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DEPRESSIONAL WETLAND VEGETATION TYPES: A QUESTION OF PLANT COMMUNITY DEVELOPMENT

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Abstract: When wetland restoration includes re-establishing native plant taxa as an objective, an understanding of the variables driving the development of plant communities is necessary. With this in mind, we examined soil and physiographic characteristics of depressional wetlands of three vegetation types (cypress-gum swamps, cypress savannas, and grass-sedge marshes) located in a fire-maintained longleaf pine ecosystem in southwestern Georgia, USA. Our objective was to establish whether plant community development in these wetlands is controlled primarily by hydrogeomorphic features or by different disturbance histories. We did not identify physical features that uniquely separate the wetland vegetation types. Instead, we observed a range of topo-edaphic conditions that likely drive variations in hydrologic regimes, which in turn, are probable influences on fire regime. We propose that several long-term successional trajectories may be initiated in the prolonged absence of fire, altered hydrology, or both, which link the distinctive vegetation types. Thus, a range of vegetation types may be suitable as potential restoration goals for these depressional wetlands. We suggest that the opportunities or constraints for use of prescribed fire in the long-term management of restored wetlands and adjacent uplands should be a significant consideration in the development of restoration strategies targeting specific plant communities.

Key Words: depressional wetlands, isolated wetlands, non-alluvial wetlands, wetland plant communities, reference wetlands, wetland restoration, fire, succession

INTRODUCTION

Depressional wetlands are a distinctive feature of the southeastern USA. These intermittently inundated wetlands are significant because they provide important functions and values, including the maintenance of regional biodiversity (Sutter and Kral 1994, Golladay et al. 1997, Kirkman et al. 1998, Semlitsch and Brodie 1998, Battle and Golladay 1999, Kirkman et al. 1999), floodwater storage, and water quality (Rowell et al. 1995). These depressions are often shallow and easily drained, and smaller ones have received less protection than other types of wetlands under Section 404 of the Clean Water Act (National Research Council 1995, Federal Register 1996). Consequently, depressional wetlands are increasingly impacted by agricultural practices (e.g., center pivot irrigation, runoff, cultivation), urban development, and forestry operations (Bennett and Nelson 1990, Folkerts 1997).

Increased interest in restoration and management of depressional wetlands presents a need for identification of wetland types that could be used as reference sites to guide restoration or mitigation efforts. The use of reference sites has gained acceptance in ecosystem management and restoration as a desirable means to compare ecosystem processes and structures of less disturbed systems with those of sites targeted for management or restoration (Kentula et al. 1993, Brinson and Rheinhardt 1996, Fulé et al. 1997, Palik et al. 2000). When wetland restoration objectives include reestablishing native plant taxa, an understanding of the variables driving the development of biotic communities in reference sites is necessary (Bedford 1996, Kirkman et al. 1999, Palik et al. 2000).

Vegetation patterns have been described for some depressional wetland types in the southeastern US, such as Carolina bays (Sharitz and Gibbons 1982, Kirkman and Sharitz 1994, Sharitz and Gresham 1998), cypress ponds (Ewel 1998), non-forested upland ponds (LaClaire 1995), and wetlands of southern Florida (Duever 1984, 1986). However, in non-peat depressional wetlands, there is little understanding of site-vegetation and successional relationships (Ewel 1998, Sharitz and Gresham 1998). Although recognition of these differences is often problematic in reference site selection (Simberloff 1990, Pickett and Parker 1994), it is particularly acute for depressional wetlands in many areas of the Gulf Coastal Plain because so little is known about their vegetative variation or the conditions that led to their development. More specifically, we do not know if some different wetland plant communities represent multiple vegetation states due to variable disturbances, if geomorphic characteristics primarily constrain community development, or how these factors are interrelated.

Non-alluvial depressional wetlands of the Dougherty Plain in southwestern Georgia are an important example. They are thought to originate from dissolution of underlying limestone and subsidence of surface soils (Hendricks and Goodwin 1952). These wetlands range in size from small (several m^2) holes with steep sides to shallow, flat expanses of many hectares with depths of up to 8 m. Many of these wetlands have impervious clay bottoms and hydrologic regimes that are driven by precipitation and evapotranspiration, while others appear to have direct connections to regional ground-water sources (Hendricks and Goodwin 1952, Torak et al. 1991). Additionally, seasonal, annual, and inter-annual water levels fluctuate widely (Hendricks and Goodwin 1952, Blood et al. 1997). The resultant vegetation varies from open grassy meadows to cypress savannas and cypress-hardwood forests. Although differences in vegetation types have been attributed to geologic or successional age of the wetland (Hendricks and Goodwin 1952) or sources of water (i.e., ground water versus surface water) (Sutter and Kral 1994), these relationships have not been substantiated.

Limesink depressional wetlands are embedded in landscapes that were once, if not presently, dominated by *Pinus palustris* Mill. (longleaf pine) or *P. elliotii* Engelm. (slash pine) communities that are fire-dependent. Thus, fire has been a recurring disturbance in these wetlands, spreading from upland sites during dry periods (Ewel 1990, 1995, Kirkman 1995, Sharitz and Gresham 1998). Although hydrologic regime is usually the controlling factor in the development of vegetation types in wetlands, landscape position, soils, and fire often interact with hydrology to influence this development (Cypert 1961, Duever 1984, 1986). In turn, landform and hydrology may influence landscape disturbance processes.

The objective of our study was to establish if plant community development in limesink depressional wetlands is controlled primarily by differences in hydrogeomorphic features or by different disturbance histories. Specifically, our goals were 1) to characterize relationships among three vegetation types, soil characteristics and physiographic variables for depressional wetlands in the Dougherty Plain of southwestern Georgia using multifactor analyses and 2) to develop a conceptual model that relates abiotic components observed in this study and potential disturbance regimes to patterns of vegetative development.

METHODS

Study Area

The study site is located at Ichauway, a 115-km^2 ecological reserve in the Coastal Plain of southwestern Georgia, USA. The climate for this region is characterized as humid subtropical (Christensen 1981), with an average annual precipitation of 131 cm, which is evenly distributed throughout the year. Mean daily temperatures range from 21 to 34°C in summer and 5 to 17°C in winter (National Climate Data Center, Asheville, NC). Ichauway is located within the Dougherty Plain physiographic region in the Gulf Coastal Plain Province of Walker and Coleman (1987) or the Lower Coastal Plain and Flatwoods (LCPF) section (Plains and Wiregrass Plains subsections) of McNab and Avers (1994). The LCPF Province is a karst landscape, characterized by flat, weakly dissected alluvial deposits over Ocala Limestone (Hodler and Schretter 1986). Parent materials are marine and continental sand and clay deposits formed during the Mesozoic (65 to 225 million years BP) and Cenozoic Eras (present to 65 million years BP) (Keys et al. 1995). Most upland soils are Paleudults and Hapludults, with some localized Quartzipsamments. Ichauway has one of the most extensive and contiguous tracts of second-growth longleaf pine and wiregrass (*Aristida beyrichiana* Trin. & Rupr.) in the Southeast and has been managed with low intensity, dormant season prescribed fires for several decades at a frequency of 1 to 3 years. Many of the embedded wetlands at Ichauway are relatively undisturbed by agricultural practices, recent timber harvest, or altered hydrology. Cypress stumps and evidence of old railroad beds are present in or near the forested wetlands, indicating that timber was harvested, presumably prior to 1938 (based on aerial photography). Surrounding upland longleaf pine forests were prescription-burned on a 2- to 3-year return interval; however, we do not know the history of fire in specific wetlands. Although some of the depressional wetlands once had plowed firebreaks or are currently adjacent to agricultural fields, all of the wetlands show some evidence of prior fire (charcoal fragments, fire scars on trees, etc.).

