

VEGETATION ALONG HYDROLOGIC AND EDAPHIC GRADIENTS IN A NORTH CAROLINA COASTAL PLAIN CREEK BOTTOM AND IMPLICATIONS FOR RESTORATION

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Abstract: We described the vegetation of two alluvial swamp forest stands along Durham Creek in Beaufort County, North Carolina, USA in relation to elevation, hydrologic, and edaphic gradients. Over 3,000 surveyed elevations of individual plant microsites were used in conjunction with 26 years of stream gage data to examine individual species responses to annual and growing season flooding frequencies. Direct gradient analyses combined with plot ordinations derived from detrended correspondence analysis and canonical correspondence analysis suggested that differences in vegetation between the stands were primarily the result of variations in elevation, growing season flooding frequency, percent base saturation, exchangeable acidity, and soil physical properties. Although the stands were less than 4.5 km apart and without significant intermediate tributaries, growing season flooding frequency and duration were magnified in the lowest elevations of the downstream stand. An elevation difference of as little as 10 cm resulted in a 20% difference in the frequency of surface flooding during the growing season. Species distributions were significantly correlated with depth to mottling ($r^2 = 0.75$), flooding frequency ($r^2 = -0.57$), elevation ($r^2 = 0.70$), and several soil chemical properties. The two stands had very similar annual surface flooding regimes, but subtle differences in growing season flooding frequency, soil characteristics, and disturbance history have apparently resulted in dissimilar plant community composition and structure. These results suggest that the lack of quantitative data on vegetation-environment interactions occurring at the microtopographic scale (10^{-1} m) in alluvial swamp forests makes precise prediction, planning, or design of created or restored wetland composition and function a formidable challenge.

Key Words: swamp forests, riverine wetlands, bottomland hardwoods, species-environment relationships, microtopography, wetland hydrology, edaphic factors, gradient analysis, detrended correspondence analysis, canonical correspondence analysis, wetland restoration

INTRODUCTION

Factors influencing the composition of plant communities in the coastal plain swamp forests of the southeastern United States are extremely complex and difficult to quantify (Daubenmire 1976, Wharton et al. 1982, Brinson 1990, Sharitz and Mitsch 1993). Development of the soil substrate in alluvial swamp forests is a dynamic process governed by vegetation, hydrology, geology, and fluvial processes. Slight variations in elevation, soil texture, and soil structure have

pronounced effects on moisture, aeration, soil chemistry, and the frequency and magnitude of flooding in swamp forests (Robertson et al. 1978, Wharton et al. 1982, Smith 1996). Topographic heterogeneity on the scale of individual plants, or microtopography, creates a complex mosaic of microsites with substrates that differ structurally, hydrologically, and chemically (Mohler 1979, Huenneke and Sharitz 1986, Titus 1990).

Initial attempts to explain the composition of flood-

plain forests were often directed at determining differential survival among species subjected to various artificial flooding regimes in controlled environments. Studies on tree seedling survival generally indicated that the varying degrees of flooding tolerance among species are related to their distribution along flood frequency gradients (McDermott 1954, Hall and Smith 1955, Hosner 1957, 1958, 1960, Briscoe 1961, Hosner and Boyce 1962, Bonner 1965, Hook 1984, Pezeshki et al. 1996). Many early field studies focused on describing general relationships among vegetation communities, flooding, and other environmental parameters in swamp forests (Hall and Penfound 1939, 1943, Shelford 1954, Monk 1966, Gemborys and Hodgkins 1971, Nixon et al. 1977). Small differences in the depth of the water table result in significant differences in herbaceous and woody vegetation (Wistendahl 1958, Gemborys and Hodgkins 1971, Bell 1974a, 1974b, Conner and Day 1976, Bell and del Moral 1977, Franz and Bazzaz 1977, Nixon et al. 1977, Barnes 1978, Wharton et al. 1982). Direct gradient analyses of vegetation along elevational gradients in floodplain and other wetland areas have demonstrated the individualistic responses of plant species to varying degrees of surface flooding (Hall and Smith 1955, Bell 1974a, 1974b, Bell and del Moral 1977, Franz and Bazzaz 1977, Theriot 1988, Smith 1996). Titus (1990) found that elevation over a 1.5-m gradient was the environmental factor most strongly correlated with species distribution of tree seedlings in a floodplain swamp forest in Florida. Studies in floodplain forests have yet to link on-site measurements of growing season hydrology with elevation, soils, and other environmental factors at the scale of individual plants.

With increased use of complex statistical and ordination techniques, phytosociological studies of wetland vegetation have become more quantitative. Robertson et al. (1978) suggested that indirect gradient analysis with multivariate interpretation is an appropriate approach to floodplain community analysis since elevation alone did not adequately represent the "site inundation, soil drainage-aeration complex" gradient. Indirect gradient analyses of swamp forest vegetation have demonstrated the complex interaction of edaphic and hydrologic factors but have yet to provide the type of predictive and quantitative tools needed for site-specific hydrologic management and restoration of swamp forests.

A greater understanding of the hydrologic regimes and other environmental factors governing community structure in swamp forest ecosystems could prove valuable in attempts to protect and restore the functions of swamp forest ecosystems. Although supporters and detractors have yet to resolve most of the philosophical and technical issues surrounding ecological

restoration, it is increasingly practiced and mandated as part of environmental management programs. Besides proactively restoring wetlands and riparian areas for ecological and economic benefits, wetland regulatory programs often mandate compensation for unavoidable losses of wetland functions in accordance with the U.S. Environmental Protection Agency's goal of achieving no net loss of the United States' remaining wetlands base. In eastern North Carolina, commonly permitted activities such as highway construction and land development often result in impacts to swamp forests along relatively small blackwater tributaries. Restoring these systems to some approximation of their pre-disturbance hydrologic and vegetative characteristics remains a challenge.

Although many researchers have qualitatively described swamp forest ecosystems and their hydrologic regimes, quantitative data needed for planning and hydrologic design of swamp forest restoration projects rarely exist. Some have suggested emulating relatively undisturbed wetlands with similar landscape positions and hydrologic attributes when attempting to develop appropriate restoration design criteria (Westman 1985, Brinson and Rheinhardt 1996). Destruction of swamp forests and mitigation projects aimed at replacing lost swamp forest functions proceed without adequate quantitative description of the subtle relationships between plant community structure, hydrologic gradients, and microtopography.

In an effort to provide more detailed information for management and restoration design, we analyzed the plant community composition of a swamp forest in relation to long-term surface-water flooding regimes, elevational gradients, soils, and other environmental factors in southern Beaufort County, North Carolina, USA. Our objectives were to 1) provide quantitative comparisons of flooding regimes along different sections of a floodplain in relation to precise measurements of microtopographic changes in elevation at the scale of individual plants; 2) elucidate the relative influence of hydrology, soils, and other environmental factors on swamp forest composition; 3) assess the potential for matching appropriate assemblages of swamp forest vegetation to restored hydrologic regimes; and 4) identify the implications of our methods and results for planning and hydrologic design of swamp forest restoration projects in the region.

