Journal of the Torrey Botanical Society 132(1), 2005, pp. 72–89

Changes in plant species composition along an elevation gradient in an old-growth bottomland hardwood-*Pinus taeda* forest in southern Arkansas[1]

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GRELL, A. G. (Arkansas Forest Resources Center, School of Forest Resources, University of Arkansas-Monticello, Monticello, AR 71656-3468), M. G. SHELTON (USDA Forest Service, Southern Research Station, Monticello, AR 71656-3516), AND E. HEITZMAN (Arkansas Forest Resources Center, School of Forest Resources, University of Arkansas-Monticello, Monticello, AR 71656-3468). Changes in plant species composition along an elevation gradient in an old-growth bottomland hardwood-*Pinus taeda* forest in southern Arkansas. J. Torrey Bot. Soc. 132: 72–89. 2005.—Old-growth bottomland hardwood-*Pinus taeda* L. forests are rare in Arkansas, and the complex relationships between plant communities and environmental conditions have not been well described in these forests. To investigate these relationships, a digital elevation model was developed for a 16.2 ha old-growth bottomland hardwood-*Pinus taeda* forest in southern Arkansas. Overstory trees, saplings, seedlings, and herbaceous plants were analyzed in three 0.5 m elevation classes and by using indirect gradient analysis. Information was also collected on site factors (canopy cover, forest floor litter cover, and elevation), soil physical factors (bulk density and soil texture), soil moisture, and soil chemical factors (pH, electrical conductivity, organic matter, N, P, K, Ca, Mg, S, Fe, Mn, Zn, Cu, and Na). Importance values for 35% of seedling species, 30% of overstory species, 22% of herbaceous species, and 8% of sapling species differed significantly by elevation class. Significant differences by elevation in species diversity, richness, and evenness were identified in the seedling stratum, while only sapling evenness differed by elevation. Seventy-four percent of the environmental characteristics produced significant differences by elevation except for soil texture (sand, silt, and clay), September soil moisture content, Mn, and Cu. Seventy percent of environmental variables were significantly correlated with elevation. Dominant environmental influences on species composition in all strata included elevation as well as many other correlated variables such as Fe, forest floor litter cover, bulk density, and Na. Results from this study suggest that differences in vegetation were primarily the result of subtle elevational variations. Restoration or management of these forests should carefully consider microtopographical influences.

Key words: direct gradient analysis, forest ecosystems, indirect gradient analysis, vegetation-microtopography relationships, ordination.

Researchers have given considerable attention to the distribution of plant communities within bottomland hardwood forests (BHF), which are undergoing a rapid reduction in area in the southern United States. Most studies that characterize the distribution of BHF vegetation along elevation gradients typically involve only woody vegetation (Gemborys and Hodgkins 1971, Bell and del Moral 1977, Bell 1980, Huenneke and Sharitz 1986, Nixon et al. 1987, Titus 1990), or only non-woody vegetation (Barnes 1978, Menges and Waller 1983). However, few studies have examined the effects of elevation and other environmental variables on the distributions of both woody and non-woody plant communities (Wikum and Wali 1974, Hutchinson et al. 1999), and even fewer have investigated these relationships in BHF old-growth forests (Robertson et al. 1978).

[1] The authors thank Potlatch Corporation, Arkansas Natural Heritage Commission, Arkansas Forest Resources Center, and USDA Forest Service, Southern Research Station for supporting our research at the Lost Forty.

[2] We would like to acknowledge Julie Bowen, Jeff Earl, Ray Galloway, Natasha Gibson, David Higgins, and Michael Marter for providing excellent field assistance. This manuscript has greatly benefited from suggestions offered by Robert Weih, Eric Sundell, and two anonymous reviewers.

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Received for publication June 21, 2003, and in revised form September 9, 2004.

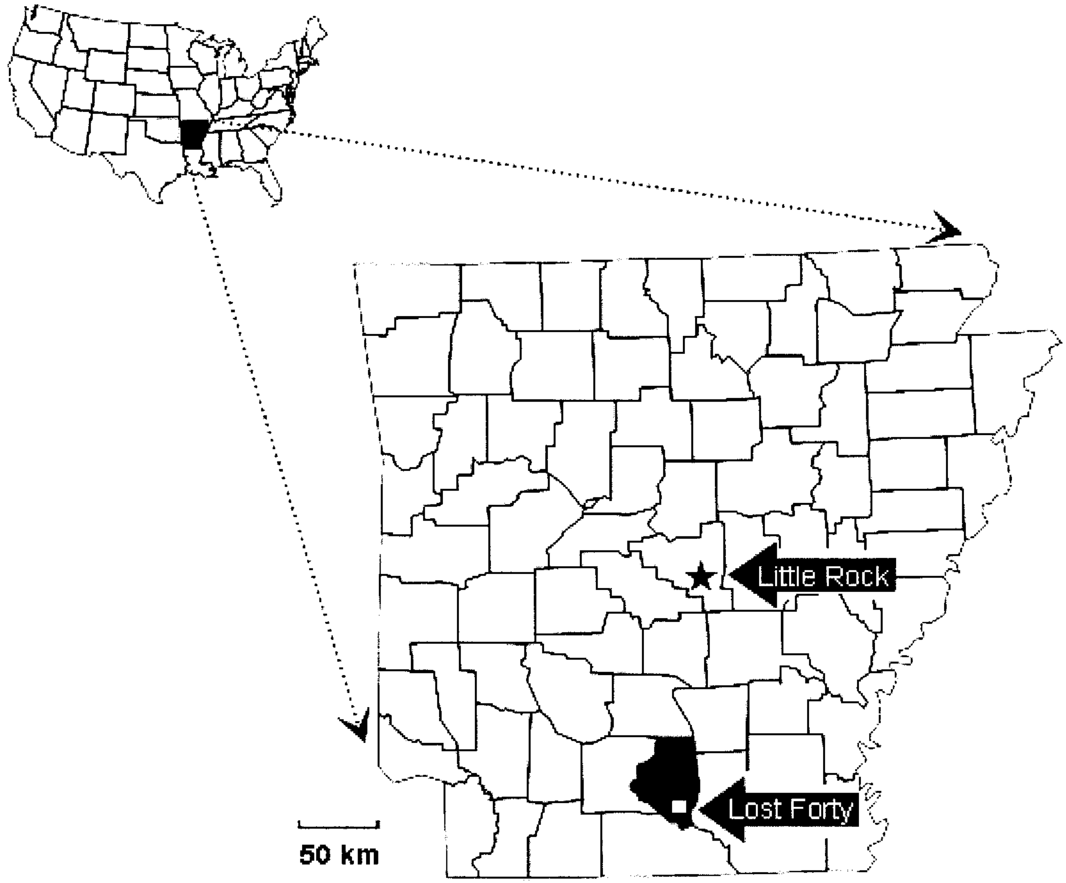

Figure 1. Location of the Lost Forty in Calhoun County, Arkansas.

In Arkansas, older and relatively undisturbed BHF communities are rare. Where they occur, they provide excellent opportunities to observe and study plant distributions. One such community is the ''Lost Forty'', a 16.2 ha old-growth mixed bottomland hardwood-*Pinus taeda* L. forest located in southern Arkansas that is characterized by distinct microtopographical features (e.g., ridges, flats, and sloughs). Moreover, the Lost Forty is home to a diverse array of woody and non-woody plant species providing excellent opportunities for studying various influences of environmental conditions on plant distributions. This study examines if and how plant communities at the Lost Forty are influenced by changes in environmental conditions. Since considerable interest exists in the conservation and restoration of BHF, results of this research should serve as a reference for other small and fragmented southern old-growth BHF. Our objectives were: 1) to create a digital elevation model and quantify environmental characteristics of the Lost Forty, and 2) to characterize woody and non-woody vegetative communities and their relationships to environmental conditions of an old-growth BHF.