Field Procedures

Based on field reconnaissance of Ichauway and review of the literature, we identified three major vegetation types that occur in wetland depressions: cypress-gum swamp, cypress savanna, and grass-sedge marsh. We selected 27 depressional wetlands, 10 of which were cypress-gum swamps, six cypress savannas, and 11 grass-sedge marshes. In each wetland, we established three to five 500-m^2 circular sample plots in areas that most represented the dominant vegetation of the wetland. The wetlands met the following criteria: a) minimum of 1 ha in size; b) majority of overstory trees (>10 cm dbh) older than 70 years, in the two forested categories (indicating that the stand was not the result of recent canopy disturbance); and c) no evidence of recent soil disturbance.

In each 500-m^2 plot, the diameter at breast height (dbh, 1.4 m) of all living overstory trees (>10 cm dbh) and saplings (2.5 to 10 cm dbh) was recorded in 2.5-cm-diameter classes. Shrubs (woody plants <2.5 cm dbh but >30 cm tall) and the coverage of the ground flora (both woody and herbaceous plants <30.0 cm tall) were recorded in each of four 0.5-m^2 quadrats located in cardinal directions from the center point of the 500-m^2 plot. Ground flora coverages were estimated using the following six coverage classes: <1%, 1–5%, 6–15%, 16–30%, 31–60%, and 61–100%. Voucher specimens were collected for any species of uncertain identity. Vouchers were checked against specimens located in the Jones Ecological Research Center Herbarium, The Florida State University Herbarium in Tallahassee, Florida or the A.K. Gholson Herbarium in Chattahooche, Florida.

At one of the sample plots at each site, we examined soil profiles to a depth of 1.5 m with a bucket auger. We made a complete soil description following Natural Resources Conservation Service procedures (Soil Survey Division Staff 1993). We also collected bulk soil samples from each horizon. Particle-size fractionation of soil samples was conducted on air-dried samples using the pipette method (Kilmer and Alexander 1949). Soil pH was determined by a 1:1 soil:water suspension (Soil Survey Division Staff 1996).

The perimeters of each basin of each wetland depression (defined by hydric soil boundary) were surveyed, and elevation above sea level was determined using standard surveying equipment and methods. Point locations (0.1-m elevation change) were obtained within the interior of the basin. We did not survey three of the large forested depressions due to logistical problems of surveying such areas. Staff gauges were placed in the lowest point of each depression, and water levels were measured quarterly during 1995.

Data Analyses

Soil texture classes were calculated as weighted averages of percent sand classes (>0.1 mm), silt (0.1–0.001 mm), and clay (<0.001 mm) from each horizon and combined into the following depth classes: 0–50 cm, 51–100 cm, and 101–150 cm. Textural data were transformed using a square root arcsine prior to statistical analyses. Contour maps were obtained from the basin surveys using Arc/Info software (ESRI 1997). From these contour maps, we determined several metrics for each wetland to describe basin characteristics. These included basin surface area (m^2), basin total volume (m^3), volume development (a measure of basin shape relative to volume of a cone), mean depth of basin (m), maximum depth of basin (m), and shoreline development (a measure of shoreline configuration relative to circumference of a circle) (Wetzel and Likens 1991). These basin variables, along with soil texture variables, were used as continuous physiographic factors in multivariate analyses. Those wetlands for which we did not have data from field surveys (n = 3) were not included in the multivariate analyses; however, we used all available data for calculations of means.

Before analyses of vegetation data, we deleted taxa not identifiable to species level. Nomenclature for species follows Clewell (1985) except for the genus *Panicum* (Lelong 1986). We calculated overstory species

Table 1. Overstory importance values (IV) of depressional wetland ecosystem types of Ichauway.

Species	Cypress-gum Swamp	Cypress Savanna	Grass-sedge Marsh
Acer rubrum	5.0 (2.1)[a]	—[b]	—
Crataegus aestivalis	—	0.9 (0.9)	—
Diospyros virginiana	1.4 (0.5)	—	—
Liquidambar styraciflua	2.0 (1.6)	—	—
Nyssa biflora	44.4 (5.5)	9.5 (4.0)	—
Pinus elliottii	1.2 (0.5)	18.4 (13.7)	18.0 (12.1)
Quercus virginiana	—	1.1 (1.1)	—
Taxodium ascendens	46.4 (7.3)	70.2 (12.5)	2.0 (2.0)

[a] Mean (± 1 standard error).
[b] — indicates species not sampled in wetland type.

importance values (IV) in each wetland by averaging the relative dominance (as expressed by basal area), relative density, and relative frequency for each sample area. Using the method described by Host et al. (1993), we calculated an importance percentage (IP) of each ground flora species for each sample area. For each species, importance percentage 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) by frequency (i.e., the number of 0.5-m^2 quadrats in which the species was present). Because a shrub layer was present in only one vegetation type, these data were used only for descriptive purposes and not in the multivariate analyses.

We used principal components analysis (PCA), an indirect ordination technique, to summarize the variation among the physiographic and soil variables. Biplots relating individual wetlands with environmental factors were created to visually interpret the PCA. In a biplot, arrows indicate the direction and strength of each environmental factor on the distribution of the wetlands.

TWINSPAN, a divisive classification technique (Hill 1979) was used to categorize ecological species groups of ground flora. A species group identifies several species that consistently occur together in sample plots. Default settings and 7 pseudospecies cut levels (an abundance scale) corresponding to the midpoint values of the percent cover classes were used for the ground flora data. These analyses produced ordered species-by-sample tables that formed the basis of ecological species groups. Ecological species groups for the ground flora stratum were generated for each wetland type and were identified using the species with the greatest ecological amplitude and importance (*sensu* Spies and Barnes 1985).

We examined the influence of environmental variables on the distribution of ground flora species by using canonical correspondence analyses (CCA) with CANOCO software (ter Braak 1990). CCA is a direct gradient analysis that employs multiple regression techniques to develop ordination diagrams of a primary matrix (e.g., overstory IVs and ground flora IPs data) that is constrained by a secondary matrix (e.g., environmental data). Because overstory species were lacking for a group of wetlands (grass-sedge marsh), we categorized these sites with a dummy variable to describe the overstory vegetation (Jongman et al. 1995). We performed several iterations, eliminating variables that accounted for minor variation in vegetation patterns. Triplots relating individual wetlands and species with environmental factors were created to visually interpret the CCAs. Arrows indicate the direction and strength of each environmental factor on the distribution of the sample wetlands and vegetation. Finally, a sequential deletion technique was used to assess the influence of each environmental factor on each canonical axis using Monte Carlo Permutation Procedures (Hix and Pearcy 1997).

RESULTS

Wetland Vegetation Descriptions

The cypress-gum swamp is dominated by *Taxodium ascendens* Brongn (pond cypress) and *Nyssa biflora* Walter (black gum) in the overstory, with sparse ground-cover vegetation, primarily patches of sedge species or seedlings of woody species (Tables 1 and 2). Few shrubs are present (except along margins), and species include *Styrax americana* Lam. (storax), *Leucothoe racemosa* (L.) Gray (fetterbush), *Clethra alnifolia* L. (sweet pepperbush), and *Lyonia lucida* (Lam.) K. Koch. (fetterbush). The grass-sedge marsh has no distinct overstory but contains occasional *Pinus elliotii* or *T. ascendens*. It is dominated by several species of perennial grasses and sedges and has the greatest species diversity. The cypress savanna consists of an open canopy of pond cypress and grass-sedge ground cover (Tables 1 and 2).

Ground flora species groups resulting from TWIN-

Table 2. Ground flora importance percentages (IP) by ecological species group for wetland ecosystem types of Ichauway.

