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Forest ecosystems of a Lower Gulf Coastal Plain landscape: multifactor classification and analysis[1]

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GOEBEL, P. C., B. J. PALIK, L. K. KIRKMAN, M. B. DREW, AND L. WEST (J.W. Jones Ecological Research Center, Newton, GA 31770). Forest ecosystems of a Lower Gulf Coastal Plain landscape: multifactor classification and analysis. J. Torrey Bot. Soc. 128:47–75. 2001.—The most common forestland classification techniques applied in the southeastern United States are vegetation-based. While not completely ignored, the application of multifactor, hierarchical ecosystem classifications are limited despite their widespread use in other regions of the eastern United States. We present one of the few truly integrated ecosystem classifications for the southeastern Coastal Plain. Our approach is iterative, including reconnaissance, plot sampling, and multivariate analysis. Each ecosystem is distinguished by differences in physiographic setting, landform, topographic relief, soils, and vegetation. The ecosystem classification is ground-based, incorporating easily observed and measured factors of landform, soil texture, and vegetative cover associated into ecological species groups identified by two-way indicator species analysis. Canonical correspondence analyses (CCA) that measure the degree of distinctness among ecosystems using different combinations of physiographic, soil, and vegetation datasets are used to verify the classification. The hierarchical ecosystem classification provides a framework for sustainable resource management of our study landscape as an alternative to traditional cover-type or vegetation-based classifications in the southeastern Coastal Plain. This ecosystem classification provides a structural framework that mimics biological organization, by physical drivers, ensuring that information on various ecosystem components are available to assist management decisions made at the ecosystem level.

Key words: ecosystem classification, geomorphology, longleaf pine (*Pinus palustris* Mill.), wiregrass (*Aristida stricta* Michx.), ground-flora.

There are many different classification systems available to resource managers to help understand the complexities of landscapes and map them into manageable components. These tools must meet two basic requirements to be useful for developing sustainable management strategies (Pregitzer et al. 2001). First, the classification should be structured hierarchically, reflecting physical drivers of biological systems. Second, the classification system must be dynamic, with the ability to seamlessly integrate new information, as it becomes available.

Multifactor ecosystem classification that characterize inter-relationships among ecosystem components, i.e., geomorphology, physiography, soil, and vegetation, is an example of one such classification scheme that meets these requirements. Ecosystem classifications provide a framework for understanding the range of natural variation among landscape ecosystems and for delineating their boundaries (Barnes et al. 1982). Ecosystem factors are arrayed hierarchically mimicking biological organization (Rowe and Sheard 1981; Bailey 1996), with the higher levels constraining the development of lower levels. When coupled with information on current vegetation distribution and composition, the hierarchical classification provides an ecological platform that can guide management, conservation, and restoration initiatives (Palik et al. 2000).

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Regional ecosystem (e.g., Keys et al. 1995) and vegetation classifications (e.g., Peet and Allard 1993; Grossman et al. 1998) are common for the Lower Coastal Plain of the southeastern United States. However, few integrated ecosystem classifications are available at the local level (e.g., Van Lear and Jones 1987; Carter et al. 1999). Rather, most land management organizations in the Southeast rely on local vegetation classifications such as cover type maps. One explanation for the reliance on single-factor classifications may be the complex nature of the environment, e.g., high species richness, a broad array of soil types, and many different disturbance agents.

In this paper, we present one of the first truly integrated, hierarchical ecosystem classifications for a local landscape in the southeastern United States. Specifically, we 1) develop and confirm an iterative, multifactor classification of local ecosystems for a Lower Gulf Coastal Plain karst landscape of southwestern Georgia; and 2) identify and examine the abiotic factors, e.g., physiography, soils, and disturbances influencing patterns of vegetation development.

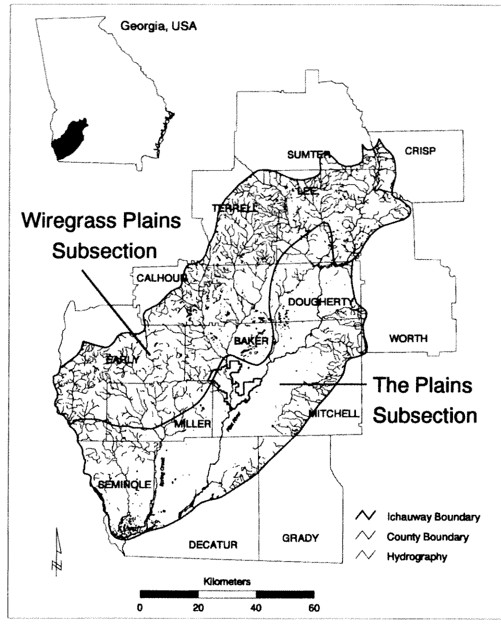

Fig. 1. Location of the Joseph W. Jones Ecological Research Center at Ichauway within The Plains and Wiregrass Plains Subsections of the Lower Gulf Coastal Plain.

Study Area. LOCATION AND CLIMATE. We developed the ecosystem classification for the Joseph W. Jones Ecological Research Center at Ichauway (31°13′N, 84°29′W), located in southwestern Georgia, U.S.A. (Fig. 1). The 11 300 ha property is located within The Plains (232Bi) and Wiregrass Plains Subsections (232Bp) of the Lower Coastal Plains and Flatwoods Section (232B; ECOMAP 1993; Keys et al. 1995). The climate is characterized by long, hot summers and short cool winters (Lynch et al. 1986). Mean annual temperature is 20°C; summer daily temperatures range from 21°C to 34°C, while winter temperatures range from 5°C to 17°C. These mild winter temperatures result in a growing season of 200 to 280 days per year (Keys et al. 1995). While variable afternoon thunderstorms and tropical depressions influence the weather patterns of the study area from mid-summer to late fall, precipitation still is evenly distributed throughout the year and averages 131 cm (National Climate Data Center, Asheville, NC). Average relative humidity ranges from 55% during the day to over 90% at night (Lynch et al. 1986).

GEOMORPHOLOGY AND SOILS. The Lower Coastal Plain and Flatwoods Section is composed of flat, weakly dissected alluvial deposits formed by deposition of continental sediments onto a submerged, continental shelf during the Mesozoic and Cenozoic Eras (McNab and Avers 1994). These deposits were then exposed with sea level subsidence. Most parent materials are marine (sands, clays, thin fossiliferous layers of sands and clays) and continental (sands and clays) deposits formed during the Mesozoic and Cenozoic Eras (Keys et al. 1995). Some Quaternary Period deposits (coarse sands) are common locally. Most soils are Paleudults and Hapludults, with some localized Quartzipsamments (Keys et al. 1995). These soils have thermic temperature (warm) and udic moisture (humid) regimes, and are deep, with fine to moderately fine textured loamy or clayey subsoils. Drainage classes range from excessively- to poorly-drained.

Irregular karst plains characterize the study area with elevations ranging from 30 to 100 m above sea level, with local relief ranging from 3 to 9 m. Two major types of karst topography characterize the landscape: 1) doline karst with numerous sinkholes, and 2) fluviokarst where soluble and less soluble rock is exposed at the surface. No major stream systems drain the doline karst materials (Fig.1). Consequently, most upland landforms, including ancient terraces, are of marine origin. Two major streams dissect the fluviokarst topography including the Flint River, a brownwater stream originating in the Piedmont of northern Georgia, and Ichawaynochaway Creek, a blackwater Coastal Plain stream with the headwaters originating in a large wetland complex. Landforms within the fluviokarst parent material were formed during the Holocene through downcutting in the two stream valleys.

VEGETATION. Ichauway contains approximately 4000 ha of fire-maintained longleaf pine (*Pinus palustris* Mill.) and wiregrass (*Aristida stricta* Michx. or *Aristida beyrichiana* Trin. and Rupr.) savannas. Historic fire regimes consisted of low to mid-intensity growing season (May–September) surface fires occurring every 2 to 10 years, depending on site conditions (Robbins and Myers 1992; Ware et al. 1993). Frequent surface fires result in floristically diverse savanna-like forests with few hardwoods in the overstory (Wahlenberg 1946; Walker and Peet 1983; Platt et al. 1988). Peet and Allard (1993) report ground-flora richness values for longleaf pine ecosystems of over 40 species per m^2, exceeding all other richness values reported for North America.

However, along many of the riparian corridors, or where surface fires are naturally excluded (e.g., depressions, natural fire breaks), southern mixed hardwood forests locally known as hammocks, are the dominant vegetation type (Quarterman and Keever 1962; Monk 1968; Ware et al. 1993). Unlike the longleaf pine-dominated ecosystems, these ecosystems have dense canopies often exceeding 30 woody species per 1000 m^2 and sparse ground-flora layers (Quarterman and Keever 1962).

LAND-USE HISTORY. Many native tribes and early European settlers frequently burned the forests with annual, dormant season surface fires to improve livestock forage and turpentine production (Bartram 1791; Wright and Bailey 1982; Denevan 1992; Robbins and Meyers, 1992). By the early to mid 1800s, large cotton plantations and small farms were common in the region (Brueckheimer 1979). With the demise of the cotton industry after the American Civil War, northern speculators purchased most of the large cotton plantations. Many of these landowners became interested in game bird hunting, primarily for bobwhite quail (*Colinus virginianus*). At the same time, forested areas were turpentined or commercially clearcut. Most of the forestland in the region had been cut over by the 1920s, and with the development of center-pivot irrigation systems in the 1960s, many of the relatively infertile lands were converted to agricultural production (Lynch et al. 1986). As a result, the natural fire regimes of most longleaf pine and associated ecosystems have been modified extensively.

At Ichauway, the first commercial harvesting activities began in the mid- to late 1800s. Following these harvesting activities, the practice of prescribed surface fires during the dormant season was continued to prevent hardwood regeneration and to promote game bird habitat. During this period, the use of plowed fire breaks to limit the extent of prescribed surface fires increased at Ichauway, especially the fluvial terraces in agricultural production and surrounding depressional wetlands. The legacy of these activities is a landscape dominated by a matrix of naturally regenerated, second-growth longleaf pine forests at least 70 to 90 years old. Embedded within this matrix are relatively undisturbed riparian areas and wetlands, commercial pine plantations, old abandoned fields, and active agricultural fields.

Our ecosystem classification is based on the least disturbed examples of ecosystems managed under these historic land-uses. Consequently, the vegetation of the ecosystems described here does not reflect those of pre-European settlement. Rather, the vegetative component of each ecosystem identified represents the influence of long-term and low intensity, dormant season surface fires, or degrees of fire in the case of hardwood systems. The vegetative composition of these ecosystems will likely change with corresponding changes in fire regimes.

Methods. SAMPLING DESIGN. The development of an ecosystem classification for Ichauway involved several repetitive, integrated steps similar to those described in Barnes et al. (1982). First, extensive reconnaissance of the study area resulted in a tentative classification based on perceived interactions between moisture availability and fire frequency (Fig. 2). Second, a minimum of three stands or sample areas were located randomly and stratified within tentatively identified ecosystems (wetland ecosystems are excluded from this work and classified using different methodologies; Kirkman et al. 2000). These samples included only those areas that were the least disturbed examples of naturally regenerated ecosystem types relative to the surrounding matrix of forest.

A total of four hundred plots were established

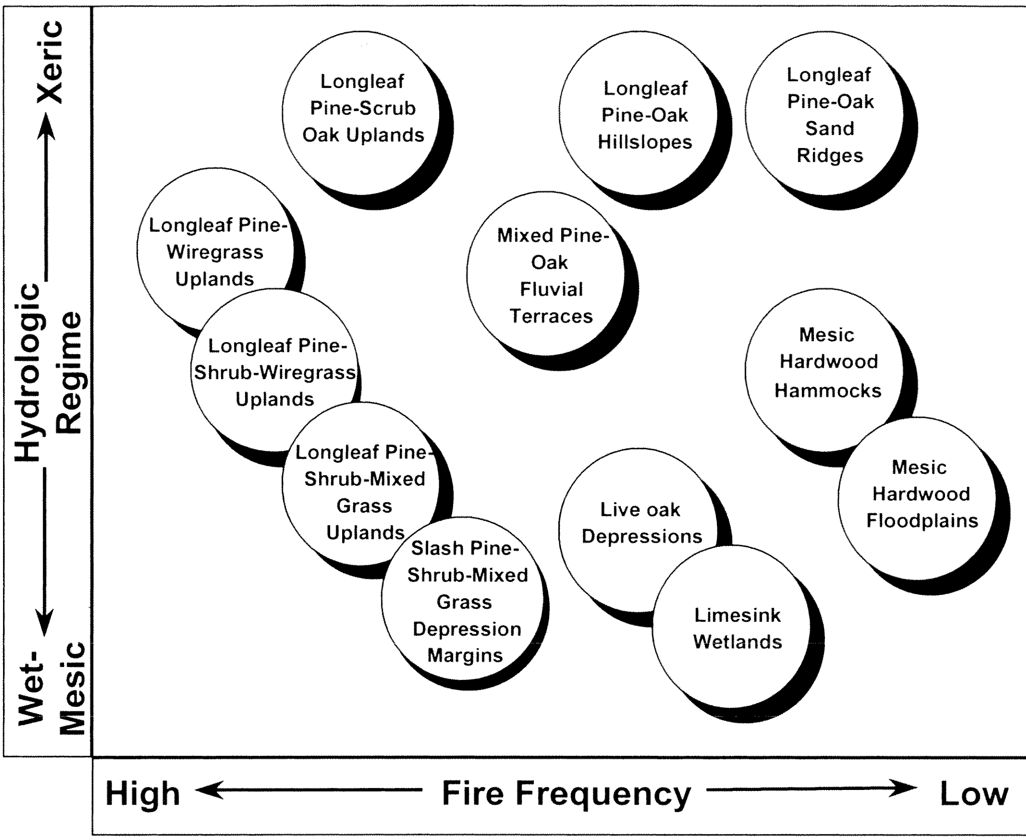

Fig. 2. Potential distribution of ecosystems of the Joseph W. Jones Ecological Research Center along fire frequency and hydrologic gradients.

in 104 stands representative of the tentative ecosystems. Field reconnaissance and data layers of physiographic and vegetation features produced by a geographic information system (GIS) were used to aid in the selection of potential sampling areas within tentative ecosystems. Each stand met the following criteria: 1) minimum of 1 ha in size; 2) majority of overstory trees (> 10 cm dbh) greater than 70 years old; 3) no evidence of recent major disturbance (e.g., fire-breaks, food plots, roads); 4) located in an area of similar physiography and soils, and 5) no evidence of past agriculture, by noting the presence or absence of wiregrass in the ground layer because it is not found in abandoned fields. Wiregrass is believed to be an indicator of undisturbed soil conditions in longleaf pine ecosystems of the Coastal Plain (Clewell 1985; Lynch et al. 1986; Clewell 1989).

