

APPLYING WETLAND REFERENCE DATA TO FUNCTIONAL ASSESSMENT, MITIGATION, AND RESTORATION

Richard D. Rheinhardt, Mark M. Brinson, and Paul M. Farley¹

*Department of Biology
East Carolina University
Greenville, North Carolina 27858*

¹ *Present address: Land Management Group
P.O. Box 2522
Wilmington, NC 28402*

Abstract: This study demonstrates an approach for rapidly collecting quantitative field data on reference wetland sites and using those data to assess functions (ecological processes) in wetlands. We demonstrate the hydrogeomorphic (HGM) assessment procedure by identifying ecological functions performed by mineral soil wet flats, obtaining quantitative field data from 19 wet flats (reference sites) in southeastern North Carolina, and modeling wetland functions using variables derived from those field data. We chose a subset of the 19 reference sites to demonstrate how HGM assessment can be used to measure ecosystem functions before and after a project site is altered and the degree to which ecosystem restoration can compensate for a reduction in functions caused by a project's impact.

We also illustrate how HGM assessment can be used to determine the minimum area over which restoration should be applied to achieve a no-net-loss in function objective. This minimum area can be determined by dividing the degree to which a function is reduced through project alteration by the degree to which a function is increased through restoration. The ratio of wetland area restored to wetland area altered by a project impact (compensatory mitigation ratio) varies among functions and is influenced by (1) the magnitude to which any given function occurs at a project site both before and after the site is altered, (2) the magnitude to which any given function occurs at a compensatory mitigation site both before and after restoration is applied, and (3) the rate at which any given function is restored.

Key Words: compensatory wetland mitigation, ecosystem restoration, fire, functional assessment, hydrogeomorphic assessment, impact assessment, longleaf pine, *Pinus palustris*, North Carolina, wet pine flats, reference standards, reference wetlands

INTRODUCTION

The hydrogeomorphic (HGM) assessment approach for measuring wetland functions differs from earlier assessment approaches in two fundamental ways: it requires that wetlands be classified by hydrologic and geomorphic properties within a narrowly defined regional subclass (Brinson 1993) and that information on other wetland sites of the same HGM class (i.e., reference wetland sites) be used to develop and calibrate standards for assessment (Smith et al. 1995, Brinson and Rheinhardt 1996).

The HGM assessment procedure was developed to assess ecosystem functions of a wetland sub-class prior to project impact or restoration and to estimate the degree of change in functions after alteration. Critical assumptions made in applying HGM assessments are that (1) ecological processes (functions) in relatively

unaltered wetlands occur at levels that are sustainable and predictable for any given HGM wetland-type (barring severe natural perturbations), (2) that these ecological processes are so similar in form and magnitude within any narrowly defined regional subclass that they shape biotic and abiotic components in ways characteristic for the subclass, (3) some of these biotic and abiotic parameters can be measured in the field using standard and relatively rapid techniques, and (4) variables derived from field measurements can be combined to coarsely model functions of the subclass. Thus, the assumption is that one can use rapidly measured field parameters to assess functions rather than doing so by measuring ecological processes directly (usually a time-consuming and expensive process). Assessment of functions using modeled field parameters is possible because model variables and functions are indexed relative to variables and functions of rel-

actively unaltered wetlands belonging to the same regional HGM wetland subclass (Brinson et al. 1995, Smith et al. 1995).

The HGM assessment method was developed for use in determining compliance with Section 404(b)(1) guidelines of the Clean Water Act (40 CFR 230), including alternatives analysis and wetland mitigation (avoidance, minimization, and compensation). This functional assessment approach is not intended to supersede the 404 public review process; it was developed as a tool for providing information for use in public review decision-making. If appropriately modified, this assessment technique could also be used to assess the relative condition of any ecosystem because it relies on relatively intact, natural ecosystems for defining standards.

This study demonstrates the HGM assessment approach for rapidly collecting quantitative field data on reference wetland sites and using those data to assess functions in wetlands. It does not provide reliable reference standards for assessing or regulating wetlands in North Carolina or elsewhere; to determine the natural variation of relatively unaltered sites, more data are needed than we used to demonstrate the assessment procedure. Therefore, within this limitation, our objectives were to (1) identify ecological functions generally attributed to forested, mineral soil wet flats in North Carolina, (2) develop procedures to rapidly measure field parameters that are attributes of functions performed by such flats, (3) locate and quantitatively characterize reference sites representing a range of relatively unaltered and altered conditions typical of wet flats in southeastern North Carolina, (4) assess changes in ecological functions expected to occur under a hypothetical alteration of one of the reference sites, and (5) predict the potential effects that two restoration alternatives could have on restoring altered functions.

This paper is divided into two parts. Part I establishes reference wetland conditions for mineral soil wet flats. It provides the historic and biogeographic context for wet flats in the southeastern United States, outlines methods used to obtain data on reference sites in North Carolina, provides field data on those reference sites, and relates reference sites to one another.

Part II defines functions, provides rationale for modeling functions with field variables, calculates reference standards for model variables, illustrates how function models and reference standards can be used to assess restoration alternatives, and determines compensatory mitigation ratios (wetland area restored to wetland area altered by a project impact) required to achieve a no-net-loss in function objective.

PART I. ESTABLISHING REFERENCE CONDITIONS

Classification: Historic and Geomorphic Setting

This study was conducted in Carteret, Craven, and Onslow Counties in southeastern North Carolina, USA in the vicinity of 35° north latitude and 77° west longitude. The southeastern North Carolina coastal plain, east of the Suffolk Scarp, is underlain by an extensive Pleistocene marine terrace that is flat and poorly drained. Seasonal saturation has led to the formation of hydric soils and extensive wetlands. Except for flats adjacent to coastal embayments where sea level directly influences the water table, most wet flats receive precipitation as their sole source of water and lose water by evapotranspiration, overland flow, and gradual, year-round seepage to the underlying aquifer (Heath 1975, Skaggs et al. 1980, Daniel 1981). Soils of wet flats range from histosol to mineral. Organic soil flats, overlain with peat, generally support pocosin or "bay" vegetation (dominated by ericaceous shrubs), while poorly drained mineral soil flats generally support trees.

Prior to the arrival of European colonists, vast areas of the southeastern coastal plain were subjected to frequent fire. Fires were caused by lightning (Komarek 1964, 1974) and by indigenous people to improve habitat for game (Bartram 1791, Ware et al. 1993). Because extensive areas of the lower (outer) coastal plain are so flat, one lightning strike could initiate a burn over vast areas of the landscape (Ware et al. 1993), including both wet flats and adjacent upland flatwoods. Thus, the only areas immune to frequent fire were small areas isolated by open water or by soils saturated for long periods (such as pocosins, stream bottom swamps, and marshes). Fire was much less frequent in isolated compartments because they were less likely to be struck by lightning than larger areas (Ware et al. 1993).

Frequent ground fires prevented the accumulation of fuel and destructive crown fires (Schwarz 1907, Chapman 1932, Heinselman 1981, Abrahamson and Harnette 1990). These fires also encouraged ground cover dominance by pyrophytic grasses and forbs and recruitment of longleaf pine (*Pinus palustris*) and pond pine (*Pinus serotina*) while suppressing recruitment of loblolly pine (*Pinus taeda*) and hardwoods (Schwarz 1907, Christensen 1981, Platt et al. 1988, Stout and Marion 1993). Longleaf requires mineral soil for seed germination (Chapman 1932, Christensen 1977), and pond pine tends to release large quantities of seeds following scorching of its cones by fire (Crutchfield and Trew 1961, Burns and Honkala 1990). Both species are relatively resistant to frequent, low intensity

fires, yet such fires usually kill loblolly and hardwood seedlings.

Fire was once so common in the southeast that most coastal plain forests from southeastern Virginia to northern Florida and eastern-most Texas were dominated by pyrogenic grass savannas and wet longleaf and pond pine savannas (Pinchot and Ashe 1897, Schwarz 1907, Ashe 1915, Wells 1928, Heyward 1939, Braun 1950, Christensen 1981, Ware *et al.* 1993). Land-clearing for agriculture, exploitation of longleaf for the naval stores industry, a proliferation of free-ranging hogs, and the suppression of wild-fires led to the complete extirpation of virgin longleaf savannas by the early 1800s (Ashe 1894, 1915, Pinchot and Ashe 1897, Ware *et al.* 1993). In the wake of this widespread degradation, loblolly pine displaced longleaf on most wet flats in North Carolina.

Loblolly, formally only a minor canopy component of wet flats and stream bottoms (Ashe 1894, Pinchot and Ashe 1897, Ashe 1915, Wells 1942, Braun 1950), was able to displace longleaf because (1) loblolly grows more rapidly than longleaf in its early stages, (2) loblolly produces more consistent and abundant mast, and (3) loblolly seeds are carried by wind much further than heavier longleaf seeds. Although large loblolly pines can withstand frequent, low intensity fire, hardwoods invade and eventually displace loblolly when fire is totally eliminated (Allen 1960, McNab 1977, Villarrubia and Chambers 1978). Under such conditions (i.e., fire suppression, the accumulation of humus, and loss of seed source), longleaf has no opportunity to re-establish itself.

Wet flats isolated from fire were extremely rare prior to European settlement. Therefore, hardwood-dominated stands and forests of mixed pine and hardwood were probably also relatively rare, particularly on the outer coastal plain where the landscape is flat over extensive areas. However, as human settlements began to compartmentalize the landscape with farms and towns, hardwoods displaced loblolly on uplands and wet flats where fire and logging were prevented (Ashe 1894, Pinchot and Ashe 1897). Today, although a policy of wildfire suppression is now diligently practiced throughout the south, mature wet hardwood flats are probably at least as rare today as they were prior to European colonization (Quarterman and Keever 1962, Christensen 1988). This is because agriculture, intensive loblolly pine silviculture, and hardwood timbering are so pervasive that there is little opportunity for succession to mature hardwood forest. As a consequence of three centuries of draining, clear-cutting, and conversions to agriculture and silviculture, the landscape and vegetation of the southeastern U.S. is one of the most altered in North America (Campbell and Hughes 1991, Ware *et al.* 1993), and as a result, relatively un-

altered mineral soil wet flats (both pine and hardwood) are extremely rare today.

Methods for Collecting Reference Wetland Data

Sixty-nine wet flats had been visited during the summer of 1993 as part of an Advanced Identification (ADID) study to inventory and characterize wetland resources for mapping and management purposes. Nineteen of the 69 wet flats initially visited were chosen for more intensive characterization because these 19 sites seemed to represent the typical range of disturbance, soil type, and seral stage exhibited by wet flats on mineral soils (pocosin peatlands excluded) on the outer coastal plain of North Carolina. Field parameters selected for measurement were those that could be rapidly measured and used for modeling functions. Data on sites were collected between April 27 and May 17, 1994; a pair of investigators was generally able to sample two sites per day.