Species	Cypress-gum Swamp	Cypress Savanna	Grass-sedge Marsh
Ludwigia-Rhexia	0.1 (0.1)[a]	8.7 (4.7)	20.4 (7.4)
Gratiola-Justicia	—[b]	18.6 (3.8)	7.4 (3.8)
Proserpinaca-Eupatorium	0.2 (0.2)	10.6 (2.6)	7.2 (1.8)
Lespedeza-Panicum	—	9.6 (2.0)	30.4 (8.0)
Panicum-Andropogon	0.5 (0.5)	28.4 (8.7)	32.2 (5.4)
Panicum-Juncus	31.9 (8.6)	18.7 (6.0)	2.3 (1.6)
Nyssa-Taxodium	67.3 (8.9)	2.2 (0.9)	—
Total	100.0	100.0	100.0

[a] Mean (± 1 standard error).
[b] — indicates species not sampled in wetland type.

SPAN analysis include *Ludwigia-Rhexia, Gratiola-Justicia, Proserpinaca-Eupatorium, Leersia-Panicum, Panicum-Andropogon, Panicum-Juncus,* and *Nyssa-Taxodium* seedlings (Appendix I). The presence of 7 species groups reflects the variability in plant species composition and abundance in the ground cover vegetation within and among these wetlands. No species groups of the ground flora were distinctly associated with wetlands having cypress canopy, as opposed to those wetlands lacking overstory vegetation, except the *Nyssa-Taxodium* group. All of the other ecological groups occur in the grass-sedge marsh type of wetland (Tables 1 and 2, Appendix I).

Principal components analysis of environmental variables indicates that two distinct gradients exist among the wetland vegetation types (cumulative explained variance of the first four principal components = 86%). Although no physical feature discretely separated the three vegetation types, the vegetation types were clearly distributed along an environmental continuum. Greater variability of environmental factors occurred within the cypress-gum group than the other vegetation types (Figure 1). Separation along PC 1 was strongly related to clay depth, thickness of organic material, elevation, and inundation ratio (mean annual volume of water in depression: total volume of depression) (adjusted variance scores (AVS) = -0.92, 0.83, 0.51, and 0.51, respectively). This suggests that thicker organic layers are associated with longer periods of inundation and lower elevations in the cypress-gum swamps (Table 3). The second PC separated samples on the basis of sand content (%) and thickness of the sandy epipedon (AVS = 0.93 and 0.56, respectively) (Figure 1). Thus, grass-sedge marshes are as-

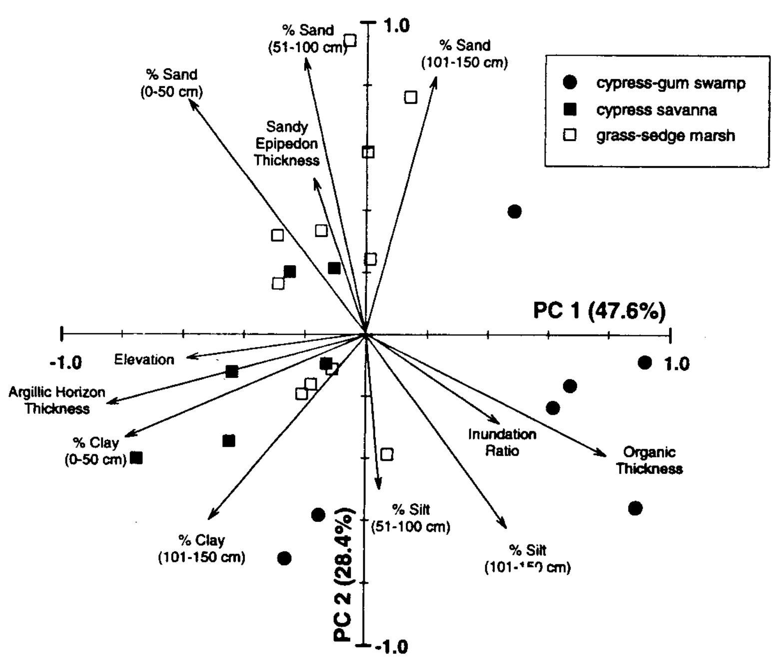

Figure 1. Principle Components Analysis of environmental variables of depressional wetlands.

Table 3. Physiographic and edaphic characteristics of depressional wetland ecosystem types of Ichauway.

Variable	Cypress-gum Swamp (n = 10)[a]	Cypress Savanna (n = 6)	Grass-sedge Marsh (n = 11)
Surface area (m^2)	50 247 (8909)[b]	16 476 (2343)	128 969 (75493)
Total volume (m^3)	22 151 (6810)	5 939 (1383)	150 766 (123631)
Elevation (m)[c]	47.1 (0.9)	54.9 (0.5)	48.3 (1.7)
Mean depth of basin (m)	0.4 (0.1)	0.4 (0.04)	0.7 (0.1)
Maximum depth of basin (m)	1.0 (0.2)	0.9 (0.1)	1.7 (0.3)
Volume development	1.2 (0.1)	1.3 (0.1)	1.2 (0.1)
Mean annual water volume (m^3)	7 184 (1709)	1 179 (544)	3 019 (940)
Inundation ratio	0.4 (0.1)	0.2 (0.04)	0.1 (0.05)
Shoreline development (m)	1.2 (0.03)	1.1 (0.05)	1.1 (0.1)
PH	5.2 (0.1)	5.6 (0.1)	5.9 (0.1)
Surface color	3.4 (0.2)	1.1 (0.1)	1.5 (0.2)
Organic layer thickness (cm)	37.6 (12.8)	—[d]	0.6 (0.6)
Sandy epidedon thickness (cm)	25.3 (8.2)	22.0 (3.4)	33.1 (5.6)
Argillic horizon thickness (cm)	22.3 (14.6)	77.4 (12.4)	50.3 (7.5)
Particle size distribution:			
% Sand (0–50 cm)	8.3 (3.4)	42.5 (3.3)	50.8 (5.5)
% Silt (0–50 cm)	15.5 (6.8)	27.7 (3.4)	20.7 (3.6)
% Clay (0–50 cm)	15.9 (7.3)	26.6 (2.7)	22.6 (3.6)
% Organic (0–50 cm)	58.0 (16.9)	2.9 (2.9)	—
% Sand (51–100 cm)	24.5 (4.0)	35.8 (3.3)	38.6 (6.2)
% Silt (51–100 cm)	27.6 (4.9)	18.5 (1.9)	13.7 (3.2)
% Clay (51–100 cm)	30.3 (5.7)	46.3 (3.4)	33.8 (3.6)
% Organic (51–100 cm)	17.1 (11.3)	—	—
% Sand (101–150 cm)	34.6 (5.5)	38.6 (6.2)	46.6 (5.5)
% Silt (101–150 cm)	29.0 (1.7)	14.0 (2.0)	10.1 (2.7)
% Clay (101–150 cm)	37.4 (5.9)	49.9 (6.2)	35.0 (2.6)

[a] Number of wetlands sampled.
[b] Mean (± 1 standard error).
[c] Jurisdictional boundary.
[d] — Indicates not sampled in wetland type.

sociated with sandy, coarse-textured soils, while cypress savannas tend to be finer-textured, with a higher percentage of clay below 50 cm (Table 3).