Sample plots consisted of an 800 m^2 circular plot, a nested 1x15 m subplot running from the plot center to the periphery at an azimuth of 0°, and two 0.5 m^2 quadrats centered at 5 and 10 m within the 1x15 m transect. The quadrats were moved in 1 m increments if they coincided with a tree trunk or other obstruction, e.g., stump, gopher tortoise burrow, or harvester ant mound until the influence of the disturbance was minimized. The center of each large 800 m^2 plot was tagged and geo-referenced using a global positioning system (GPS).

FIELD AND LABORATORY PROCEDURES. Physiography, soils, and vegetation of each sample plot were measured systematically. Physiographic measurements included: landform class, topographic relief class, and slope percent. Landform classes included: sand ridges, marine and alluvial terraces, floodplains, hillslopes, depression margins, and shallow, non-wetland depressions. Topographic relief classes (Soil Survey Division Staff 1993) included steeply sloping (> 8 %), undulating (1–8 %), or nearly level (1–3 %).

A bucket auger was used to sample soil characteristics to a depth of 3.4 m (or to a restrictive layer) at the center plot of each sample area. A complete soil description was made following Soil Conservation Service procedures (Soil Survey Division Staff 1993) and bulk soil samples were collected from each horizon for the entire profile. Sand (particle size > 0.1 mm), silt (particle size 0.1–0.001 mm), and clay (particle size < 0.001 mm) fractions were determined after air drying using the pipette method.

Vegetation sampling included measurements of four different strata, each believed to have specific species assemblages useful to stratifying longleaf pine ecosystems. The diameter at breast height (dbh, 1.4 m) of all living trees ≥ 2.5 cm was recorded by species in 2.5 cm diameter classes in each 800 m^2 plot. Living trees > 10.0 cm dbh were considered overstory, while stems between 2.5 cm and 10.0 cm dbh were considered midstory. Understory vegetation, woody plants < 2.5 cm dbh, but > 30 cm tall, were tallied by species within the 1 by 15 m subplot. The ground flora (both woody and herbaceous species ≤ 30 cm tall) coverage was visually estimated in each of the 0.5 m^2 quadrats using the following six coverage classes: < 1%; 1–5%; 6–15%; 16–30%; 31–60%, and 61–100%. Voucher specimens were collected for many species of uncertain identity. Nomenclature follows Clewell (1985), except for the genus *Panicum* (Lelong 1986).

NUMERICAL ANALYSES. Soil and physiographic data were summarized for each plot, including the thickness (cm) of a sandy epipedon (sandy textures above an argillic horizon). Depth (cm) to redoximorphic depletions or mottling with a chroma of 2 or less, indicative of reduced or anoxic conditions and seasonal zones of saturation, were also summarized for each plot. Soil textures were calculated as weighted averages of percent total sand, silt, and clay for the following depth classes: 0–50 cm, 51–150 cm, and 151–300 cm. A color development equivalent (CDE; Buntley and Westin 1965) that is representative of soil drainage was also calculated for each horizon and a weighted average generated for each of the three soil depth classes. CDE is a measure of the hue-chroma interaction in soil. Hues, the dominant spectral color, are given a ranking based on tendencies toward yellow or red. These rankings are multiplied by the chroma, a measure of the hue purity or departure from neutral gray, to generate the index. Available water above a restrictive layer, or to 3.4 m, was computed for each horizon of a given sample area by assigning a numerically based value of soil texture that reflects centimeters of water per centimeter of soil multiplied by the depth of each horizon. These values were 0.05-cm water/cm soil for sands and sandy loams, 0.20 cm water/cm soil for silt loams and silty clay loams, and 0.15 cm water/cm soil for all other textures. These values of available water for each horizon were then converted to a weighted average for the complete soil profile. Finally, categorical variables, including landform and terrain shape were arrayed along a theoretical gradient of soil moisture, transforming the variables to a semi-continuous variable for use in multivariate statistical analyses. Soil textural data were standardized using a square root arcsine transformation.

Before analyses, the few plants not identified to species were deleted from the dataset. Additionally, due to the high species richness and diverse array of lifeforms in longleaf pine ecosystems, the growth form (species of large stature with canopy potential; species of small stature and relegated to the subcanopy; shrubs and vines) of each species was determined to help illustrate the differences among ecosystems. Overstory and midstory species importance values (IV) of each sample area were calculated by averaging the relative dominance (as expressed by basal area), relative density, and relative frequency for each sample area. Relative densities were computed for the understory species. Finally, an importance percentage (IP) of each ground-flora species was calculated for each sample area (Host et al. 1993). The IP was generated by multiplying the median value of the cover class midpoint (0.5, 3.0, 10.5, 22.0, 45.5, and 80.5) for each ground-flora species by its frequency, i.e., the number of 1 m^2 quadrats in which the species was present.

Two Way Indicator Species Analysis (TWINSPAN), a divisive polythetic classification based on repeated division of a reciprocal averaging ordination (Hill 1979), was used to explore the initial and revised classifications in terms of vegetative composition. TWINSPAN was run using the default settings and nine pseudospecies cut levels for the overstory, midstory, and understory datasets. Default settings and six pseudospecies cut levels corresponding to the midpoint values of the percent cover classes were used for the ground-flora dataset. These analyses produced ordered species-by-sample tables that formed the basis of ecological species groups. Ecological species groups for each strata and growth form were generated for each ecosystem using TWINSPAN and named for the species with the greatest ecological amplitude and importance (*sensu* Spies and Barnes, 1985).

We used a variation of canonical correspondence analysis (CCA; ter Braak 1994) to measure the degree of distinctness of each ecosystem and to confirm various iterations of the field-based classification. Four canonical analyses were conducted using the CCA routine in CANOCO (ter Braak 1988). For each, we used a subset of the original sample area data: 1) physiography and soil dataset, 2) overstory and midstory species group datasets as determined by TWINSPAN, 3) understory and ground-flora species group datasets as determined by TWINSPAN, and 4) all ecosystem component datasets. Typically, CCA relates a primary matrix of vegetative data to a secondary matrix of environmental data. It also can be used, as we did here, to verify a classification by relating our primary environment and vegetation matrices to a classification matrix, i.e., matrix of each sample area and the ecosystem it represents. Such an analysis is an improvement over canonical variates analysis (CVA; Williams 1983) because the number of sites does not need to greatly outnumber the total number of species and classes (Jongman et al. 1995). Because small within-group sample sizes tend to dominate the CCA, ecosystems with less than four sample plots were not included in these confirmation analyses (ecosystems 4 and 17; see Results).

Results. MULTIFACTOR CLASSIFICATION. We identified seventeen non-wetland ecosystems in the final iteration of the classification. Eight are found exclusively within the fluvial valleys of Ichawaynochaway Creek and the Flint River, while five ecosystems are found only in the karst uplands (Table 1). Four ecosystems (sandy depressions, clayey depressions, depression margins, and terrace escarpments) are commonly found in both the fluvial and upland physiographic zones (Table 1). Each ecosystem is named for dominant physiography, soil drainage, and soil textures, or characteristic vegetation, e.g., FSR = fluvial sand ridge; HAM = mesic hardwood hammock; SEUT = somewhat excessively drained upland terrace.

The multifactor classification has a hierarchical structure consisting of six levels (Table 1). The first level of the classification differentiates between fluvial, i.e., ecosystems located within the stream valley of Ichawaynochaway Creek and the Flint River, and upland karst physiographic zones. The second and third levels of the classification divides ecosystems based on topography, primarily landform and terrain shape, respectively. The fourth level distinguishes ecosystems on the basis of soil drainage class, while the fifth level is based on differences in soil texture. The final level separates ecosystems based on vegetation. Because physiography and soils are relatively stable compared to vegetation, these factors formed the primary basis for the higher levels of the classification (Table 1).

The upland and fluvial ecosystems all have repeatable patterns of occurrence. Seven occupy unique positions on the landscape, including floodplains, sand ridges, terrace escarpments, depression margins, and shallow, non-wetland depressions. The most extensive upland ecosystems are the longleaf pine-dominated moderately-drained and well-drained upland terraces (ecosystems 10 and 11). The well-drained fluvial terraces with longleaf pine (ecosystem 4) and mesic hardwood hammocks (ecosystem 5) are the dominant fluvial ecosystems. Both of these ecosystems occur on similar landforms and have similar topographic relief. Most slope or terrace escarpment (ecosystem 15) ecosystems are found within the fluvial physiographic zone, while the majority of sandy and clayey shallow depressions (ecosystem 16 and 17, respectively), as well as the depression margins (ecosystem 14), are found in the upland physiographic zone. For comparative purposes, ecosystem 15 (SCARP) is grouped with the fluvial ecosystems, while the sandy and clayey shallow (non-wetland) depressions (ecosystem 16 and 17, respectively), as well as the depression margins (ecosystem 14), are considered with the upland ecosystems. We identified two additional fluvial ecosystems through mapping for a related project (Palik et al. 2000). However, both are rare at Ichauway. These include ecosystem 1, the somewhat poorly drained fluvial terraces with overstories of longleaf pine, loblolly pine (*Pinus taeda* L.), and water oak (*Quercus nigra* L.) and ecosystem 3, the longleaf pine-dominated, well-drained fluvial terraces. For these ecosystems, information from field reconnaissance during mapping was used to describe the soil and vegetative components.

FLUVIAL ECOSYSTEM ANALYSIS. The canonical ordinations of fluvial ecosystems illustrate the

Table 1. Characteristics of fluvial and upland ecosystems of Ichauway, southwest Georgia.

Ecosystem[a]	Physiographic zone	Landform	Topographic relief class[b]	Soil drainage class	Soil texture	Soil classification	Overstory vegetation	Ground-flora species groups
1 (SPFT)	fluvial	terrace	complex, nearly level	somewhat poorly drained	sand to sandy loam over sandy clay loam to clay	Aquic & Aquic Arenic Plaeudults	longleaf pine-loblolly pine-water oak	not sampled
2 (MWFT)	fluvial	terrace	complex, nearly level	moderately drained	sandy clay loam over fine sand	Typic Paleudults, Aquic Dystrochrepts	longleaf pine-loblolly pine-short leaf pine	*Vaccinium—Ruellia/Dyschoriste—Scleria/Panicum—Erianthus*
3 (WFT)	fluvial	terrace	complex, nearly level-undulating	well drained	loamy sand over sandy loam to sandy clay loam	Typic & Arenic Paleudults, Typic Dystrochrepts, Typic Hapludults	longleaf pine	not sampled
4 (EFT)	fluvial	terrace	complex, nearly level-undulating	well to somewhat excessively drained	sand and loamy sand	Grossarenic Paleudults & Typic Quartzipsamments	longleaf pine	*Aristida—Andropogon/Dyschoriste—Scleria*
5 (HAM)	fluvial	terrace	complex, nearly level-undulating	somewhat excessively drained	sand	Typic Quartzipsamments	laurel oak-pignut hickory-Southern magnolia	*Parthenocissus—Bignonia/Quercus—Ilex/Mitchella—Euonymus*
6 (FSR)	fluvial	sand ridge	complex, nearly level-undulating	excessively drained	sand	Typic Quartzipsamments	longleaf pine-turkey oak-sand post oak	*Aristida—Andropogon/Dyschoriste—Scleria*
7 (FR)	fluvial	floodplain	complex, undulating	moderately well drained	sand clay loam over sandy loam	Aquic & Typic Dystrochrepts	live oak-sweet gum-southern sugar maple	*Parthenocissus—Bignonia/Dioscorea—Viola*
8 (FC)	fluvial	floodplain	complex, undulating	moderately well drained	sandy loam over loamy sand	Aquic & Typic Dystrochrepts	live oak-sweet-gum-southern sugar maple	*Parthenocissus—Bignonia/Quercus—Ilex/Mitchella—Euonymus*
9 (SPUT)	upland	terrace	complex, nearly level	somewhat poorly to poorly drained	sandy loam over sandy clay loam to clay	Aquic Arenic Paleudults	longleaf pine	*Aristida—Dyschoriste/Scleria—Aster*
10 (MWUT)	upland	terrace	complex, nearly level-undulating	moderately well drained	loamy sand over sandy clay loam to clay	Arenic Paleudults	longleaf pine	*Aristida—Dyschoriste/Scleria—Aster*

Table 1. Continued.