At the center of each site, soil was excavated to at least 0.25 m depth and examined to determine soil type, soil texture, redoximorphic features (chroma, mottling, etc.), and depth to water table (if < 0.25 m). The proximity and dimensions of ditches were recorded at sites where they appeared to be effective in transporting water away from the site. Increment cores were extracted from the largest trees at each site to estimate stand age.

Field parameters were recorded from three locations at each site. Each location was located approximately 30 m from the center of the site in a randomly chosen compass direction and oriented at 120° from one another relative to the center point. Data from each of the three sampled locations were later pooled for each site.

At each of three sample locations per site, the following data were collected: (1) basal area (m² per ha cross-sectional area at 1.5 m above ground) of trees, by species, greater than 10 cm dbh using the Bitterlich plotless technique (Grosenbaugh 1952, Lindsey *et al.* 1958), (2) number of canopy trees, by species, greater than 10 cm dbh (diameter at 1.5 m above ground) within a 10-m radius of each Bitterlich point, (3) number of standing dead stems (snags) greater than 10 cm dbh within a 10-m radius of each Bitterlich point, (4) number of subcanopy trees and shrubs (by species) greater than 1 m tall, but less than 10 cm dbh, located within a 5-m radius of each Bitterlich point, and (5) lengths and numbers of coarse woody debris (CWD), defined as dead stems greater than 10-cm diameter, prostrate or leaning more than 45°, and located within a 10-m radius of each Bitterlich point.

Canopy species were defined as trees capable of dominating the canopy, such as loblolly pine, longleaf

pine, and red maple (*Acer rubrum*), while subcanopy species were defined as woody life-forms generally restricted to the understory and shrub layer, such as fetter-bush (*Lyonia lucida*), titi (*Cyrilla racemiflora*), and red bay (*Persea borbonia*). Taxonomic nomenclature follows Radford et al. (1968), except that *Nyssa sylvatica* var. *sylvatica* and *Nyssa sylvatica* var. *biflora* are herein referred to as *Nyssa sylvatica* and *Nyssa biflora*, respectively.

At each of the three Bitterlich points, three 5-m-long transects were established, each of which radiated outward from the three Bitterlich points and were oriented at 120° from one another. Thickness of litter layer and relative elevation (using a stadia rod and hand level) were measured at each 0.5-m interval along the three transects (10 points per transect $\times$ 3 transects per sample point $\times$ 3 sample points per site = 90 measurements per site). Two 1-m² quadrats were placed along each transect between the 2 and 3 m position and the 4 and 5 m position. For each quadrat (18 per site), we recorded percent cover for each of the following categories: (1) graminoids, (2) forbs (non-graminoid herbaceous plants), and (3) subcanopy and canopy seedlings less than 1 m tall. Percent cover was estimated as the midpoint of one of eight cover classes (modified from Daubenmire 1968): 0% (0%), 2.5% (0–5%), 15% (5–25%), 37.5% (25–50%), 67.5% (50–75%), 85% (75–95%), 97.5% (95–100%), 100% (100%).

Analysis of Reference Wetland Data

Measured field parameters and units of measurement are defined in Table 1. Counts of stems were converted to absolute density and presented in numbers per hectare. Relative basal area and relative density were calculated for each canopy species and averaged to obtain importance values, by species. Relative density and relative frequency of occurrence were averaged for subcanopy species to obtain importance values, by species. Importance values for canopy and subcanopy were combined for each site and used to construct an ordination diagram using Detrended Correspondence Analysis (DCA) (Hill 1979, Hill and Gauch 1980), with CANOCO software developed by Ter Braak (1988). CANOCO was also used to construct environmental biplots for the ordination. We used the DCA algorithm, rather than a direct ordination technique, because we did not want the ordination to be constrained by the parameters we measured. Rather, our objective was to assess how the measured field parameters were related to intrinsic differences in vegetation among sites.

Microtopographic complexity for each site was calculated by (1) subtracting the lowest elevation measured in each transect (30 per transect) from all other

Table 1. Field parameters measured in wet flats. Measurements provided in Table 3. Variables used to model functions were derived from these field parameters.

Variable	Definition
V _{DITCH}	Lack of ditches near (<50 m) and within assessment site
V _{GRAM}	Percent cover of graminoids
V _{FORB}	Percent cover of forb (non-graminoid herbs)
V _{TREE}	Total basal area (m ² ha ⁻¹) for all trees > 10 cm dbh
V _{TDEN}	Density (stems/ha) of canopy trees > 10 cm dbh
V _{TDIA}	Average tree diameter (m)
V _{SUBC}	Density (stems/ha) of subcanopy > 1 m tall and < 10 cm dbh
V _{SIDL}	Percent cover of trees and shrubs < 1 m tall
V _{MICR}	Microtopographic complexity (measured as variance in elevation divided by mean elevation, n = 90)
V _{LTR}	Depth of litter layer (cm), n = 90
V _{SNAG}	Density (stems/ha) of standing dead stems > 10 cm diameter
V _{CWD}	Volume (cm ³ /ha) of coarse woody debris > 10 cm diameter
V _{CVEG}	Sorensen similarity index of canopy Importance Values (average of relative basal area and relative density of trees > 10 cm dbh)
V _{SVEG}	Sorensen similarity index of subcanopy Importance Values (average of relative density and relative frequency of occurrence for subcanopy species > 1 m tall and < 10 cm dbh)

elevation measurements within the transect (thus, zero was assigned to the lowest elevation in each transect) and (2) dividing the pooled variance in elevation for each of the 9 transects by the mean elevation of the site.

Relationship Among Reference Wetlands

The 19 reference sites for wet flats were classified into four forest cover-types (Table 2): natural pine (3 sites), loblolly pine plantation (6 sites), pine-hardwood (6 sites), and hardwood (4 sites). Field measurements used to establish reference standards and derive model variables for assessing functions are summarized in Table 3.

The DCA ordination separated wet hardwood flats to the right side of the ordination diagram and natural wet pine flats to the left side (Figure 1). These represent the two seral endpoints possible for mineral soil wet flats: fire-maintained pine savanna dominated by longleaf or pond pine and fire-suppressed, and closed canopy forest dominated by admixtures of hardwoods.

Ordination biplot arrows, which depict the direction

and relative strengths of changes along environmental gradients, suggest that wet pine flats possess lower basal area, lower snag density, and higher graminoid cover than wet hardwood flats. Wet pine flats also tend to possess less living and dead biomass than wet hardwood flats because fire increases tree mortality and burns woody debris (snags and CWD). The higher graminoid cover measured in wet pine flats likely results from a sparse canopy, which allows more light penetration to the forest floor (Wells 1932, Lemon 1949, Frost 1987, Ware 1993). In fact, graminoids, such as wiregrass, broom-straw (*Andropogon* spp. L.), or switch-cane (*Arundinaria gigantea* Michaux) are often dense in relatively natural wet pine flats in North Carolina. The flammability of graminoids contributes to a pine flat's susceptibility to fire (Lemon 1949). It is these frequent, low-intensity fires that prevent hardwood and loblolly pine recruitment (Frost 1978, Ware 1993).

Mature, fire-maintained wet flats are represented by site 10 on the far left side of the ordination; this site is believed to most closely represent fire-maintained coastal plain wet pine flats. Its vegetative composition, physiognomy, and soil are similar to remnant fire-maintained wet pine flats in the southeastern U.S. and historic accounts described in the scientific literature (Bartram 1791, Ashe 1915, Wells 1928, Heyward 1939, Braun 1950, Christensen 1981, Bridges and Orzell 1989, Ware et al. 1993). Because site 10 was the only completely intact wet pine flat located within the study area, field variables measured at this site were used to establish reference standards for assessing functions at other sites.

Ideally, 15 or more sites should be used to characterize the natural variation in relatively unaltered wetlands and provide reference standards, but the global rarity of relatively unaltered wet pine flats and our restricted study area prevented us from locating more sites. More extensive field data from relatively unaltered wet pine flats from across a broader wetness continuum would be required to characterize the natural range of conditions exhibited by unaltered wet flats; such data would also enable us to sub-classify pine flats by wetness regime using vegetation. For example, sites with mostly pond pine or pond pine and bald cypress (*Taxodium distichum*) could be classified (with enough data) separately from sites with mostly longleaf and sparse pond pine (site 10). With such data, separate reference standards could be determined for each subclass.

The canopy of site 10 is overwhelmingly dominated by longleaf pine (IV = 68.9). Pond pine (IV = 17.6), loblolly pine (IV = 8.9), and red maple (IV = 4.4) contribute to the remainder of canopy composition. The sparse and patchy woody understory of site 10 is

comprised of inkberry (*Ilex glabra*: IV = 21.8) loblolly bay (*Gordonia lasianthus*: IV = 21.6), fetter-bush (IV = 12.1), and blueberry (*Vaccinium* spp.: IV = 14.8). The herbaceous stratum is dominated by graminoids (cover = 66.8%), primarily wiregrass (*Aristida stricta* Michaux).

Site 9 is a wet pine savanna from which fire has been suppressed. Its canopy lacks longleaf pine but contains pond pine and loblolly pine. It was judged to be a bit wetter than site 10 because it supported pond pine in its canopy, and pepperbush (*Clethra alnifolia*) and titi in its subcanopy. Although in relatively good condition, it appeared that fire had been suppressed in site 9 for some time due to its (1) high density of understory shrubs (potential fuel), (2) preponderance of fire-intolerant saplings (especially red maple), and (3) lack of graminoids. Invasion of shrubs and hardwoods probably occurred rapidly due to the initially low density of pines. Continual fire-suppression will cause its composition to eventually change from dominance by pines to a mixture of hardwood species.

Site 6 is a selectively cut-over pond pine stand. This site appears to have been similar to site 9 before it was logged, but it now contains less than half the basal area of site 9 (Table 2). Site 8 is a 50-year old loblolly pine plantation with an understory dominated by pepperbush, blueberry, and wax myrtle (*Myrica cerifera*).

Sites enclosed by the dotted line on the right side of the ordination (Figure 1) represent the composition and site characteristics of mature hardwood stands found on mineral soil wet flats where fire has been excluded. Long-term fire exclusion may allow soils to accumulate high levels of organic matter, which would encourage higher soil moisture, resistance to ground fires, and further organic matter accumulation. Thus, long-term fire suppression and protection from disturbance may stimulate a positive feedback loop that encourages wet flats to switch from pine to hardwood dominance (Streng and Harcombe 1982).