Vegetation-Environment Relationships of Depressional Wetland Ecosystems

The first two axes of the overstory CCA accounted for 61.0 % of the total variation in wetland types. Of this, 76.1 % is attributable to the environmental factors included in the analysis (Table 4). The few species (total in all wetlands sampled = 7) and the wide environmental amplitude of each of the species is likely a factor in the lack of separation among these wetlands (Figure 2a). Grass-sedge marshes were separated from the cypress savannas and cypress-gum swamp, probably due to the few overstory individuals present. Sand content (0–50 cm; $F = 4.48$, df = 11, $p < 0.01$), elevation ($F = 1.72$, df = 11, $p < 0.11$), and organic matter thickness ($F = 4.72$, df = 11, $p < .01$) all are significantly correlated with CCA axis 1, slightly separating the cypress-gum swamps dominated by pond cypress and blackgum from cypress savanna (Figure 2a, Table 4). Only silt content (101–150 cm) was found to be significantly correlated with CCA axis 2 ($F = 3.62$, df = 11, $p < .02$).

The ground flora CCA also showed strong correlations among the ground flora species and environmental factors; however, only 22 % of the total variation in wetland types was explained by the first two axes. Of this variation, only 34 % was explained by the measured environmental factors (Table 4). For the ground flora analysis, the cypress-gum wetlands, dominated by members of the *Panicum-Juncus* and *Nyssa-Taxodium* groups, separated primarily along CCA axis 1 and were associated with greater organic thickness ($F = 2.27$, df = 11, $p < 0.01$), lower elevations ($F = 1.50$, df = 11, $p < 0.02$), and greater inundation ratios ($F = 1.04$, df = 11, $p < 0.39$). The second CCA axis is a textural gradient, having significant associations with sandy epipedon thickness (depth to clay increase) ($F = 1.42$, df = 11, $p < 0.05$). Although not significant, the grass-sedge marsh-

Table 4. Summary statistics for canonical correspondence analysis of overstory and ground-flora IVs by species and environmental factors.

Overstory	CCA Axis 1	CCA Axis 2
Eigenvalue	0.724	0.368
Species-environment correlation	0.95	0.963
Cumulative percent variance of overstory	40.4	61.0
Cumulative % variance of overstory-environment relation	54.4	76.1
Correlation of individual factors with canonical axis:		
Elevation	0.33*	0.52
Volume development	0.31	0.19
Inundation ratio	−0.23	−0.45
Organic matter thickness	−0.44*	−0.35
Sandy epipedon thickness	0.13	−0.17
Argillic horizon thickness	0.08	0.10
% Sand, 0–50 cm	0.56*	0.41
% Silt, 0–50 cm	0.06	−0.03
% Clay, 0–50 cm	0.06	−0.08
% Sand, 51–100 cm	0.27	0.52
% Silt, 51–100 cm	−0.28	−0.48
% Clay, 51–100 cm	0.31	0.14
% Sand, 101–150 cm	0.05	0.47
% Silt, 101–150 cm	−0.47	−0.57*
% Clay, 101–150 cm	0.21	−0.17
Ground flora	**CCA Axis 1**	**CCA Axis 2**
Eigenvalue	0.826	0.535
Species-environment correlation	0.982	0.976
Cumulative percent variance of ground flora	13.2	21.8
Cumulative % variance of ground flora-environment relation	20.5	33.7
Correlation of individual factors with canonical axis:		
Elevation	−0.31*	0.11
Volume development	0.13	0.28
Inundation ratio	0.62	−0.05
Organic matter thickness	0.72*	0.39
Sandy epipedon thickness	−0.02	−0.63*
Argillic horizon thickness	−0.35	−0.08
% Sand, 0–50 cm	−0.71	−0.33
% Silt, 0–50 cm	−0.24	−0.19
% Clay, 0–50 cm	−0.23	−0.13
% Sand, 51–100 cm	−0.44	−0.26
% Silt, 51–100 cm	0.52*	−0.24
% Clay, 51–100 cm	−0.31	−0.19*
% Sand, 101–150 cm	−0.33	0.07
% Silt, 101–150 cm	0.77	0.04
% Clay, 101–150 cm	−0.12	−0.11

* Variable is significantly correlated with the canonical axis based on Monte Carlo Permutation Procedure, $P < 0.10$.

es tend to have a higher percentage of sand in the upper 100 cm (Figure 2b, Table 3). Conversely, the cypress savannas have a high percentage of clay (>35%) within 51–100 cm, while the lowest depths sampled averaged approximately 50% clay (Table 3). Ground flora species also appear to be arrayed along this textural gradient, with the diverse *Ludwigia-Rhexia* and *Lespedeza-Panicum* groups characterizing the grass-sedge marshes and members of the *Gratiola-Justicia* group characterizing the cypress savannas. Members of the *Panicum-Andropogon* group are distributed along the textural gradient.

DISCUSSION

Although we did not identify distinctive physical features that uniquely correlate with each of the wetland vegetation types, this study demonstrated a general predictability for the occurrence of cypress-gum

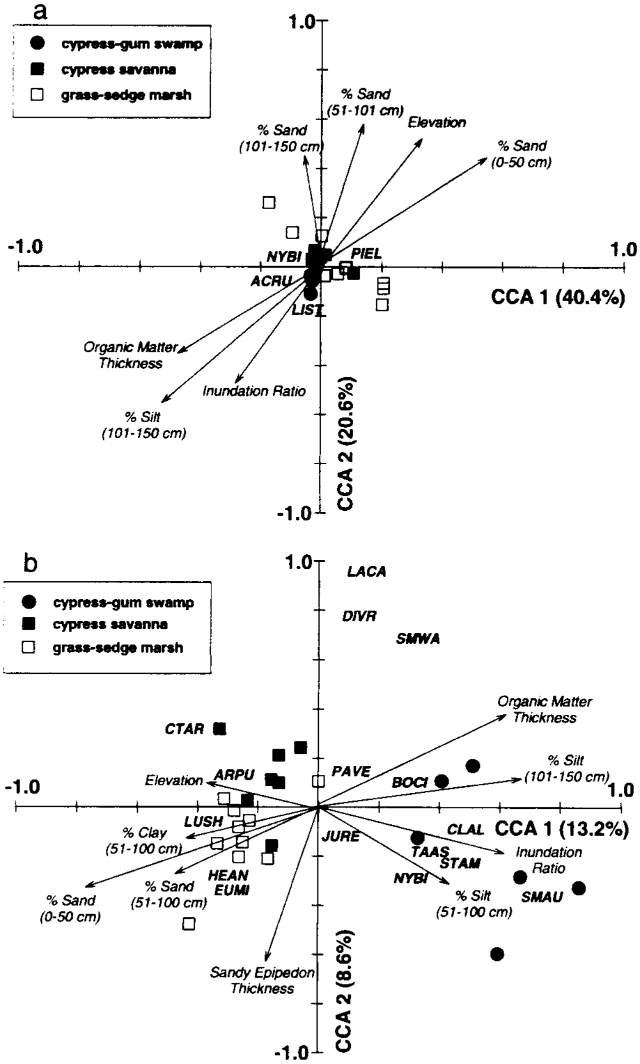

Figure 2. Canonical correspondence analysis (CCA) relating a) overstory and b) ground flora composition to physiographic and edaphic characteristics of depressional wetlands. PIEL = *Pinus elliotii;* NYBI = *Nyssa biflora;*ACRU = *Acer rubrum*; LIST = *Liquidambar styraciflua*; SMWA = *Smilax walteri*; DIVR = *Diospyros virginiana*; LACA = *Lacnanthes caroliniana*; PAVE = *Panicum verrucosum*; BOCY = *Boehmeria cylindrica*; CLAL = *Clethra alnifolia*; TAAS = *Taxodium ascendens*; STAM = *Styrax americana*; JURE = *Juncus repens*; SMAU = *Smilax auriculata*; HEAN = *Helianthus angustifolius*; EUMI = *Euthamia minor*; ARPU = *Arisitida purpurescens*; LUSH = *Ludwigia sphaerocarpa*; CTAR = *Ctenium aromaticum.*

swamps in depressions with organic accumulations of soil and those that have more extended hydroperiods than the depressional wetlands with cypress savanna or grass-sedge marsh vegetation. Little predictability between ground flora and physical factors as a means for separating cypress savannas and grass-sedge marshes was observed. The low cumulative variance explained by the CCA of the ground flora might reflect large variation associated with the large number of total species (170), within-site microsite differences, or other environmental factors not assessed in the study.