METHODS

Study Stands

The two study stands were located in the Durham Creek watershed in southern Beaufort County, North Carolina, USA (Figure 1). Durham Creek is a fourth

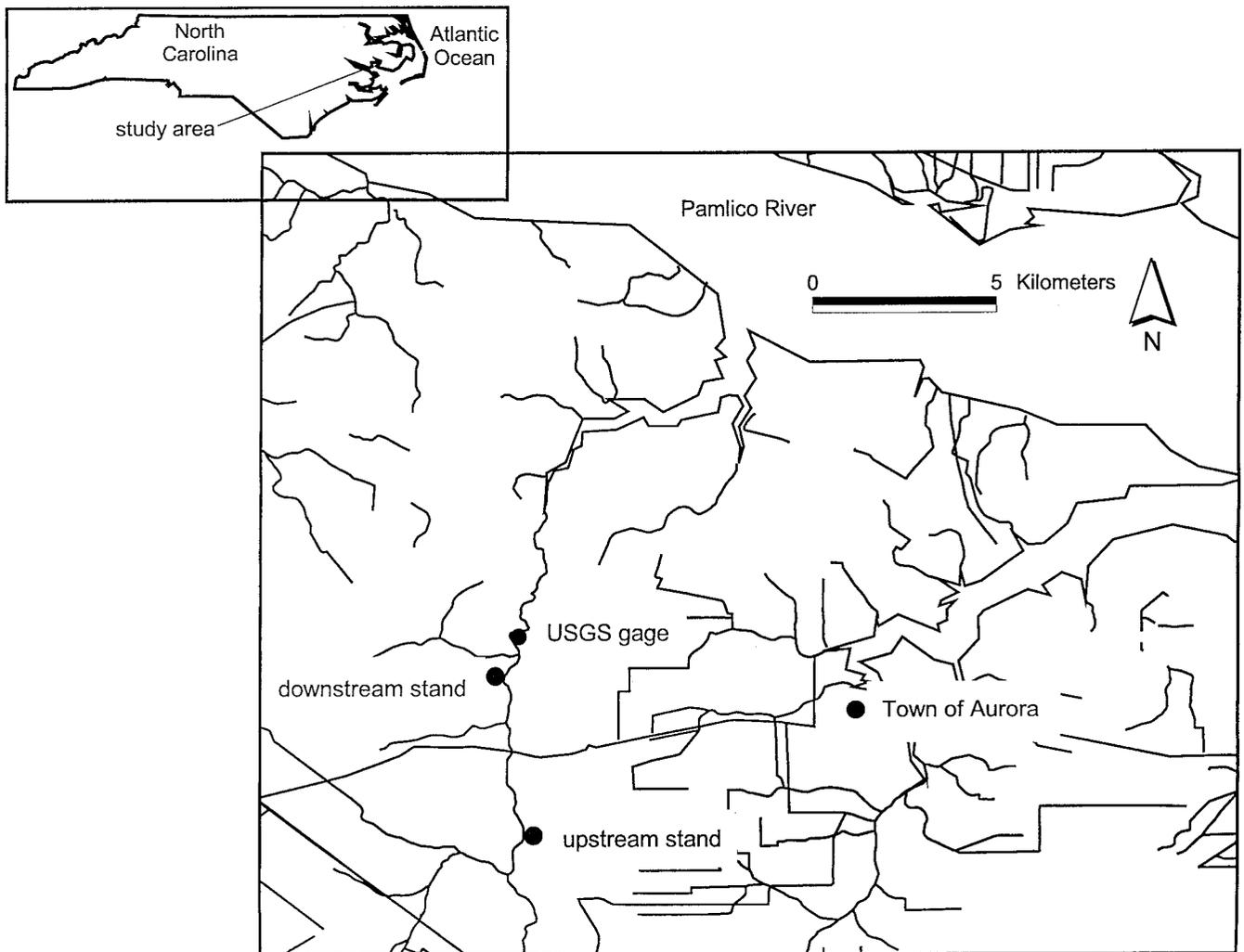


Figure 1. Vicinity map of study sites along Durham Creek.

order stream that flows north into the Pamlico River. Both study sites were classified as *coastal plain small stream swamps, blackwater sub-type* (Schafale and Weakley 1990). There had been no apparent major disturbances (*e.g.*, timber harvesting, ditching) in the past thirty years, and the plant communities were representative of mid-successional bottomland hardwood forests of southern Beaufort County. The stands were probably high-graded for *Taxodium distichum* (baldcypress), as there were considerable and nearly equal numbers of very large rotted stumps in both stands. The stream had been monitored by a United States Geological Survey (USGS) gaging station at Edward since 1965. The watershed above the gage contains 67 km² of forest in various successional stages, drained agricultural land, and managed pine plantations. One study stand (designated the downstream stand) was located approximately 1.25 km upstream from the USGS gage, and the other study stand (designated the upstream stand) was located approximately 5.6 km up-

stream from the gage (at 35°18'48" N/76°52'30" W and 35°16'55" N/76°52'15" W, respectively). The downstream stand had a stream width of 5–6 m, and upstream the stream width was 4–5 m. The floodplain width of both stands typically was 225–300 m.

Hydrology

To estimate long-term surface flooding regimes by correlation with the USGS gage, we installed a continuous water-level recorder in each stand. The upstream stand stage was monitored from November 1990 to February 1993. The downstream stand was monitored from July 1992 to February 1993. Stream flow and precipitation during the study represented normal conditions over the period of record for the USGS gage (1965–1991). Mean daily discharges for Durham Creek at the USGS gage were significantly correlated with the upstream stand water levels ($r^2 = 0.94$), and this regression model was used to hindcast

water levels in the upstream stand for the period of record. Due to *Castor canadensis* Kuhl (beaver) activity in the vicinity of the USGS gage in late summer 1991, only gage data collected before August 1991 were used in the regression analysis. It therefore became necessary to correlate stage in the downstream stand to stage in the upstream stand to allow hind-casting. Different models were best for the growing season (April 1–October 31, as defined by Natural Resources Conservation Service 1995) and the dormant season. For the growing season, downstream stage was a function of upstream stage and temperature expressed as degree days (average daily degrees $> 10^{\circ}\text{C}$, $r^2 = 0.96$). During the dormant season, downstream stage was related to upstream stage alone. The USGS gage record and the long-term estimates of surface flooding in the study stands were analyzed for frequency and duration of flooding by elevational increments for the period of record.