Ecosystem[a]	Physiographic zone	Landform	Topographic relief class[b]	Soil drainage class	Soil texture	Soil classification	Overstory vegetation	Ground-flora species groups
11 (WUT)	upland	terrace	complex, undulating	well drained	loamy sand over sandy loam to sandy clay loam	Typic Hapludult, Typic, Arenic & Grossarenic Paleudults	longleaf pine	*Aristida—Dyschoriste/Scleria—Aster/Rhynchosia—Crotolaria*
12 (SEUT)	upland	terrace	undulating	well to excessively drained	loamy sand to sandy loam	Grossarenic Paleudults	longleaf pine	*Aristida—Dyschoriste/Centrosema—Schrankia/Rhynchosia—Crotolaria*
13 (USR)	upland	sand ridge	complex, nearly level-undulating	excessively drained	sand	Typic Quartzipsamments	longleaf pine-turkey oak-sand post oak	*Aristida—Dyschoriste/Croton—Stylisma*
14 (MARG)	fluvial & upland	slope	simple, gentle	well drained to poorly drained	loamy sand over sandy loam to clay	Grossarenic Paleaquults, Aquic, Aquic Arenic, Typic, & Arenic Paleudults	longleaf pineslash pine	*Aristida—Dyschoriste/Scleria—Aster/Hypericum—Solidago*
15 (SCARP)	fluvial & upland	slope	simple, moderately steep	well drained to somewhat excessively drained	loamy sand over sandy loam to sandy clay loam	Grossarenic, Arenic, & Typic Paleudults	longleaf pine-sand post oak	*Aristida—Andropogon/Dyschoriste—Scleria*
16 (CD)	fluvial & upland	shallow depression	complex, nearly level	moderately to poorly drained	sand to sandy loam over sandy clay loam to clay	Grossarenic Paleaquults, Aquic, Aquic Arenic, Typic, & Arenic Paleudults,	live oak-water oak-swamp laurel oak	*Quercus—Campsis/Quercus—Smilax*
17 (SD)	fluvial & upland	shallow depression	complex, nearly level	well to moderately drained	sand over sandy clay loam	Grossarenic Paleaquults, Aquic, Aquic Arenic, Typic, & Arenic Paleudults	sand live oak-longleaf pine-live oak	*Aristida—Dyschoriste/Quercus—Campsis*

[a] Ecosystem number and corresponding acronym.
[b] Topographic relief classes: complex slopes include nearly level (0–3%) and undulating (1–8%); simple slopes include gentle (1–8%) and moderately steep (10–30%).
[c] Overstory vegetation named for dominant members of each ecological species groups derived using TWINSPAN. Mean importance values by ecosystem and complete list of species by ecological species group available by request.
[d] Ground-flora vegetation named for dominant members of each ecological species groups derived using TWINSPAN. Mean percent cover by ecosystem and complete list of species by ecological species group available by request.

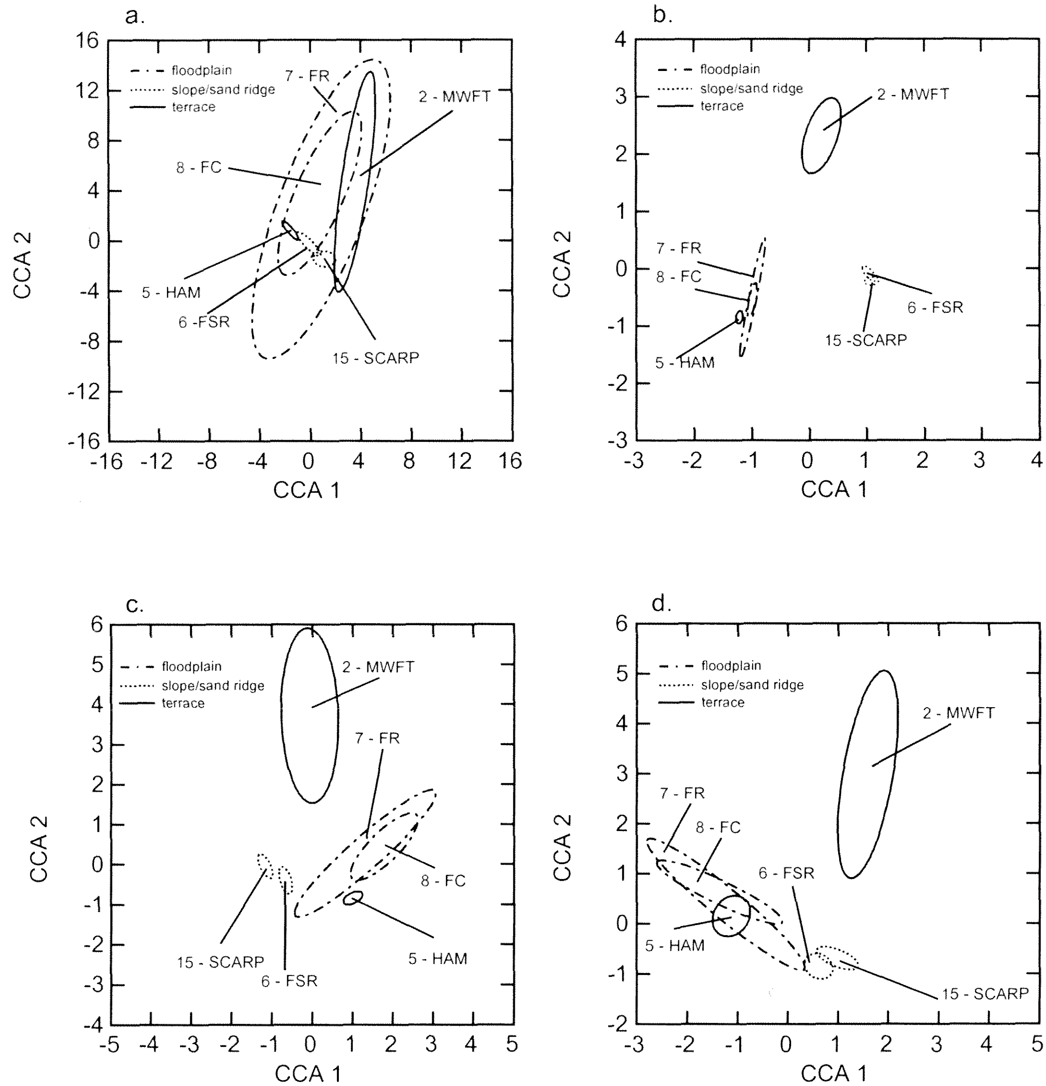

Fig. 3. Confirmation canonical correspondence analysis (CCA) relating a) physiography-soils, b) overstory-midstory composition, c) understory-ground-flora composition, and d) all ecosystem components to a matrix of fluvial ecosystem membership. See Table 1 for ecosystem acronyms.

degree of similarity among ecosystems (Fig. 3). Based on physiography and soil variables, there is considerable overlap in ordination space among the ellipses of the floodplain ecosystems (FR and FC) and other fluvial ecosystems (Fig. 3a). However, because the floodplains occupy a different landform than the other ecosystems they are identified easily in the field (Table 2). Two other fluvial ecosystems also occupy specific landscape positions: ecosystem 6 (FSR) and ecosystem 15 (SCARP). Additionally, there are differences in the soil between the two ecosystems. The sand ridges have on average ($\pm$ 1 SE) thick sandy epipedons (263.8 $\pm$ 27.6 cm) and lower subsoil CDE values typical of excessively drained soils, while the terrace escarpments have thinner sandy epipedons (107.4 $\pm$ 18.5 cm) and higher subsoil CDE values indicative of well drained soils (Table 2). Ecosystems 2 (MWFT), 4 (WFT), and 5 (HAM) all occupy fluvial terraces along Ichawaynochaway Creek and the Flint River, however, each can be distinguished by sandy epipedon thickness, soil texture, and surface CDE values (Table 2).

When the overstory and midstory datasets are used in the analysis, differences among fluvial

Table 2. Physiographic and edaphic characteristics of selected fluvial ecosystems of Ichauway, southwest Georgia.

	Fluvial Ecosystem						
Variable	MWFT (n = 5)[a]	EFT (n = 3)	HAM (n = 8)	FSR (n = 8)	FR (n = 4)	FC (n = 5)	SCARP (n = 9)
Ecosystem Number	2	4	5	6	7	8	15
Landform[b]	TR	TR	TR	SR	FP	FP	SL
Terrain shape[c]	NL	NL	NL	U	U	U	MS
Percent slope (%)	3.0 (0.7)[e]	0.7 (0.3)	0.9 (0.4)	2.0 (0.3)	2.0 (1.4)	0.8 (0.2)	10.6 (0.7)
Sandy epipedon thickness (cm)	15.2 (5.4)	138.7 (84.4)	300.0 (0.0)	263.8 (27.6)	174.0 (73.8)	95.6 (29.2)	107.4 (18.5)
Depth to redoximorphic features (cm)	74.0 (45.2)	146.0 (23.0)	188.3 (30.6)	230.0 (20.8)	151.5 (54.1)	67.8 (32.1)	201.7 (18.0)
Available water (cm water/cm soil)	34.2 (3.3)	24.0 (6.2)	15.0 (0.0)	15.9 (0.6)	31.5 (2.1)	21.4 (4.3)	31.7 (2.4)
% sand (0–50 cm)	45.8 (9.4)	82.7 (5.8)	92.4 (2.5)	94.1 (1.0)	54.7 (12.2)	76.1 (9.8)	82.5 (1.8)
% silt (0–50 cm)	20.0 (2.2)	9.5 (2.5)	4.8 (1.5)	4.3 (0.8)	21.2 (6.1)	10.3 (4.1)	10.4 (0.8)
% clay (0–50 cm)	34.2 (8.9)	7.9 (3.5)	2.9 (1.0)	1.6 (0.4)	24.1 (6.4)	13.6 (5.9)	7.0 (1.7)
% sand (51–150 cm)	38.4 (8.9)	76.7 (8.3)	94.8 (0.7)	93.2 (2.1)	61.1 (8.0)	86.6 (4.7)	74.9 (3.0)
% silt (51–150 cm)	11.4 (2.1)	10.2 (2.7)	3.0 (0.6)	4.0 (0.8)	15.2 (2.6)	3.8 (1.0)	8.9 (0.8)
% clay (51–150 cm)	50.1 (6.9)	13.1 (5.8)	2.2 (0.2)	2.8 (1.5)	23.7 (6.0)	9.7 (3.9)	16.2 (3.2)
% sand (151–300 cm)	78.7 (9.2)	90.4 (4.6)	96.0 (0.7)	96.1 (0.8)	77.0 (13.2)	77.5 (6.5)	61.5 (5.3)
% silt (151–300 cm)	7.4 (4.6)	3.7 (2.4)	2.7 (0.7)	1.7 (0.4)	10.2 (6.7)	6.9 (2.4)	7.2 (0.9)
% clay (151–300 cm)	13.9 (4.6)	5.9 (2.5)	1.3 (0.3)	2.2 (0.5)	12.9 (6.7)	15.7 (4.6)	31.2 (4.9)
CDE[d] (0–50 cm)	16.1 (3.2)	15.1 (3.7)	9.2 (1.1)	10.8 (1.5)	13.4 (1.8)	7.4 (1.1)	11.7 (1.4)
CDE (51–150 cm)	17.7 (5.7)	17.2 (4.6)	16.7 (1.3)	15.2 (2.3)	17.6 (4.2)	10.3 (2.2)	20.8 (2.8)
CDE (151–300 cm)	11.8 (2.9)	13.5 (0.8)	9.9 (1.6)	11.7 (1.2)	17.4 (1.2)	5.4 (1.3)	22.7 (4.6)

[a] Number of sample areas.
[b] FP, floodplain; TR, terrace; SR, sand ridge; SL, slope.
[c] NL, nearly level (0–3%); U, undulating (1–8%); MS, moderately steep (10–30%).
[d] Color development equivalent.
[e] Mean (± 1 standard error).

ecosystems are more pronounced (Fig. 3b). The *Liquidambar-Quercus, Celtis-Ulmus*, and *Acer-Quercus* overstory groups, as well as the *Acer-Celtis* and *Ostrya-Carpinus* midstory groups dominate ecosystems 5 (HAM), 7 (FC) and 8 (FR). Other overstory and midstory communities characterize the remaining fluvial ecosystems (Table 1). For example, although both ecosystem 2 (MWFT) and ecosystem 5 (HAM) occur on fluvial terraces, the overstory of ecosystem 2 is dominated by loblolly pine, shortleaf pine (*P. echinata* Mill.), and post oak (*Quercus stellata* Wang.) rather than mixed hardwoods (Table 1). Similarly, the composition of the midstory separates ecosystem 5 from ecosystems 7 and 8 (Fig. 3b).

Similar results are found when understory and ground-flora datasets are analyzed (Fig. 3c). However, the differences among ecosystems 6 (FSR) and 15 (SCARP) are more distinct (Fig. 3c). Although both ecosystems have overstories and midstories of longleaf pine and scrub oaks, each has different understory and ground-flora communities. Similarly, the distinctions between the floodplain ecosystems (ecosystems 7 and 8) and the mesic hardwood hammock ecosystem (ecosystem 5) are more pronounced when the understory and ground-flora composition are used in the analysis. While distinct groups of understory species are found among the three ecosystems (Table 1), members of the *Parthenocissus-Bignonia* and *Mitchella-Euonymus* ground-flora species groups (Table 1) dominate the ground-flora of each ecosystem.

The similarities in physiography, soils, and ground-flora vegetation among fluvial ecosystems tend to lessen the differences among ecosystems as seen when all ecosystem components (e.g., physiography, soils, overstory, midstory, understory, and ground-flora data) are included in the analysis (Fig. 3d). Sample areas tend to cluster into distinct groups with similar physiography, soils, and vegetation. However, distinguishing ecosystems in these groups is possible. Although the fluvial ecosystems appear to be similar in terms of soils and vegetation, landform differences easily observed in the field provide the basis for identifying fluvial ecosystems.