Similar vegetation types have been identified in depressional wetlands elsewhere in the southeastern US. However, no consensus has emerged regarding relationships among these wetland vegetation types to physical characteristics of the depressions nor the role of fire, particularly among those wetlands lacking thick peat (Ewel 1998, Sharitz and Gresham 1998). Nonalluvial swamps, cypress savannas, and depression meadows are wetland types that have been described in clay-based (i.e., lacking histosols) Carolina bay wetlands of the Atlantic Coastal Plain (Bennett and Nelson 1990, Schafale and Weakley 1990). Depression marshes and dome swamps (cypress- or hardwood-dominated) have been described for depressional wetlands with peaty soils in Florida (Duever 1986, Florida Natural Areas 1990), and Georgia (Cypert 1961), although Ewel (1998) described pond cypress swamps and gum ponds in northern Florida and Georgia as also occurring in sandy soils underlain by clay. Although geomorphic controls are not well established, the formation of smaller wetlands in some areas of Florida has been suggested as occurring in karst sinkholes as opposed to larger basin swamps that may have been formed in ox-bows of former rivers (Florida Natural Areas Inventory 1990).

Wetland Ecosystem Development

The correlative association between organic soils and cypress-gum swamps in this study does not imply a causal relationship; organic soil development processes and woody vegetation establishment are likely influenced by similar external environmental conditions (Sharitz and Gibbons 1982, Lockaby and Walbridge 1998). The greater inundation ratio, also associated with presence of organic matter in this study, is consistent with that of several studies that indicate that organic matter accumulation in freshwater wetlands tends to be greater under extended, but not continuously flooded hydroperiods (Day 1982, Yates and Day 1983, Megonigal and Day 1988), even though many other factors contribute to decomposition rates (Webster and Benfield 1986, Mitsch and Gosselink 1993, Craft 2000). The tendency for the cypress-gum swamps to occur locally at lower elevation is consistent with the observation that the landscape position of these cypress-gum swamps is in valleys (inter-ridge position), whereas the other vegetation types occur as depressions along ridge tops within the study area (E. Blood, unpublished data). Although we are not suggesting that elevation is a general predictor of organic depth or hydrology, this observation suggests a possible relationship between geomorphic origin, hydrology, and plant community development.

Although more coarsely-textured soils in the upper horizons tend to be associated with grass-sedge marshes and more finely textured soils (clays and loams) are often associated with cypress-savannas, the overlapping results of the CCAs suggest that other factors may be responsible for the development of the plant communities. Wetlands with longer hydroperiods would likely have less potential for burning if fire occurs in surrounding uplands. Thus, the long-term establishment of hardwood species is more probable in wetlands with more extended hydroperiods (and less frequent fire) than in wetlands where fire is more frequent. Although woody species require occasional periods of drawdown for germination and establishment (Demaree 1932, DuBarry 1963), young hardwoods are intolerant of fire (Ewel and Mitsch 1978). Similarly, less frequent fire would contribute to more rapid organic matter accumulation (Hamilton 1984).

Most of the wetlands in this study appear to have an impervious clay layer, resulting in a perched water table that fluctuates with precipitation; they are not directly maintained by the regional ground water table (Hendricks and Goodwin 1952). Also, water chemistry of these wetlands suggests that there is no direct ground-water interaction (Battle and Golladay 1999). In spite of evidence that the surficial hydrology of depressions is independent of the regional ground water, the grass-sedge marshes that lack deep clay horizons may be indirectly maintained by regional ground-water tables. In these wetlands, water-level variations through time (beyond that of this study) are inconsistent with those of most of the other wetlands and appear to reflect regional ground-water levels, as opposed to precipitation only (E. Blood, unpublished data).

Discerning developmental constraints of vegetation types in these wetland ecosystems due to inherent site characteristics or identification of multiple successional pathways resulting from variations in disturbance regimes will require long-term experimental manipulations and hydrologic studies to test developmental postulates. Below, we describe a conceptual model of vegetative development from which testable hypotheses can be generated.

Conceptual Model of Wetland Ecosystem Development

We propose a model depicting the interactions of abiotic components and potential disturbances that influence patterns of vegetative development in depressional wetlands. The scenarios presented result in three major vegetation types (Figure 3). The basis of our model is that stable physical factors of topographic position and soil texture are primary drivers influencing the hydrologic regime in this region. We suggest that inter-ridge depressions generally have a hydrologic regime of greater duration of inundation than wetland depressions occurring on ridges. Among the ridge depressions, those with more sandy textures and thicker sandy epipedons have greater permeability to surface water that results in shorter hydroperiods.

Reminiscent of successional pathways proposed for wetlands in southern Florida (Duever 1984, Duever et al. 1986), this conceptual model features fire and hydrology as having dominant roles in ecosystem development. Both fire and hydrology similarly serve as environmental filters (*sensu* van der Valk 1981) in determining the establishment of woody propagules in a wetland (Figure 3). Thus, the proposed sequence of events that could lead to each of the three endpoints is as follows.

The frequency of drawdown in a wetland that results in dry, combustible fuels is an obvious controlling factor of the potential frequency of fire. Therefore, it is likely that the probability of fire (where frequent fire is a component of surrounding upland landscape) is inversely related to the length of hydroperiod and depth of flooding (Figure 3). Presumably, in these depressional wetlands, conditions suitable for woody plant establishment are dependent on climatic conditions. Drawdown must be sufficiently prolonged for seed germination and for adequate plant height growth to occur in order to survive subsequent fire and/or deep inundation. The timing of the prolonged drawdown must also correspond with seed dispersal for those species that do not persist in a soil seed bank (Kirkman and Sharitz 1994, Sharitz and Gresham 1998). Consequently, a combination of such conditions may occur infrequently in a particular site; thus, herbaceous plants, once established, are predicted to dominate for extensive periods. Evidence supporting this view has been documented for similar intermittently ponded wetlands in South Carolina, in which cyclical patterns in vegetation change occurred as a result of prolonged drawdown or prolonged inundation driven by extremes in precipitation patterns (Kirkman and Sharitz 1994, Kirkman 1995). Additionally, the relative stability of dominance by herbaceous species over several decades, even where fire has been excluded (Kirkman et al. 1996), suggests that woody species establishment in the wetlands is partly controlled by hydrologic regime. Inundation following establishment of woody species serves to filter out those species that are unable to withstand flooded conditions (Figure 3).