Vegetation

We divided each stand into three elevational zones, chosen because they appeared to represent significant differences in soil moisture regimes: (1) from the creek level to the 46 cm contour; (2) from 46 cm to the 122 cm contour; and (3) from the 122 cm contour to slightly above the wetland/upland ecotone. Five 0.04-ha plots (20 m \times 20 m) were randomly established in each of the three topographic zones, for a total of 30 plots. Each 0.04-ha plot contained 20 contiguous 1-m² subplots for sampling understory vegetation; all plots were on the same side of the stream, and all subplots were oriented perpendicular to the stream.

In each 0.04-ha plot, all woody plants over 1 m tall were counted by species, and measured for diameter at 1.3-m height (DBH). Saplings were defined as woody stems > 1 m height and with DBH < 6.4 cm. Saplings with DBH < 1.3 cm or height < 1.3 m were recorded as 0.25 cm DBH. Understory consisted of all plants < 1 m tall. Percent cover for each understory plant species was determined visually. Tree seedling density by species was determined from plot counts. Any woody specimen > 6.4 cm DBH was considered a tree, and any woody species that typically grows to more than 6.4 cm DBH was considered a tree species. Species identification followed Radford et al. (1968). Increment cores were taken at DBH from several mature *Pinus taeda* (loblolly pine) on the fringes of the stand and from hardwoods within the swamp to estimate stand age.

The elevation of each woody plant > 1 m tall in each 1-m² plot was measured with a free-standing surveyor's leveling rod placed at plot center. A hand level mounted on a staff was placed next to each plant at

the average root collar elevation, and the elevation relative to the plot center was determined by sighting the surveyor's rod. The elevation at the center of each 1-m² subplot was determined the same way. Elevations of plot centers relative to mean sea level were determined from an established benchmark using a surveyor's level. An elevation was assigned to each 0.04-ha plot by averaging the elevations of the twenty 1-m² subplots along its centerline, within-plot topographic heterogeneity in the lowest topographic zone was calculated as the variance of these twenty plots. Plots from the two zones of higher elevation were not used in analyses of topographic heterogeneity due to steep elevational gradients at the edges of the floodplain, which were not appropriate for consideration as microtopography.

Soils

Both stands occurred on soils of the Muckalee series, which is classified as a coarse-loamy, siliceous, non-acid, thermic Typic Fluvaquents (Natural Resources Conservation Service 1995). Soil cores were extracted from the upper 25 cm of the profile at five locations along the centerline in each plot. A Mehlich-3 (Mehlich 1984a) extract of each composite sample from each plot was tested for percent humic matter (Mehlich 1984b), cation exchange capacity, percent base saturation, pH, exchangeable acidity, and by inductively coupled plasma spectrometry, for concentrations of calcium, magnesium, exchangeable phosphorus, and potassium. Soil profiles were determined at the plot centers in at least two plots within each topographic zone per stand to a depth of 100 cm. Soil characteristics measured included texture and depth to the least permeable horizon (highest percent clay); the depth to, abundance, and Munsell color (Munsell Color 1990) of distinct mottling; and the color and thickness of each horizon. Soil texture of the upper 25 cm and the least permeable horizon for each plot were determined by a modified Bouyococ hydrometer method (Foth 1978, Gee and Bauder 1986).

Data Analyses

We summarized vegetation data by calculating tree seedling, sapling, and tree densities, along with tree and shrub basal areas for each stand, combining all individuals from all plots for each stand—averages of plot totals were not used. Relative basal area for each species was calculated as the proportion of basal area of all species. Relative frequency and relative cover were calculated within elevational increments for each understory species. Mean elevations were calculated for each species within each stand and by size class for tree species. A coenocline of selected tree species

was constructed to provide a model of the vegetation in the downstream stand. Normal Gaussian distributions were fit to species importance values across the elevational increments as delineated above to estimate species responses to the elevational continuum (Gauch and Whittaker 1972). Both direct and indirect gradient analyses of vegetation and environmental factors were performed. For direct gradient analyses, individual overstory plants and understory 1-m² plots were first sorted by elevation. Relative basal area and relative density of overstory species were then calculated within nine elevational increments of 15, 30, or 45 cm. The importance value (IV) for a species within a plot or elevational increment was calculated as the average of its relative basal area and relative density within a given plot or increment. A primary matrix of IVs of 26 tree species in the 30 plots from both stands was ordinated by detrended correspondence analysis (DCA) (Hill and Gauch 1980) using DECORANA (Hill 1979) and by canonical correspondence analysis (CCA) using CANOCO (ter Braak 1987a, 1987b). CCA was also applied to the matrices derived from each stand separately. We used multiple regression to examine the relationships between environmental factors and the DCA ordination axes. We used cluster analyses (Wards method and the centroid group linkage method in PC-ORD (McCune 1991)) of the vegetation plots in conjunction with the DCA ordinations to classify plant community types.

RESULTS

Hydrology

Stage fluctuations in the two study stands were closely related during the period of observation (Fig-

ure 2). Two large rain events were recorded for both stands: one occurring during the growing season in August and the other during dormancy in December. For the summer period, the magnitude of flooding in each stand was affected by antecedent moisture conditions that were, in part, determined by differing rates of evapotranspiration. Stage recession rates and diurnal fluctuations were 2–3 times greater in the upstream stand than in the downstream stand between precipitation events during the summer study period. The downstream stand hydrograph indicated a relative flooding depth considerably greater than that of the upstream stand during the August rain event. However, no differences were observed in flooding events occurring after October.

Vegetation Characteristics

The forest stands on Durham Creek are similar in composition, with structural characteristics that reflect historical and environmental differences. Differences in succession and disturbance histories are often reflected by differences in basal area and stem density. The 18 percent lower basal area and 32 percent higher tree stem density of the upstream stand (Table 1) may reflect more intense and recent disturbance. Increment cores suggested that the upstream and downstream stands had been harvested around the late-1940s and mid-1950s, respectively. The stands were similar in the occurrence and total number of species, but compositional and structural differences were considerable. Plots in the upstream and downstream stands contained 74 and 76 species of vascular plants, respectively, 57 of which were common to both stands. The

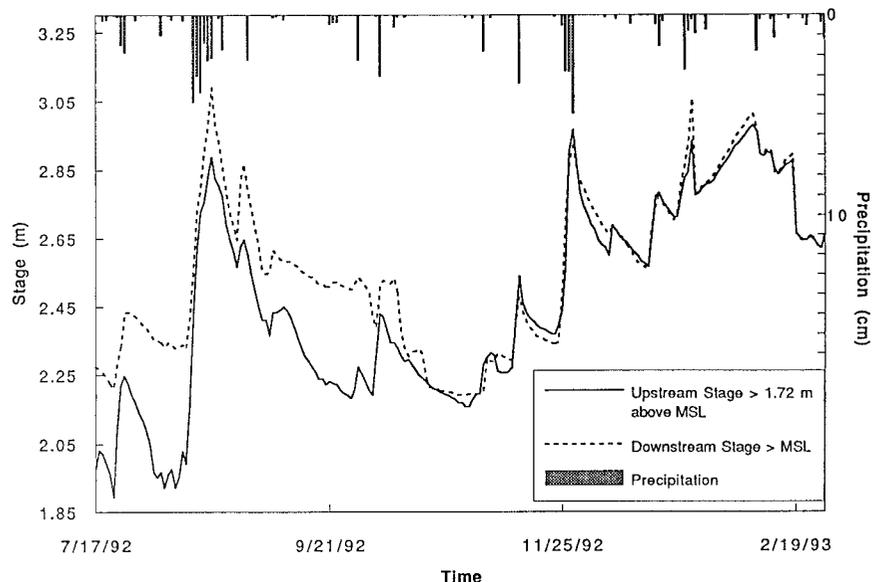


Figure 2. Stage relationship of the two study sites.

