgia*. Georgia Department of Natural Resources. Atlanta, GA.
- Whittaker, R.H. 1954. The vegetational response to serpentine soils. *Ecology* 35:275-288.
- Wolfe, S.H., J.A. Reidenauer and D.B. Means. 1988. An ecological characterization of the Florida panhandle. U.S. Department of Interior, Fish and Wildlife Service, FWS Biological Report 88(12).
- Woodwell, G.M. 1956. *Phytosociology of coastal plain wetlands of the Carolinas*. M.S. Thesis. Duke University, Durham, NC.