Methods. STUDY SITE. The study site is the Lost Forty, a 16.2 ha forested tract located in Calhoun County, Arkansas in the West Gulf Coastal Plain ecoregion (Fig. 1). Uncertainty surrounds how the area received its name; possibilities include its inaccessibility, uncertainty over ownership, or the fact that it was never harvested. Regardless, a sequence of owners have valued the undisturbed tract as a unique natural area and refrained from commercially harvesting it. The Lost Forty is located at 33° 22′ 58″ North and 92° 23′ 49″ West. The forest's stand structure, species composition, and age distribution have been described by Heitzman et al. (2004). Overstory vegetation consists primarily of *Pinus taeda*, *Liquidambar styraciflua* L., *Quercus* spp., and *Carya* spp. Some trees reach as tall as 46 m and are more than 200 years old. The understory and midstory are mainly *Ostrya virginiana* (Miller) K. Koch, *Carpinus caroliniana* Walter, *Ilex opaca* Aiton, and *Nyssa sylvatica* Marsh. Species most common in the seedling layer include *Quercus nigra* (L.), *Callicarpa americana* L., *Carpinus caroliniana*, *Quercus phellos* L., *Ilex opaca*, *Symplocos tinctoria* (L.) L'Her., and *Quercus michauxii* Nuttall.

Wolf Creek, the largest of several small streams that meander through the Lost Forty, is a tributary of Moro Creek. Moro Creek flows about 0.5 km west of the Lost Forty. Generally, Wolf Creek dries during the summer and autumn (June–September) and floods periodically during the winter and spring (November–May). The growing season of the study area is about 220 days. The mean annual temperature is 17 °C, and the average annual precipitation is 130 cm, with generally wet winters and dry autumns. Soils are Guyton (Typic Glossaqualfs) silt loam (frequently flooded) and Ruston (Typic Paleudults) fine sandy loam with 1% to 3% slopes (Gill et al. 1980).

Potlatch Corporation and the Arkansas Natural Heritage Commission cooperatively manage the Lost Forty. Other than about 5 to 10 large pine trees that were salvaged in the last decade, no evidence exists of harvesting in the tract.

DIGITAL ELEVATION MODEL. In November and December 2001, elevations were measured across the tract using a Topcon 6000 series Total Station® and a Tripod Data Systems® datalogger. A total of 1836 coordinates (latitude, longitude, and elevation) were collected across the study area; areas that exhibited greater topographic diversity were sampled more intensively (Grell 2003). Known coordinates were obtained at two locations near the Lost Forty using survey-grade global positioning system units to establish a baseline. All other coordinates were referenced from these known locations. To create a digital elevation model, the spline interpolation technique was employed in ArcView 3.2® Spatial Analyst™ at a cell size of 1.5 m (Environmental Systems Research Institute 1998). This method delineated five elevation classes in 0.5 m intervals. Since the lowest (≤ 27.7 m) and highest (> 29.2 m) elevation classes constituted only 5% of the total area of the Lost 40, these areas were eliminated from the analysis. Thus, the three 0.5-m elevation classes (0–0.5, > 0.5–1.0, and > 1.0–1.5) sampled were > 27.7–28.2 m (low), > 28.2–28.7 m (mid), and > 28.7–29.2 m (high) above mean sea level. The classes respectively constitute 31, 47, and 17% of the total area of the Lost Forty.

PLOT LOCATION. Using ArcView 3.2®, six 500 m^2 plots were randomly located in each of the three elevation classes. Random X and Y coordinates were selected for tentative plot location, and then all interior 1.5 m^2 cells within the tentative plot were evaluated to see if they fell within the designated elevation class. If they did, the plot location was accepted; if they did not, the plot was rotated 45° and the new set of cells evaluated. If no rotations qualified, new X and Y coordinates were selected and evaluated. This procedure was continued until six plots were randomly selected for each elevation class. Coordinates for the selected 500 m^2 plots were obtained, and subsequently established at the study site using the Topcon 6000 series Total Station®.

VEGETATION SAMPLING. In August 2002, all overstory trees (≥ 9.1 cm dbh) were tallied by species and dbh in each 500 m^2 overstory plot. Within each overstory plot, six nested 20 m^2 circular understory plots (2.54 m in radius) and six nested 4 m^2 circular ground flora plots (1.14 m in radius) were also established. In the understory plots, all saplings (≥ 1.5 cm dbh and < 9.1 cm dbh), including vines, were tallied by species and dbh in August, 2002. In the ground flora plots, all seedlings (< 1.5 cm dbh), including vines, were tallied by species in August 2002. In addition, herbaceous vegetation (non-woody and non-vine) in the ground flora plots were tallied by species and percentage cover four times during 2002 on May 5, June 19, July 9, and September 7. Botanical nomenclature and species identification followed Radford et al. (1968) and Smith (1994). Voucher specimens of herbaceous plants are on file at the University of Arkansas–Monticello herbarium.

ENVIRONMENTAL VARIABLES. In July 2002, soil samples were collected for chemical analysis and particle size analysis. These samples were collected using a 1.9 cm diameter soil probe at 10 randomly selected locations within each overstory plot. Soil cores were collected from 0–15 cm and 15–30 cm depths. In each overstory plot, all 10 soil cores were combined by depth, resulting in a total of 36 samples for the study. Samples were air dried and processed through a 2-mm sieve. Rock content (> 2 mm) was calculated on one-half of the samples and was found to be minor (< 7%). Soil samples were analyzed for total N, P, K, Ca, Mg, Na, S, Fe, Mn, and Cu concentrations as well as pH and electrical conductivity. Except for total N, all soil nutrients were analyzed using the inductance coupled plasma analysis, after a Mehlich 3 extraction (Donohue 1992). All extractions maintained a 1:10 soil to Mehlich 3 ratio. Electrical conductivity and pH were analyzed at a 1:2 soil to water ratio. Total N was determined by combustion with a LECO® CN2000 (Bremner 1996). Organic matter was estimated by weight loss on ignition in a muffle furnace at 375° C for 16 hr (Nelson and Sommers 1996). After digesting organic matter using 30% hydrogen peroxide, the Bouyoucos-hydrometer method was used for particle size analysis (Gee and Bauder 1986).

Gravimetric moisture content samples were collected using a 1.9 cm diameter soil probe at 10 randomly selected locations within each overstory plot. Soil cores were collected from 0–15 cm and 15–30 cm depths. Collection dates were May 20, July 7, and September 6, 2002 for a total of 108 samples (36 for each sampling date). To prevent moisture loss, samples were immediately sealed in metal tins after being collected. Samples were weighed before and after oven drying (24 hr at 105 °C).

A total of 72 bulk density samples were collected on June 25, 2002 using a 139 cm^3 sampler at two random locations and at two depths in each overstory plot. Weights were obtained after oven drying.

Forest floor litter and canopy coverage were quantified in each ground flora plot. Forest floor litter was ocularly estimated as the percent of leaf and woody litter covering the mineral soil in each ground flora plot on September 6, 2002. Canopy cover was estimated using a densiometer held at 1.37 m in height at each subplot on July 10, 2002.

CALCULATIONS AND DATA ANALYSIS. Depending on stratum, density (number ha^{-1}), basal area (m^2 ha^{-1}), and/or coverage (%) were calculated for each species and plot. A species' frequency of occurrence for seedlings, saplings, and herbaceous layers was the percentage of subplots within a plot that contained at least one individual of that species. For the overstory, frequency of occurrence of a species was expressed as present or absent.

Importance values (IVs) were calculated for each vegetative stratum (Curtis and MacIntosh 1951). They were calculated for each species by plot using relative values as follows: overstory (density, basal area, and frequency), saplings (density, basal area, and frequency), seedling (density and frequency), and herbaceous (cover and frequency). Measures of diversity were calculated from species IVs for each stratum by plot as described by Odum (1971). Mean elevation was calculated for each plot by averaging the elevation values for all surveyed points that fell within the plot's boundary; on average, there were four to five surveyed points per plot. In order to reduce the number of soil variables, weighted means were calculated for both depths using bulk density as the weighting factor.

Correlation coefficients among site factors (elevation, forest floor litter cover, and canopy cover), soil physical factors (bulk density, sand, silt, and clay), soil moisture, and soil chemical factors (pH, organic matter, electrical conductivity, total N, P, K, Ca, Mg, S, Fe, Mn, Zn, Cu, and Na) were computed using Pearson correlation analysis (SAS 1989).