Table 1. Composition and structure of the swamp forests of Durham Creek. Density is stems/ha; basal area is m²/ha; importance value (IV) is the average of relative density (of saplings and trees) and relative basal area (of saplings and trees).

Species	Upstream Stand					Downstream Stand				
	Seedling Density	Sapling Density	Tree Density	Basal Area	IV	Seedling Density	Sapling Density	Tree Density	Basal Area	IV
<i>Nyssa sylvatica</i> var. <i>biflora</i> (Walter) Sargent	2,970	20	190	13	19		5	67	12	13
<i>Liquidambar styraciflua</i> L.	21,600	92	228	9	17	17,700	47	70	5	9
<i>Ilex opaca</i> Aiton	2,130	387	163	2	14	267	93	37	<1	4
<i>Acer rubrum</i> L.	20,600	163	148	6	13	29,700	260	248	9	24
<i>Liriodendron tulipifera</i> L.	100		57	5	7	167		18	2	2
<i>Quercus michauxii</i> Nuttall	467	27	47	3	4	367	5	7	<1	1
<i>Quercus nigra</i> L.	1,130	17	15	2	3		7	2	<1	<1
<i>Persea borbonia</i> (L.) Sprengel		140	8	<1	3		48	3	<0.1	2
<i>Taxodium distichum</i> (L.) Richard	67		10	1	2	1,470		75	11	12
<i>Pinus taeda</i> L.			7	1	2	667		8	2	2
<i>Quercus laurifolia</i> Michaux		32	25	1	2	33	3	2	<1	<1
<i>Leucothoe racemosa</i> (L.) Gray		75		<0.1	2		37		<0.1	1
<i>Magnolia virginiana</i> L.		25	23	<1	2	100	13	5	<0.1	<1
<i>Cyrilla racemiflora</i> L.		55	3	<0.1	1		33		<0.1	1
<i>Leucothoe axillaris</i> (Lam.) D. Don		62		<0.1	1		3		<0.1	<1
<i>Amelanchier canadensis</i> (L.) Medicus		27		<0.1	<1					
<i>Vaccinium</i> spp. L.		67		<0.1	1		22		<0.1	<1
<i>Symplocos tinctoria</i> (L.) L'Her.		58	8	<0.1	1		57	2	<0.1	2
<i>Fraxinus caroliniana</i> Miller		30	2	<0.1	<1		125	77	<1	7
<i>Ilex coriacea</i> (Pursh) Chapman		13		<0.1	<1					
<i>Itea virginica</i> L.		2		<0.1	<1		10		<0.1	<1
<i>Gordonia lasianthus</i> (L.) Ellis		2	3	<0.1	<1					
<i>Ilex verticillata</i> (L.) Gray		2		<0.1	<1		2		<0.1	<1
<i>Fagus grandifolia</i> Ehrhart	100	17	2	<1	<1					
<i>Lyonia lucida</i> (Lam.) K. Koch		32		<0.1	<1					
<i>Ulmus americana</i> L.		2		<0.1	<1		2	3	<1	<1
<i>Quercus alba</i> L.	33	5	2	<1	<1					
<i>Myrica cerifera</i> L.		3		<0.1	<1					
<i>Quercus falcata</i> Michaux			2	<1	<1					
<i>Rhododendron</i> spp. L.		2		<0.1	<1					
<i>Oxydendron arboretum</i> (L.) DC.		20	7	<1	<1	33	18	3	<0.1	<1
<i>Nyssa aquatica</i> L.							18	52	4	6
<i>Fraxinus pennsylvanica</i> Marshall								33	8	2
<i>Hamamelis virginiana</i> L.							8		<0.1	<1
<i>Cornus florida</i> L.							3		<0.1	<1
<i>Ligustrum sinense</i> Lour							3		<0.1	<1
<i>Morus rubra</i> L.							2		<0.1	<1
<i>Carya tomentosa</i> (Poiret) Nuttall								2	<1	<1
<i>Carpinus caroliniana</i> Walter	33					533	5	2		<1
<i>Nyssa</i> spp. L.						2,770				
<i>Asimina triloba</i> (L.) Dunal						233				
<i>Clethra alnifolia</i> L.		230		<0.1	5		62		<0.1	2
<i>Quercus</i> spp. L.	1,770					1,030				
<i>Fraxinus</i> spp. L.	267					12,100				
TOTAL	51,267	1,578	950	46		67,170	892	715	56	

Table 2. Elevation by growth form for selected tree species. Data are mean elevations > datum (m) followed by standard deviations.

	Upstream Stand			Downstream Stand		
	Seedlings	Saplings	Trees	Seedlings	Saplings	Trees
<i>Taxodium distichum</i>	4.32 (0.04)		4.45 (0.15)	2.83 (0.06)		2.72 (0.12)
<i>Liquidambar styraciflua</i>	4.52 (0.45)	4.45 (0.41)	4.79 (0.72)	2.79 (0.30)	3.20 (0.82)	3.14 (0.43)
<i>Acer rubrum</i>	4.46 (0.41)	4.69 (0.72)	5.00 (0.88)	2.92 (0.42)	3.02 (0.49)	3.05 (0.38)
<i>Ilex opaca</i>	4.47 (0.41)	4.82 (0.48)	5.05 (0.60)	3.80 (0.74)	3.45 (0.70)	3.74 (0.90)
<i>Quercus michauxii</i>	5.08 (0.28)	5.22 (0.61)	5.33 (0.55)	4.49 (0.84)	3.58 (0.16)	4.56 (0.46)
<i>Liriodendron tulipifera</i>	4.83 (0.37)		6.04 (0.86)	3.92 (0.87)		4.37 (0.47)

upstream stand was dominated by *Nyssa sylvatica* var. *biflora* (swamp tupelo) with *Acer rubrum* (red maple) and *Liquidambar styraciflua* (sweetgum) as major associates throughout most of the stand. The most important tree species in the downstream stand, as indicated by IV (Table 1), was *A. rubrum*. *Acer rubrum* occurred abundantly throughout the stand in all sizes, and its IV was influenced by a high density of small trees. *Taxodium distichum* dominated the wettest areas, and *N. sylvatica* var. *biflora* was important on all but the wettest substrates. *Fraxinus pennsylvanica* (green ash) achieved canopy dominance only in small areas of the downstream stand. *Nyssa aquatica* (water tupelo) was also unique to the downstream stand, occurring only in the lowest plots along the stream channel.