Differences in fire tolerance among woody species are the basis for the separation of plant communities among flood-tolerant species in the proposed model

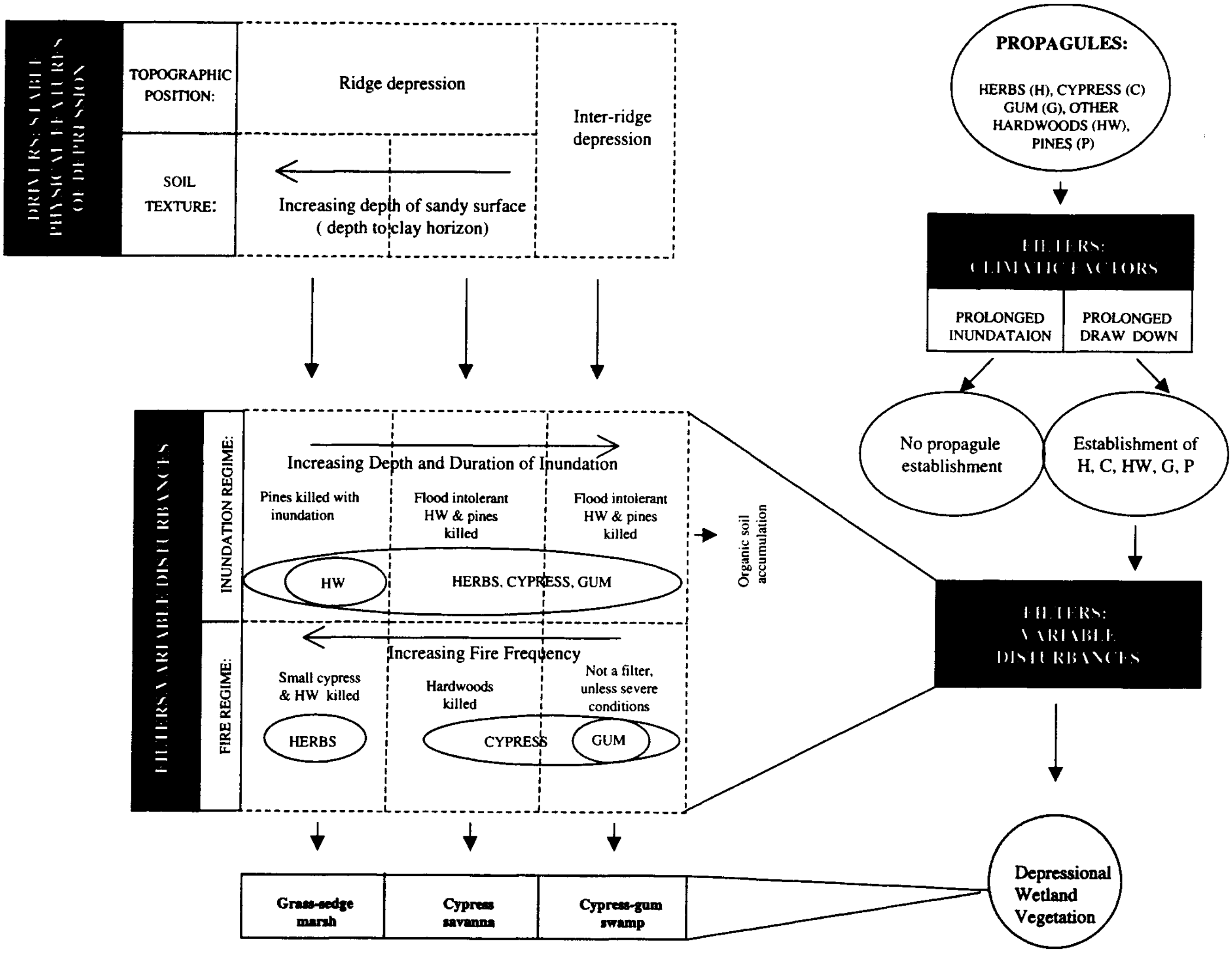

Figure 3. Conceptual model of ecosystem development in depressional wetlands. Drivers (stable physical features of depression that control hydrologic and disturbance regimes) and filters (climatic and disturbance factors that control the establishment of species) are identified in black boxes. Bold arrows from these boxes indicate the resulting environmental conditions or vegetation from each influencing factor. A generalization of the propagules and establishing vegetation that emerge through the filters are identified in ovals. Resulting depressional wetland vegetation is indicated in shaded boxes.

(Figure 3). In the prolonged absence of fire, *T. ascendens* and flood-tolerant hardwood species dominate the community (e.g., cypress-gum swamp) once they become established. However, as an established tree, *T. ascendens*, is believed to have a greater fire tolerance than hardwood species (Hare 1961, Ewel and Mitsch 1978, Ewel 1998). Our model suggests that *T. ascendens* will continue to dominate with frequent fire, once it becomes established. Frequent, low intensity fires will diminish peat accumulation (Hamilton 1984), lessening the probability of future fire that would kill adult cypress (Ewel and Mitsch 1978). With very frequent fire, cypress (in addition to hardwood species) is eliminated and a grass-sedge community prevails. Because fire and inundation both inhibit establishment of woody species, the absence of one may be off-set by the presence of the other, and consequently, change in community composition may occur very slowly.

Potential Influences of Surrounding Land-Use on Ecosystem Development

Many depressional wetlands in the region are no longer susceptible to fire due to the presence of firebreaks or the close proximity to agricultural or urban development. In such cases, plant community development is primarily controlled by hydrology. The current use of prescribed fire in the management of upland fire-maintained ecosystems also has ramifications for the probability of fire occurrence in these wetlands. Prescribed fire in much of the remaining pine-dominated uplands in the southeastern Coastal Plain is usually carried out in late winter to early spring, differing from the late spring to summer season that was most prevalent for lightning-ignited fires (Robbins and Myers 1992) when drawdown of a wetland is most likely. As a consequence, the potential for fire entering a wetland may be lessened due to the earlier timing of managed burns.

The implications of differing hydrologic controls among depressional wetlands are that the vegetative communities of some wetlands will be more regulated by regional ground-water withdrawals than others, potentially altering rates of successional change, particularly where fire is excluded.

Implications for Restoration of Depressional Wetlands

Identification of reference conditions to quantify a range of conditions that represent a structurally intact and fully functioning ecosystem has been key to the hydrogeomorphic approach to assessing wetland functions for wetland regulatory activities (Brinson and Rheinhardt 1996). Determining appropriate reference wetlands for a particular disturbed wetland site implies an understanding of the relationship between vegetation, physiography, geologic substrate, and hydrologic regime in relatively unaltered situations. Presumably, in the absence of vegetation, geomorphic characteristics and water source can predict a range of potential restored plant communities. In regions such as the southeastern US, where fire frequency was once a critical factor influencing plant community development, identifying potential vegetation of a disturbed depressional wetland site is problematic because this relationship is often intricately linked with past land uses and altered disturbance regimes in even the least altered sites.

In this study, we observed a range of topo-edaphic conditions that likely drive variations in hydrologic regimes, which in turn, are probable influences on fire regime. We propose that long-term successional trajectories may be initiated in the prolonged absence of fire, altered hydrology, or both, which link the distinctive vegetation types examined in this study. Thus, a range of vegetation types may be suitable as potential restoration goals for these depressional wetlands. We suggest that the opportunities or constraints for use of prescribed fire in the long-term management of restored wetlands and adjacent uplands should be a significant consideration in the development of restoration strategies where specific plant communities are an objective.

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LITERATURE CITED

Battle, J. and S. Golladay. 1999. Water quality and aquatic macroinvertebrates in 3 types of seasonally-inundated limesink wetlands in southwest Georgia. p. 439–442. *In* K. J. Hatcher (ed.) Proceedings of 1999 Georgia Water Resources Conference. University of Georgia, Athens, GA, USA.

Bedford, B. 1996. The need to define hydrologic equivalence at the landscape scale for freshwater wetland mitigation. Ecological Applications 5:57–68.

Bennett, S. H. and J. B. Nelson. 1990. Distribution and status of Carolina bays in South Carolina. South Carolina Wildlife and Marine Resources Department, Columbia, SC, USA.

Blood E. R., J. S. Phillips, D. Calhoun, and D. G. Edwards. 1997. The role of the Floridan Aquifer in depressional wetlands hydrodynamics and hydroperiod. p. 273–279. *In* Proceedings of the Georgia Water Resources Conference. University of Georgia; Athens, Georgia, USA.

Brinson, M. M. and R. Rheinhardt. 1996. The role of reference wetlands in functional assessment and mitigation. Ecological Applications 6:69–76.

Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. p. 112–136. *In* H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reinsers (eds.) Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26.

Clewell, A. F. 1985. Guide to the Vascular Plants of the Florida Panhandle. University Presses of Florida, Tallahassee, FL, USA.