UPLAND ECOSYSTEM ANALYSIS. The ordination of upland ecosystems using the physiography and soils dataset successfully separates six of the seven ecosystems that are commonly found in the upland physiographic zone (Fig 4a). The one ecosystem not separated from the others, ecosystem 14 (MARG), occurs on gentle slopes adjacent to both non-wetland (ecosystems 16 and 17) and wetland (not described here) ecosystems. Consequently, distinguishing this ecosystem from the other upland ecosystems can be determined in the field based on landform. Two of the remaining six ecosystems (ecosystems 13 and 16) also occur on unique landforms and have edaphic characteristics that are clearly distinguishable from the other upland ecosystems (Fig 4a; Table 3). The remaining four upland ecosystems occur on marine terraces and are separated with minimal overlap; each is separated based on their soil properties (Fig 4a). Nearly level terrain, shallow depths to redoximorphic features (46.2 ± 4.3 cm), and low CDE values reflecting poor drainage (Table 3) characterize ecosystem 9 (SPUT). Ecosystem 10 (MWUT) also has nearly level terrain and low CDE values, however, the average depth to redoximorphic features is deeper (94.4 ± 3.0) cm than ecosystem 9 (Table 3). Ecosystems 11 (WUT) and 12 (SEUT) both have undulating terrain and high CDE values, indicative of good drainage (Table 3). Nevertheless, other soil characteristics, primarily sandy epipedon thickness and depth to redoximorphic features, separate ecosystems 11 and 12 (Table 3).

The CCA analysis based on overstory and midstory IVs results in considerable overlap among ecosystems (Fig. 4b). Only ecosystem 16 (CD) with overstories and midstories of live oak (*Quercus virginiana* Mill.), water oak, and swamp laurel oak (*Q. laurifolia* L.), and ecosystem 13 (USR) comprised of longleaf pine and turkey oak (*Q. laevis* Walt.), are separated from the other five ecosystems (Table 1). Although grouped with ecosystems 9 (SPUT), 10 (MWUT), and 11 (WUT), ecosystem 14 (MARG) is readily distinguished in the field by the presence of slash pine (*Pinus elliottii* Engelm.) which comprises 30.4% of the overstory (Table 1). The overstories of the remaining upland ecosystems are dominated by longleaf pine (Table 1). Differences in the subcanopy composition, i.e., importance of members of the subcanopy *Quercus* group, can be used to help distinguish these ecosystems dominated by overstories of longleaf pine (ecosystems 9, 11, 12).

Comparable separation among the upland ecosystems is found when the understory and ground-flora species groups are analyzed (Fig 4c). Both ecosystem 13 (USR) and 16 (CD) are separated from the other five ecosystems (Fig 4c.). The upland sand ridges have understories

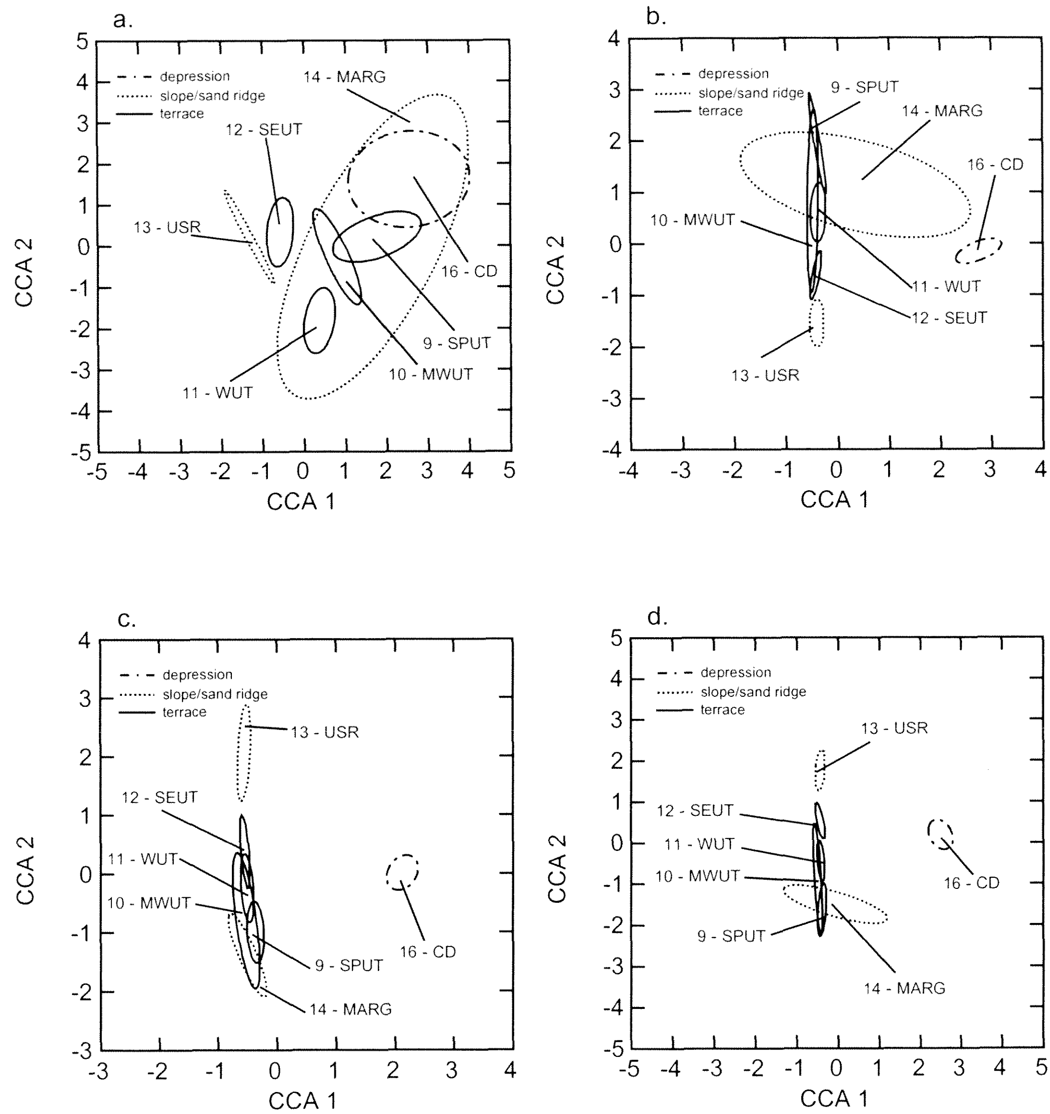

Fig. 4. Confirmation canonical correspondence analysis (CCA) relating a) physiography-soils, b) physiography-soils and overstory-midstory composition, c) physiography-soils and understory-ground-flora composition, and d) all ecosystem components to a matrix of upland ecosystem membership. See Table 1 for ecosystem acronyms.

of subcanopy scrub oaks such as turkey oak, sand post oak (*Q. margaretta* Ashe), and bluejack oak (*Q. incana* Bartr.), and a ground-flora dominated by the *Croton-Stylisma* and *Aristida-Dyschoriste* groups (Table 1). The clayey depressions (CD) have relatively sparse understories of water oak, persimmon (*Diospyros virginiana* L.), and blueberry (*Vaccinium elliottii* Chapm.), and ground-floras comprised of the *Quercus-Campsis* and *Quercus-Smilax* species groups (Table 1). Although members of the *Aristida-Dyschoriste* ground-flora species group are abundant in all longleaf pine-dominated upland ecosystems, there are differences in the dominance of the other species groups. Ecosystems 9 (SPUT) and 10 (MWUT) are characterized by members of the *Scleria-Aster* group, while members of the *Centrosema-Schrankia* and *Solidago-Cassia* groups are common to ecosystems 11 (WUT) and 12 (SEUT; Table 1).

The analysis of all ecosystem components results in a similar ordination diagram as the over-

Table 3. Physiographic and edaphic characteristics of selected upland ecosystems of Ichauway, southwest Georgia.

Variable	Ecosystem							
	SPUT (n = 6)[a]	MWUT (n = 5)	WUT (n = 16)	SEUT (n = 10)	USR (n = 6)	MARG (n = 5)	CD (n = 10)	SD (n = 3)
Ecosystem number	9	10	11	12	13	14	16	17
Landform[b]	TR	TR	TR	TR	SR	SL	DEP	DEP
Terrain shape[c]	NL	NL	U	U	U	GS	U	U
Percent slope (%)	0.9 (0.3)[e]	1.2 (0.2)	1.6 (0.3)	2.0 (0.3)	3.4 (1.2)	1.9 (0.3)	1.1 (0.2)	0.8 (0.2)
Sandy epipedon thickness (cm)	46.2 (4.3)	62.0 (8.3)	68.1 (16.6)	150.8 (17.8)	250.8 (29.6)	42.6 (7.22)	52.5 (13.1)	131.7 (37.3)
Depth to redoximorphic features (cm)	59.8 (7.2)	94.4 (3.0)	164.6 (19.3)	185.2 (21.6)	290.2 (9.8)	71.8 (18.7)	34.4 (7.9)	82.3 (22.0)
Available water (cm water/cm soil)	40.3 (0.2)	38.8 (0.9)	38.1 (2.0)	27.6 (2.2)	18.5 (2.3)	38.0 (4.6)	37.6 (3.1)	25.3 (2.2)
% sand (0–05 cm)	69.6 (5.3)	76.2 (2.1)	74.2 (4.3)	85.4 (1.2)	92.5 (1.1)	76.0 (2.1)	65.5 (4.5)	93.8 (0.6)
% silt (0–50 cm)	21.9 (2.1)	19.0 (2.1)	15.5 (2.0)	10.6 (0.9)	5.2 (0.8)	12.4 (0.8)	20.7 (2.7)	5.0 (0.8)
% clay (0–50 cm)	8.6 (3.7)	4.8 (1.1)	10.3 (2.7)	4.0 (0.4)	2.3 (0.5)	11.7 (2.4)	13.8 (2.7)	1.2 (0.1)
% sand (51–150 cm)	49.8 (4.9)	57.3 (2.6)	64.0 (4.8)	83.3 (2.0)	93.2 (0.9)	65.7 (3.4)	57.4 (5.9)	83.1 (4.1)
% silt (51–150 cm)	13.4 (1.8)	14.1 (2.9)	11.2 (1.1)	9.3 (0.9)	4.4 (0.6)	8.6 (0.9)	13.6 (2.0)	5.0 (2.0)
% clay (51–150 cm)	36.9 (5.5)	28.6 (3.5)	24.8 (4.3)	7.4 (1.5)	2.4 (0.4)	25.7 (3.1)	29.1 (5.5)	11.9 (5.8)
% sand (151–300 cm)	34.4 (5.7)	39.6 (5.6)	55.9 (4.8)	66.3 (5.0)	89.1 (2.9)	59.6 (5.7)	50.7 (5.6)	70.7 (3.7)
% silt (151–300 cm)	9.4 (3.8)	10.0 (1.8)	8.9 (0.7)	7.0 (1.0)	4.5 (0.8)	6.1 (1.6)	10.0 (1.6)	3.3 (1.9)
% clay (151–300 cm)	56.3 (8.5)	50.4 (5.8)	35.2 (4.6)	26.7 (4.3)	6.4 (2.3)	34.3 (6.4)	39.3 (5.7)	25.9 (5.7)
CDE[d] (0–50 cm)	7.0 (0.7)	8.4 (0.5)	11.1 (1.8)	7.5 (0.5)	14.0 (1.3)	8.8 (1.6)	4.5 (0.5)	4.1 (1.0)
CDE (51–150 cm)	8.9 (1.7)	11.2 (1.4)	19.5 (2.6)	13.4 (1.4)	18.8 (0.8)	14.0 (2.7)	6.6 (1.4)	5.9 (0.9)
CDE (151–300 cm)	2.2 (0.5)	2.8 (0.4)	14.7 (2.4)	14.2 (2.5)	25.3 (5.0)	10.0 (3.9)	5.4 (2.2)	4.0 (0.2)

[a] Number of sample areas.
[b] TR, terrace; SR, sand ridge; DEP, depression; SL, slope.
[c] NL, nearly level (0–3%); U, undulating (1–8%); GS, gently sloping (0–8%).
[d] Color development equivalent.
[e] Mean (± 1 standard error).

story-midstory and understory-ground flora ordinations (Fig. 4d). Consequently, physiographic and soil characteristics form the basis for distinguishing among upland ecosystems. However, identification of ecosystem 14 (MARG) that has a wide range of soil characteristics, can be easily identified in the field because it occurs on a unique landform and has an overstory dominated by slash pine.

Discussion and Conclusions. Regional studies of the Atlantic and Gulf Coastal Plains suggest that differences in climate, soil texture, and fertility are responsible for the differences in composition, structure, and diversity of most longleaf pine-dominated ecosystems (Wahlenberg 1946; Peet and Allard 1993). Using an iterative approach based on an understanding of the inter-relationships among physiography, soils, and vegetation, we successfully produced a hierarchical ecosystem classification that segregates these complex gradients into discrete units. Our classification is also ground-based, incorporating easily observed and measured factors, including landform, soil texture, and vegetative cover. Because the classification is hierarchical, individual ecosystems can be associated into ecological units at higher scales, such as local physiographic zones or Bailey's (1996) EcoRegion classification. Such integrated and hierarchical classifications are rare for the southeastern Coastal Plain.

Ecosystem classifications developed for other regions of the United States (e.g., Archambault et al. 1990; Hix 1988; Van Kley and Parker 1993; Zogg and Barnes 1995; Hix and Pearcy 1997), have seldom been examined for applicability on the ground. We measured the accuracy of our classification by systematically mapping individual ecosystems. Using a geographical information system (GIS), aerial photos, field soil sampling, and vegetative descriptions of each ecosystem as defined by the classification, we developed a map of local ecosystems at Ichauway (Palik et al. 2000). By classifying and mapping ecosystems simultaneously, we assessed how well the classification could be applied in this Coastal Plain landscape. Of the more than 11,000 hectares, we identified only two ecosystems during the mapping phase that were not identified by earlier iterations of the classification (ecosystems 1 and 3), each of which comprised less than 5% of the total land area (Palik et al. 2000). The results of the mapping phase confirm that integrated multifactor ecosystem classifications can be applied successfully and fully implemented in this complex environment of the southeastern United States.