The shrub-sapling stratum was much more dense in the upstream stand and dominated by *Ilex opaca* (American holly), *Clethra alnifolia* (sweet-pepperbush), and *Persea borbonia* (red bay). The greater abundance of shrubs and saplings in the upstream stand was accompanied by greater stratification of the canopy, more standing dead trees, and more prevalent tree falls and tip-up mounds. In the more open understory of the downstream stand, *Fraxinus caroliniana* (Carolina ash), *I. opaca*, *C. alnifolia*, *P. borbonia*, and *Symplocos tinctoria* (sweetleaf) were the dominant shrub-sapling species. *Acer rubrum* and *L. styraciflua* were the only canopy species with abundant seedlings and saplings in both stands. Regeneration of *Fraxinus* spp. was also occurring in the downstream stand (most saplings were *F. caroliniana*). The understory of the upstream stand was dominated by *Leucothoe axillaris* (doghobble); mosses, *Woodwardia areolata* (netted chainfern), and *Saururus cernuus* (lizard's tail) were increasingly abundant with decreasing elevation. *Woodwardia areolata* and *S. cernuus* were by far the most abundant species in the ground-layer vegetation of the downstream stand. *Mitchella repens* (partridge-berry), mosses, and *Rhus radicans* (poison ivy) were also commonly encountered in the downstream stand

understory, with *L. axillaris* abundant only at higher elevations.

Fraxinus spp. seedling density was significantly correlated ($r^2 = 0.63$) with topographic heterogeneity in plots within the lowest elevational zone of the downstream stand but was strongly influenced by an outlier plot. Otherwise, no relationship was found between topographic heterogeneity and density or absolute cover of seedlings in the lowest stratum of either stand.

Direct Gradient Analyses

Elevation accounted for much more variation in species distributions in the more mature downstream stand than in the upstream stand ($r^2 = 0.87$ and 0.51). Tree species occurrence relative to elevation varied by size class (Table 2). However, the elevational distributions of seedlings and saplings of most tree species were similar to the distribution of canopy members of the species. Some species (e.g., *A. rubrum* and *N. sylvatica* var. *biflora*) showed a broad tolerance to soil moisture conditions, while *T. distichum* occurred within a very narrow range of elevations. With the exception of *I. opaca*, elevations of tree species were more variable in the upstream stand.

A coenocline of selected tree species in the downstream stand revealed individualistic responses of species to the elevational gradient (Figure 3). A comprehensive summary of results from the direct gradient analyses is provided in Appendix Tables 1a–d. Sorting of species into discrete elevational increments was most apparent in the downstream stand. Although the stands were flooded with almost equal frequency on an annual basis, the corresponding elevational increments in the downstream stand were considerably wetter in the growing season. Within the elevational increments, species richnesses of trees, shrubs, and saplings were greater in the upstream stand, while the forest floor of the downstream stand had the highest overall species richness (Appendix Tables 1a–d).

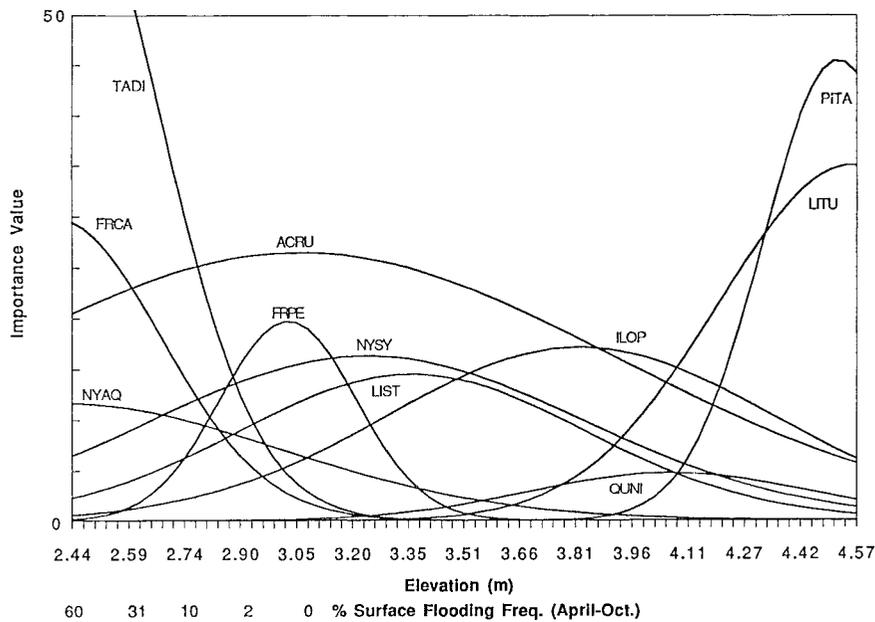


Figure 3. Coenocline of the downstream stand derived from species importance values within elevational increments. Species are *Acer rubrum* (abbreviated ACRU), *Fraxinus caroliniana* (FRCA), *Fraxinus pennsylvanica* (FRPE), *Ilex opaca* (ILOP), *Liquidambar styraciflua* (LIST), *Liriodendron tulipifera* (LITU), *Nyssa aquatica* (NYAQ), *Nyssa sylvatica* var. *biflora* (NYSY), *Pinus taeda* (PITA), *Quercus nigra* (QUNI), and *Taxodium distichum* (TADI).

Ordination Analyses

A more comprehensive view of the plant community—environment complex was developed with the two multivariate ordination techniques that arranged plots along axes on the basis of species composition and, in the case of CCA, environmental factors. Each axis in DCA or CCA ordination may be interpreted as a multidimensional vector that represents a complex gradient of multiple environmental factors, which maximally accounts for the variation in species composition.

A combination of hydrologic and soil fertility factors was the best predictor of plot ordination scores when plots from both stands were analyzed collectively. Many of the environmental variables were correlated with the first axis since flooding regime has a strong influence on nutrient availability/leaching and soil texture (Table 3). Depth to mottling, flooding frequency, elevation, and several soil chemical properties were all significantly correlated. Exchangeable acidity was the single variable of highest correlation ($r = 0.40$) with the collective DCA ordination second axis (Figure 4). As in the direct gradient analysis, elevation accounted for a considerably greater portion of the variation in species composition in the downstream stand than in the upstream stand. Elevation was the most parsimonious model of compositional variation along the first DCA axis for the downstream stand ($r^2 = 0.88$, $p < 0.001$). Hydrologic factors and soil nutrient status

were also related to the first DCA ordination axis for the upstream stand. The second axis in each ordination was weakly correlated with a few of the hydrologic and soil fertility factors linked with the first axis.