Weighted means of soil variables, means for forest floor litter and canopy cover, IVs of vegetation data by species and stratum, diversity, richness, and evenness were analyzed by elevation class. Homogeneity of variances and normality of the data were tested using Levene's test (Levene 1960) and Shapiro-Wilks test, respectfully (SAS 1989). For this and other statistical tests, significance was accepted at $\alpha \leq 0.05$. Most of these tests indicated non-homogenous and non-normal data despite several transformations. As a result, the non-parametric Kruskal-Wallis test of group comparisons was used since it makes no assumptions about homogeneity and normality (Lehmann 1975).

Nonmetric multidimensional scaling was used to show the arrangement of sampling units and species. Vegetation data and environmental data were summarized by plot. After eliminating species occurring in $<$ 5% of the plots, each stratum was analyzed separately as the main matrices (four separate matrices) with the same environmental data, which served as the secondary matrix. Analyses used a Sorenson (Bray-Curtis) distance measure, 400 iterations, random starting coordinates, and 40 runs (McCune and Grace 2002) and were conducted using PC-ORD (McCune and Mefford 1999). Preliminary results suggested a two-dimensional solution should be used for sapling and seedling strata, while a three-dimensional solution was optimal for the overstory and herbaceous strata. However, two-dimensional solutions were conducted

Table 1. Environmental variable values and concentrations by elevation class at the Lost Forty.

Environmental variables	Elevation class[1]			*P*
	Low	Mid	High	
Site Factors				
Elevation (m)	27.97	28.40	28.88	**0.001**[2]
Canopy Cover (%)	94	98	98	**0.004**
Litter Cover (%)	34	80	90	**0.002**
Soil Physical Factors				
Bulk Density (Mg m^{-3})	1.40	1.27	1.17	**0.012**
Sand (%)	49.3	53.2	56.7	0.402
Silt (%)	26.0	24.5	22.0	0.423
Clay (%)	24.6	22.1	21.3	0.421
Soil Moisture Contents				
May 21, 2002 (%)	37.8	33.4	25.8	**0.015**
July 10, 2002 (%)	30.5	21.5	23.1	**0.008**
September 6, 2002 (%)	14.9	13.7	14.2	0.751
Soil Chemical Factors				
pH	4.64	4.73	4.89	**0.012**
Electrical Conductivity (μmho^{-1})	52.6	38.7	42.8	**0.002**
Organic Matter (%)	2.53	2.50	4.10	**0.004**
N (mg kg^{-1})	1110	1040	1710	**0.011**
P (mg kg^{-1})	9.07	5.89	10.90	**0.013**
K (mg kg^{-1})	48.1	43.2	72.8	**0.012**
Ca (mg kg^{-1})	138	73.7	76.7	**0.050**
Mg (mg kg^{-1})	55.7	27.9	22.2	**0.013**
S (mg kg^{-1})	14.0	12.8	19.1	**0.007**
Fe (mg kg^{-1})	206	146	80.4	**0.001**
Mn (mg kg^{-1})	59.8	79.3	126	0.065
Zn (mg kg^{-1})	1.92	0.92	1.06	**0.006**
Cu (mg kg^{-1})	1.85	1.47	2.01	0.081
Na (mg kg^{-1})	28.6	16.1	14.5	**0.003**

[1] Class ranges: Low > 27.7–28.2 m, Mid > 28.2–28.7 m, and High > 28.7–29.2 m.
[2] Bold numbers highlight $P \leq 0.05$.

for those layers since the third dimension provided only slight improvements (McCune et al. 1997, Grace et al. 2000). Subsequently, 10 two-dimensional ordinations were performed on each stratum, and the one with the least amount of overall stress was selected for further analysis. Most ecological community data sets have stress between 10 and 20, with values towards the lower limit being quite satisfactory for interpretation (McCune and Grace 2002). Ordination axes were rotated using the varimax method. The vectors in the ordination graphs represent the correlation between environmental variables and the ordination axes; the lines' length and direction indicate the strength and sign (positive or negative) of this relationship.

Results. ENVIRONMENTAL VARIABLES. *Differences by elevation class.* Twenty-four site and soil physical, moisture, and chemical variables were identified in the three elevation classes. Eighteen of these variables differed significantly by elevation class (Table 1). Values for canopy cover, litter cover, organic matter, pH, N, K, and S were greatest at high elevations. In contrast, maxima at low elevations occurred for bulk density, Mg, Fe, Na, Ca, and Zn. Electrical conductivity and P exhibited their lowest values in the mid-elevation class. May soil moisture content decreased with increases in elevation, but the driest soils in July were in the mid-elevation class. All three elevation classes were predominantly sand (49–57%), with 22–26% silt and 21–25% clay; textural classes were sandy clay loams and sandy loams. There was a trend for higher sand and lower silt and clay concentrations as elevation increased.

Correlations among variables. Elevation was significantly correlated with 16 environmental variables; this was the highest number of significant correlations observed for any variable (Table 2). Only soil texture, September soil moisture content, P, Ca, and Cu were not significantly correlated with elevation. Fifteen variables were significantly correlated with Na and 14 with Fe. Sodium showed significant correlations with all of the site factors, soil physical factors, and soil moisture contents as well as electrical conductivity, Ca, Mg, Fe, and Zn. Iron exhibited significant correlations with elevation, forest floor litter cover, canopy cover, bulk density, May and July soil moisture content determinations, pH, electrical conductivity, organic matter, N, K, S, and Mn. Electrical conductivity and Mg also showed many significant correlations (both with 12). The strongest correlations occurred between N and organic matter (0.97), silt and sand (-0.93), Fe and elevation (-0.91), and K and N (0.90). Variables with the least number of significant correlations included Cu (three), P (four), Mn (five), and September soil moisture content (five). Variables with positive correlation coefficients increased with increasing elevations, while those with negative correlation coefficients decreased.

DIRECT GRADIENT ANALYSIS. Twenty-three tree species were identified in the overstory (Table 3). However, only the IVs of *Acer rubrum* L., *Carpinus caroliniana*, *Ilex opaca*, *Liquidambar styraciflua*, *Nyssa sylvatica*, *Ostrya virginiana*, and *Tilia americana* L. differed significantly by elevation class. Of these species, *Liquidambar styraciflua* (26%) had the highest IV in the low-elevation class followed by *Nyssa sylvatica* (19%) and *Carpinus caroliniana* (12%). In the mid-elevation class, *Carpinus caroliniana* (20%), *Ilex opaca* (18%), *Liquidambar styraciflua* (14%), and *Nyssa sylvatica* (11%) were the most important species. In the high class, *Ilex opaca* (24%), *Ostrya virginiana* (14%), and *Liquidambar styraciflua* (7%) were the most important species. Shannon and Simpson diversity, as well as richness, increased with elevation although differences were not significant.

Twenty-four species were identified in the sapling stratum (Table 4), but only *Carpinus caroliniana* and *Ilex opaca* had IVs that differed significantly by elevation class. *Carpinus caroliniana* had the greatest IVs for the low- and mid-elevation classes (63% in each case), while *Ilex opaca* was the most important species (32%) on the high sites. Evenness was significantly different by elevation class, while diversity and richness were nonsignificant. Diversity generally increased with elevation, while richness was the greatest and evenness the least in the mid-elevation class.

Thirty-five species were identified in the seedling layer (Table 5). The IVs of 12 species were significantly different between elevation classes. These species include *Asimina triloba* (L.) Dunal, *Berchemia scandens* (Hill) K. Koch, *Callicarpa americana*, *Carya* spp., *Ilex opaca*, *Liquidambar styraciflua*, *Ostrya virginiana*, *Parthenocissus quinquefolia* (L.) Planchon, *Pueraria lobata* (Willd.) Ohwi, *Quercus michauxii*, *Quercus pagoda* (Raf.), and *Vaccinium* spp. Of these species, only *Berchemia scandens* (6%) was noteworthy in the low-elevation class. In the mid-elevations, *Vaccinium* spp. (6%), *Parthenocissus quinquefolia* (5%), *Carya* spp. (5%), and *Callicarpa americana* (4%) were relatively important species. At high elevations, *Parthenocissus quinquefolia* (15%), *Carya* spp. (7%), *Callicarpa americana* (6%), *Ostrya virginiana* (6%), and *Asimina triloba* (5%) were the most important species. Diversity, richness, and evenness increased with increases in elevation.