Hardwood stands in the reference data are dominated by a mixture of hardwood species, including ash (*Fraxinus* spp.), swamp chestnut oak (*Quercus michauxii*), swamp tupelo (*Nyssa biflora*), sweetgum (*Liquidambar styraciflua*), laurel oak (*Q. laurifolia*), tulip poplar (*Liriodendron tulipifera*), and red maple (Table 2). The understory of wet hardwood flats is comprised of red bay, American holly (*Ilex opaca*), leucothoe (*Leucothoe axillaris*), and ironwood (*Carpinus caroliniana*).

Stands in the middle of the ordination are altered, managed, or naturally succeeding towards one of the two reference standard conditions. Altered sites sampled in this study included mid-successional wet pine-hardwood flats (sites 7, 13, 14, 15, 17), recently logged sites (sites 6, 12), a fire-suppressed wet savanna (site

Loblolly Pine Plantations

for intact wet pine flats and stands 11, 18, and 19 for 1981											
trees >10 cm dbh. Site 20 (an agricultural field) had no vegetation											
Site #	Natural Pine Flatwoods				Loblolly Pine Plantations						
	10	9	6	2	4	5	8	3	1	7	
Basal Area (m ² ha ⁻¹)	15	17	7	0	25	0	15	5	21	26	
Density (no. ha ⁻¹)	244	360	318	0	1,198	0	286	254	753	519	
<i>Pinus palustris</i> Miller	68.9	—	—	—	—	—	—	—	—	—	
<i>Pinus serotina</i> Michaux	17.6	33.3	93.3	—	—	—	—	—	—	—	
<i>Pinus taeda</i> L.	8.9	49.9	—	100.0	100.0	93.4	100.0	44.3	80.8	56.5	
<i>Acer rubrum</i> L.	4.4	16.8	—	—	—	6.6	—	44.3	2.8	17.6	
<i>Liquidambar styraciflua</i> L.	—	—	—	—	—	—	—	11.3	11.3	21.2	
<i>Prunus serotina</i> Ehrhart	—	—	—	—	—	—	—	—	—	1.0	
<i>Taxodium distichum</i> (L.) Richard	—	—	6.7	—	—	—	—	—	—	3.3	
<i>Nyssa sylvatica</i> Walter	—	—	—	—	—	—	—	—	—	—	
<i>Fraxinus</i> spp. Ash	—	—	—	—	—	—	—	—	—	—	
<i>Magnolia virginiana</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Nyssa biflora</i> Walter	—	—	—	—	—	—	—	—	—	—	
<i>Quercus laurifolia</i> Michaux	—	—	—	—	—	—	—	—	—	—	
<i>Quercus michauxii</i> Nuttall	—	—	—	—	—	—	—	—	—	—	
<i>Quercus nigra</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Gordonia lasianthus</i> (L.) Ellis	—	—	—	—	—	—	—	—	—	—	
<i>Quercus phellos</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Liriodendron tulipifera</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Fagus grandifolia</i> Ehrhart	—	—	—	—	—	—	—	—	—	—	
<i>Ulmus rubra</i> Muhl.	—	—	—	—	—	—	—	—	—	—	
SUBCANOPY	12,550	11,702	636	6,963	2,586	18,402	13,314	7,632	127	3,165	
Density (stems ha ⁻¹)	21.8	19.2	—	8.9	—	63.9	13.1	32.0	—	—	
<i>Ilex glabra</i> (L.) Gray	21.6	4.8	—	—	—	—	5.7	—	58.8	—	
<i>Gordonia lasianthus</i> (L.) Ellis	14.8	7.0	11.7	—	—	—	11.6	—	—	—	
<i>Vaccinium</i> sp. L.	12.1	20.1	—	10.5	—	10.2	5.7	—	—	5.2	
<i>Lyonia lucida</i> (Lam.) K. Koch	8.3	—	—	16.2	—	—	—	—	—	—	
<i>Rhus copallina</i> L.	6.0	11.2	11.7	8.7	86.7	10.4	7.3	10.6	—	50.7	
<i>Persea borbonia</i> Miller	4.3	8.8	41.7	6.8	13.3	5.1	3.4	5.4	—	4.5	
<i>Magnolia virginiana</i> L.	3.7	—	—	—	—	—	—	9.7	—	—	
<i>Myrica heterophylla</i> Raf.	3.7	—	—	—	—	—	—	—	—	5.8	
<i>Gaylussacia baccata</i> (Wang) K. Koch	3.5	5.6	—	3.3	—	—	—	—	—	—	
<i>Ilex coriacea</i> (Pursh) Chapman	—	11.1	—	5.9	—	—	38.6	6.9	—	—	
<i>Clethra alnifolia</i> L.	—	5.8	—	18.6	—	—	—	12.4	—	—	
<i>Cyrilla racemiflora</i> L.	—	3.4	—	2.7	—	—	—	—	—	—	
<i>Baccharis halimifolia</i> L.	—	2.1	20.0	2.7	—	—	—	—	—	—	
<i>Symplocos tinctoria</i> (L.) L'Her.	—	0.7	—	—	—	5.1	13.0	10.6	—	4.5	
<i>Myrica cerifera</i> L.	—	—	15.0	—	—	—	—	—	—	—	
<i>Vaccinium arboreum</i> Marshall	—	—	—	15.3	—	—	—	—	—	—	
<i>Rubus</i> spp. L.	—	—	—	—	—	5.1	—	12.0	—	11.0	
<i>Vaccinium corymbosum</i> L.	—	—	—	—	—	—	—	—	41.6	4.5	
<i>Ilex opaca</i> Aiton	—	—	—	—	—	—	—	—	—	13.5	
<i>Vaccinium stamineum</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Ilex decidua</i> Walter	—	—	—	—	—	—	—	—	—	—	
<i>Leucothoe axillaris</i> (Lam.) D. Don	—	—	—	—	—	—	—	—	—	—	
<i>Ligustrum sinense</i> Lour.	—	—	—	—	—	—	—	—	—	—	
<i>Sabal minor</i> (Jacquin) Persoon	—	—	—	—	—	—	—	—	—	—	
<i>Cornus stricta</i> Lam.	—	—	—	—	—	—	—	—	—	—	
<i>Carpinus caroliniana</i> Walter	—	—	—	—	—	—	—	—	—	—	
<i>Oxydendrum arboreum</i> (L.) DC.	—	—	—	—	—	—	—	—	—	—	
<i>Callicarpa americana</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Aralia spinulosa</i> L.	—	—	—	—	—	—	—	—	—	—	
<i>Viburnum nudum</i> L.	—	—	—	—	—	—	—	—	—	—	

Table 2. Extended.

Pine-Hardwood Flats						Hardwood Flats			PCC
15	12	13	14	17	11	19	18	16	20
32	3	26	20	31	18	23	27	25	0
784	233	689	509	763	403	572	435	562	0
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
54.9	28.2	15.8	31.8	25.2	13.7	—	—	10.7	—
37.8	48.2	20.2	1.0	3.2	1.3	31.5	25.6	25.6	—
4.1	14.5	—	16.9	0.7	13.9	10.9	17.0	16.3	—
—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
3.0	9.1	56.3	—	70.2	—	—	—	—	—
—	—	—	7.6	—	20.5	11.4	2.4	39.3	—
—	—	7.4	—	—	—	1.5	1.5	5.1	—
—	—	—	4.2	—	14.0	24.5	19.5	—	—
—	—	—	7.2	—	6.3	8.1	—	0.9	—
—	—	—	3.8	—	16.0	10.1	2.4	—	—
—	—	—	21.4	—	—	0.9	—	1.9	—
—	—	—	1.1	—	—	—	—	—	—
—	—	—	3.8	—	—	—	—	—	—
—	—	—	1.7	—	5.8	—	35.3	—	—
—	—	—	—	—	8.1	—	—	—	—
—	—	—	—	—	—	0.9	—	0.9	—
551	7,208	9,794	1,950	424	886	3,307	1,781	10,048	0
—	18.4	—	—	—	—	—	—	7.7	—
—	—	—	12.3	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—
10.4	15.3	22.8	—	13.4	—	—	—	21.9	—
—	—	—	—	—	—	—	—	—	—
35.4	7.9	13.5	13.2	18.3	32.1	28.9	25.5	6.9	—
18.7	10.6	9.5	—	28.3	—	4.8	—	5.7	—
—	—	—	—	—	—	—	5.7	—	—
—	—	—	—	—	—	—	—	—	—
—	—	27.8	7.8	—	—	20.6	—	—	—
10.4	—	—	—	—	—	—	—	—	—
—	—	6.1	—	—	—	—	—	15.7	—
—	3.2	—	—	—	—	—	—	—	—
14.6	4.3	—	—	—	—	—	—	—	—
—	17.3	—	11.1	13.4	—	5.4	16.1	2.0	—
—	5.0	—	—	—	—	—	—	7.7	—
—	—	—	—	—	—	—	—	—	—
10.4	5.5	—	13.2	—	—	6.0	—	6.9	—
—	—	9.8	24.3	13.4	23.8	15.9	11.4	17.4	—
—	—	—	—	—	—	—	—	—	—
—	4.6	—	—	—	—	—	—	—	—
—	—	10.2	5.6	—	15.5	7.3	13.8	2.2	—
—	—	—	5.6	—	—	—	4.5	—	—
—	—	—	6.7	—	—	—	—	—	—
—	—	—	—	13.4	—	—	—	—	—
—	—	—	—	—	28.5	5.4	—	—	—
—	—	—	—	—	—	5.4	4.5	3.7	—
—	—	—	—	—	—	—	13.8	—	—
—	—	—	—	—	—	—	4.5	—	—
—	—	—	—	—	—	—	—	4.3	—

Table 3. Model variables derived from field measurements. Reference standards for wet pine flats obtained from site 10, the only unaltered wet pine flat located in the study area. Site 20 is based on characteristics of agricultural fields (prior-converted cropland). Table 1 provides abbreviations for model variables.