The DCA ordination of both stands was examined for discontinuities and plot groupings were initially delineated into three segments labeled wet, transitional, and mesic (Figure 4) based on discontinuities in DCA axis 1 scores. Environmental variables for each of these segments were summarized collectively and by stand (Appendix Table 2). Varying amounts of exchangeable calcium, magnesium, and acidity were the most obvious differences in soil chemical properties between the stands. Soil textures were either sandy loam or sandy clay loam (in both stands depending on topographic position), with the lowest elevations of the downstream stand containing the most clay. In both stands, clay content and cation exchange capacity were higher at lower elevations, reflecting the relatively slow flows associated with the most frequent flooding events.

Nyssa sylvatica var. *biflora*, *A. rubrum*, and *L. styraciflua* dominated the transitional zone. *Nyssa sylvatica* var. *biflora* was more abundant than *L. styraciflua* on the wettest soils of finer texture, particularly those containing high exchangeable acidity. A few plots in the transitional segment of the upstream stand that were dominated by *N. sylvatica* var. *biflora* occurred in a depression that stored surface water and were

Table 3. Pearson correlation matrix of DCA axis scores and environmental variables. DCA axes are derived from ordination of both sites together. Significant r values ($\alpha \leq 0.05$) are in bold, $n = 30$. Flood frequency is for growing season only.

	DCA Axis1	DCA Axis2	Elevation	Flooding Frequency	Depth to Mottling	% Base Saturation	Acidity	CEC	% Sand in A Horizon	% Clay in A Horizon	[K]	[Ca]
DCA axis2	0.01											
Elevation	0.70	-0.33										
Flooding frequency	- 0.58	0.28	- 0.66									
Depth to mottling	0.75	-0.06	0.37	-0.21								
% base saturation	- 0.75	-0.21	-0.33	0.19	- 0.68							
Acidity	-0.11	0.40	- 0.49	0.63	0.18	-0.24	0.78					
Cation exchange capacity (CEC)	- 0.54	0.30	- 0.65	0.69	-0.27	0.41	0.78	- 0.69				
% sand in the A horizon	0.68	-0.24	0.48	- 0.59	0.65	- 0.57	-0.32	0.73	- 0.94			
% clay in the A horizon	- 0.68	0.26	- 0.57	0.69	- 0.59	0.54	0.39	0.10	-0.07	0.11		
[phosphorus]	-0.11	-0.27	0.19	0.07	0.01	0.21	0.02	0.73	- 0.58	0.56	0.26	
[potassium]	- 0.43	0.11	- 0.39	0.55	-0.30	0.35	0.55	0.73	- 0.53	0.50	0.12	0.20
[calcium]	- 0.73	-0.19	-0.33	0.15	- 0.65	0.99	-0.26	0.38	- 0.53	0.50	0.12	0.20
[magnesium]	- 0.68	-0.20	-0.28	0.28	- 0.66	0.80	-0.14	0.39	- 0.59	0.56	0.25	0.67

flooded for longer periods than some of the plots placed in the wet segment. The wet segment contained only plots from the downstream stand, reflected by a strong presence of *T. distichum* and some *N. aquatica*.

Cluster analyses were used with plot vegetation abundance summaries and the DCA ordination to designate community types derived from the flooding-fertility gradient (Figure 4 and Table 4). Pronounced differences in flooding regime and soil fertility appeared to influence the dominant species, with *F. pennsylvanica* only attaining dominance in a narrow range of flooding frequencies and at relatively high base saturation. Although *A. rubrum* and *L. styraciflua* commonly occurred together throughout the stands, they only appeared as codominants at or beyond the upper limit of growing season flooding.

Canonical correspondence analysis bolstered the interpretation of the flooding-fertility gradient. In the ordination of the upstream stand (Figure 5), axes 1 and 2 accounted for 23 percent and 11 percent, respectively of the variance of all covariances between species and environment. Elevation and flooding frequency strongly correlated with the first axis, while percent base saturation was the variable with highest correlation on the second axis ($r = 0.66$). Exchangeable acidity had a stronger correlation with axis 1 than did percent base saturation. On the upstream ordination biplot, flooding frequency, exchangeable acidity, and depth to mottling were closely associated with those species occurring in the wettest plots, such as *T. distichum* and *N. sylvatica* var. *biflora* (Figure 5). Soil texture was strongly related to the occurrence of several species in the more mesic segment of the upstream gradient, including *I. opaca* and *S. tinctoria*.

The first axis of the downstream stand ordination was also very strongly correlated with elevation; axis 1 accounted for 29 percent and axis 2 accounted for 12 percent of the variance of all covariances between species and environmental factors (Figure 6). Exchangeable acidity was closely linked with axis 2 and the occurrence of *N. sylvatica* var. *biflora*. Distributions of almost all species were apparently influenced by elevation, with the species of wetter plots split into two expressions of a flooding-fertility gradient (Figure 6). *Fraxinus pennsylvanica* was strongly associated with base saturation.

In general, species such as *Quercus michauxii* (swamp chestnut oak), *S. tinctoria*, *Liriodendron tulipifera* (tulip-poplar), *Oxydendrum arboreum* (sourwood), and *P. taeda* reach maximum abundance under more mesic conditions. These species were closely associated with soil texture and elevation, which reflect the moisture regime beyond the area of flooding. Species with broad tolerances (e.g., *A. rubrum* and *L. styraciflua*) were generally placed in the center of the CCA