Although it is difficult to determine exactly why hierarchical ecosystem classification has largely been ignored in the southeastern United States, there are some potential drawbacks from implementing such a classification. First, ecosystem classifications are expensive to develop (Pregitzer et al. 2001). Second, most organizations, both public and private, have existing vegetation-based classifications on which they base most of their day to day management decisions. While it would be an expensive proposition for many organizations to abandon existing vegetation classifications, there may be instances where an ecosystem classification provides a more appropriate management framework.

When we compare our ecosystem classification to a forest cover type map for Ichauway, we find that many of the undisturbed longleaf pine dominated ecosystems (ecosystems 9, 10, 11, and 12) are lumped into one or two cover type units. At first glance, the CCAs appear to support this simple stratification, as there is little differentiation among vegetation of the upland longleaf pine-dominated ecosystems (ecosystems 9, 10, 11, and 12). One possible explanation for these similarities is the dominance of wiregrass across the gradient, masking trends in abundance in rarer species among the longleaf pine dominated ecosystems. Another may be the use of long-term dormant season prescribed fires to promote game bird habitat. Frequent dormant season fires over long periods may act to decouple the natural vegetation-environment relationships, resulting in an increase in abundance of hardwoods, such as oaks (Jacqmain et al. 1999).

Regardless of the vegetation, there are physiographic and edaphic differences indicative of a subtle gradient of moisture availability among the pine–dominated ecosystems. Recent work also shows that forest productivity is strongly related to moisture availability among these upland longleaf pine–dominated ecosystems at Ichauway (Mitchell et al. 1999). Specifically, annual net primary productivity (ANPP) of ecosystem 9 (SPUT) is nearly twice that of ecosystem 12 (SEUT). Although longleaf pine and wiregrass remain dominant across the gradient of upland ecosystems, species richness follows a similar pattern to that of productivity (Kirkman, unpublished data). Thus, small differences in soil moisture may result in significant productivity increases, providing a functional basis for delineating ecosystems that appear similar in terms of vegetation. The use of a single-factor classification, such as a cover type map, would fail to detect these subtle changes in soil moisture and its influence over productivity. Consequently, a multifactor classification similar to the one presented here may be better suited for sustainable management initiatives, regardless of the region where it is applied.

Describing the variability in composition, structure, and function of the landscape is one goal of ecosystem classification. Another goal is to provide a framework on which to base management decisions. The classification provides a structural framework that could facilitate research and local sustainable management initiatives. For example, understanding the mechanisms that maintain biodiversity requires detailed information of the various ecosystem components that are responsible for biodiversity. Because these components (compositional, structural, and functional) are inherent in the structure of ecosystem classifications (Pregitzer et al. 2001), biodiversity surveys that are framed around the ecosystem classification can provide insights into the factors that mediate levels of biodiversity across the landscape.

In the future, the multifactor ecosystem classification presented here will continue to be refined by examining more closely the relationships among physiography, soils, and vegetation under a changing fire regime and at smaller spatial scales. Additionally, functional differences among ecosystems, primarily the productivity and diversity of the longleaf pine-dominated ecosystems, will continue to be a major focus of investigation at Ichauway. The results of these ecosystem studies, framed around our hierarchical classification, will greatly increase our understanding of how various ecosystem components interact. Our multifactor classification system, as one of the first such complete efforts in the southeastern United States, serves as a model for developing similar local ecosystem classifications throughout the region.

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Appendix A - Tables.

The following tables describe the ecosystem composition (mean + 1 stand error) of each ecosystem by ecological species group (see Appendix B for members) and forest strata. See figure below for an explanation of each vegetative stratum.

[a] Growth form determined by stature at maturity

Overstory importance values (IV) of selected fluvial and upland ecosystems of Ichauway, southwest Georgia.

Fluvial Ecosystem

Ecological Species Group by Lifeform[a]	MWFT (n = 5)	EFT (n = 3)	HAM (n = 8)	FSR (n = 8)	FR (n = 4)	FC (n = 5)	SCARP (n = 9)
Ecosystem Number	2	4	5	6	7	8	15
Canopy Species							
Pinus	76.9 (2.3)[b]	—	1.7 (0.8)	—	8.5 (3.4)	2.7 (1.1)	0.8 (0.8)
Liquidambar-Quercus	13.1 (2.3)	—	1.6 (0.5)	—	27.2 (8.1)	20.2 (4.2)	0.6 (0.6)
Celtis-Ulmus	—	—	2.4 (0.6)	—	29.6 (8.3)	8.7 (1.7)	—
Acer-Quercus	1.5 (0.6)	—	73.4 (1.8)	—	26.8 (5.7)	56.0 (5.4)	2.0 (1.3)
Pinus-Quercus	6.6 (1.9)	96.5 (3.5)	3.2 (0.9)	52.7 (8.6)	—	1.8 (1.4)	80.2 (8.1)
Subcanopy Species							
Quercus	—	3.5 (3.5)	0.3 (0.2)	47.3 (8.6)	—	—	16.4 (7.9)
Ostrya-Carpinus	1.9 (1.2)	—	5.8 (1.8)	—	7.6 (2.0)	4.4 (2.2)	—
Bumelia-Osmanthus	—	—	11.6 (2.0)	—	0.3 (0.3)	6.2 (2.3)	—

Upland Ecosystem

Ecological Species Group by Lifeform[a]	SPUT (n = 6)	MWUT (n =5)	WUT (n =16)	SEUT (n =10)	USR (n =6)	MARG (n=5)	CD (n = 10)	SD (n =3)
Ecosystem Number	9	10	11	12	13	14	16	17
Canopy Species								
Quercus-Nyssa	—	—	—	—	—	1.3 (1.3)	40.2 (5.6)	8.3 (4.7)
Quercus	3.3 (1.5)	1.5 (1.5)	3.9 (1.8)	1.3 (0.9)	2.3 (2.3)	31.7 (16.4)	56.7 (5.6)	12.4 (1.5)
Pinus-Quercus	95.6 (2.1)	97.3 (1.7)	91.6 (3.4)	95.2 (2.7)	58.4 (7.7)	67.0 (17.6)	1.0 (0.6)	71.1 (6.0)
Subcanopy Species								
Quercus	1.1 (1.1)	1.2 (1.2)	4.5 (3.2)	3.5 (2.5)	39.3 (7.6)	—	0.2 (0.2)	8.2 (8.2)
Crataegus	—	—	—	—	—	—	1.9 (0.8)	—

[a] See Appendix B for ecological species group members. Ecological species groups derived using TWINSPAN.
[b] Mean (+ 1 standard error).

Midstory importance values (IV) of selected fluvial and upland ecosystems of Ichauway, southwest Georgia.

	Fluvial Ecosystem						
Ecological Species Group by Lifeform[a]	MWFT (n = 5)	EFT (n = 3)	HAM (n = 8)	FSR (n = 8)	FR (n = 4)	FC (n=5)	SCARP (n = 9)
Ecosystem Number	2	4	5	6	7	8	15
Canopy Species							
Pinus	56.4 (4.7)[b]	—	0.4 (0.2)	—	1.4 (0.6)	0.4 (0.4)	—
Acer-Celtis	16.2 (5.3)	19.0 (9.6)	40.3 (2.6)	2.9 (2.5)	56.0 (4.9)	42.5 (5.6)	1.4 (1.4)
Pinus-Quercus	15.2 (5.0)	50.9 (24.9)	0.6 (0.2)	15.4 (5.3)	4.3 (2.2)	0.4 (0.3)	50.9 (12.5)
Subcanopy Species							
Bumelia	6.4 (4.4)	—	9.1 (0.9)	—	3.1 (0.7)	6.3 (0.9)	—
Osmanthus-Prunus	—	—	18.7 (2.9)	—	0.9 (0.3)	7.4 (4.3)	—
Ostrya-Carpinus	5.8 (4.1)	—	24.0 (3.3)	3.3 (1.6)	27.1 (2.4)	31.5 (5.9)	—
Quercus	—	30.1 (15.3)	0.6 (0.5)	78.4 (5.2)	—	0.4 (0.3)	47.7 (12.1)
Shrub & Vine Species							
Viburnum	—	—	0.5 (0.3)	—	1.1 (0.6)	—	—
Campsis	—	—	0.3 (0.2)	—	—	1.3 (0.5)	—
Vitis	—	—	3.7 (0.8)	—	6.1 (2.0)	9.8 (2.1)	—
Vaccinium	—	—	1.8 (0.4)	—	—	—	—

	Upland Ecosystem							
Ecological Species Group by Lifeform[a]	SPUT (n = 6)	MWUT (n =5)	WUT (n =16)	SEUT (n =10)	USR (n =6)	MARG (n=5)	CD (n = 10)	SD (n =3)
Ecosystem Number	9	10	11	12	13	14	16	17
Canopy Species								
Quercus-Nyssa	—	—	—	—	—	14.7 (14.7)	40.5 (4.5)	8.0 (4.5)
Quercus	—	—	8.2 (6.3)	10.5 (6.4)	1.2 (0.8)	6.7 (6.7)	38.9 (4.3)	13.1 (2.9)
Pinus-Quercus	100.0 (0.0)	69.0 (23.7)	63.8 (9.8)	20.0 (7.5)	14.1 (2.4)	69.9 (27.0)	0.7 (0.5)	39.9 (10.3)
Subcanopy Species								
Vaccinium	—	—	—	—	1.0 (0.7)	—	0.9 (0.6)	17.3 (8.8)
Quercus	—	31.0 (23.7)	24.9 (9.2)	69.5 (13.2)	83.7 (2.7)	—	—	18.7 (18.7)
Crataegus	—	—	3.1 (3.1)	—	—	—	11.9 (3.8)	—
Shrub & Vine Species								
Campsis	—	—	—	—	—	5.7 (5.7)	7.1 (1.7)	1.0 (1.0)

[a] See Appendix B for ecological species group members. Ecological species groups derived using TWINSPAN.
[b] Mean (+ 1 standard error).

Understory relative densities of selected fluvial and upland ecosystems of Ichauway, southwest Georgia.

Ecological Species Group by Lifeform[a]	Fluvial Ecosystem MWFT (n = 5)	EFT (n = 3)	HAM (n = 8)	FSR (n = 8)	FR (n = 4)	FC (n = 5)	SCARP (n = 9)
Ecosystem Number	2	4	5	6	7	8	15
Canopy Species							
Pinus-Quercus	17.2 (6.4)[b]	7.4 (4.1)	—	1.6 (1.2)	4.0 (4.0)	—	4.6 (1.4)
Diospyros-Liquidambar	30.0 (6.3)	2.0 (1.2)	0.3 (0.3)	2.3 (1.1)	2.0 (1.4)	0.4 (0.4)	4.9 (1.8)
Acer-Celtis	10.0 (5.8)	—	6.4 (3.0)	—	4.5 (2.1)	16.4 (5.2)	—
Quercus	—	0.7 (0.7)	30.0 (6.9)	3.0 (1.5)	13.5 (10.3)	0.8 (0.5)	0.2 (0.2)
Subcanopy Species							
Quercus	0.4 (0.4)	34.7 (25.7)	0.5 (0.5)	58.1 (12.3)	—	—	55.1 (9.9)
Vaccinium	15.6 (5.5)	2.0 (2.0)	2.8 (0.9)	17.0 (8.1)	4.5 (1.7)	2.8 (1.5)	2.8 (1.3)
Chionanthus	4.4 (2.6)	—	43.8 (5.4)	—	10.0 (4.1)	25.2 (8.4)	—
Shrub & Vine Species							
Rubus-Rhus	7.6 (3.2)	53.2 (21.7)	—	15.7 (9.3)	—	—	32.4 (7.3)
Vaccinium	10.8 (6.3)	—	7.8 (2.2)	2.3 (1.6)	—	7.6 (7.6)	—
Sebastiania-Sabal	4.0 (2.5)	—	8.4 (3.1)	—	61.5 (13.6)	46.8 (7.0)	—

Ecological Species Group by Lifeform[a]	Upland Ecosystem SPUT (n = 6)	MWUT (n =5)	WUT (n =16)	SEUT (n =10)	USR (n =6)	MARG (n=5)	CD (n = 10)	SD (n =3)
Ecosystem Number	9	10	11	12	13	14	16	17
Canopy Species								
Pinus-Quercus	36.3 (14.3)	26.4 (16.7)	11.2 (2.2)	6.0 (2.1)	6.7 (3.3)	14.0 (3.4)	16.8 (5.2)	2.0 (1.2)
Quercus-Nyssa	—	—	—	—	—	—	12.7 (3.4)	—
Quercus	11.0 (5.0)	—	6.5 (2.7)	2.2 (1.4)	—	4.0 (4.0)	33.8 (7.1)	51.9 (21.4)
Subcanopy Species								
Crataegus	4.7 (4.7)	3.6 (2.6)	1.7 (1.0)	—	—	—	1.8 (1.4)	—
Quercus	7.7 (3.2)	14.0 (7.9)	30.2 (8.4)	46.6 (8.5)	84.3 (4.2)	2.4 (1.9)	4.7 (3.4)	12.0 (2.3)
Shrubs & Vines								
Vaccinium-Serenoa	—	—	—	—	1.0 (1.0)	—	22.0 (7.8)	28.7 (22.9)
Asimina-Rhus	35.3 (9.1)	44.0 (12.1)	36.9 (6.8)	39.2 (8.4)	8.0 (4.6)	54.8 (16.3)	3.6 (2.8)	4.7 (1.8)
Myrica-Vaccinium	5.0 (4.3)	12.0 (7.6)	13.5 (6.1)	6.0 (4.6)	—	24.8 (14.1)	4.6 (4.6)	0.7 (0.7)

a See Appendix B for ecological species group members. Ecological species groups derived using TWINSPAN.
b Mean (+ 1standard error).

Ground-flora ecological species group importance percentages (IP) for selected fluvial and upland ecosystems of Ichauway, southwest Georgia.