Site	Age	V _{DITC}	V _{GRAM}	V _{FORB}	V _{TREE}	V _{TDEN}	V _{TDIA}	V _{SUBC}	V _{SDLG}	V _{MICR}	V _{LIR}	V _{SNAG}	V _{CWD}
1	26	0.5	52.4	34.4	21.3	753	0.19	127	15.4	4.49	2.8	212.0	0.62
2	5	0.1	69.0	20.5	0.0	0	0.00	6,963	34.0	6.60	2.9	0.0	0.00
3	11	0.1	64.0	5.7	4.7	254	0.15	7,632	17.8	21.25	4.5	0.0	0.00
4	12	0.1	5.7	55.2	24.7	1,198	0.16	2,586	3.9	8.33	9.3	0.0	0.85
5	26	0.5	0.0	2.8	0.0	0	0.22	18,402	12.2	4.17	13.1	0.0	1.77
6	10	0.5	62.1	42.9	6.7	318	0.16	636	9.6	5.89	0.5	0.0	0.00
7	60	1.0	38.1	43.3	26.0	519	0.25	3,165	15.1	6.52	10.2	0.0	6.92
8	50	0.5	4.7	0.0	14.6	286	0.25	13,313	43.6	2.53	5.9	0.0	0.00
9	60	1.0	0.0	6.0	16.7	360	0.24	11,702	51.4	3.53	6.4	42.4	0.00
10	60	1.0	66.8	33.3	14.7	244	0.28	12,550	60.3	2.48	5.7	8.0	2.07
11	64	1.0	17.0	52.0	18.0	403	0.24	886	22.5	4.86	6.1	169.6	5.52
12	5	0.1	58.4	37.5	3.3	233	0.13	7,208	26.6	4.63	2.6	84.8	9.52
13	50	0.5	0.0	8.4	26.7	689	0.22	9,794	28.8	6.84	9.0	0.0	7.07
14	50	0.5	15.0	14.6	20.0	509	0.22	1,950	17.8	3.96	8.6	84.8	0.00
15	50	0.5	48.7	6.0	32.0	784	0.23	551	17.5	6.86	20.1	84.8	8.10
16	35	1.0	11.4	5.6	29.3	560	0.26	10,048	15.1	8.40	11.1	0.0	4.60
17	46	0.5	2.8	24.9	30.7	763	0.23	424	1.9	3.16	4.7	127.2	0.00
18	118	0.5	11.7	60.0	28.0	435	0.29	1,781	26.0	6.08	6.0	84.8	1.35
19	67	1.0	2.8	41.3	22.7	572	0.22	3,307	21.8	6.35	5.9	42.4	3.12
20	0	0.0	0.0	0.0	0.0	0	0.00	0	0.0	0.00	0.0	0.0	0.00

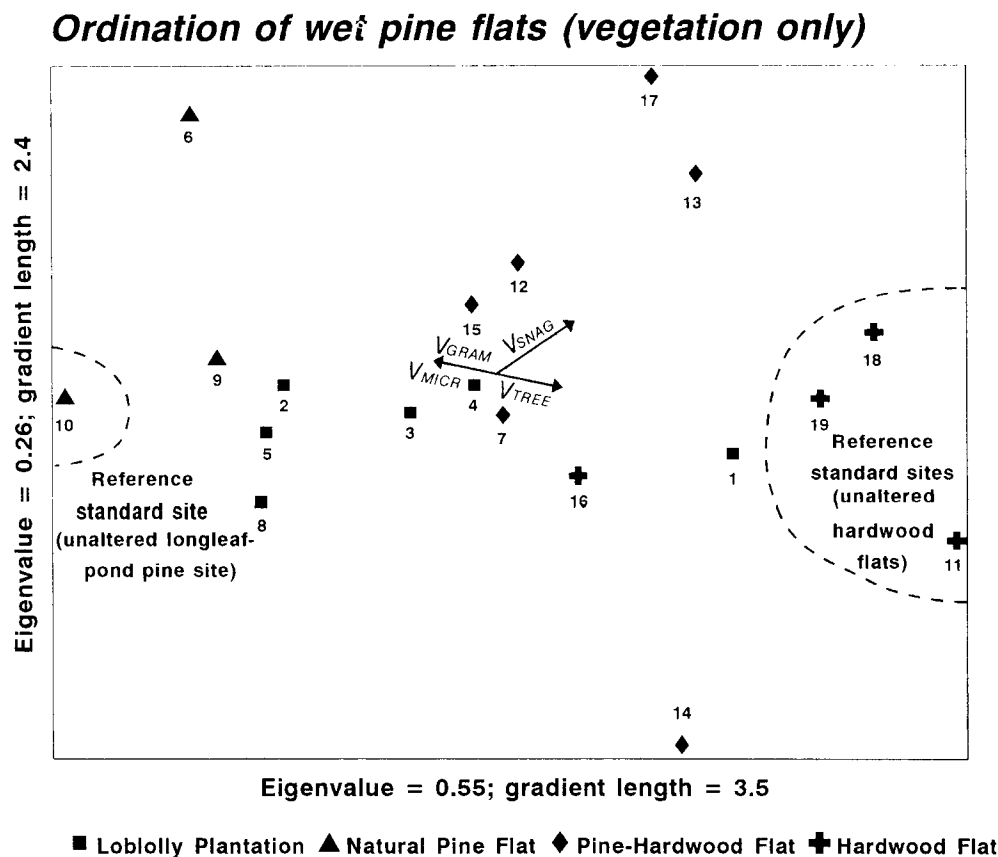


Figure 1. Ordination of vegetation on mineral soil flats based on Importance Values of canopy and subcanopy species. Biplot arrows illustrate relative strengths of environmental gradients. Variables defined in Table 1.

9), and managed pine plantations (sites 1, 3, 4, 5, 8). Pine plantations are managed for loblolly pine, some more intensively than others. Wet pine-hardwood flats are stands in various stages of secondary succession; they support admixtures of loblolly pine and hardwoods (mostly red maple and sweetgum).

PART II: ASSESSING, MITIGATING, AND RESTORING WETLAND FUNCTIONS

Functions are defined by Smith *et al.* (1995) as “the normal or characteristic activities that take place in wetland ecosystems or simply the things wetlands do.” One goal of functional assessment is to determine how well a wetland is doing. This can only be done if one knows what a given wetland is capable of doing or how it functions under relatively unaltered conditions. HGM assessment assumes that hydrogeomorphic and regional edaphic-climatic constraints determine natural variation, while human-induced alterations induce a form of variation that should be captured by the assessment method.

To reduce the amount of natural variability that has to be considered in assessment, the HGM procedure separates (classifies) wetlands by regional sub-class. Then a wetland's potential is determined from reference data from relatively unaltered sites within its regional wetland subclass (background presented in Part I). General information about unaltered conditions and locations of relatively unaltered sites are obtained from scientific literature and from ecologists familiar with regional variability of the subclass. HGM assessments rely on knowledge about unaltered conditions because the degree of functioning is expressed relative to intact wetlands of the same limited regional subclass. Degree of functioning is determined from both site data and the structure of function models.

Function models used in HGM assessment are coarse logic statements that portray general ecological processes or conditions; they should not be confused with sophisticated models depicting ecological rates and fates of nutrients and energy (Brinson and Rheinhardt 1996). The HGM assessment method was designed to be a rapid technique for use in the regulatory arena where lack of sufficient time, money, and personnel limit the application of more sophisticated procedures. Fortunately, wetlands possess numerous biotic and abiotic parameters that can be measured rapidly and can be used to model functions using coarse logic models.

For simplicity of illustrating the application of functional assessment, we focus only on pine-dominated, mineral soil wet flats. Because both relatively unaltered pine and mature wet hardwood flats are relatively rare, they both warrant consideration for restoration in

the southeastern U.S. coastal plain. With modifications and much additional data, we expect our reference data set to provide a starting point for expansion to more extensive regions of the coastal plain where climatic conditions and edaphic features are similar (*i.e.*, South Carolina to east Texas). More geographically extensive sampling will be required to support or refute this opinion.

Identifying and Modeling Functions

Field measurements collected at each site show differences in biotic and abiotic characteristics among sites (Table 3). We used these field measurements to produce model variables. Some model variables were used to model several functions. Their form was retained for all functions to which they were applied, but the rationale for using them differed among functions. Rationale for using each variable is explained below when defining functions and their models.

Scaling for model variables was continuous, except for cases where continuous measurements were not possible. A simple linear relationship for model variables was assumed because we could not justify a more sophisticated curvilinear relationship without adequate supporting data. For example, if the reference standard condition for tree basal area were 16 m²/ha, a site with 8 m²/ha would score 0.5 while a site with 4 m²/ha would score 0.25. Had we obtained a larger data set of intact sites, natural variation of reference standard sites could have been used to scale the models, thus allowing a range of basal areas (*e.g.*, 14–20 m²/ha) that could be scaled to 1.0.

Instead, model variables from the one relatively unaltered wet pine flat in our reference set (site 10) were defined to be reference standards and indexed to 1.0. Model variables from assessment sites were then normalized relative to those of site 10, thus scoring between zero and 1.0. In most cases, model variables that scored higher than 1.0 after normalization were reduced to 1.0 or less, the assumption being that a higher level of any given function or model variable is not sustainable in natural, relatively unaltered wetlands without negatively affecting other functions (Brinson and Rheinhardt 1996). For plant density-related variables, indices that scored considerably higher than 1.0 after initial normalization were considered to be so detrimental to the expression of their associated functions that their indices were automatically reduced to 0.5.

Model variables were applied to model functions as defined by the mathematical formula developed for each function. By definition, each function was indexed to 1.0 for the reference standard and between zero and 1.0 for assessed sites. The actual relationship

between model variables and functions has not been tested specifically for wet pine flats or any wetland. Therefore, we applied general knowledge about ecosystem structure and function to provide our basis for modeling functions. Also, functions were not weighted in importance relative to one another or to any preconceived notion. Such weighting would require an assignment of societal value, which must take place within regulatory and policy arenas.

We identified four functions performed by mineral soil, wet pine flats: (1) Maintain Characteristic Hydrologic Regime, (2) Maintain Characteristic Nutrient and Elemental Cycling Processes, (3) Maintain Characteristic Plant Community, and (4) Maintain Characteristic Physiognomic Structure. For each function, we provide its definition, describe on-site and off-site effects of the function, list processes that control the function, provide rationale for choosing specific field measurements that we used to represent those processes and model the function, and justify our approach for the way we structured model variables to estimate functions.

Our models could be improved in a variety of ways, ranging from more quantitatively scaling field measurements to adjusting the relative importance of each model variable based upon appropriate data. Both are needed to justify a more sophisticated modeling of functions. However, achieving higher levels of sophistication and resolution must be balanced with practical considerations for a rapid approach that meets the needs of the regulatory end-user.

Functions

(1) Maintain Characteristic Hydrologic Regime. This hydrologic function represents the capacity of an ecosystem to maintain hydrologic processes characteristic of relatively unaltered wet pine flats, including evapotranspiration (ET), long and short-term surface water storage, and subsurface storage. Precipitation and flow from adjacent areas (surface and subsurface) are the only sources of water to wet pine flats. Outputs are restricted to ET, surface and subsurface lateral flow, and minor downward seepage to ground-water. Water is stored in vegetation, in small-scale depressions associated with variations in microtopographic relief (hummocks, depressions, and other irregularities of less than 0.25 m relief), and below ground.