Twenty-eight species of herbaceous plants were identified (Table 6). *Carex* spp. dominated all elevations. However, only *Carex flaccosperma* Dewey, *Chasmanthium laxum* (L.) Yates subsp. *laxum*, *Chasmanthium laxum* (L.) Yates subsp. *sessiliflorum* (Poir.) L. Clark, *Commelina virginica* L., *Elephantopus tomentosus* L., and *Triadenum walteri* (Gmelin) Gleason had IVs that were significantly different by elevation class. Of these species, *Chasmanthium laxum* subsp. *laxum* (8%), *Triadenum walteri* (4%), and *Commelina virginica* (4%) had their highest IVs in the low-elevation class. In the mid-elevation class, *Chasmanthium laxum* subsp. *laxum* (19%), and *Carex flaccosperma* (11%) comprised a substantial amount of herbaceous vegetation. In the high class, *Chasmanthium laxum* subsp. *sessiliflorum* (17%) and *Carex flaccosperma* (17%) were the most important species. Diversity, richness, and evenness of herbaceous plants were not significantly different by elevation class.

INDIRECT GRADIENT ANALYSIS. For overstory vegetation, the two-dimensional ordination had a final stress of 13.9; Axis 1 explained 74.3% of the observed distances, while Axis 2 explained an additional 12.3% (cumulative of 84.6%). Sample plots representing the low-elevation class were clustered towards the left side of the graph, plots of the mid-elevation classes were positioned in the middle, and plots of the high-elevation class were clustered on the right (Fig. 2A). Thus, Axis 1 appeared to be associated

Table 2. Pearson correlation coefficients between environmental variables at the Lost Forty.

Variables[1]	Elev	Cacv	Licv	BD	Sand	Silt	Clay	MMC	JMC	SMC	pH	EC	OM	N
Cacv	**0.67***[2]													
Licv	**0.77***	**0.79***												
BD	**−0.72***	**−0.52**	**−0.66***											
Sand	0.42	0.39	0.42	−0.14										
Silt	−0.35	−0.35	−0.37	0.10	**−0.93***									
Clay	−0.42	−0.35	−0.37	0.15	**−0.82***	**0.55**								
MayMC	**−0.70***	−0.32	−0.45	**0.47**	**−0.52**	0.37	**0.61***							
JulyMC	**−0.57***	−0.37	−0.42	0.27	**−0.61***	**0.49**	**0.63***	**0.54**						
SeptMC	−0.17	−0.14	−0.12	−0.09	**−0.70***	0.45	**0.88***	0.36	**0.57***					
pH	**0.76***	**0.55**	**0.56**	**−0.58***	0.23	−0.20	−0.22	−0.45	−0.39	−0.17				
EC	**−0.60***	**−0.61***	**−0.57***	0.41	**−0.47**	0.32	**0.58**	0.47	**0.87***	**0.49**	−0.34			
OM	**0.72***	0.35	**0.60***	**−0.52**	0.18	−0.26	0.00	−0.34	−0.06	0.27	**0.51**	−0.04		
N	**0.63***	0.31	**0.51**	**−0.49**	0.14	−0.27	0.11	−0.21	0.05	0.35	**0.50**	0.07	**0.97***	
P	0.29	0.05	0.11	−0.16	0.38	**−0.52**	−0.05	−0.09	0.10	0.08	0.20	0.32	**0.58***	**0.67***
K	**0.58***	0.22	0.38	**−0.50**	−0.12	0.00	0.26	−0.19	0.10	0.48	**0.53**	0.08	**0.87***	**0.90***
Ca	−0.43	−0.24	−0.31	0.34	−0.33	0.16	**0.50**	**0.62***	**0.61***	0.27	0.06	**0.71***	−0.06	0.11
Mg	**−0.66***	**−0.57***	**−0.75***	0.40	**−0.64***	**0.48**	**0.70***	**0.50**	**0.63***	0.43	−0.22	**0.72***	−0.42	−0.28
S	**0.60***	0.24	0.35	−0.34	0.05	−0.12	0.06	**−0.52**	−0.03	0.25	**0.50**	−0.03	**0.69***	**0.65***
Fe	**−0.91***	**−0.59***	**−0.62***	**0.70***	−0.25	0.19	0.27	**0.64***	**0.58***	0.13	**−0.87***	**0.58***	**−0.58***	**−0.50**
Mn	**0.61***	0.47	0.33	**−0.50**	0.07	−0.09	−0.03	−0.43	−0.23	−0.04	**0.88***	−0.20	0.35	0.37
Zn	**−0.62***	**−0.65***	**−0.72***	0.33	−0.38	0.26	**0.47**	0.38	**0.55**	0.29	−0.28	**0.79***	−0.33	−0.22
Cu	0.16	0.15	0.04	−0.13	**0.50**	**−0.49**	−0.36	−0.25	−0.14	−0.22	0.14	0.11	0.06	0.10
Na	**−0.73***	**−0.63***	**−0.70***	**0.56**	**−0.66***	**0.52**	**0.69***	**0.60***	**0.79***	**0.49**	−0.45	**0.85***	−0.33	−0.22

[1] Abbreviations are: Elev = elevation; Cacv = canopy cover; Licv = forest floor litter cover; BD = bulk density; MMC = soil moisture content on May 20, 2002; JMC = soil moisture content on July 7, 2002; SMC = soil moisture content on September 6, 2002; EC = electrical conductivity; OM = organic matter.

[2] Bold indicates $P \leq 0.05$; * indicates $P \leq 0.01$.

Table 2. Continued.

Variables	P	K	Ca	Mg	S	Fe	Mn	Zn	Cu
K	0.47								
Ca	0.33	0.05							
Mg	−0.02	−0.13	**0.68***						
S	0.37	**0.77***	−0.17	−0.14					
Fe	−0.10	**−0.54**	0.37	0.44	**−0.59***				
Mn	0.13	0.43	0.09	0.06	**0.48**	**−0.80***			
Zn	−0.24	−0.12	**0.57***	**0.83***	−0.14	0.50	−0.09		
Cu	**0.64***	−0.04	0.09	−0.05	0.05	−0.06	0.14	0.31	
Na	0.08	−0.13	**0.70***	**0.86***	−0.11	**0.65***	−0.28	**0.76***	−0.07

with elevation and a host of associated variables, while Axis 2 appeared to be indicative of soil texture. Species such as *Sassafras albidum* (Nuttall) Nees, *Ulmus alata* Michaux, *Tilia americana*, *Cornus florida* L., and *Ostrya virginiana* were clustered on the right side of the graph, which was indicative of higher elevations (Fig. 2B). In contrast, *Quercus phellos*, *Taxodium distichum* L. and *Diospyros virginiana* L. were clustered on the left side of the graph, which represented lower elevations.

Multiple runs of a two-dimensional ordination for sapling vegetation produced unstable solutions, indicating that a useful ordination was not found. Thus, the ordination was not presented for this layer.

The ordination for seedling vegetation had a final stress of 11.4; Axis 1 explained 62.9% of the observed distances, while Axis 2 explained an additional 27.1% (cumulative of 90.0%). Sample plots were distributed the same as with overstory vegetation (Fig. 3A). Elevation and six other associated environmental variables were strongly related to Axis 1, while July soil moisture content and N more closely related with Axis 2. Species such as *Parthenocissus quinquefolia*, *Ostrya virginiana*, *Hamamelis virginiana* L., *Asimina triloba*, and *Carya spp*. were clustered on the right side of the graph (Fig. 3B). In contrast, *Quercus phellos*, *Brunnichia ovata* (Walt.) Shinners, *Diospyros virginiana*, and *Ilex decidua* Walter were clustered on the left side of the graph.