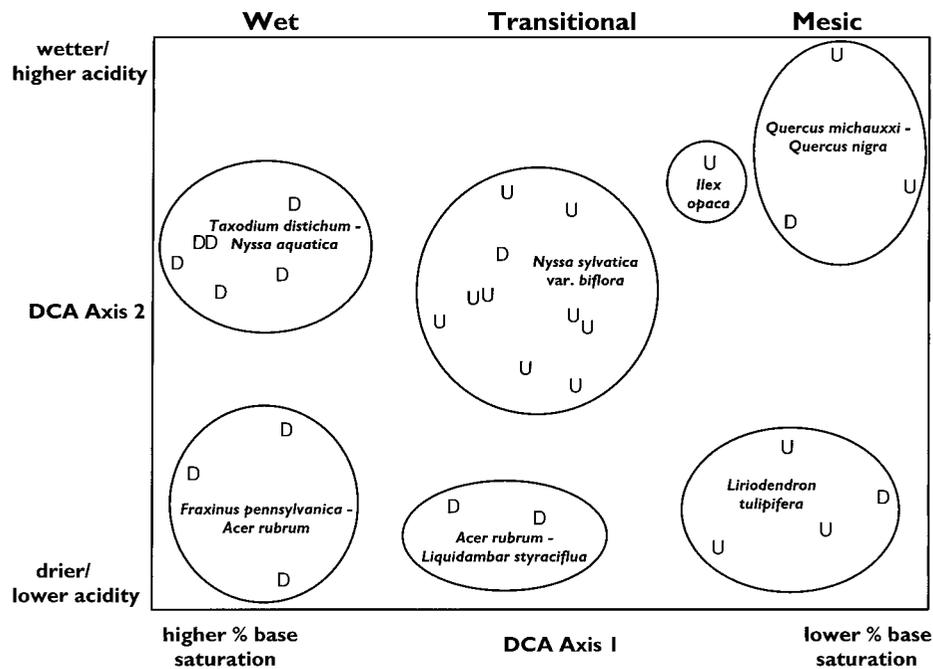


Figure 4. DCA ordination of 29 plots from both stands. Plots from the upstream and downstream stands are labeled U and D, respectively. Three segments of the flooding gradient are labeled wet, transitional, and mesic. Environmental variables on axes are derived from multiple regression analysis of plot scores. Plot dominants were determined by cluster analysis and plot summaries. Axis 1 eigenvalue = 0.56; axis 2 eigenvalue = 0.22.

biplots and were not readily interpreted in relation to environmental variables.

In an attempt to separate the effects of soil nutrient status from the background variation resulting from elevation and flooding, partial canonical ordination was applied to the full data matrix with elevation, flooding frequency, and depth to mottling represented as “covariables.” Base saturation had an inter-set correlation of $r = 0.68$ with the first CCA axis, while

exchangeable acidity and percent sand in the A horizon were more closely associated with the second axis ($r = 0.44$ and 0.52 , respectively). The only strong single species-site relationship was between *F. pennsylvanica* and axis 1. *Nyssa sylvatica* var. *biflora* and *P. taeda* appeared to be associated with both increasing exchangeable acidity and finer texture in the A horizon.

The results of both ordinations pointed to the dual

Table 4. Selected environmental characteristics of segments by community type (as depicted in Figure 4). Categories were derived from DCA ordination, cluster analysis, and plot summaries. Data are means followed by standard deviations.

Environmental Variable	<i>Taxodium distichum</i> - <i>Nyssa aquatica</i>	<i>Nyssa sylvatica</i> var. <i>biflora</i>	<i>Fraxinus pennsylvanica</i> - <i>Acer rubrum</i>	<i>Acer rubrum</i> - <i>Liquidambar styraciflua</i>
% sand in the A horizon	54 (8)	49 (14)	62 (11)	65 (4)
% clay in the A horizon	27 (7)	28 (8)	23 (9)	15 (0)
% humic matter	2 (0)	4 (2)	3 (1)	4 (2)
CEC, cmol _c /kg	8 (1)	8 (2)	7 (1)	5 (1)
Acidity, cmol _c /kg	5 (1)	6 (2)	4 (0)	4 (0)
% base saturation	32 (8)	27 (16)	47 (7)	20 (3)
Calcium, % of CEC	22 (6)	18 (13)	38 (8)	12 (2)
Magnesium, % of CEC	8 (2)	7 (3)	7 (2)	6 (0)
% surface flooding in the growing season	20 (9)	16 (9)	5 (5)	0 (0)
Duration of flooding (days) after the Storm of August 1992	15 (4)	12 (6)	7 (4)	0 (0)
Duration of flooding (days) after the Storm of December 1992	13 (6)	14 (10)	5 (2)	0 (0)
Maximum duration of flooding (days) Sept.–Nov. 1971	33 (8)	30 (16)	18 (9)	0 (0)

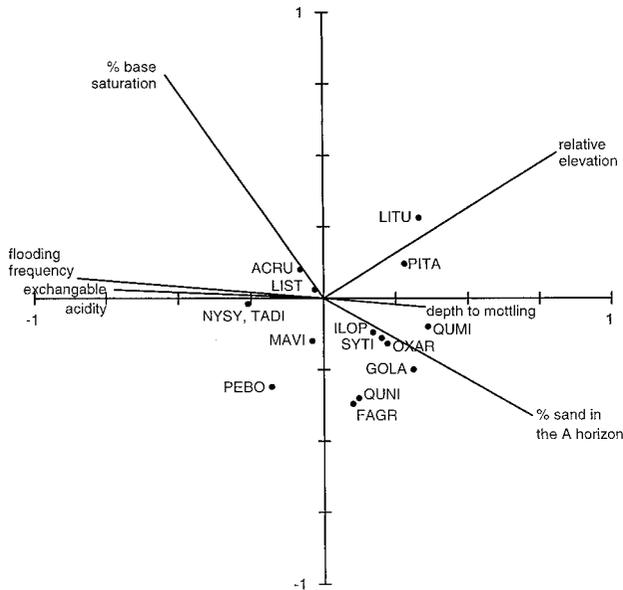


Figure 5. CCA biplot of species points and environmental vectors from the ordination of 15 plots from the upstream stand. Species are *Acer rubrum* (abbreviated ACRU), *Fagus grandifolia* (FAGR), *Gordonia lasianthus* (GOLA), *Ilex opaca* (ILOP), *Liquidambar styraciflua* (LIST), *Liriodendron tulipifera* (LITU), *Magnolia virginiana* (MAVI), *Nyssa sylvatica* var. *biflora* (NYSY), *Oxydendrum arboreum* (OXAR), *Persea borbonia* (PEBO), *Pinus taeda* (PITA), *Quercus michauxii* (QUMI), *Quercus nigra* (QUNI), *Symplocos tinctoria* (SYTI), and *Taxodium distichum* (TADI). NYSY is hidden beneath axis 1 and the acidity and perfflood vectors, just above TADI.

importance of soil moisture and fertility. Both ordination techniques also indicated that elevation was a key variable in the downstream stand. More variation in the upstream stand vegetation was accounted for by the CCA ordination than by the DCA ordination. The CCA ordination suggested a stronger relationship between acidity and the upstream ordination second axis than the DCA ordination.