On-site effects of this function include supporting conditions favorable for biogeochemical processes that require anoxic conditions (oxidation and reduction reactions), maintaining wetland vegetation, and providing fire-breaks during wet periods (Schwarz 1907). Off-site effects include maintaining regional water quality, recharging surficial aquifers, sustaining base

flow to streams, and delaying and reducing discharge peaks to riparian areas draining wet flats. For some wet flats, downstream sites are primary nursery areas for fish and shellfish (Brinson 1991).

A direct way to assess hydrologic regime is to monitor shallow ground-water wells and compare hydrographs with those of relatively unaltered sites. However, long-term hydrologic monitoring is not feasible in most regulatory situations. An alternative way to assess hydrologic regime is to measure field parameters that indicate the degree of hydrologic functioning and compare (index) those parameters with relatively unaltered wet flats.

The presence of canopy and subcanopy vegetation indicates that transpiration is occurring. Since basal area of canopy trees is rapidly measured and is roughly proportional to tree leaf area available for transpiration (Barbour et al. 1980), we used total tree basal area (V_{TRF}) to indicate transpiration potential of trees relative to the relatively unaltered wet pine flat. By comparing basal area (and by inference, transpiration) relative to the unaltered site, we assessed sites relative to a characteristic transpiration rate for the unaltered condition, rather than choosing the highest or lowest potential for water loss in defining standards. Likewise, since density of subcanopy stems is an indirect indication of subcanopy leaf area available for transpiration, we used total density of subcanopy stems (V_{SUBC}) to assess subcanopy transpiration relative to transpiration in the unaltered wet pine flat. However, an index score of 0.5 was assigned to sites with a density greater than 125% of the relatively unaltered pine flat. The reasoning for scaling down high densities was that considerably higher densities would subject a site to higher rates of transpiration than the relatively unaltered pine flat and thus alter the hydrologic regime relative to its characteristic condition.

The presence of microtopographic relief indicates that surface water can be held on site. Microtopographic variation contributes to the capacity of a site to retain surface water in small depressions. Low areas surrounded by slightly higher elevations impede overland flow of water away from a site. Therefore, microtopographic complexity (V_{MICR}) was assessed relative to complexity measured in the unaltered pine flat.

An absence of ditches indicates that water is not being artificially removed from a site. We assumed that normal lateral surface and subsurface flow are intact if ditches capable of removing water from a site are absent. By more rapidly transporting water to creeks, ditches reduce the duration of short-term storage of water and reduce water availability to vegetation and small depressions. Assessment sites without ditches (V_{DTC}) were assigned an index score of 1.0 because relatively unaltered wet pine flats lacked ditches. Sites

without ditches within their assessment area, but present within 50 m and capable of removing water, received an index score of 0.5. Sites with ditches present within their assessment area, and capable of removing water, received an index score of 0.1. While this categorical assignment of model variables is used as a first approximation, in reality, the index for the model variable would be a continuum ranging from the reference standard (Index = 1.0) to absent (Index = 0.0) in sites that have been intensively drained. More information on ditch density and soil drainage capacity effects on water removal under varying conditions of soil type and vegetation cover in wet pine flats would be needed to improve our model for this function.

Our model for "Maintain Characteristic Hydrologic Regime" is

Index of Function

$$= \left[\left(\frac{V_{\text{TREE}} + V_{\text{SUBC}} + V_{\text{MICR}}}{3} \right) \times V_{\text{DITC}} \right]^{1/2}$$

Because the presence of ditches affects the expression of the three other hydrologic variables, the model of this function is structured such that the V_{DITC} variable is used as a multiplier of the other factors and the square root is taken from the resulting product. This makes the index zero if either multiplied term scores zero.

(2) *Maintain Characteristic Nutrient and Elemental Cycling Processes.* This function represents the capacity of an ecosystem to maintain nutrient and elemental cycling processes characteristic of relatively unaltered wet pine flats. Cycling includes biotic and abiotic processes that convert elements from one form to another. For nutrients to be cycled, both living and dead biomass (which contain organic carbon and nutrients) must be present. We assumed that living biomass in a mature forest is relatively stable; i.e., mature wet pine flats probably maintain a balance between carbon input (net primary production) and output (oxidation via fire and respiration by decomposers). The living carbon storage compartment represents the capacity of an ecosystem to convert atmospheric carbon dioxide into above-ground plant biomass, and in the process, incorporate other elements into biomass. With similar reasoning, detritus (litter and humus, fine woody debris, snags, and coarse woody debris) represents the nutrient pool available for mineralization.

The primary on-site effect of this function is to supply nutrients required for sustaining living components of the ecosystem and maintain characteristic rates of primary production and decomposition. The primary off-site effect is to provide a reservoir for storing elements and nutrients that may be exported if not internally cycled.

Cycling processes can be measured directly by tracing transformations of essential elements over seasonal and meteorological cycles. However, such studies are time-consuming and require analytical lab support, and so are clearly outside the bounds of rapid assessment procedures. An alternative way to assess this function is to measure field parameters that indicate the degree to which the function occurs at a site.

Snags and coarse woody debris (CWD) represent some of the more refractory forms of detritus undergoing decomposition. As decomposition progresses, these coarse materials are reduced to the fine litter component (explained below) at the same time they release elements for uptake by plants. The density of snags and volume of CWD indicates the relative amount of coarse organic material available for these processes. Therefore, snag density (V_{SNAG}) and volume of CWD (V_{CWD}) were assessed relative to the unaltered pine flat.

Fine litter (leaves, needles, twigs) is mineralized and fragmented to smaller particles during decomposition. Litter depth reflects the relative amount of nutrients available for mineralization. Therefore, mean litter depth (V_{LTR}) was assessed relative to the unaltered wet pine flat. As a consequence of frequent fires, only sparse quantities of snags, CWD, and litter occur in fire-maintained wet pine flats. However, these small stocks are characteristic of nutrients that have been previously released (Garren 1943, Christensen 1987).

Living plants assimilate inorganic nutrients and other elements released by decomposition. Plants from all strata (canopy trees, subcanopy trees and shrubs, seedlings, herbaceous plants) contribute to this process. Tree basal area indicates the relative amount nutrients and elements being incorporated in tree biomass; subcanopy density indicates the amount of biomass being incorporated in understory shrubs and trees; seedling cover indicates the amount of biomass being incorporated in seedlings; and cover of forbs and graminoids indicates the relative amount of biomass incorporated in herbaceous plants. Therefore, canopy basal area (V_{TREE}), subcanopy density (V_{SUBC}), seedling cover (V_{SDLG}), and herbaceous cover ($V_{\text{GRAM}} + V_{\text{FORB}}$) were assessed relative to the unaltered pine flat.

Our model for "Maintain Characteristic Nutrient and Elemental Cycling Processes" is

Index of Function

$$= \left\{ \frac{\left(V_{\text{TREE}} + V_{\text{SUBC}} + V_{\text{SDLG}} + \left[\frac{V_{\text{GRAM}} + V_{\text{FORB}}}{2} \right] \right)}{4} + \left(\frac{V_{\text{LTR}} + V_{\text{SNAG}} + V_{\text{CWD}}}{3} \right) \right\} / 2$$

Because we assumed a relative balance between decomposition and assimilation in mature ecosystems, the model of this function is structured to first average living and decomposing nutrient pools and then determine the average for both compartments.

(3) *Maintain Characteristic Plant Community.* This plant community function represents the capacity of an ecosystem to maintain a plant community that is characteristic of relatively unaltered wet pine flats. Characteristic plant community is defined as a species composition and structure of strata typical of unaltered conditions. Regional climate, geomorphic position, site-specific edaphic factors, competition, herbivory, disease, disturbance, and chance combine to control plant-community composition. Sites that are similar in these respects tend to have similar composition. Hydrogeomorphic classification is one way to ensure that sites with the capacity to support a similar community are assessed relative to their potential.

On-site effects include maintaining local diversity of flora and fauna and providing propagules to nearby wet pine flats. The primary off-site effect is to help maintain regional and global diversity of flora and fauna. Once extensive, natural wet pine flats are now extremely rare. As a consequence, they support a remarkable number of rare and endangered plant and animal species.

Importance values (IV) are used extensively by ecologists to characterize plant composition and analyze community structure (Barbour et al. 1980). A direct comparison of compositional similarity between an assessed site and the relatively unaltered wet pine flat would provide direct evidence on whether the function is occurring in a site. Assessing composition by stratum provides the most useful comparison. This is fairly easily done for the canopy and subcanopy of wet pine flats. However, the herbaceous stratum of fire-maintained, relatively unaltered wet flats is noted for its extremely rich herbaceous stratum. Sometimes as many as 40 species of forbs and graminoids inhabit a single 1 m² plot (Walker and Peet 1983), and a large number of those species are graminoids.

The taxonomic expertise required to identify herbs, particularly graminoids, and their phenological variability (particularly in flowering and fruiting), prevent a rapid assessment of herb composition. However, two more rapidly measured differences in the character of the herb stratum were noted between altered and relatively unaltered wet flats in our study sites: (1) percent herb cover and species richness are much higher in relatively unaltered wet pine flats than in altered flats and (2) the proportion of graminoids to forbs is

higher in relatively unaltered flats than altered sites. We used these two distinctions to develop the herb component of our plant community model (outlined below). For developing a more thorough reference set throughout the southeast, we would suggest that biogeographically focused lists of rare and common species be compiled for relatively unaltered flats and that these lists be used to develop reference standards for assessing wet flats.

For the plant community function, composition of canopy and subcanopy strata and average percent cover for the herbaceous stratum were assessed relative to relatively unaltered wet pine flats. Importance values for canopy (V_{cveg}) and subcanopy (V_{svveg}) species were used to derive a Sorensen Index (Barbour et al. 1980) for each stratum, weighted by importance value (IV). Sorensen's Index is a type of similarity index obtained by summing IVs for each species that is common to any two sites being compared. In this case, assessed sites are compared with the relatively unaltered wet pine flat.

Forb and graminoid cover were measured separately because the proportion of graminoid cover to forb cover is higher in relatively unaltered wet pine flats than in altered flats or fire-suppressed sites in our study area. The invasion of hardwoods in stands protected from fire and silvicultural management to maximize pine production reduces light penetration to the forest floor, which in turn suppresses grasses, and in some instances, encourages forbs. Therefore, we decided that a separate estimate of forb and graminoid cover would be sufficient to detect differences between the herb stratum of altered and relatively unaltered wet flats. Therefore, forb cover (V_{forb}) and graminoid cover (V_{gram}) were assessed relative to relatively unaltered pine flats.