The two-dimensional ordination for herbaceous vegetation had a final stress of 13.8; Axis 1 explained 49.8% of the observed distances, while Axis 2 explained an additional 35.7% (cumulative of 85.5%). Sample plots representing low elevation classes were grouped on the left side of the graph, while plots representative of high elevations were clustered towards the right (Fig. 4A). Elevation, Fe, pH, Mg, and Na were strongly associated with Axis 1, while no variables were closely related to Axis 2. Species such as *Elephantopus tomentosus*, *Carex flaccosperma*, *Chasmanthium laxum* subsp. *sessiliflorum*, *Galium pilosum* Aiton, and *Oxalis dillenii* Jacq. were clustered on the right side of the graph (Fig. 4B). In contrast, *Panicum dichotomum* L., *Triadenum walteri*, and *Lycopus* sp. were clustered on the left side.

Discussion. ENVIRONMENTAL VARIABLES. Processes leading to the formation of southern bottomland hardwood forests result in differences in

Table 3. Species importance values (%) and diversity measures of overstory vegetation (≥9.1 cm dbh) by elevation class at the Lost Forty.

Species or diversity measure	Elevation class[1] Low	Mid	High	*P*
Acer rubrum	2.1	6.2	0.0	**0.05**[2]
Carpinus caroliniana	11.8	19.7	3.1	**0.02**
Carya aquatica	1.0	0.0	0.0	0.37
Carya glabra	0.0	0.0	1.8	0.37
Carya ovata	0.0	0.0	1.4	0.37
Carya tomentosa	0.0	1.6	6.5	0.09
Cornus florida	0.0	0.0	1.0	0.37
Diospyros virginiana	2.4	0.0	0.0	0.12
Ilex opaca	1.6	17.6	23.7	<**0.01**
Liquidambar styraciflua	25.7	14.3	6.7	**0.02**
Nyssa sylvatica	19.5	10.9	3.1	**0.02**
Ostrya virginiana	0.0	0.0	14.4	<**0.01**
Pinus taeda	1.3	11.7	4.9	0.10
Quercus alba	0.0	0.0	3.8	0.12
Quercus lyrata	7.1	0.0	2.1	0.12
Quercus michauxii	15.6	13.4	3.8	0.26
Quercus nigra	3.6	0.0	6.6	0.16
Quercus pagoda	0.0	3.2	3.8	0.59
Quercus phellos	4.0	0.0	0.0	0.12
Sassafras albidum	0.0	0.0	2.8	0.37
Taxodium distichum	2.8	0.0	0.0	0.12
Tilia americana	0.0	0.0	6.2	**0.04**
Ulmus alata	1.8	1.5	4.2	0.49
Shannon Diversity	1.6	1.7	2.0	0.09
Simpson Diversity	0.8	0.8	0.8	0.08
Richness	6.0	6.2	8.0	0.08
Evenness	0.9	1.0	1.0	0.07

[1] Class ranges: Low > 27.7–28.2 m, Mid > 28.2–28.7 m, and High > 28.7–29.2 m.
[2] Bold numbers highlight $P \leq 0.05$.

their hydrology, geomorphology, and soils. Large stream size, broad topographic features, and soils from regional sources are indicative of major bottoms, while smaller stream sizes, narrow topographic features, and soils of local origins are more representative of minor bottoms (Hodges 1997). Soil variations in floodplains may be pronounced, reflecting differences in relief, drainage, and depositional patterns (Hodges 1998). When streams overflow their banks, the velocity of the water slows and rapid deposition occurs. Generally, sand (or coarser material) is deposited first forming the ridges of the floodplain, which are more indicative of higher elevations. As the velocity of the water slows, silts and clays (finer material) are deposited in flats and sloughs that are more representative of lower elevated sites (Hodges 1997). At the Lost Forty, soil textural variations by elevation were not statistically significant, which may reflect the fact that it is a minor bottom. However, our results indicated a trend toward higher concentrations of sand and lower concentrations of silt and clay as elevation increased, which correspond with results from other studies (Smith 1996, Axt and Walbridge 1999, Bledsoe and Shear 2000).

We found elevation significantly correlated with more variables than any other environmental factor at the Lost Forty. The strong association between elevation and other environmental variables reflects the soil forming processes that occur in bottomlands. The depositional patterns that occur when bottomlands flood create a varied topography. These microsite conditions are influenced by elevation, substrate, and distance from the active channel (Hughes 1997). Lower elevation sites will become or remain saturated for longer periods of time than higher elevation sites. Moreover, pH is affected by saturated conditions, which in turn influences soil nutrient concentrations (Ponnamperuma 1984, Vepraskas and Faulkner 2001).

We identified many significant relationships between environmental variables at the Lost Forty; however, examples will be discussed for the major ones. The relationship between soil bulk density and organic matter is well known. Increases in organic matter are typically asso-

Table 4. Species importance values (%) and diversity measures of sapling vegetation (≥1.5 cm dbh and <9.1 cm dbh) by elevation class at the Lost Forty.

Species or diversity measure	Elevation class[1] Low	Mid	High	*P*
Acer rubrum	0.0	1.2	0.0	0.37
Asimina triloba	0.0	0.0	22.2	0.12
Berchemia scandens	4.6	0.0	0.0	0.12
Brunnichia ovata	1.8	0.0	0.0	0.37
Callicarpa americana	0.0	1.0	0.0	0.37
Carpinus caroliniana	62.9	63.1	7.3	**0.01**[2]
Cornus florida	0.0	0.0	2.4	0.37
Cornus foemina	8.0	0.0	0.0	0.37
Crataegus marshallii	0.0	1.5	0.0	0.37
Diospyros virginiana	7.5	0.0	0.0	0.37
Hamamelis virginiana	0.0	0.0	7.8	0.37
Ilex decidua	1.2	0.0	0.0	0.37
Ilex opaca	0.0	15.5	31.7	**0.02**
Liquidambar styraciflua	2.5	0.0	0.0	0.37
Nyssa sylvatica	7.0	7.0	5.6	0.95
Ostrya virginiana	0.0	2.8	11.1	0.11
Quercus lyrata	0.8	0.0	0.0	0.37
Quercus michauxii	0.0	0.8	0.0	0.37
Quercus nigra	2.2	0.0	0.0	0.37
Quercus phellos	0.8	0.0	0.0	0.37
Tilia americana	0.0	0.0	2.9	0.37
Ulmus alata	0.0	4.4	0.0	0.12
Vaccinium spp.	0.0	1.2	0.0	0.37
Vitis spp.	0.6	1.5	8.8	0.25
Shannon Diversity	0.7	1.0	1.0	0.83
Simpson Diversity	0.4	0.5	0.5	0.75
Richness	3.2	3.8	3.2	0.39
Evenness	0.9	0.7	0.9	**0.02**

[1] Class ranges: Low > 27.7–28.2 m, Mid > 28.2–28.7 m, and High > 28.7–29.2 m.
[2] Bold numbers highlight $P \leq 0.05$.

ciated with reductions in bulk density (Collins and Kuehl 2001). Although this strong relationship holds true for most bottomland studies, there have been discrepancies reported along elevational gradients (Table 7). Some studies report increasing bulk density and decreasing organic matter with elevational gains (Axt and Walbridge 1999, Burke et al. 2000). In contrast, we found bulk density to decrease and organic matter to increase with increases of elevation. The relationship between organic matter and bulk density can be attributed to the duration and intensity of flooding at the Lost Forty. There, the floods are often short-term and quickly recede with little standing water left behind. Similar to findings of Barnes (1978), these swift and strong floodwaters remove much of the annual increment of litter along the lowest elevations, but leave litter in adjacent higher elevations intact. However, bottomlands that exhibit higher organic matter contents in the lower elevations most likely experience prolonged periods of flooding and associated anaerobic conditions. These saturated conditions lead to accumulations of organic matter by slowing decomposition (Patrick 1981, Wharton et al. 1982, Stanturf and Schoenholtz 1998).

Soil organic matter also plays a significant role in determining soil N concentrations (Dunn and Stearns 1987). We observed a strong and significant relationship between organic matter and N. This is consistent with results reported from floodplains in northern Italy (Gerdol et al. 1985) and South Carolina (Burke et al. 1999).