Ground-flora Ecological Species Group[a]	Fluvial Ecosystem MWFT (n = 5)	EFT (n = 3)	HAM (n = 8)	FSR (n = 8)	FR (n = 4)	FC (n = 5)	SCARP (n = 9)
Ecosystem Number	2	4	5	6	7	8	15
Bulbostylis-Opuntia	—	0.5 (0.5)[b]	—	11.1 (3.7)	—	—	0.2 (0.1)
Aster-Galactia	3.2 (1.2)	2.2 (0.2)	—	2.4 (0.8)	—	—	1.5 (0.5)
Panicum-Erianthus	21.3 (6.7)	0.3 (0.3)	—	0.1 (0.1)	—	—	0.1 (0.1)
Dyschoriste-Scleria	24.0 (4.2)	28.1 (2.6)	0.7 (0.5)	29.2 (3.9)	—	0.2 (0.2)	21.4 (1.6)
Aristida-Andropogon	3.1 (2.8)	44.8 (8.8)	0.5 (0.3)	45.4 (5.1)	—	3.2 (2.9)	41.4 (1.4)
Eupatorium-Rhynchospora	—	3.1 (2.5)	—	1.7 (0.9)	—	—	0.3 (0.2)
Rubus-Schizachyrium	2.6 (1.7)	7.3 (4.4)	—	1.7 (1.0)	—	—	5.3 (1.3)
Gaylussacia-Crotalaria	—	2.3 (1.0)	—	1.5 (0.7)	—	—	6.2 (1.8)
Pteridium-Polygala	—	4.3 (3.2)	—	0.5 (0.2)	—	—	10.3 (1.9)
Sorghastrum-Rhynchosia	—	6.2 (3.0)	—	1.7 (0.9)	—	—	12.0 (1.9)
Vaccinium-Ruellia	26.9 (4.7)	0.7 (0.4)	3.1 (0.8)	3.5 (1.3)	14.7 (3.9)	11.8 (2.5)	1.0 (0.3)
Trachelospermum-Lygodium	3.0 (3.0)	—	—	—	2.1 (1.6)	1.0 (1.0)	—
Dioscorea-Viola	0.3 (0.3)	—	0.7 (0.5)	—	25.7 (2.8)	4.7 (2.1)	—
Parthenocissus-Bignonia	14.3 (6.0)	—	35.6 (5.1)	0.3 (0.2)	41.0 (3.6)	47.3 (4.8)	0.1 (0.1)
Mitchella-Euonymus	0.7 (0.7)	—	26.9 (3.6)	0.2 (0.1)	14.9 (1.9)	15.6 (1.8)	0.1 (0.1)
Quercus-Ilex	0.6 (0.6)	0.2 (0.2)	32.5 (4.9)	0.7 (0.4)	1.6 (0.9)	16.2 (6.1)	0.1 (0.1)

Ground-flora Ecological Species Group[a]	Upland Ecosystem SPUT (n = 6)	MWUT (n =5)	WUT (n =16)	SEUT (n =10)	USR (n =6)	MARG (n=5)	CD (n = 10)	SD (n =3)
Ecosystem Number	9	10	11	12	13	14	16	17
Croton-Stylisma	3.8 (1.0)	6.0 (2.2)	6.1 (0.8)	8.3 (1.0)	43.3 (4.7)	1.6 (0.6)	1.4 (1.4)	13.2 (8.8)
Aristida-Dyschoriste	55.6 (2.5)	47.3 (2.0)	46.9 (1.9)	50.0 (2.2)	48.4 (2.4)	46.5 (6.5)	0.2 (0.2)	41.7 (14.8)
Hypericum-Solidago	5.2 (1.6)	1.2 (0.9)	2.9 (1.6)	0.2 (0.2)	—	11.2 (8.7)	—	5.2 (5.2)
Scleria-Aster	23.2 (2.3)	20.8 (3.4)	12.9 (1.4)	7.8 (1.2)	1.3 (0.9)	21.7 (1.2)	—	3.5 (3.5)
Rhyncosia-Crotollaria	6.6 (1.1)	10.5 (1.4)	10.3 (1.2)	10.5 (1.0)	1.4 (1.0)	5.9 (1.6)	—	1.3 (1.3)
Centrosema-Schrankia	2.9 (1.1)	4.4 (0.8)	9.1 (1.3)	10.8 (1.7)	2.9 (1.6)	7.2 (1.9)	—	2.4 (2.4)
Solidago-Cassia	1.9 (0.9)	8.2 (2.1)	9.4 (1.3)	10.4 (1.5)	1.3 (1.0)	3.5 (1.9)	—	—
Quercus-Campsis	0.4 (0.3)	0.5 (0.5)	0.4 (0.2)	1.1 (0.7)	—	0.1 (0.1)	71.3 (8.9)	20.3 (18.4)
Quercus-Smilax	0.1 (0.1)	—	0.5 (0.3)	0.5 (0.2)	1.4 (0.5)	—	16.2 (8.5)	2.5 (2.5)
Diospyros-Smilax	0.3 (0.2)	1.1 (0.6)	1.5 (1.1)	0.4 (0.3)	—	2.3 (1.2)	10.9 (3.3)	9.9 (6.5)

a See Appendix B for ecological species group members. Ecological species groups derived using TWINSPAN.
b Mean (+ 1 standard error).

Appendix B - Ecological Species Groups

The following lists describe the individual species that comprise each ecological species groups. The ecological species groups were derived from TWINSPAN and were generated for each physiographic zone (fluvial ecosystems and upland ecosystems), forest strata (overstory, midstory, understory, and ground-flora), and growth form (canopy, subcanopy, shrub-vine, and ground-flora). See figure below for an explanation of each vegetative stratum and potential growth form.

[a] Growth form determined by stature at maturity

Fluvial ecosystems

Fluvial ecosystems

Overstory species groups—Canopy species

Pinus

Carya tomentosa (Poir. In Lam.) Nutt.
Nyssa sylvatica Marsh.
Pinus echinata Mill.
Pinus elliottii Engelm.
Pinus taeda L.
Quercus alba L.
Quercus phellos L.
Quercus stellata Wang.

Liquidambar—Quercus

Fraxinus americana L.
Liquidambar stryaciflua L.
Quercus laurifolia Michx.
Quercus nigra L.
Ulmus alata Michx.

Celtis—Ulmus

Acer rubrum L.
Aesculus pavia L.
Carya aquatica (Michx. f.) Nutt.
Carya cordiformis (Wang.) K. Koch
Carya ovata Mill. K. Koch
Celtis laevigata Willd.
Diospyros virginiana L.
Fagus grandifolia Ehrh.
Fraxinus pennsylvanica Marsh.
Pinus glabra Walt.
Quercus lyrata Walt.
Quercus michauxii Nutt.
Quercus shumardii Buckl.
Quercus velutina Lam.
Taxodium distichum (L.) L. Rich.
Ulmus americana L.

Acer—Quercus

Acer saccharum subsp. *floridanum* Marsh.
Carya glabra (Mill.) Sweet
Catalpa bignonioides Walt.
Juniperus virginiana L.
Magnolia grandiflora L.
Morus rubra L.
Prunus serotina Ehrh.
Quercus austrina Small
Quercus hemisphaerica Bartr.
Quercus virginiana Mill.
Sassafras albidum (Nutt.) Nees.
Taxodium ascendens Brongn.
Tilia americana L.

Pinus—Quercus

Pinus palustris Mill.
Quercus falcata Michx.
Quercus geminata Small

Overstory species groups—Subcanopy species

Quercus

Crataegus flava Ait.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe

Ostrya—Carpinus

Carpinus caroliniana Walt.
Cercis canadensis L.

Appendix B. Continued.

Chionanthus virginicus L.
Cornus florida L.
Crataegus spp
Halesia carolina L.
Halesia diptera Ellis
Ostrya virginiana (Mill.) K. Koch

Bumelia—Osmanthus

Amelanchier arborea (Michx. f.) Fern.
Bumelia lanuginosa (Michx.) Pers.
Ilex ambigua (Michx.) Torr.
Ilex opaca Ait.
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray
Persea borbonia (L.) Spreng.
Prunus caroliniana (Mill.) Ait.
Prunus umbellata Ell.
Vaccinium arboreum Marsh.

Midstory species groups—Canopy species

Pinus

Carya tomentosa (Poir. In Lam.) Nutt.
Nyssa sylvatica Marsh.
Pinus echinata Mill.
Pinus elliottii Engelm.
Pinus taeda L.
Quercus alba L.
Quercus phellos L.
Quercus stellata Wang.

Acer—Celtis

Acer rubrum L.
Acer saccharum subsp. *floridanum* Marsh.
Carya aquatica (Michx. f.) Nutt.
Carya cordiformis (Wang.) K. Koch
Carya glabra (Mill.) Sweet
Catalpa bignonioides Walt.
Celtis laevigata Willd.
Diospyros virginiana L.
Fraxinus americana L.
Fraxinus pennsylvanica Marsh.
Juniperus virginiana L.
Liquidambar stryaciflua L.
Magnolia grandiflora L.
Morus rubra L.
Pinus glabra Walt.
Prunus serotina Ehrh.
Quercus austrina Small
Quercus geminata Small
Quercus hemisphaerica Bartr.
Quercus laurifolia Michx.
Quercus lyrata Walt.
Quercus michauxii Nutt.
Quercus shumardii Buckl.
Quercus velutina Lam.
Quercus virginiana Mill.
Taxodium distichum (L.) L. Rich.
Tilia americana L.
Ulmus alata Michx.
Ulmus americana L.

Pinus—Quercus

Pinus palustris Mill.
Quercus falcata Michx.
Quercus nigra L.
Sassafras albidum (Nutt.) Nees.

Midstory species groups—Subcanopy species

Bumelia

Bumelia lanuginosa (Michx.) Pers.
Cornus florida L.
Halesia carolina L.
Ilex opaca Ait.
Prunus umbellata Ell.

Osmanthus—Prunus

Amelanchier arborea (Michx. f.) Fern.
Asimina parviflora (Michx.) Dunal
Halesia spp.
Hamamelis virginiana L.
Ilex vomitoria Ait.
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray
Persea borbonia (L.) Spreng.
Prunus caroliniana (Mill.) Ait.

Ostrya—Carpinus

Aesculus pavia L.
Carpinus caroliniana Walt.
Cercis canadensis L.
Chionanthus virginicus L.
Cornus asperifolia Michx.
Crataegus spp
Cyrilla racemiflora L.
Halesia diptera Ellis
Ilex ambigua (Michx.) Torr.
Linaria canadensis (L.) Dumont
Ostrya virginiana (Mill.) K. Koch
Vaccinium arboreum Marsh.

Quercus

Crataegus flava Ait.
Prunus angustifolia Marsh.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe

Midstory species groups—Shrub & vine species

Viburnum

Parthenocissus quinquefolia (L.) Planch.
Viburnum rufidulum Raf.

Campsis

Berchemia scandens (Hill) K. Koch
Campsis radicans (L.) Seem. ex Bureau
Vaccinium elliottii Chapm.
Vitis aestivalis Michx.

Vitis

Toxicodendron radicans (L.) Kuntze
Vitis rotundifolia Michx.

Vaccinium

Castanea pumila (L.) Mill.
Vaccinium stamineum L.

Understory species groups—Canopy species

Pinus-Quercus

Carya cordiformis (Wang.) K. Koch
Pinus palustris Mill.
Prunus serotina Ehrh.
Quercus alba L.
Quercus falcata Michx.
Quercus nigra L.

Appendix B. Continued.

Quercus phellos L.
Quercus pumila Walt.
Quercus stellata Wang.

Diospyros

Carya tomentosa (Poir. In Lam.) Nutt.
Diospyros virginiana L.
Liquidambar stryaciflua L.
Sassafras albidum (Nutt.) Nees.

Acer—Celtis

Acer saccharum subsp. *floridanum* Marsh.
Acer rubrum L.
Celtis laevigata Willd.
Morus rubra L.

Quercus laurifolia **Michx.**

Ulmus alata Michx.

Quercus
Carya glabra (Mill.) Sweet
Fraxinus pennsylvanica Marsh.
Magnolia grandiflora L.
Quercus geminata Small
Quercus hemisphaerica Bartr.
Quercus lyrata Walt.
Quercus virginiana Mill.
Tilia americana L.

Understory species groups—Subcanopy species

Quercus

Aesculus pavia L.
Crataegus flava Ait.
Prunus angustifolia Marsh.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe

Vaccinium

Asimina parviflora (Michx.) Dunal
Bumelia lanuginosa (Michx.) Pers.
Carpinus caroliniana Walt.
Cercis canadensis L.
Chionanthus virginicus L.
Cornus asperifolia Michx.
Cornus florida L.
Crataegus spp.
Crataegus viridis L.
Halesia diptera Ellis
Hamamelis virginiana L.
Ilex opaca Ait.
Ilex vomitoria Ait.
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray
Ostrya virginiana (Mill.) K. Koch
Persea borbonia (L.) Spreng.
Prunus caroliniana (Mill.) Ait.
Prunus umbellata Ell.
Symplocos tinctoria (L.) L'Her.
Vaccinium arboreum Marsh.

Understory species groups—Shrub & vine species

Rubus—Rhus

Amorpha fruticosa L.
Asimina longifolia Kral
Baptisia alba (L.) R. Br.
Gaylussacia dumosa (Andrz.) T. & G.
Indigofera caroliniana Mill.
Rhus copallina L.
Rubus cuneifolius Pursh
Vaccinium darrowii Camp
Vaccinium myrsinites Lam.
Yucca flaccida Haw.

Vaccinium

Euonymus americanus L.
Rubus flagellaris Willd.
Serenoa repens (Bartr.) Small
Vaccinium corymbosum L.
Vaccinium stamineum L.