Our model for "Maintain Characteristic Plant Community" is

Index of Function

$$= \left[\frac{V_{\text{cveg}} + \left(\frac{V_{\text{svveg}} + \left[\frac{V_{\text{gram}} + V_{\text{forb}}}{2} \right]}{2} \right)}{2} \right]$$

Because canopy composition in wet pine flats is a dependable indicator of the presence or absence of periodic, low-intensity fire (the main controlling factor of composition in all strata), the arrangement of model variables in the function is structured to allocate more weight to canopy composition. The model also combines graminoids and forbs into an herbaceous com-

ponent, which is weighted equally with the subcanopy composition variable.

(4) *Maintain Characteristic Physiognomic Structure.*

The physiognomic structure function represents the capacity of an ecosystem to maintain habitat and structural characteristics typical of relatively unaltered wet pine flats. Physiognomic structure pertains to physical or architectural features and not to floral composition *per se*, although each influences the other. The number and types of strata, their heights, and general physical characteristics of forests have long been known to be important in affecting the structure and composition of animal communities (Elton and Miller 1953, MacArthur and MacArthur 1961, Perry 1994). For example, red-cockaded woodpecker (*Picoides borealis* Vieillot) requires forests with tall, living pines and an open midstory; almost any species of pine is acceptable (including loblolly, longleaf pine, and pond pine) in providing suitable nest cavities (Copeyon 1990), as long as the midstory is also sparse (Van Balen and Doerr 1978). Shade-intolerant herbs also require a sparse canopy and understory. Relatively unaltered wet pine flats are noted for their sparse tree density, relatively open canopies, dense herb layer, high graminoid cover, and susceptibility to frequent fire. Many rare plants and animals adapted to these conditions are restricted to relatively unaltered wet pine flats. The primary on-site effects of this function are to provide shelter and structure for feeding, nesting, and reproductive behavior of animals and essential microclimatic conditions for characteristic plant species. The primary off-site effect is to maintain regional and global biodiversity of flora and fauna. Because relatively unaltered wet pine flats are so rare, many rare and endangered species inhabit these systems.

Canopy basal area in conjunction with canopy tree density is generally useful in determining maturity and canopy structure of a forest; older stands (under similar climatic and edaphic constraints) generally possess a higher basal area and lower density of trees than younger forests. Mature wet pine flats support larger, taller, and fewer trees than less mature sites and sites managed for timber production. Therefore, we determined relative canopy tree size by dividing stand basal area by stand density to obtain average tree diameter. We assumed that tree diameter is positively related to tree size and height. We then assessed average tree diameter (V_{TDA}) relative to the relatively unaltered wet pine flat.

The density of canopy trees and subcanopy vegetation indicates the relative openness of a forest canopy and midstory. More dense (closed) stands function less effectively in supporting habitat for plants that are shade-intolerant or animals that require an open midstory. Therefore, canopy tree density (V_{TDEN}) and sub-

canopy density (V_{SUBC}) were assessed relative to the relatively unaltered wet pine flat. However, an index score of 0.5 was assigned to any site with a density greater than 125% that of the relatively unaltered wet pine flat. The reason for scaling down high density scores was that considerably higher densities would severely restrict light penetration to the forest floor for shade-intolerant plants and restrict space in the canopy and midstory for animals that need open space for normal behavioral requirements. Subcanopy density is also generally sparse where fire is frequent.

Herbaceous vegetation influences soil moisture conditions, provides forage for herbivores, and provides fuel for fire. Low subcanopy biomass and sufficient graminoid biomass to fuel low-intensity fire are essential for maintaining an appropriate fire frequency and intensity. Many rare and endangered plants associated with relatively unaltered wet pine flats are adapted to and require frequent fires to eliminate competitors and complete their life cycles. Thus, pyrophytic forbs and grasses both influence and are modified by physiognomy in relatively unaltered wet pine flat ecosystems. Herbaceous cover is a useful parameter for comparing herbaceous biomass among sites. Therefore, graminoid cover (V_{GRAM}) and forb cover (V_{FORB}) were assessed relative to the unaltered wet pine flat.

Snags and coarse woody debris (CWD) provide shelter, nesting, and feeding habitat for an array of invertebrates, microbes, and small vertebrates (salamanders, herptiles, and small mammals). Large CWD can act as a localized barrier to low-intensity ground fires (Schwartz 1907). However, snags and CWD can smolder for weeks after rain has dampened a grass fire and can re-ignite grasses when conditions again become favorable. Because frequent fires burn snags and CWD, fire-maintained mineral wet flats tend to contain less CWD than fire-suppressed sites. Therefore, we determined that the density of snags and volume of CWD would be useful for assessing physiognomic structure. Therefore, snag density (V_{SNAG}) and volume of CWD (V_{CWD}) were assessed relative to the unaltered wet pine flat.

Our model for "Maintain Characteristic Physiognomic Structure" is

Index of Function

$$= \left\{ V_{TDA} + V_{TDEN} + \left[\left(V_{SUBC} + \left[\frac{V_{GRAM} + V_{FORB}}{2} \right] + \left[\frac{V_{SNAG} + V_{CWD}}{2} \right] \right) / 3 \right] / 3 \right\}$$

Table 7. Predicted changes in "Maintain Characteristic Physiognomic Structure" function resulting from jetport construction on a 50-year old pine plantation (site #8) and conducting restoration at two alternative sites: an agricultural field (site #20) and a 26-year old pine plantation (site #5). All values predicted to occur five years after initiating restoration. Index of function = $(V_{TDA} + V_{TDEN} + (V_{SUBC} + ((V_{GRAM} + V_{FORB})/2) + ((V_{NNAG} + V_{CWD})/2)))/3$.

Variables	Unaltered Wet Pine Flat (site #10)		Jetport Site Before Impact		Jetport Site After Impact		Agricultural Field Before Restoration		Agricultural Field After Restoration		Pine Plantation Before Restoration		Pine Plantation After Restoration	
	Raw	Index	Raw	Index	Raw	Index	Raw	Index	Raw	Index	Raw	Index	Raw	Index
V_{TDA}^1	0.28	1.0	0.25	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.22	0.8	0.28	1.0
V_{TDEN}^1	244	1.0	286	1.0	0.0	0.0	0.0	0.0	0.0	0.0	403	0.5	185	1.0
V_{SUBC}^1	12,550	1.0	13,314	1.0	0.0	0.0	0.0	0.0	6,963	0.5	18,402	0.5	9,800	0.8
V_{GRAM}^1	66.8	1.0	4.7	0.1	0.0	0.0	0.0	0.0	69.0	1.0	30.0	0.4	70.0	1.0
V_{FORB}^1	33.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	20.5	0.6	2.8	0.1	20.5	0.6
V_{NNAG}^1	8.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.0	1.0
V_{CWD}^1	2.07	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.77	0.8	3.0	1.0
Function index:		1.0		0.75		0.0		0.0		0.14		0.56		0.96

Analysis of alternatives:

Jetport impact¹: 0.0 minus 0.75 = -0.75 (reduction)

Restoration impact to PC cropland¹: 0.14 minus 0.0 = 0.14 (increase)

Compensation ratio²: (0.75/0.14) = 5.4:1

Restoration impact to pine plantation¹: 0.96 minus 0.56 = 0.40 (increase)

Compensation ratio²: (0.75/0.40) = 1.9:1

¹ Change in function = post-impact index minus pre-impact index.

² Required compensatory mitigation ratio = function reduced by jetport construction/function increase five years after initiating restoration.

signed to achieve compensatory mitigation within five years.

We do not provide mitigation specifications such as the number of trees to plant, performance standards on survivorship, or achievement of short-term project targets in any regulatory context. Rather, we assumed that if appropriate specifications were met, the restoration would thereafter progress toward the reference standard condition with natural succession and continued fire management. The two compensatory mitigation options compared were (1) restoration using a wet flat converted to agricultural production (site 20) and (2) restoration using a wet flat converted to a loblolly pine plantation (site 5).

Agricultural Field. Agricultural fields typically function poorly with respect to most wetland functions. Data for the hypothetical agricultural field to which we applied our alternatives analysis are typical for cropland in southeastern North Carolina. These fields have a relatively smooth surface (no microtopographic complexity), no litter layer, no vegetation, no coarse woody debris, and are effectively drained by dense networks of ditches. Therefore, all functions would score zero prior to initiating restoration (Tables 2 and 3).

Restoring a converted agricultural field to a natural wet pine flat would require plugging or otherwise rendering ditches incapable of removing water, creating

microtopographic complexity similar to the relatively unaltered wet pine flat, planting longleaf and pond pine at a density sufficient to achieve a vegetative composition similar to reference standards at maturity, and instituting appropriate long-term fire-management. Values used to predict conditions five years after initiating restoration were based on field data from a five-year-old loblolly pine plantation (site 2) that was an altered natural wet flat, except that management during restoration would be for longleaf and pond pine rather than for loblolly pine. Increases in functions anticipated from conducting the above restoration were predicted to range from 0.14 to 0.71 five years after initiating restoration (Tables 4--7).

The hydrologic function (Table 4) would be expected to show the greatest increase (0.71) at the agricultural field site after five years. This increase in functioning would primarily be achieved by restoring natural drainage to the site (i.e., the V_{DTC} variable would increase from 0.0 to 1.0). Therefore, our assessment shows that restoring natural drainage at the agricultural field site would compensate for the reduction in the hydrologic function caused by removing vegetation (transpiration variables) at the jetport site. This means that to compensate for the reduction in the hydrologic function at the jetport site, one unit of land would have to be restored for each unit of land impacted by construction (compensatory mitigation ratio

= degree to which a function is reduced by jetport construction/degree to which a function is increased by year 5 after initiating restoration = $0.71/0.71 = 1.0$, ratio = 1:1). Of course, this ratio (1:1) assumes that all restoration objectives will be met as outlined above.

The nutrient cycling function (Table 5) was expected to increase by 0.27, primarily because appropriate vegetation would be established and a fire regime favoring graminoids would be initiated. However, neither living nor dead components of nutrient pools would be sufficiently developed in an agricultural field (based on site 2 data) to achieve reference standards by year 5. Therefore, at least 1.9 units of the agricultural field site would have to be allocated to restoration for every unit impacted by jetport construction ($0.51/0.27 = 1.9$) to compensate for the expected reduction in nutrient cycling. This means that 1.9:1 is the minimum compensatory mitigation ratio needed to meet a no-net-loss in function objective for nutrient cycling.