Numerous factors affect the availability of soil nutrients in bottomland systems, but identifying these factors can be difficult due to the complex nature of bottomland soils (Mollitor et al. 1980, Peterson and Rolfe 1982). For example, Fe and Mn are usually affected similarly under variable reduced-oxygenated conditions (Vepraskas 2001). However, Fe and Mn are negatively correlated in the Lost Forty's soil. Turner and Patrick (1968) found Fe concentrations to increase with time after inundation, but found the relationship for Mn to be more complicated.

Table 5. Species importance values (%) and diversity measures of seedling vegetation (<1.5 cm dbh) by elevation class at the Lost Forty.

Species or diversity measure	Elevation class[1] Low	Mid	High	*P*
Acer rubrum	0.6	2.4	2.0	0.16
Arundinaria gigantea	2.4	1.9	0.0	0.36
Asimina triloba	0.0	0.0	5.4	**0.01**[2]
Berchemia scandens	6.4	0.5	1.2	**0.02**
Bignonia capreolata	0.7	3.0	0.7	0.30
Brunnichia ovata	9.7	0.6	0.2	0.07
Callicarpa americana	0.5	4.5	6.4	**0.03**
Carpinus caroliniana	5.6	4.7	1.4	0.19
Carya spp.	0.4	4.9	7.4	<**0.01**
Cornus foemina	1.9	0.0	0.0	0.37
Crataegus marshallii	0.5	0.0	0.0	0.37
Diospyros virginiana	3.3	0.0	0.5	0.28
Hamamelis virginiana	0.0	0.0	0.8	0.12
Ilex decidua	1.9	0.0	0.0	0.12
Ilex opaca	0.6	1.0	3.3	**0.05**
Liquidambar styraciflua	0.0	1.6	0.0	**0.04**
Nyssa sylvatica	3.3	2.1	1.1	0.54
Ostrya virginiana	0.0	0.5	5.6	<**0.01**
Parthenocissus quinquefolia	0.7	4.9	15.2	<**0.01**
Planera aquatica	0.6	0.0	0.0	0.37
Prunus serotina	0.0	0.0	0.3	0.37
Pueraria lobata	0.0	1.6	4.2	<**0.01**
Quercus lyrata	0.0	0.3	0.0	0.37
Quercus michauxii	0.0	3.1	0.6	**0.04**
Quercus nigra	10.7	4.3	6.3	0.78
Quercus pagoda	0.0	2.8	0.8	**0.04**
Quercus phellos	1.8	0.0	0.0	0.12
Rubus spp.	0.0	0.0	0.3	0.37
Smilax spp.	39.4	34.5	23.1	0.06
Taxodium distichum	0.4	0.0	0.0	0.37
Toxicodendron radicans	3.6	9.6	9.1	0.06
Trachelospermum difforme	0.6	0.0	0.0	0.37
Ulmus alata	0.0	0.2	0.0	0.37
Vaccinium spp.	1.0	5.5	0.0	**0.04**
Vitis spp.	1.6	5.5	3.2	0.09
Unknown	2.0	0.0	0.0	**0.04**
Shannon Diversity	1.7	2.1	2.3	**0.01**
Simpson Diversity	0.7	0.8	0.9	**0.01**
Richness	9.0	13.2	13.5	**0.02**
Evenness	0.8	0.8	0.9	**0.02**

[1] Class ranges: Low > 27.7–28.2 m, Mid > 28.2–28.7 m, and High > 28.7–29.2 m.
[2] Bold numbers highlight $P \leq 0.05$.

They reported exchangeable Mn increases with increased time after inundation, while easily reducible Mn decreased. Although the scope of our project was to obtain baseline concentrations of Fe and Mn at different elevations, results from Turner and Patrick (1968) indicate that this relationship is complicated and requires a more detailed investigation of the processes involved.

Reported soil chemical and physical properties from this study and other studies often show inconsistent patterns along elevational gradients in bottomlands (Wharton et al. 1982, Fuad 1995, Smith 1996, Axt and Walbridge 1999, Burke et al. 1999, Bledsoe and Shear 2000, Burke et al. 2000). We speculate that this wide variation indicates that each bottomland comprises a unique set of environmental conditions, which are most often related to the sites' flooding frequency and intensity as well as the nature of the alluvium deposited.

VEGETATION. *Environmental effects.* Bottomland vegetation is influenced by complex environmental gradients associated with flooding frequency, intensity, and duration (Bell 1974, Nixon et al. 1977, Adams and Anderson 1980, Hupp and Ostercamp 1985, Wall and Darwin 1999, Bledsoe and Shear 2000). For example,

Table 6. Species importance values (%) and diversity measures of herbaceous vegetation by elevation class at the Lost Forty.

Species or diversity measure	Elevation class[1]			P
	Low	Mid	High	
Asclepias perennis	1.0	0.0	0.0	0.12
Boehmeria cylindrica	4.2	0.0	0.0	0.37
Carex debilis	4.4	8.9	8.8	0.27
Carex festucacea	0.8	2.9	0.0	0.11
Carex flaccosperma	2.3	10.6	16.6	**0.02**[2]
Carex intumescens	7.5	9.0	2.0	0.13
Carex typhina	6.2	1.4	0.0	0.36
Carex spp.	21.7	21.5	24.0	0.83
Chasmanthium laxum subsp. *laxum*	8.1	18.5	8.8	**0.03**
Chasmanthium laxum subsp. *sessiliflorum*	0.0	0.0	16.8	<**0.01**
Commelina virginica	4.0	0.0	0.0	**0.04**
Elephantopus carolinianus	0.0	0.0	0.3	0.37
Elephantopus tomentosus	0.0	0.0	2.8	**0.04**
Galium pilosum	0.0	0.0	1.4	0.12
Justicia ovata var. *lanceolata*	1.6	0.0	0.0	0.12
Leersia lenticularis	4.0	0.0	0.0	0.12
Leersia sp. *vel aff.*	11.8	18.2	9.8	0.12
Lycopus sp. *vel aff.*	1.1	0.6	0.0	0.59
Mitchella repens	3.9	6.5	4.4	0.50
Oxalis dillenii	0.0	0.3	1.6	0.11
Panicum commutatum	2.2	1.0	0.6	0.47
Panicum dichotomum	1.5	0.6	0.0	0.33
Panicum rigidulum	0.5	0.0	0.0	0.37
Sanicula canadensis	0.0	0.0	0.6	0.37
Saururus cernuus	2.0	0.0	0.0	0.37
Triadenum walteri	4.2	0.0	0.0	**0.01**
Viola palmata	0.0	0.0	0.2	0.37
Viola sororia	3.2	0.0	1.1	0.29
Unknown	3.7	0.0	0.0	**0.01**
Shannon Diversity	2.0	2.0	2.0	0.61
Simpson Diversity	0.8	0.8	0.8	0.85
Richness	9.3	8.0	9.0	0.60
Evenness	0.9	0.9	0.9	0.56

[1] Class ranges: Low > 27.7–28.2 m, Mid > 28.2–28.7 m, and High > 28.7–29.2 m.
[2] Bold numbers highlight $P \leq 0.05$.

improved growth is often a direct benefit from dormant season flooding. Spring floods were found to provide additional water later in the growing season for various hardwood species (Broadfoot and Williston 1973). However, prolonged flooding can be detrimental to bottomland vegetation by decreasing aerobic respiration (Armstrong 1978, Osmond et al. 1987, McKevlin et al. 1998), and producing and accumulating toxic levels of ferrous Fe, nitrates, sulfides, and Mn (Broadfoot and Williston 1973).

Seedbed conditions can also affect the establishment of species. For example, Shelton (1995) reported that increases in the amount of forest floor litter reduced the establishment of woody and non-woody vegetation, indicating that establishment of most light-seeded species is favored in a mineral soil seedbed. However, our results suggest that seedbed conditions are a minor factor in species establishment at the Lost Forty. Woody seedling and herbaceous species were most prevalent in the high elevation class, which had the greatest forest floor litter cover. Thus, environmental factors, such as the direct effects of flooding on seed germination (Guo et al. 1998) or the loss of seeds due to scouring, probably exert a more dominant effect.