Sebastiania—Sabal

Amelanchier arborea (Michx. f.) Fern.
Arundinaria gigantea (Walt.) Muhl.
Callicarpa americana L.
Calycocarpum lyonii (Pursh) Gray
Campsis radicans (L.) Seem. ex Bureau
Crataegus uniflora Muenchh.
Forestiera ligustrina (Michx.) Poir.
Nandina domestica Thunb.
Ptelea trifoliata L.
Rhus glabra L.
Rubus cuneifolius Pursh.
Sabal minor (Jacq.) Pers.
Sebastiania fruticosa (Bartr.) Fern.
Vaccinium elliottii Chapm.
Viburnum dentatum L.
Viburnum obovatum Walt.

Ground-flora species groups

Bulbostylis—Opuntia

Agalinis obtusifolia Raf.
Amsonia ciliata Walt.
Anthaenantia villosa (Michx.) Beauv.
Asclepias humistrata Walt.
Aureolaria pedicularia (L.) Raf.
Bulbostylis ciliatifolia (Ell.) Fern.
Chamaesyce cordifolia (Ell.) Small
Chloris floridana (Chapm.) Wood
Commelina erecta L.
Erigeron strigosus Muhl. ex Willd.
Fimbristylis autumnalis (L.) R. & S.
Galium hispidulum Michx.
Helianthemum corymbosum Michx.
Helianthemum rosmarinifolium Pursh
Indigofera caroliniana Mill.
Lespedeza intermedia (S. Watts.) Britt.
Leersia virginica Willd.
Licania michauxii Prance
Liatris tenuifolia Nutt.
Opuntia humifusa (Raf.) Raf.
Paronychia rugelii Shuttlew ex Chapm.
Polygonella gracilis (Nutt.) Meisn.
Quercus laevis Walt.
Rumex hastatulus Baldw. ex. Ell.
Seymeria pectinata Pursh
Stylodon carneus (Medic.) Moldenke
Stipulicida setacea Michx.
Stylisma humistrata (Walt.) Chapm.
Triplasis americana Beauv.
Tradescantia ohiensis Raf.

Appendix B. Continued.

Aster—Galactia

Aster tortifolius Michx.
Asclepias verticillata L.
Diodia teres Walt.
Gaillardia aestivalis (Walt.) Rock
Galactia microphylla (Chapm.) Hall & Ward
Liatris graminifolia (Walt.) Willd.
Paspalum setaceum Michx.
Petalostemon pinnatum (Walt. ex. Gmel.) Blake
Zornia bracteata (Walt.) Gmel.

Panicum—Erianthus

Aristida palustris (Chapm.) Vasey
Aster sagittifolius Wedem. ex Willd.
Carya tomentosa (Poir. in Lam.) Nutt.
Ceanothus americanus L.
Crataegus spathulata Michx.
Desmodium glabellum Michx.) DC.
Dioclea multiflora (T. & G.) Mohr
Elephantopus elatus Bertol.
Erianthus alopecuroides (L.) Ell.
Euthamia minor (Michx.) Greene
Gnaphalium obtusifolium L.
Gymnopogon ambiguus (Michx.) BSP
Hypericum crux-andreae (L.) Crantz
Oxalis corniculata L.
Oxypolis filiformis Walt.) Britt.
Panicum aciculare Desv. ex Poir
Penstemon laevigatus Solander
Pinus taeda L.
Vaccinium stamineum L.

Dyschoriste—Scleria

Aristida purpurascens Poir.
Aster dumosus L.
Cassia fasciculata Michx.
Cassia nictitans L.
Desmodium lineatum DC.
Desmodium marilandicum (L.) DC.
Dyschoriste oblongifolia (Michx.) Kuntze
Galium pilosum Ait.
Lespedeza angustifolia (Pursh) Ell.
Lespedeza repens (L.) Bart.
Panicum acuminatum Sw.
Panicum angustifolium Ell.
Panicum virgatum L.
Rhynchospora harveyi Boott
Scleria ciliata Michx.
Scutellaria integrifolia L.
Schrankia microphylla (Dry.) MacBride
Solidago leavenworthii T. & G.
Stylosanthes biflora (L.) BSP
Tephrosia florida (Dietr.) Wood
Tephrosia spicata (Walt.) T & G
Vernonia angustifolia Michx.

Aristida—Andropogon

Acalypha gracilens Gray
Andropogon virginicus L.
Aristida stricta Michx.
Aster concolor L.
Centrosema virginianum (L.) Benth.
Clitoria mariana L.
Cnidoscolus stimulosus (Michx.) Engelm. & Gray
Croton argyranthemus Michx.
Cyperus filiculmis Vahl
Desmodium ciliare (Muhl. ex Willd.) DC.
Euphorbia pubentissima Michx.
Gaura filipes Spach.
Hedyotis procumbens (Walt. ex Gmel.) Fosb.
Ipomoea pandurata (L.) G. F. W. Meyer
Lechea minor L.
Lechea sessiliflora Raf.
Panicum ovale Ell.
Panicum tenue Muhl.
Penstemon australis Small
Physalis angulata L.
Piriqueta caroliniana (Walt.) Urban
Pityopsis graminifolia (Michx.) Nutt.
Pinus palustris Mill.
Quercus margaretta Ashe
Rhus copallina L.
Sporobolus clandestinus (Biehler) Hitchc.
Sporobolus junceus (Michx.) Kunth
Stylisma humistrata (Walt.) Chapm.
Toxicodendron toxicarium (Salisb.) Gillis
Tragia urens L.

Eupatorium—Rhynchosia

Cyperus globulosus Aubl.
Eupatorium cuneifolium Willd.
Eupatorium mohrii Green
Helianthemum carolinianum (Walt.) Michx.
Hedyotis corymbosa (L.) Lam.
Hypericum gentianoides (L.) BSP
Rhynchospora grayi Kunth
Rudbeckia hirta L.
Tragia urticifolia Michx.

Rubus—Schizachyrium

Ambrosia artemisiifolia L.
Erianthus strictus Baldw.
Helianthus radula (Pursh) T. & G.
Rubus cuneifolius Pursh
Schizachyrium tenerum Nees
Vaccinium myrsinites Lam.
Gaylussacia-Crotalaria
Ageratina aromatica (L.) Spach
Anagallis arvensis L.
Asimina longifolia Kral
Crotalaria purshii DC.
Crotalaria rotundifolia Walt. ex Gmel.
Cyperus plukenetii Fern
Desmodium lineatum DC.
Desmodium obtusum (Muhl ex Willd.) DC.
Eriogonum tomentosum Michx.
Gaylussacia dumosa (Andrz.) T. & G.
Galactia volubilis (L.) Britt.
Hypericum pseudomaculatum Bush
Lespedeza procumbens Michx.
Liatris elegans (Walt.) Michx.
Liatris gracilis Pursh
Psoralea canescens Michx.
Quercus falcata Michx.
Scutellaria integrifolia L.
Sisyrinchium nashii Bickn
Verbesina aristata (Ell.) Heller
Viola villosa Walt.

Pteridium—Polygala

Chrysopsis mariana (L.) Ell.

Appendix B. Continued.

Eupatorium hyssopifolium L.
Polygala grandiflora alt.
Pteridium aquilinum (L.) Kuhn
Quercus incana Bartr.
Silphium simpsonii Greene
Stillingia sylvatica Garden ex L.
Tephrosia virginiana (L.) Pers.

Sorghastrum—Rhynchosia

Aralia spinosa L.
Aster adnatus Nutt.
Aster linariifolius L.
Chrysopsis gossypina (Michx.) Ell.
Chloris petraea (Sw.) Desv.
Desmodium strictum (Pursh) DC.
Galactia erecta (Walt.) Vail
Galactia mollis Michx.
Gnaphalium pensilvanicum Willd.
Helianthus angustifolius L.
Hexastylis arifolia (Michx.) Small
Hieracium gronovii L.
Hypericum hypericoides (L.) Crantz
Hypericum suffruticosum Adams & Robson
Lactuca graminifolia Michx.
Lespedeza capitata Michx.
Lygodesmia aphylla (Nutt.) DC.
Muhlenbergia capillaris (Lam.) Trin.
Onosmodium virginianum (L.) A. DC.
Panicum strigosum Muhl.
Petalostemon albidum (T.& G.)Small
Physalis pubescens L.
Polygonum hydropiperoides Michx.
Prunus serotina Ehrh.
Psoralea lupinellus Michx.
Rhynchospora microcarpa Baldw. ex Gray
Rhynchosia reniformis (Pursh) DC.
Sida elliottii T. & G.
Sorghastrum elliottii (Mohr) Nash
Sorghastrum nutans (L.) Nash
Sorghastrum secundum (Ell.) Nash
Solidago odora Alt.
Tephrosia mohrii (Rydb.) Godfrey
Tragia smallii Shinners
Viola septemloba LeConte

Vaccinium—Ruellia

Aristolochia serpentaria L.
Chasmanthium sessiliflorum (Poir.) Yates
Erianthus brevibarbis Michx.
Liquidambar stryaciflua L.
Panicum commutatum Schutt.
Rubus argutus Link
Rubus trivialis Michx.
Ruellia caroliniensis (Walt. ex Gmel.) Steud
Sassafras albidum (Nutt.) Nees
Serenoa repens (Bartr.) Small
Smilax bona-nox L.
Smilax glauca Walt.
Vaccinium arboreum Marsh
Viola sororia Willd.

Trachelospermum—Lygodium

Agrimonia microcarpa Wallr.
Eupatorium semiserratum DC.
Lygodium japonicum (Thunb.) Sw.
Paspalum floridanum Michx.
Quercus phellos L.
Trachelospermum difforme (Walt.) Gray

Dioscorea—Viola

Acer rubrum L.
Amorpha fruticosa L.
Arundinaria gigantea (Walt.) Muhl.
Aristolochia tomentosa Sims
Calycanthus floridus L.
Carex abscondita Mackenz.
Carpinus caroliniana Walt.
Carya cordiformis (Wang.) K. Koch
Carex digitalis Willd.
Carex floridana Schw.
Chasmanthium latifolium (Michx.) Yates
Dioscorea quaternata (Walt.) Gmel.
Diospyros virginiana L.
Elephantopus carolinianus Raeusch.
Fagus grandifolia Ehrh.
Hymenocallis occidentalis (J. LeConte) Kunth
Ilex opaca Ait.
Justicia ovata (Walt.) Lindau
Lonicera sempervirens L.
Matelea flavidula (Chapm.) Woodson
Polygala nana (Michx.) DC.
Quercus nigra L.
Sambucus canadensis L.
Scutellaria incana Biehler
Smilax auriculata Walt.
Smilax ecirrhata (Engelm. ex Kunth) Wats.
Solidago arguta Alt.
Spigelia marilandica L.
Thelypteris quadrangularis var. *versicolor* (St. John) AR Smith
Uvularia floridana Chapm.
Vernonia gigantea subsp. *ovalifolia* (T&G) Urbatsch
Viola affinis LeConte
Viola walteri House

Parthenocissus—Bignonia

Arisaema dracontium (L.) Schott
Bignonia capreolata L.
Campsis radicans (L.) Seem. ex Bureae
Cornus asperifolia Michx.
Parthenocissus quinquefolia (L.) Planch.
Smilax smallii Morong
Smilax tamnoides L.
Toxicodendron radicans (L.) Kuntze
Trichostema dichotomum L.
Vitis rotundifolia Michx.

Mitchella—Euonymus

Acer saccharum subsp. *floridanum* Marsh.
Carya glabra (Mill.) Sweet
Celtis laevigata Willd.
Conyza canadensis (L.) Cronq.
Euonymus americanus L.
Mitchella repens L.
Ostrya virginiana (Mill.) K. Koch
Sebastiania fruticosa (Bartr.) Fern.

Quercus—Ilex

Amelanchier arborea (Michx. f.) Fern.
Asimina parviflora (Michx.) Dunal

Appendix B. Continued.

Berchemia scandens (Hill) K. Koch
Bumelia lanuginosa (Michx.) Pers.
Calamintha georgiana (Harper) Shinners
Cardamine pensylvanica Muhl. ex Willd.
Cercis canadensis L.
Chionanthus virginicus L.
Clematis glaucophylla Small
Conopholis americana (L.) Wallr.
Cocculus carolinus (L.) DC.
Commelina virginica L.
Diodia virginiana L.
Forestiera ligustrina (Michx.) Poir.
Galium uniflorum Michx.
Gelsemium sempervirens (L.) Alt.f.
Halesia diptera Ellis
Hamamelis virginiana L.
Ilex vomitoria Ait.
Juniperus virginiana L.
Lonicera japonica Thunb.
Morus rubra L.
Nyssa sylvatica Marshall
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray
Passiflora lutea L.
Persea borbonia (L.) Spreng.
Prunus caroliniana (Mill.) Alt.
Quercus geminata Small
Quercus hemisphaerica Bartr.
Quercus laurifolia Michx.
Quercus virginiana Mill.
Smilax pumila Walt.
Tillandsia usneoides (L.) L.
Ulmus alata Michx.
Viburnum obovatum Walt.

<u>**Upland ecosystems**</u>

Overstory species groups—Canopy species

Quercus—Nyssa

Acer rubrum L.
Diospyros virginiana L.
Liquidambar stryaciflua L.
Nyssa biflora Walt.
Nyssa sylvatica Marsh
Pinus taeda L.
Prunus serotina Ehrh.
Quercus hemisphaerica Bartr.
Quercus laurifolia Michx.

Quercus

Pinus echinata Mill.
Pinus elliottii Engelm.
Quercus nigra L.
Quercus virginiana Mill.

Pinus—Quercus

Pinus palustris Mill.
Quercus falcata Michx.
Quercus geminata Small

Overstory species groups—Subcanopy species

Quercus

Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe
Crataegus aestivalis (Walt.) T. & G.
Crataegus spp
Ilex opaca Ait.