The plant community function (Table 6) was expected to increase by 0.30 after five years because the site would be revegetated with appropriate species and a fire regime would be established to encourage the appropriate cover of graminoids and fire-adapted forbs. Even this modest increase in the plant community function would compensate for the expected reduction in function anticipated from construction because the jetport site functioned so poorly prior to its alteration (0.15). This means that in order to compensate for the reduction in plant community function caused by jetport construction, restoration would have to be performed on one half unit of agricultural field for each unit of the jetport site impacted ($0.15/0.30 = 0.50$, ratio = 0.5:1).

The physiognomic structure function (Table 7) would be expected to increase by 0.14 five years after initiating restoration. We expected that this function would show the smallest increase, primarily because tree diameter, tree density, snag density, and CWD volume could not be restored within five years at an agricultural site (thus, all variables would be expected to score 0.0). Based on site 2 data, only forb and graminoid cover and subcanopy density would be expected to show any increase. Because the jetport site was a 50-year-old pine plantation, it had sufficient canopy structure to score relatively high (0.75) for this habitat function prior to impact. Thus, we anticipated a substantial reduction in the habitat function (0.75) due to jetport construction and a minimal increase in the function (0.14) five years after initiating restoration at the agricultural field. This means that one would have to allocate 5.4 times as much area to restoration as that impacted by jetport construction ($0.75/0.14 = 5.4$, ratio = 5.4:1) to compensate for the reduction in habitat function anticipated from construction.

The above analysis shows that compensatory mitigation ratios required to meet no-net-loss objectives differ for each function. This is partly due to the magnitude to which each function occurred at the project site before impact and partly due to the inability of an agricultural field to recover functions (relative to reference standards) within five years. Assuming restoration is successful, we expect that all functions would achieve reference standards (1.0) after about 60 years. However, after initiating restoration at an agricultural site, we do not expect any functions that depend on the presence of mature canopy trees to function anywhere near those of relatively unaltered sites after only five years. That is why the hydrologic function scored high relative to the other functions; it is more dependent on the absence of drainage than the presence of canopy trees.

26-Year-Old Pine Plantation. Function indices in the 26-year-old loblolly pine plantation (site 5) considered for restoration in this study ranged from 0.16 to 0.64 prior to initiating restoration (Tables 4–7). The 26-year-old pine plantation seemed to function at a magnitude comparable to the project or jetport site (50-year-old pine plantation), except for the physiognomic structure function. The younger pine plantation functions less effectively in maintaining characteristic structure (Index = 0.56 vs. 0.75) because it had smaller and higher density of trees than the older pine plantation and it entirely lacked CWD.

Restoring site 5 to a natural wet pine flat would require rendering nearby ditches incapable of removing water, culling small-diameter pines to open the canopy, creating a mosaic of open space and thinned loblolly stands to mimic patchiness in relatively unaltered longleaf pine wet flats, planting longleaf and pond pine seedlings in openings at a density sufficient to reach reference standards at maturity, planting wiregrass, creating appropriate microtopographic complexity (at reference standard magnitude) for surface water storage, creating snags in the appropriate density by girdling some pines, creating an appropriate volume of CWD, and initiating long-term fire management. Increases in functions anticipated from conducting the above restoration were predicted to range from 0.27 to 0.40 after five years (Tables 4–7).

The hydrologic function (Table 4) was predicted to show the least increase ($0.91 - 0.64 = 0.27$) even though natural drainage would be restored (V_{DTC} improved from 0.5 to 1.0). This is because some canopy trees would have to be removed to plant longleaf and pond pine (thus reducing the V_{TREE} index from 1.0 to 0.7), a condition that would adversely alter site hydrology by reducing transpiration. In addition, only minimal change could be obtained by restoring sub-

canopy density (V_{SUBC} from 0.8 to 1.0). Because hydrologic improvement would be minimal, 2.6 units of pine plantation would have to be allocated to restoring the hydrologic function to site 5 for every unit of jetport constructed ($0.71/0.27 = 2.6$, ratio = 2.6:1).

The nutrient cycling function (Table 5) was expected to show an increase of 0.37 (0.91–0.54) after five years, about half the decline in the function anticipated from jetport construction. This small increase in the cycling function is based on our prediction that (1) canopy basal area for the stand would decline in response to culling trees to plant longleaf and pond pine, (2) because litter depth was already equivalent to the reference standard, it could not be improved, (3) CWD and snags could be increased to reference standards by selectively felling trees, and (4) herbaceous, subcanopy, and seedling cover could be increased by planting and managing the site with fire. Therefore, 1.4 units of pine plantation would have to be allocated to restoration to compensate for the reduction in this function due to jetport construction ($0.51/0.37 = 1.4$, ratio = 1.4:1).

The plant community function (Table 6) was predicted to realize a 0.34 (0.50–0.16) increase after five years. This prediction is based on the assumption that characteristic graminoid and herb cover could be completely restored through planting and by managing the site with fire, and that subcanopy composition could be restored rapidly (most characteristic subcanopy species are present in pine plantations, although their relative proportions vary). Canopy composition was predicted to be only 0.1 that of reference standard after five years because planted longleaf and pond pine would still be too small to meet our minimum 10-cm-dbh size definition for trees.

The predicted 0.34 increase in the plant community function is slightly more than twice the reduction in function (0.15) anticipated from jetport construction. Therefore, restoration of only 0.4 unit to natural wet pine flat would be required at site 5 to compensate for this reduction in function. Even this marginal increase in the function would compensate for the jetport impact because the function was operating at a low level at the jetport prior to impact (i.e., its composition was not very similar to natural wet pine flats).

The physiognomic structure function (Table 7) was predicted to approach the reference standard (0.96) within five years after initiating restoration, thus realizing a moderate (0.40) increase ($0.96 - 0.56 = 0.40$). However, because jetport impacts would lead to a large reduction (0.75) in this function, 1.9 units of land would have to be allocated to restoration for every unit of land negatively impacted by jetport construction ($0.75/0.40 = 1.9$, ratio = 1.9:1).

Note that five years after initiating restoration, the

hydrologic, nutrient cycling, and physiognomic structure functions would all be expected to be operating near reference standards (indices = 0.91 to 0.96); i.e., we expect that they would function similarly to relatively unaltered wet pine flats. The nutrient cycling and physiognomic structure functions would be similar to reference standards because many of the components (trees, CWD, snags) driving those functions would already have been in place before initiating restoration and restoration of these parameters could be achieved relatively quickly by just manipulating the site. Only plant-community composition would be expected to function at a low level relative to the unaltered condition, primarily because the planted longleaf and pond pines would require decades to grow to maturity. Only at maturity would canopy composition be expected to achieve reference standard.

In comparing the potential of the two restoration options to compensate for jetport impacts, we see that both options would require roughly the same amount of land to restore the nutrient cycling and plant community functions. By applying restoration to an agricultural field, less land would be required to restore the hydrologic function and more land to restore the physiognomic structure function than would be required using the 26-year-old pine plantation as a restoration site. However, applying restoration to the pine plantation would bring all functions closer to reference standards in the shortest period of time, particularly the physiognomic structure function.

DISCUSSION

In approaching assessment from an ecosystem perspective, one can determine how alterations affect ecosystem processes and what has to be done to restore an altered wetland to a fully functioning, self-sustaining ecosystem. For example, lack of coarse woody debris (CWD) and snags in pine plantations results from intensive extraction of those sites for timber; trees never have a chance to grow old, die, and decompose. Moreover, harvesting results in the export of elements that would otherwise remain on site at reference standard levels. Therefore, pine plantations do not function at recycling nutrients in a manner characteristic of relatively unaltered wet pine flats. Measures of CWD and snags are useful for assessing the relative degree to which cycling processes have been altered and provide guidance on what can be done to restore the decomposing portion of the nutrient pool to conditions existing in intact wet pine flats.

The two restoration options we discussed in this study (applying restoration to an agricultural field and to a loblolly pine plantation) show how important it is to assess several functions in an ecosystem. Five years

after initiating restoration, the agricultural field site would not be expected to show much structural resemblance to a relatively unaltered wet pine flat (physiognomic structure function index = 0.14); however, by manipulating the physiognomy of the loblolly pine site, its functions could be restored to levels indicative of the relatively unaltered wet pine flat (index = 0.96) within only 5 years. This is because the site already had a 26-year-old forest on it that possessed structure (Index = 0.56) that would take the agricultural field 26 years to achieve. If we had failed to assess the physiognomic structure function, we would have missed an important piece of the ecological picture of the system and our assessment of project and restoration impacts would have been deficient.

Although the ultimate goal of restoration set forth in the HGM approach is to achieve reference standards for all functions, no restoration project is likely to restore all functions at the same rate (as shown by differing restoration impacts in Tables 4–7), nor would any given function be restored at the same rate among competing restoration alternatives (as shown by differences between the two restoration alternatives discussed in this paper). That is why compensatory mitigation ratios required to achieve a no-net-loss-in-function objective vary among the four functions and the two restoration alternatives used for illustration in this study.

Another issue that affects a no-net-loss-in-function objective is the loss of functions expected between the time a project is initiated and the point at which compensatory mitigation is achieved (defined as year 5 in our study). Loss of functions usually occurs immediately after a project is initiated; recovery of functions usually progresses gradually over time. Therefore, unless restoration is initiated prior to project impacts (in the above scenario, five years earlier), increases in function would fail to compensate for reductions in functioning accrued between project impact and assessment of the restoration site. However, this loss may be compensated over the long term because functions would continue to increase in magnitude from time of initial post-restoration assessment (year 5) to ecosystem maturity, at which time reference standards would be achieved. This is particularly true for forested wetlands, for which succession to maturity occurs over many decades.

Because restoration ratios do not dictate specific actions, all the above issues should be considered when negotiating for an appropriate compensatory mitigation ratio for a specific restoration project or in setting regional policy. For example, if water quality is given priority, then one might choose restoration sites that maximize the recovery of hydrologic functions in the shortest time. However, if recovery of endangered spe-

cies habitat is assigned priority, then one might choose a restoration alternative that would lead to recovery of habitat-related functions in the shortest time. In any case, the main objective of HGM assessment is to restore wetland ecosystems, not individual functions.

In summary, the HGM assessment procedure applies basic knowledge of ecosystems to rapidly assess wetland functions. It was designed as a tool to improve the application of science to the management of wetland resources. The key element of the HGM procedure is that all model variables are indexed relative to standards derived from intact natural ecosystems of the appropriate regional HGM-type, the assumption being that mature, relatively unaltered ecosystems function at a magnitude that is sustainable in the absence of severe perturbation. In doing this, direct measurements of ecological processes need not be measured; one only needs to measure field parameters controlled by such processes. Using metrics from intact ecosystems also provides standards for restoring wetland ecosystems; it therefore requires that ecosystems, not just individual functions, be restored.