Although this study was limited in its geographic scope, its fine-scale approach to quantifying various environmental characteristics and relating them to species composition can provide some information for restoration efforts. This research suggests that differences in vegetation were primarily the result of subtle elevational variations. Restoration or management of bottomland hardwood forests should carefully consider microtopographical influences. Our find-

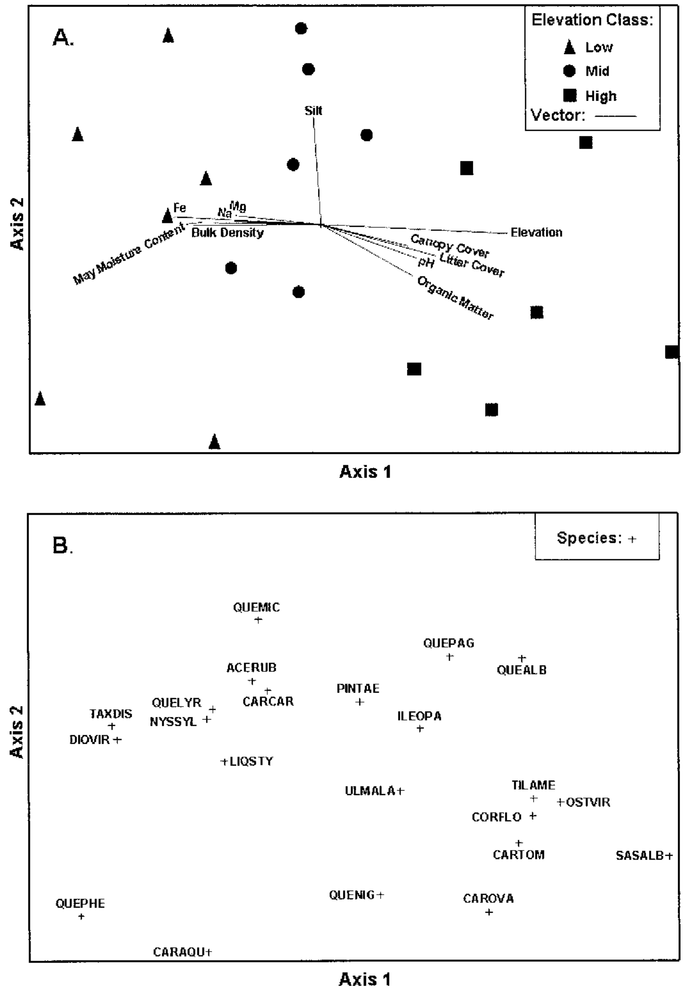

Figure 2. Ordination of (A) sampling units for overstory vegetation in the Lost Forty, including vectors (the lines originating at the graph's center) for environmental variables with $r^2 > 0.35$, and (B) species. Abbreviations for species consist of the first three letters of the genus and specific epithet as listed in Table 3.

ings from the Lost Forty indicate that species tolerant of flooding should be emphasized in lower sites and/or areas that experience annual or periodic flooding. On high sites that rarely flood, species moderately tolerant to intolerant of saturated conditions should be emphasized.

Direct gradient analysis. The importance of *Acer rubrum*, *Liquidambar styraciflua*, and *Nyssa sylvatica* in the overstory and midstory of bottomland forests among various elevations has been documented in this study and by others (Gemborys and Hodgkins 1971, Nixon et al. 1977, Nixon et al. 1987, Smith 1996, Bledsoe and Shear 2000). Additionally, researchers have found *Smilax* spp. (Bell 1974, Bledsoe and Shear 2000) and *Acer rubrum* (Bledsoe and Shear 2000) in the seedling stratum across a variety of elevations. Such species have the ability to grow in widely varied microsite conditions, which accounts for their ubiquitous occurrence (Burns and Honkala 1990).

However, some of the vegetative patterns in the Lost Forty differ from those identified in other bottomlands. For instance, Nixon et al. (1987) found *Ilex opaca* to be an important species in the low areas, and *Ostrya virginiana* important in mid-elevational sites for overstory and midstory layers in eastern Texas. Conversely, we found *Ilex opaca* to be important in the mid- to high elevations and *Ostrya virginiana* to be important in the high sites. Other research reported similar results to this study for *Ilex opaca* (Gem-

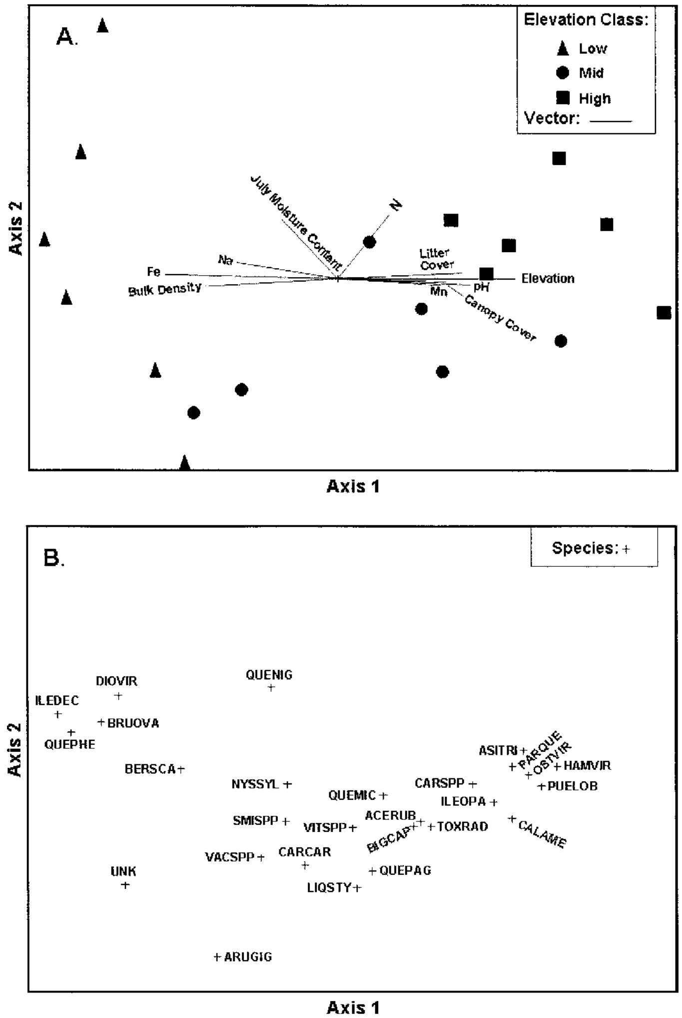

Figure 3. Ordination of (A) sampling units for seedling vegetation in the Lost Forty, including vectors (the lines originating at the graph's center) for environmental variables with $r^2 > 0.35$, and (B) species. Abbreviations for species consist of the first three letters of the genus and specific epithet as listed in Table 5.

borys and Hodgkins 1971, Bledsoe and Shear 2000), however, *Ostrya virginiana* was not reported in these studies. In the seedling layer, Bledsoe and Shear (2000) report *Liquidambar styraciflua* important across all elevations, whereas it was low in importance in the understory across all elevations at the Lost Forty.

These anomalies in the overstory, sapling, and seedling vegetative layers might reflect differences in flooding patterns and criteria for which sampling plots were established. For instance, the Lost Forty usually floods annually leaving only the ridge tops above water. In contrast, the bottomland forest described by Nixon et al. (1987) was subjected to brief periods of flooding every 2 to 5 years. Moreover, Nixon et al. (1987) established transects parallel to the creek based on landscape position alone without accurately quantifying elevation.