Craft, C. B. 2000. Biology of wetland soils. *In* J. L. Richardson and M. J. Vepraskas (eds.) Wetland Soils: Their Genesis, Morphology, Hydrology, Landscapes and Classification. CRC Press, Boca Raton, FL, USA.

Cypert, E. 1961. The effect of fires in the Okefenokee Swamp in 1954 and 1955. American Midland Naturalist 66:485–503.

Day, Jr. F. P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63:670–678.

Demaree, D. 1932. Submerging experiments with *Taxodium.* Ecology 13:258–262.

DuBarry, Jr., A. P. 1963. Germination of bottomland tree seed while immersed in water. Journal of Forestry 61:225–226.

Duever, M. J. 1984. Environmental factors controlling plant communities of the Big Cypress Swamp. p. 127–137. *In* P. J. Gleason (ed.) Environments of South Florida: Present and Past II. Miami Geological Society, Coral Gables, FL, USA.

Duever, M. J., J. F. Meeder, and L. C. Duever. 1986. Ecosystems of the Big Cypress Swamp. p. 294–303. *In* K. C. Ewel and H. T. Odum (eds.) Cypress Swamps. University of Florida Press, Gainesville, FL, USA.

ESRI (Environmental Systems Research Institute). 1997. ArcView: The Geographic Information System for Everyone (User's Guide). Redlands, CA, USA.

Ewel, K. C. 1990. Swamps. p. 281–317. *In* R. L. Myers and J. J. Ewel (eds.) Ecosystems of Florida. University of Central Florida Press, Orlando, FL, USA.

Ewel, K. C. 1995. Fire in cypress swamps in the Southeastern United States. p. 111–116. *In* S. I. Cerulean and R. T. Engstrom (eds.) Fire in wetlands: a management perspective. Proceedings of the Tall Tiimbers Fire Ecology Conference, No. 19. Tall Timbers Research Station, Tallahassee, FL, USA.

Ewel, K. C. 1998. Pondcypress swamps. p. 405–420. *In* M. G. Messina and W. H. Conner (eds.) Southern Forested Wetlands: Ecology and Management. Lewis Publishers, Boca Raton, FL, USA.

Ewel, K. C. and W. J. Mitsch. 1978. The effects of fire on species composition in cypress dome ecosystems. Florida Scientist 41:25–31.

Federal Register. 1996. Final notice of issuance, reissuance and modification of nationwide permits. Army Corps of Engineers, DOD, Volume 61: 65916.

Florida Natural Areas Inventory and Department of Natural Resources. 1990. Guide to the natural communities of Florida. Florida Department of Natural Resources, Tallahassee, FL, USA.

Folkerts, G. W. 1997. Citronelle Ponds: little-known wetlands of the Central Gulf Coastal Plain, USA. Natural Areas Journal 17:6–16.

Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern pondersoa pine forests. Ecological Applications 7:895–908.

Golladay, S. W., B. W. Taylor, and B. J. Palik. 1997. Invertebrate communities of forested limesink wetlands in southwest Georgia, USA: habitat use and influence of extended inundation. Wetlands 7:383–393.

Hamilton, D. B. 1984. Plant succession and the influence of disturbance in Okefenokee Swamp. p. 86–11. *In* A. D. Cohen, D. J. Casagrande, M. J. Andrejko, and G. R. Best (eds.) The Okefenokee Swamp: Its Natural History, Geology, and Geochemistry. Wetland Surveys, Los Alamos, NM, USA.

Hare, R. C. 1961. Heat effects on living plants. U. S. Department of Agriculture Forest Service. Southern Forest Experiment Station, New Orleans, LA, USA. Occasional Paper 183.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-level fluctuations in limestone sinks in southwestern Georgia. U. S. Geological Survey Water-Supply Paper 1110-E.

Hill, B. H. 1979. Uptake and release of nutrients by aquatic macrophytes. Aquatic Botany 7:87–93.

Hix, D. M. and J. N. Pearcy. 1997. Forest ecosystems of the Marietta Unit, Wayne National Forest, southeastern Ohio: multifactor classification and analysis. Canadian Journal of Forest Research 27: 1117–1131.

Hodler, T. W. and H. A. Schretter. 1986. Atlas of Georgia. Institute of Community and Area Development. University of Georgia, Athens, GA, USA.

Host, G. E., C. W. Ramm, E. A. Padley, K. S. Pregitzer, J. B. Hart, and D. T. Cleland. 1993. Field sampling and data analysis methods for development of ecological land classifications: an application on the Manistee National Forest. USDA Forest Service, Washington, DC, USA. NC-162.

Jongman, R. H. G., C. J. F ter Braak, and O. F. R. Van Tongeren. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, MA, USA.

Kentula, M. E., R. P. Brooks, S. E. Gwin, C. C. Holland, A. D. Sherman, and J. C. Sifneos. 1993. Wetlands: an Approach to Improving Decision-Making in Wetland Restoration and Creation. Island Press, Washington, DC, USA.

Keys, Jr. J., C. Carpenter, S. Hooks, F. Koenig, W. H. McNab, W. Russell, and M. L. Smith. 1995. Ecological units of the eastern United States—first approximation (map and booklet of map unit tables). USDA Forest Service, Atlanta, GA, USA.

Kilmer, V. J. and L. T. Alexander. 1949. Methods of making mechanical analysis of soils. Soil Science 68:15–24.

Kirkman, L. K. 1995. Impacts of fires and hydrological regimes on vegetation in depression wetlands of southeastern USA. p. 10–20. *In* S. I. Cerulean and R T. Engstrom (eds.) Fire in wetlands: a management perspective. Proceedings of the Tall Timbers Fire Ecology Conference, No. 19. Tall Timbers Research Station, Tallahassee, FL, USA.

Kirkman, L. K. and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. Ecological Applications 4:177–188.

Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western Coastal Plain of South Carolina: 1951–1992. Wetlands 16:564–576.

Kirkman, L. K., M. B. Drew, L. T. West, and E. R. Blood. 1998. Ecotone characterization between upland longleaf pine/wiregrass stands and seasonally ponded isolated wetlands. Wetlands 18:346–364.

Kirkman, L. K., S. Golladay, L LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally-ponded isolated wetlands: management and policy perspectives for research and conservation. Journal of North American Benthological Society 18:553–562.

LaClaire, L. V. 1995. Vegetation of selected upland temporary ponds in north and north-central Florida. Bulletin of Florida Museum Natural History 38:69–90.

Lelong, M. G. 1986. A taxonomic treatment of the genus *Panicum* (Poaceae) in Mississippi. Phytologia 61:251–269.

Lockaby, B. G. and M. R. Walbridge. 1998. Biogeochemistry. p. 149–172. *In* M. G. Messina and W. H. Conner (eds.) Southern Forested Wetlands: Ecology and Management. Lewis Publishers, Boca Raton, FL, USA.

McNab, W. H. and P. E. Avers (compilers). 1994. Ecological subregions of the United States: section descriptions. USDA Forest Service, Washington, DC, USA. Administrative Publication WO-WSA-5.

Megonigal, J. P. and F. P. Day, Jr., 1988. Organic matter dynamics in four seasonally flooded forest communities of the Dismal Swamp. American Journal of Botany 75:1334–1343.

Mitsch, W. A. and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, NY, USA.

National Research Council. 1995. Wetlands: Characteristics and Boundaries. National Academy Press. Washington, DC, USA.

Palik, B. J., P. C. Goebel, L. K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecological Applications 10:189–202.

Pickett, S.T.A. and V.T. Parker. 1994. Avoiding the old pitfalls: opportunities in a new discipline. Restoration Ecology 2:75–79.