ACKNOWLEDGMENTS

This manuscript was developed, prepared, and produced by the authors with support and funding from a number of sources including the U.S. Army Engineer Waterways Experiment Station (DACW39-93-K-0023), the U.S. Environmental Protection Agency (3-B0978NTEX and X994884-95-0), the North Carolina Division of Coastal Management (F3078), and the Division of Environmental Management (J-3054) of the North Carolina Department of Environment, Health, and Natural Resources. We thank the following for assisting with various phases of field work and data management: John Russell, Dawn Cahoon, Laura Stavovich, Veronica Lance, and Joseph Hmielewski. Reviewers of previous drafts included Lyndon C. Lee, Linda Ellis, Dennis Whigham, R. Daniel Smith, Cherri Smith, John Dorney, Ron Ferrell, and at least four anonymous reviewers.

LITERATURE CITED

- Abrahamson, W.G. and D.C. Hartnett. 1990. Pine flatwoods and dry prairies. p. 103–149. *In* R.L. Myers and J.J. Ewel (eds.) *Ecosystems of Florida*. University of Central Florida Press, Orlando, FL, USA.
- Allen, P.H. 1960. Scorch and mortality after a summer burn in loblolly pine. *Fire Control Notes* 21:124.
- Ashe, W.W. 1894. The forests, forest lands, and forest products of eastern North Carolina. *North Carolina Geologic Survey* 5:1–128.
- Ashe, W.W. 1915. Loblolly or North Carolina pine. *North Carolina Geologic Survey and Economic Survey* 24:1–176.
- Barbour, M.G., J.H. Burk, and W.D. Pitts. 1980. *Terrestrial Plant Ecology*. Benjamin/Cummings Publishing Company, Menlo Park, CA, USA.

- Bartram, W. 1791 (1955). *Travels Through North and South Carolina, Georgia, East and West Florida*. Dover Publications Reprint, New York, NY, USA.
- Braun, E.L. 1950. *Deciduous Forests of Eastern North America*. Hafner Publishing, New York, NY, USA.
- Bridges, E.L. and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf coastal plain. *Natural Areas Journal* 9:246-263.
- Brinson, M. M. and R.D. Rheinhardt. 1996. The role of reference wetlands in functional assessment and mitigation. *Ecological Applications* 6:69-76.
- Brinson, M.M. 1991. Landscape properties of pocosins and associated wetlands. *Wetlands* 11:441-465.
- Brinson, M. M. 1993. A hydrogeomorphic classification for wetlands. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. Wetlands Research Program Technical Report WRP-DE-4.
- Brinson, M.M., E. R. Hauer, L. C. Lee, W. L. Nutter, R. D. Rheinhardt, R. D. Smith, and D. Whigham. 1995. A guidebook for application of hydrogeomorphic assessments to riverine wetlands. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. Wetlands Research Program Technical Report WRP-DE-11.
- Burns, R.M. and B.H. Honkala. 1990. *Silvics of North America*. Volume 1, Conifers. United States Department of Agriculture Forest Service, Washington, DC, USA. *Agricultural Handbook* 654.
- Campbell, R.G. and J.D. Hughes. 1991. Impact of forestry operations on pocosins and associated wetlands. *Wetlands* 11:467-480.
- Chapman, H.H. 1932. Is the longleaf type a climax? *Ecology* 13:328-334.
- Christensen, N.L. 1977. Fire and soil-plant relations in a pine-wiregrass savanna on the coastal plain of North Carolina. *Oecologia* 31:27-44.
- 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. Reiners (eds.) *Fire Regimes and Ecosystem Properties*. United States Department of Agriculture Forest Service, Washington, DC, USA. General Technical Report WO-26.
- Christensen, N.L. 1987. The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of the southeastern United States. p. 1-22. *In* L. Trabaud (ed.) *The Role of Fire in Ecological Systems*. SPB Academic Publishing, The Hague, the Netherlands.
- Christensen, N.L. 1988. Vegetation of the southeastern coastal plain. p. 317-363. *In* M.G. Barbour and W. D. Billings (eds.) *North American Terrestrial Vegetation*. Cambridge University Press, New York, NY, USA.
- Copeyon, C.K. 1990. A technique for constructing cavities for the red-cockaded woodpecker. *Wildlife Society Bulletin* 18:303-311.
- Daniel, C.C. 1981. Hydrology, geology and soils of pocosins: a comparison of natural and altered systems. p. 69-108. *In* C. J. Richardson (ed.) *Pocosin Wetlands*. Hutchinson Ross Publishing Co., Stroudsburg, PA, USA.
- Daubenmire, R. 1968. *Plant Communities: a Textbook of Plant Synecology*. Harper and Row Publishers, New York, NY, USA.
- Frost, C.C., J. Walker, and R.K. Peet. 1986. Fire dependent savannas and prairies of the southeast: original extent, preservation status, and management problems. p. 348-357. *In* D.L. Kulhavy and R. N. Conner (eds.) *Proceedings of a Symposium: Wilderness and Natural Areas in the Eastern United States*. Center for Applied Studies, School of Forestry, Stephen F. Austin State University, Nacogdoches, TX, USA.
- Garren, K.H. 1943. Effects of fire on vegetation of the southeastern United States. *Botanical Review* 9:617-654.
- Grosenbaugh, L.R. 1952. Plotless timber estimates—new, fast, easy. *Journal of Forestry* 50:32-37.
- Heath, R.C. 1975. Hydrology of the Albemarle-Pamlico region, North Carolina—A preliminary report on the impact of agricultural developments. United States Geological Survey Water-Resources Investigation 9-75.
- Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. p. 7-57. *In* H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.) *Fire Regimes and Ecosystem Properties*. United States Department of Agriculture Forest Service, Washington, DC, USA. General Technical Report WO-26.
- Heyward, E. 1939. The relation of fire to stand composition of longleaf pine forests. *Ecology* 20:287-304.
- Hill, M.O. 1979. DECORANA: a FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging. Section of Ecology and Systematics, Cornell University, Ithaca, NY, USA.
- Hill, M.O. and H.G. Gauch, Jr. 1980. Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- Komarek, E. V., Sr. 1964. The natural history of lightning. *Proceedings of the Tall Timbers Fire Ecology Conference* 3:139-183.
- Komarek, E.V., Sr. 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. p. 251-278. *In* T.T. Kowalski and C.E. Ahlgren (eds.) *Fire and Ecosystems*. Academic Press, New York, NY, USA.
- Lindsey, A.A., J.D. Barton, and S.R. Miles. 1958. Field efficiencies of forest sampling methods. *Ecology* 39:428-444.
- Lemon, P.C. 1949. Successional responses of herbs in the longleaf-slash pine forest after fire. *Ecology* 30:135-145.
- MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594-598.
- McNab, W.H. 1977. An overcrowded loblolly pine stand thinned with fire. *Southern Journal of Applied Forestry* 1:24.
- Mulholland, P.J. and E.J. Kuenzler. 1979. Organic carbon export from upland and forested wetland watersheds. *Limnology and Oceanography* 24:960-966.
- Perry, D.A. 1994. *Forest Ecosystems*. John Hopkins University Press, Baltimore, MD, USA.
- Pinchot, G. and W.W. Ashe. 1897. *Timber trees and forests of North Carolina*. North Carolina Geological Survey 6:1-227.
- Platt, W.J., G.W. Evans, and S.L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *The American Naturalist* 131:491-525.
- Pomeroy, K.B. and J.G. Yoho. 1964. *North Carolina Lands*. The American Forestry Association, Washington, DC, USA.
- Quarterman, E. and C. Keever. 1962. Southern mixed hardwood forest: climax in the southeastern coastal plain, U.S.A. *Ecological Monographs* 32:167-185.
- Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. The University of North Carolina Press, Chapel Hill, NC, USA.
- Schwarz, G.F. 1907. *The Longleaf Pine in Virgin Forest, a Silvical Study*. John Wiley and Sons, New York, NY, USA.
- Skaggs, R.W., J.W. Gilliam, T.J. Sheets, and J.S. Barnes. 1980. Effect of agricultural land development on drainage waters in the North Carolina Tidewater Region. Water Resources Research Institute of the University of North Carolina, Raleigh, NC, USA. Report Number 159.
- Smith, R.D., A. Ammann, C. Bartoldus, and M. M. Brinson. 1995. A approach for assessing wetland functions using hydrogeomorphic classification, reference wetlands, and functional indices. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. Wetlands Research Program Technical Report WRP-DE-9.
- Streng, D.R. and P.A. Harcombe. 1982. Why don't east Texas savannah grow up to forests? *American Midland Naturalist* 108:278-293.
- Stout, I.J. and W.R. Marion. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. p. 373-446. *In* W. H. Martin, S. G. Boyce, and A. C. Echternacht (eds.) *Biodiversity of the Southeast: Lowland Terrestrial Communities*. John Wiley and Sons, Inc., New York, NY, USA.
- Ter Braak, C.J.F. 1988. CANOCO: a FORTRAN program for Canonical Community Ordination by partial canonical correspondence analysis, Principle Components Analysis, and Redundancy Analysis (version 3.1). Agricultural Mathematics Group, Wageningen, The Netherlands.
- Van Balen, J.B. and P.D. Doerr. 1978. The relationship of understory vegetation to red-cockaded woodpecker activity. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 32:89-92.
- Villarrubia, C.H. and J.L. Chambers. 1978. Fire: its effects on

- growth and survival of loblolly pine, *Pinus taeda* L. Louisiana Academy of Sciences 41:85-93.
- Walker, J. and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55:163-179.
- Ware, S. A., C. Frost, and P.D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. p. 447-493. *In* W. H. Martin, S. G. Boyce, and A. C. Echternacht (eds.) *Biodiversity of the Southeast: Lowland Terrestrial Communities*. John Wiley and Sons, Inc., New York, NY, USA.
- Wells, B.W. 1928. Plant communities of the coastal plain of North Carolina and their successional relations. *Ecology* 9:230-242.
- Wells, B.W. 1932. *The Natural Gardens of North Carolina*. The University of North Carolina Press, Chapel Hill, NC, USA.
- Wells, B.W. 1942. Ecological problems of the southeastern United States coastal plain. *Botanical Review* 8:533-561.
- Wells, B.W. and L.A. Whitford. 1976. History of stream-head swamp forests, pocosins, and savannas in the southeast. *Journal of the Elisha Mitchell Scientific Society* 92:148-150.

Manuscript received 26 January 1996; revisions received 19 September 1996, 17 December 1996; accepted 27 January 1997.