Because emphasis has usually been given to woody plants, little is known about how herbaceous vegetation responds to changes in elevation in bottomlands. We found *Chasmanthium laxum* subsp. *sessiliflorum* and *Carex flaccosperma* to dominate higher sites, while *Commelina virginica* and *Triadenum walteri* had their highest IVs in the lower sites. There have been a few researchers who have quantified herbaceous vegetation along similar elevation gradients. Some herbaceous species showed distinctive patterns while others did not. For example, in a study of a streamside forest in Illi-

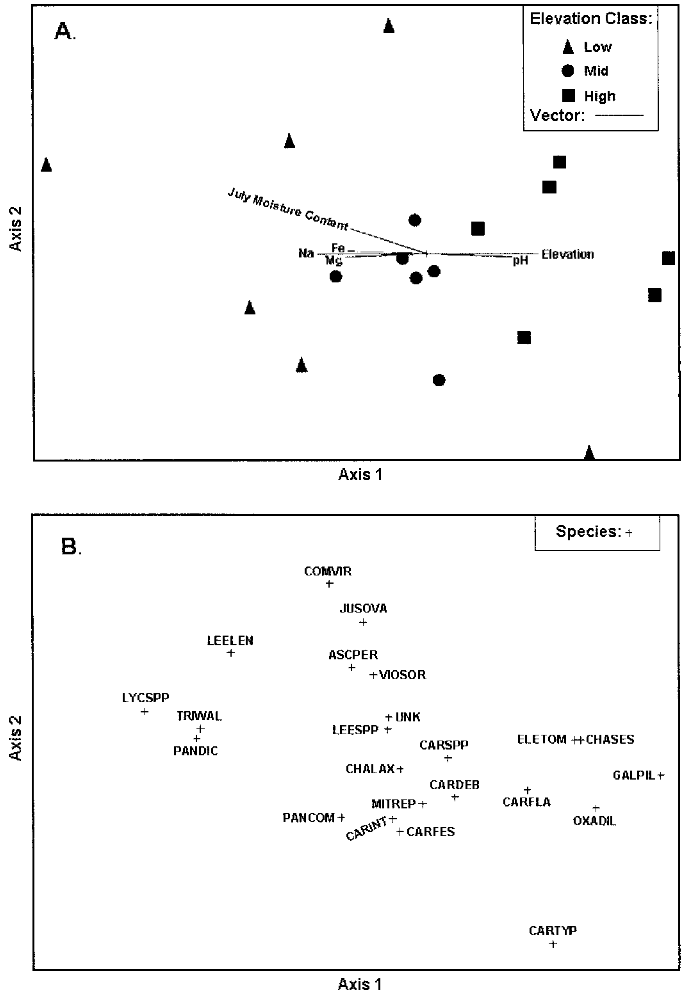

Figure 4. Ordination of (A) sampling units for herbaceous vegetation in the Lost Forty, including vectors (the lines originating at the graph's center) for environmental variables with $r^2 > 0.35$, and (B) species. Abbreviations for species consist of the first three letters of the genus and specific epithet as listed in Table 6.

nois, Bell (1974) found *Aster simplex* Willd. and *Laportea canadensis* (L.) Weddell to be the most prevalent species in lower areas, while *Impatiens pallida* Nutt. and *Erythronium albidum* Nutt. were the most abundant in high areas. Bledsoe and Shear (2000) identified *Saururus cernuus* L. as an important species in low sites, while *Mitchella repens* L. was indicative of higher sites.

Indirect gradient analysis. The variation explained by the two axes in the overstory (86.4%), seedling (90%), and herbaceous (85.5%) ordinations was much higher in this study than in others. Grace et al. (2000), studying influences of environmental conditions on vegetation in the Texas coastal tallgrass prairie, found only 42% of the variation explained by a two-dimensional ordination. McCune et al. (1997), examining lichen communities throughout southeastern United States, identified only 59% of the variation explained by a two-dimensional ordination. The considerable differences observed between our study and other studies most likely are attributed to using elevation as a criterion for randomly locating sampling plots, the small area represented by the Lost Forty, and the distinct difference in community types. Our technique assured that all cells (1.5 m) within the overstory plots were within the specified elevation class.

In contrast to other strata, no useful ordination was found for the sapling stratum. Only eight

Table 7. Soil physical and chemical characteristics of bottomland hardwood forests in the southern United States.

Author	Location	Sand (%)	Silt (%)	Clay (%)	BD[1] ($Mg\ m^{-3}$)	pH	OM[2] (%)	P ($mg\ kg^{-1}$)	K ($mg\ kg^{-1}$)	Ca ($mg\ Kg^{-1}$)	Mg ($mg\ kg^{-1}$)
Grell et al. (this publication)	Arkansas	49–57[3]	26–22	25–21	1.40–1.27	4.6–4.9	2.5–4.1	9.1–10.9	48–72	138–77	55–22
Smith (1996)	Arkansas	43–47	26–33	29–21	—	4.9–5.4	2.9–4.2	1.2–1.0	2.0–2.0	2.9–3.0	0.4–0.4
Bledsoe and Shear (2000)	North Carolina	53–73[4]	—	27–11	—	4.3–4.1	2.7–2.4	—	—	—	—
Burke et al. (1999)	South Carolina	31–79	—	50–11	—	4.8–4.5	5.5–6.0	1.1–4.2	11–48	2042–328	323–67
Burke et al. (2000)	South Carolina	—	—	—	0.88–1.34	4.7–4.6	7.1–3.0	46–71	40–23	900–227	164–64
Fuad (1995)	Virginia	53[5]	28	18	—	4.7	5.1	—	—	—	—
Axt and Walbridge (1999)	Virginia	43–71[6]	25–13	31–16	0.42–0.78	4.1–4.2	23.4–5.8	—	—	—	—
Wharton et al. (1982)	southeastern U.S.	69–74[7]	20–14	12–12	—	5.0–5.1	7.9–18.0	11–9.8	48–29	607–346	98–36

[1] BD is bulk density.
[2] OM is organic matter.
[3] Values represent low to high elevations within the bottomland.
[4] Values represent the A horizon.
[5] Values represent an average across the bottomland.
[6] Values represent soil characteristics of the top 15 cm.
[7] Value ranges represent blackwater river bottomlands in Florida, Georgia, North Carolina, and South Carolina.

species were reported for saplings after elimination of rare species. Moreover, the sapling stratum was dominated by *Carpinus caroliniana*, *Ilex opaca*, and *Nyssa sylvatica*, which accounted for 70% of the importance in the low class, 85% in the mid-elevation class, and 45% in the high class. The dominance of these species, coupled with the overall low species diversity, suggest that the sapling stratum is biologically dissimilar to the other strata across all elevations. The uniqueness of the sapling layer is also supported by the direct ordination. There were only two species with significant differences among elevation classes for saplings, compared to seven species for both overstory and herbaceous layers and 13 species for seedlings.

Results of the indirect gradient analysis generally support findings from the direct gradient analysis. For example, overstory species characteristic of higher elevations in the direct gradient analysis, such as *Tilia americana* and *Ostrya virginiana*, were found clustered together on the right side of the graph of the indirect gradient analysis, which was indicative of higher elevations. Species such as *Taxodium distichum* and *Diospyros virginiana* were clustered on the left side of the graph, which reflects lower elevations. Interestingly, environmental variables in the seedling and herbaceous ordinations revealed much weaker correlations with elevation than in the overstory ordination. Heitzman et al. (2004) propose that the closed canopy of the Lost Forty limits the successful establishment of many species in the understory, especially those that are shade intolerant. Furthermore, flood duration and frequency have been identified as the cause of mortality in ground flora layers because of saturated soil conditions (Barnes 1978, Titus 1990). While some understory plants might establish themselves in marginal microsites during periods with low flooding, mortality of these species would likely occur when major flooding resumes. Conversely, the overstory species present at the Lost Forty have survived to maturity over many years of variation in environmental conditions, which could explain the higher correlations of the environmental variables for this stratum.

Diversity. Diversity in all vegetative layers in this study was generally found to increase with elevation. This pattern was similar to that found in others studies of wetland habitats (Bell 1974, 1980, Bell and del Moral 1977, Robertson et al. 1978, Frye and Quinn 1979). Vegetation in the lower elevations is subjected to frequent and sometimes strong flooding events, which restricts successful establishment to those species highly tolerant of such conditions (Barnes 1978, Menges and Waller 1983, Titus 1990). Bell (1980) found evenness to sharply decrease with increases in elevation. However, our findings indicate that evenness is relatively uniform for all vegetative layers along the elevation gradient. This difference might be explained by the fact that Bell (1980) sampled along an elevational gradient of about 15 m whereas our gradient was only 1.5 m.

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