Midstory species groups—Canopy species

Quercus—Nyssa

Acer rubrum L.
Diospyros virginiana L.
Liquidambar stryaciflua L.
Nyssa biflora Walt.
Nyssa sylvatica Marsh.
Pinus elliottii Engelm.
Pinus glabra Walt.
Pinus taeda L.
Prunus serotina Ehrh.
Quercus laurifolia Michx.
Quercus phellos L.
Taxodium ascendens Brongn.

Quercus

Quercus hemisphaerica Bartr.
Quercus nigra L.
Quercus virginiana Mill.

Pinus—Quercus

Pinus palustris Mill.
Quercus falcata Michx.
Quercus geminata Small
Sassafras albidum (Nutt.) Nees.

Midstory species groups—Subcanopy species

Vaccinium

Chionanthus virginicus L.
Cornus florida L.
Crataegus aestivalis (Walt.) T. & G.
Crataegus flava Ait.
Crataegus spp.
Ilex opaca Ait.
Prunus umbellata Ell.
Vaccinium arboreum Marsh.

Midstory species groups—Shrubs & vine species

Campsis

Campsis radicans (L.) Seem. ex Bureau
Cephalanthus occidentalis L.
Myrica cerifera L.
Toxicodendron radicans (L.) Kuntze
Vaccinium elliottii Chapm.
Vaccinium stamineum L.
Vitis rotundifolia Michx.

Understory species groups—Canopy species

Pinus—Quercus

Diospyros virginiana L.
Pinus palustris Mill.
Prunus serotina Ehrh.
Quercus falcata Michx.
Quercus stellata Wang.
Quercus virginiana Mill.
Sassafras albidum (Nutt.) Nees.

Quercus—Nyssa

Nyssa biflora Walt.
Nyssa sylvatica Marsh.
Pinus taeda L.

Appendix B. Continued.

Quercus laurifolia Michx.
Quercus phellos L.

Quercus

Liquidambar stryaciflua L.
Quercus geminata Small
Quercus hemisphaerica Bartr.
Quercus nigra L.

Understory species groups—Subcanopy species

Crataegus

Crataegus aestivalis (Walt.) T. & G.
Crataegus flava Ait.
Crataegus spp.
Cyrilla racemiflora L.
Leucothoe racemosa (L.) Gray
Osmanthus americanus (L.) Benth. & Hook. f. ex Gray
Prunus caroliniana (Mill.) Ait.
Prunus umbellata Ell.
Quercus incana Bartr.
Quercus laevis Walt.
Quercus margaretta Ashe
Vaccinium arboreum Marsh.

Understory species groups—Shrubs & vine species

Vaccinium—Serenoa

Campsis radicans (L.) Seem. ex Bureau
Serenoa repens (Bartr.) Small
Vaccinium elliottii Chapm.

Asimina—Rhus

Asimina longifolia Kral
Crataegus uniflora Meunchh.
Licania michauxii Prance
Rhus copallina L.
Rubus cuneifolius Pursh
Stylisma sylvatica Garden ex L.
Vaccinium myrsinites Lam.

Myrica—Vaccinium

Gaylussacia dumosa (Andrz.) T. & G.
Myrica cerifera L.
Rubus argutus Link.
Rubus flagellaris Willd.
Vaccinium darrowii Camp
Vaccinium staminium L.

Ground-flora species groups

Croton—Stylisma

Ambrosia artemisiifolia L.
Andropogon ternarius Michx.
Aristolochia tomentosa Sims
Bulbostylis barbata (Rottb.) Clarke
Bulbostylis ciliatifolia (Ell.) Fern.
Chrysopsis gossypina (Michx.) Ell.
Cnidoscolus stimulosus (Michx.) Engelm. & Gray
Commelina erecta L.
Croton argyranthemus Michx.
Cyperus filiculmis Vahl
Desmodium ciliare (Muhl. ex Willd.) DC.
Eriogonum tomentosum Michx.
Eupatorium compositifolium Walt.
Eupatorium cuneifolium Willd.
Eupatorium mohrii Greene
Galactia microphylla (Chapm.) Hall & Ward
Galactia volubilis (L.) Britt.
Hedyotis corymbosa (L.) Lam.
Hieracium gronovii L.
Hypericum hypericoides (L.) Crantz
Lechea mucronata Raf.
Lechea sessiliflora Raf.
Liatris gracilis Pursh
Liatris tenuifolia Nutt.
Licania michauxii Prance
Opuntia humifusa (Raf.) Raf.
Panicum aciculare Desv. ex Poir.
Paronychia rugelii Shuttlew. ex Chapm.
Paspalum setaceum Michx.
Penstemon australis Small
Petalostemon pinnatum (Walt. ex. Gmel.) Blake
Physalis heterophylla Nees
Polygala grandiflora Walt.
Polygonella gracilis (Nutt.) Meisn.
Psoralea lupinellus Michx.
Quercus laevis Walt.
Quercus margaretta Ashe
Rhynchospora grayi Kunth
Serenoa repens (Bartr.) Small
Sorghastrum secundum (Ell.) Nash
Sporobolus junceus (Michx.) Kunth
Stipulicida setacea Michx.
Strophostyles umbellata (Muhl. ex Willd.) Britt.
Stylisma humistrata (Walt.) Chapm.
Tephrosia florida (Dietr.) Wood
Triplasis americana Beauv.
Vaccinium arboreum Marsh.
Zornia bracteata (Walt.) Gmel.

Aristida—Dyschoriste

Andropogon virginicus L.
Anthaenantia villosa (Michx.) Beauv.
Aristida stricta Michx.
Cassia nictitans L.
Chrysopsis mariana (L.) Ell.
Dyschoriste oblongifolia (Michx.) Kuntze
Euphorbia pubentissima Michx.
Gaylussacia dumosa (Andrz.) T. & G.
Lechea minor L.
Lespedeza repens (L.) Bart.
Panicum acuminatum Sw.
Panicum virgatum L.
Pityopsis graminifolia (Michx.) Nutt.
Rhynchospora harveyi Boott
Rubus cuneifolius Pursh
Schizachyrium tenerum Nees
Sorghastrum nutans (L.) Nash
Stylosanthes biflora (L.) BSP

Hypericum—Solidago

Aletris aurea Walt.
Andropogon gerardii Vitman
Aronia arbutifolia (L.) Ell.
Aster lateriflorus (L.) Britt.
Carphephorus odoratissimus (Gmel.) Herb.
Ceanothus microphyllus Michx.
Chaptalia tomentosa Vent.
Conyza canadensis var. *pusilla* (Nutt.) Cronq.
Crotonopsis linearis Michx.
Ctenium aromaticum (Walt.) Wood
Drosera brevifolia Pursh
Erianthus alopecuroides (L.) Ell.
Eupatorium capillifolium (Lam.) Small

Appendix B. Continued.

Eupatorium rotundifolium L.
Gaylussacia frondosa (L.) T. & G.
Gnaphalium spicatum Lam.
Gratiola pilosa Michx.
Habenaria quinqueseta (Michx.) A. Eaton
Helianthus angustifolius L.
Hibiscus aculeatus Walt.
Hypericum crux-andreae (L.) Crantz
Hypericum gentianoides (L.) BSP
Hypericum suffruticosum Adams & Robson
Ilex glabra (L.) Gray
Justicia ovata (Walt.) Lindau
Lespedeza procumbens Michx.
Lespedeza virginica (L.) Britt.
Ludwigia alternifolia L.
Ludwigia virgata Michx.
Mitreola sessilifolia (Walt.) G. Don
Panicum verrucosum Muhl.
Paspalum laeve Michx.
Paspalum notatum Fluegge
Polygala incarnata L.
Polygala lutea L.
Polygala nana (Michx.) DC.
Prunus umbellata Ell.
Pterocaulon pycnostachyum (Michx.) Ell.
Quercus falcata Michx.
Rhexia alifanus Walt.
Rhexia mariana L.
Rhynchospora plumosa Ell.
Sambucus canadensis L.
Scleria reticularis Michx.
Solidago fistulosa Mill.
Solidago stricta Ait.
Trichostema dichotomum L.

Scleria—Aster

Acalypha gracilens Gray
Aster adnatus Nutt.
Aster dumosus L.
Crotalaria purshii DC.
Desmodium marilandicum (L.) DC.
Diodia teres Walt.
Diospyros virginiana L.
Erianthus strictus Baldw.
Eryngium yuccifolium Michx.
Eupatorium hyssopifolium L.
Eupatorium linearifolium Walt.
Gymnopogon ambiguus (Michx.) BSP
Hedyotis procumbens (Walt. ex Gmel.) Fosb.
Helianthus radula (Pursh) T. & G.
Lespedeza angustifolia (Pursh) Ell.
Muhlenbergia capillaris (Lam.) Trin.
Myrica cerifera L.
Panicum ovale Ell.
Panicum tenue Muhl.
Pinus palustris Mill.
Scleria ciliata Michx.
Solidago leavenworthii T. & G.
Tragia smallii Shinners
Tragia urens L.
Vaccinium myrsinites Lam.

Rhynchosia—Crotalaria

Aristolochia serpentaria L.
Asimina longifolia Kral
Aster concolor L.
Aster tortifolius Michx.
Crotalaria rotundifolia (Walt.) Gmel.
Elephantopus elatus Bertol.
Galactia erecta (Walt.) Vail
Galium pilosum Ait.
Helianthemum carolinianum (Walt.) Michx.
Panicum angustifolium Ell.
Rhus copallina L.
Rhynchosia reniformis (Pursh) DC.
Tephrosia spicata (Walt.) T. & G.
Vernonia angustifolia Michx.

Centrosema—Schrankia

Aristida purpurascens Poir.
Centrosema virginianum (L.) Benth.
Clitoria mariana L.
Piriqueta caroliniana (Walt.) Urban
Pteridium aquilinum (L.) Kuhn
Ruellia caroliniensis (Walt. ex Gmel.) Steud.
Schrankia microphylla (Dry.) MacBride

Solidago—Cassia

Ageratina aromatica (L.) Spach
Ageratina jucunda (Greene) Clewell & Wooten
Asclepias obovata Ell.
Asclepias viridiflora Raf.
Aster linariifolius L.
Cassia deeringiana (Small & Pennell) Macbride
Cassia fasciculata Michx.
Chloris floridana (Chapm.) Wood
Cirsium horridulum Michx.
Claytonia virginica L.
Commelina communis L.
Crataegus flava Ait.
Croton glandulosus L.
Cyperus retrofractus (L.) Torr.
Desmodium laevigatum (Nutt.) DC.
Desmodium lineatum DC.
Desmodium obtusum (Muhl ex Willd.) DC.
Desmodium tortuosum (Sw.) DC.
Dicerandra linearifolia (Ell.) Benth.
Eragrostis hirsuta (Michx.) Nees
Euonymus americanus L.
Eupatorium leptophyllum DC.
Evolvulus sericeus Sw.
Galactia floridana T. & G.
Galactia mollis Michx.
Galium hispidulum Michx.
Gaura filipes Spach
Helianthemum rosmarinifolium Pursh
Ipomoea pandurata (L.) G. F. W. Meyer
Jacquemontia tamnifolia (L.) Griseb.
Lespedeza capitata Michx.
Lespedeza intermedia (S. Wats.) Britt.
Lygodesmia aphylla (Nutt.) DC.
Oenothera fruticosa L.
Onosmodium virginianum (L.) A. DC.
Panicum commutatum Schult.
Paspalum dilatatum Poir.
Penstemon laevigatus Solander
Pentodon pentandrus (Schum. & Thonn.) Vatke
Persea palustris (Raf.) Sarg.
Petalostemon albidum (T. & G.)Small
Physalis angulata L.
Physalis pubescens L.
Physalis virginiana Mill.

Appendix B. Continued.

Pinus elliottii Engelm.
Prunus angustifolia Marsh.
Psoralea canescens Michx.
Quercus stellata Wang.
Rhynchosia difformis (Ell.) DC.
Rhynchosia tomentosa (L.) H. & A.
Rhynchospora debilis Gale
Rudbeckia hirta L.
Scutellaria incana Biehler
Scutellaria integrifolia L.
Silphium simpsonii Greene
Sisyrinchium nashii Bickn.
Solidago nemoralis Ait.
Solidago odora Alt.
Sorghastrum elliottii (Mohr) Nash
Spiranthes tuberosa Raf.
Sporobolus clandestinus (Biehler) Hitchc.
Stillingia sylvatica Garden ex L.
Stylisma patens (Desr.) Myint.
Stylodon carneus (Medic.) Moldenke
Tephrosia virginiana (L.) Pers.
Toxicodendron toxicarium (Salisb.) Gillis
Vaccinium stamineum L.
Verbesina aristata (Ell.) Heller
Viola septemloba LeConte
Xyris ambigua Beyr. ex Kunth

Quercus—Campsis

Campsis radicans (L.) Seem. ex Bureau
Nyssa sylvatica Marsh.
Quercus hemisphaerica Bartr.
Quercus laurifolia Michx.
Quercus virginiana Mill.
Sassafras albidum (Nutt.) Nees
Smilax glauca Walt.
Smilax rotundifolia L.
Toxicodendron radicans (L.) Kuntze
Viburnum obovatum Walt.
Vitis rotundifolia Michx.

Quercus—Smilax

Leucothoe racemosa (L.) Gray
Liquidambar styraciflua L.
Mitchella repens L.
Nyssa biflora (Walt.) Sarg.
Parthenocissus quinquefolia (L.) Planch.
Pinus taeda L.
Prunus caroliniana (Mill.) Ait.
Prunus serotina Ehrh.
Quercus nigra L.
Smilax auriculata Walt.
Smilax tamnoides L.

Diodia—Smilax

Diodia virginiana L.
Panicum strigosum Muhl.
Quercus geminata Small
Rubus argutus Link
Smilax bona-nox L.
Smilax smallii Morong
Sporobolus floridanus Chapm.
Vaccinium elliottii Chapm