Robbins, L. E. and R. L. Myers. 1992. Seasonal effects of prescribed burning in Florida. Tall Timbers Research, Inc., Tallahassee, FL, USA. Miscellaneous Publication No. 8.

Rowell, M. C., C. Johnson, and V. Fasselt. 1995. Draft technical summary document for the central Dougherty Plain Advance Identification of Wetlands. U. S. Environmental Protection Agency, Region 4, Water Management Division, Wetlands Protection Section, Atlanta, GA, USA.

Schafale, M. P. and A. S. Weakley. 1990. Classification of the natural communities of North Carolina: third approximation. North Carolina National Heritage Program, North Carolina Division of Parks and Recreation, North Carolina Department of Environment, Health, and Natural Resources, Raleigh, NC, USA.

Semlitsch, R. D. and J. R. Brodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–1133.

Sharitz, R. R. and J.W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, DC, USA. FWS/OBS-82/04.

Sharitz, R. R. and C. A. Gresham. 1998. Pocosins and Carolina Bays. p. 343–378. *In* M. G. Messina and W. H. Conner (eds.) Southern Forested Wetlands: Ecology and Management. Lewis Publishers, Boca Raton, FL, USA.

Simberloff, D. 1990. Reconstructing the ambiguous: can island ecosystems be restored? p. 37–51. *In* D. R. Towns, C. H. Daugherty, and I. A. E. Atkinson (eds.) Ecological restoration of New Zealand islands. Department of Conservation, Wellington, New Zealand. Conservation Sciences Publication No. 2.

Soil Survey Division Staff, 1993. Soil Survey Manual. U. S. Department of Agriculture Handbook 18, Revised Edition. Washington, DC, USA.

Soil Survey Staff. 1996. Soil Survey Laboratory Methods Manual. USDA-NRCS. Washington, DC, USA. Soil Survey Investigations Report No. 32.

Spies, T. A. and B. V. Barnes 1985. Ecological species groups of upland northern hardwood-hemlock forest ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan. Canadian Journal of Forest Research 15:961–972.

Sutter, R. D. and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and eastern Gulf Coastal Plain, USA. Biological Conservation 68:235–243.

ter Braak, C. J. F. 1990. CANOCO: A FORTRAN Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principal Components Analysis, and Redundancy Analysis (version 3.1). ITI-TNO, Wageningen, The Netherlands.

Torak, L. J., G. S. Davis, G. A. Strain, and J. G. Herndon. 1991. Geohydrology and evaluation of the water-resource potential of the upper Floridan aquifer in the Albany area, Southwestern Georgia. U. S. Geological Survey Open-File Report 91–52.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688–696.

Walker, H. J. and J. M.Coleman. 1987. Atlantic and Gulf Coastal Province. P. 51–110. *In* W. L.Graf (ed.) Geomorphic systems in North America. Geological Society of America, Boulder, CO, USA. Centennial Special Volume 2.

Webster, J. R. and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.

Wetzel., R. G. and G. E. Likens. 1991. Limnological Analyses. Second Edition. Springer-Verlag, New York, NY, USA.

Yates, R. F. K. and F. R. Day. 1983. Decay rates and nutrient dynamics in confined and unconfined leaf litter in the Great Dismal Swamp. American Midland Naturalist 110:37–45.

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Appendix I. Ecological species groups derived using TWINSPAN. The group name reflects the two most common species (highest frequency and dominance) in a group. Species are grouped that consistently occur with these two dominant species.

***Ludwigia-Rhexia* Group**

Erianthus giganteus (Walt.) Muhl.
Eriocaulon decangulare L.
Eryngium prostratum Nutt.
Helenium pinnatifidum (Mutt.) Tydb.
Hypericum brachyphyllum (Spach) Steud.
Ludwigia linearis Walt.
Ludwigia linifolia Poir. In Lam.
Manisuris rugosa (Nutt.) Kuntze
Mitreola sessilifolia (Walt.) G. Don
Panicum tenerum Beyr. Ex Trin.
Polygala cymosa Walt.
Rhexia aristosa Britt.
Rhynchospora perplexa Britt. Ex Small
Rhynchospora pleianthea (Kuekenth.) Gale
Rhynchospora tracyi Britt.
Rudbeckia mohrii Bray
Scleria georgiana Core

***Gratiola-Justicia* Group**

Bacopa caroliniana (Walt.) Robins.
Eleocharis minima Kunth
Elephantopus carolinianus Raeusch.
Eupatorium leucolepis (DC.) T. & G.
Gratiola brevifolia Raf.
Gratiola ramosa Walt.
Hypericum harperi R. Keller
Justicia ovata (Walt.) Lindau
Ludwigia spathulata T. & G.
Lycopus rubellus Moench
Rhexia virginica L.
Rhynchospora globularis var. *pinetorum* (Small) Gale

***Proserpinaca-Eupatorium* Group**

Eupatorium leptophyllum DC.
Pluchea rosea Godfrey
Proserpinaca pectinata Lam.

***Leersia-Panicum* Group**

Acalypha gracilens Gray
Anthaenantia villosa (Michx.) Beauv.
Aristida longispica Poir. In Lam.
Axonopus furcatus (Fluegge) Hitchc.
Croton elliottii Chapm.
Diodia teres Walt.
Eragrostis refracta (Muhl.) Scribn.
Erigeron vernuus (L.) T. & G.
Eulophia ecristata (Fern.) Ames
Fimbristylis puberula (Michs.) Vahl
Iva microcephala Nutt.
Leersia hexandra Sw.
Lindernia dubia (L.) Pennell
Ludwigia suffruticosa Walt.
Mecardonia acuminata (Walt.) Small
Oxalis corniculata L.
Panicum acuminatum Sw.
Panicum hemitomon Schult.
Paspalum laeve Michx.
Paspalum setaceum Michx.
Piriqueta caroliniana (Walt.) Urban
Polygala mariana Mill.
Polygonum hydropiperoides Michx.
Polypremum procumbens L.
Raphanus raphanistrum L.
Rhynchospora filifolia Gray
Rhynchospora microcarpa Baldw. Ex Gray
Rhynchospora pusilla Champ.
Rubus cuneifolius Pursh
Tridens ambiguus (Ell.) Schult.
Triplasis americana Beauv.

***Panicum-Andropogon* Group**

Amphicarpum muhlenbergianum (Schult.) Hitchc.
Andopogon virginicus L.
Aristida purpurescens Poir.
Aster dumosus L.
Diodia virginiana L.
Eupatorium mohrii Greene
Euthamia minor (Michx.) Greene
Helianthus angustifolius L.
Ludwigia spaerocarpa Ell.
Panicum rigidulum Boxc. ex Nees
Panicum wrightianum Scribn.
Rhexia mariana L.
Stylisma aquatica (Walt.) Raf.
Viola lanceolata L.

***Panicum-Juncus* Group**

Carex verrucosa Muhl.
Diospyros virginiana L.
Juncus repens Michx.
Lachnanthes caroliniana (Lam.) Dandy
Panicum verrucosum Muhl.
Rhexia alifanus Walt.
Smilax auriculata Walt.

***Nyssa-Taxodium* Group**

Bidens frondosa L.
Boehmeria cylindrica (L.) Sw.
Carex glaucescens Ell.
Cephalanthus occidentalis L.
Clethra alnifolia L.
Itea virginica L.
Leucothoe racemosa (L.) Gray
Ludwigia palustris (L.) Ell.
Lycopus angustifolius Ell.
Mikania scandens (L.) Willd.
Nyssa biflora Walt.
Quercus laurifolia Michx.
Smilax walteri Pursh
Styrax americana Lam.
Taxodium ascendens Brongn.
Toxicodendron radicans (L.) Kuntze
Vitis rotundifolia Michx.