DISCUSSION

Although the upstream and downstream stands had very similar surface flooding regimes, particularly when considered on an annual basis, differences in flooding frequency, stage, evapotranspiration, and base flow during the growing season created considerably different conditions in the two stands. We do not know whether the period of observation was representative of site-specific variations in hydrology and microtopography prior to 1990. The limited overlap of hydrologic monitoring periods constrains conclusions regarding long-term hydrologic processes. Estimates of long-term surface-flooding regimes should be inter-

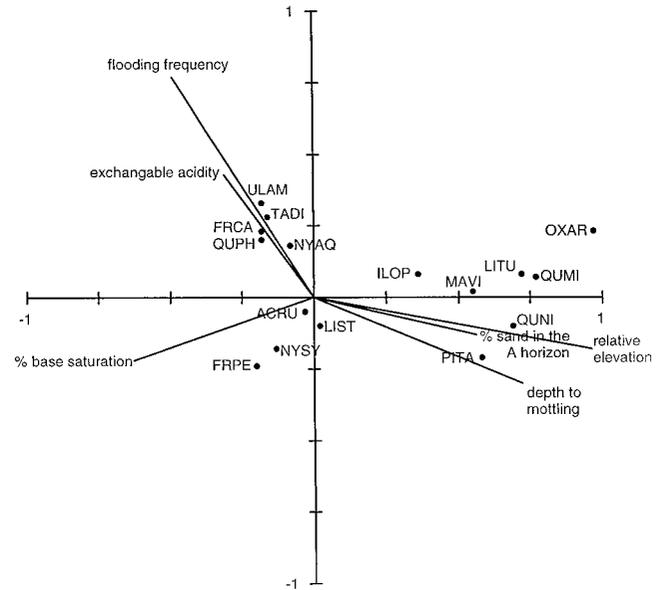


Figure 6. CCA biplot of species points and environmental vectors from the ordination of 15 plots from the downstream stand. Species are *Acer rubrum* (abbreviated ACRU), *Fraxinus caroliniana* (FRCA), *Fraxinus pennsylvanica* (FRPE), *Ilex opaca* (ILOP), *Liquidambar styraciflua* (LIST), *Liriodendron tulipifera* (LITU), *Magnolia virginiana* (MAVI), *Nyssa aquatica* (NYAQ), *Nyssa sylvatica* var. *biflora* (NYSY), *Oxydendrum arboreum* (OXAR), *Pinus taeda* (PITA), *Quercus michauxii* (QUMI), *Quercus nigra* (QUNI), *Quercus phellos* (QUPH), *Taxodium distichum* (TADI), and *Ulmus americana* (UMAM).

preted as an extrapolation of existing site-specific conditions across the stream gaging record. Despite the uncertainty associated with regression analyses and hindcasting of hydrologic data, characteristics measured during 1992–1993 clearly reveal lateral (channel to floodplain to upland), vertical (surface to subsurface), and longitudinal (upstream to downstream) hydrologic gradients in the Durham Creek watershed. Although the stands were less than 4.5 km apart and without significant intermediate tributaries, growing season flooding frequency and duration were magnified in the lowest elevations of the downstream stand. Such variation in local hydrology suggests that the common practice of linearly extrapolating *annual* surface-flooding frequencies from an established gage to some point of interest may not reflect subtle yet critical differences between forest stands in flooding frequency, stage, evapotranspiration, base flow, and microtopographic influences on drainage during the *growing season*.

An elevational difference of 10 cm resulted in a 20 percent difference in the frequency of surface flooding during the growing season. Clearly, surface flooding is not entirely representative of below-ground differ-

Table 5. Flooding frequencies (percent of growing season) at which species occur, as suggested by a variety of studies. Order of species approximates sequence from most tolerant to least tolerant of flooding.

Species	This Study	Hall & Smith (1955)	Tesky & Hinckley (1977)	Bedinger (1978)	Leitman <i>et al.</i> (1981)		Wharton <i>et al.</i> (1982)	Hook (1984)	Theriot (1988)
					Duration	Saturation			
<i>Taxodium distichum</i>	10–60+			29–40+	40–90	100	75–100	100	75–100
<i>Nyssa aquatica</i>	10–60+	<38	90–100		40–90	100	75–100	100	75–100
<i>Nyssa sylvatica</i> var. <i>biflora</i>	7–50	<27	90–100	29–40	40–90	100	75–100		
<i>Quercus lyrata</i> Walter		<40	40	10–40	13–40	42	25–75	50–75	50
<i>Acer rubrum</i>	0–30	<37	36	0–21	13–40		25–75	50	
<i>Fraxinus pennsylvanica</i>	1–10	<38			13	22	13–25	50	13–25
<i>Liquidambar styraciflua</i>	0–30	<34		0–21	4–13	13	13–25	50	0–25
<i>Populus heterophylla</i> L.		<34					13–25+		
<i>Populus deltoides</i> Marshall		<34					13–25+		
<i>Ulmus americana</i>	1–10	<24		0–21	4–13		13–25	50	13–25
<i>Quercus phellos</i> L.		<31	31	0–21			13–25	50	
<i>Platanus occidentalis</i> L.		<23	28				13–25+		
<i>Betula nigra</i> L.		<23	28				13–25	50	
<i>Quercus michauxii</i>	0–7		29		4		2–13		
<i>Quercus nigra</i>	0–7	<17	18	0–21	4		2–13		5–13
<i>Liriodendron tulipifera</i>	0	<4	9		4–13				

ences in the plant rooting environment. Soil may remain saturated for much longer than the period of surface flooding (Leitman *et al.* 1981, Day *et al.* 1988). Even after the creek stage recedes to well within the channel, many areas of the floodplain remain flooded for long periods due to microtopographic depressions and relatively low infiltration rates associated with cohesive soils (Titus 1990). The least permeable horizon in most of the soil profiles examined in the Durham Creek floodplain was the uppermost mineral horizon, which occurred under approximately 10 cm of organic muck. Drainage from the uppermost mineral into the lower horizons of coarser texture is impeded by the low conductivity of the surface layers. Minor drainages, sloughs, depressions, and other microtopographic features were observed to have moisture regimes that fluctuate somewhat independently of creek stage, especially with increasing distance from the main channel (Bledsoe 1993). Local influences on drainage might be better characterized in future studies through an index of depression storage and channel connectivity coupled with more extensive stage monitoring relative to variations in topography and soil physical properties. Ground-water discharge could also be important in creating differences in infiltration rates and baseflow between the sites. Ground-water contribution rates generally increase with drainage area. The height of the water table and the base flow contribution can vary seasonally in accordance with the water balance of the watershed (Knighton 1998). Although both stands probably receive significant ground-water con-

tributions from adjacent uplands, the downstream stand clearly has higher levels of baseflow that may result in slower rates of infiltration relative to the upstream stand.

Distributions of species within elevational increments reflect a variety of individualistic responses to differing hydrologic and edaphic gradients associated with elevation in the two stands (Appendix Tables 1a–d). Differences in elevation may also reflect dynamic changes in floodplain microtopography around trees with roots that collect and stabilize debris. Species distributions over the elevational gradient in the Durham Creek floodplain are somewhat consistent with quantitative estimates of flooding frequency reported by others (Hall and Smith 1955, Tesky and Hinkley 1977, Bedinger 1978, Leitman *et al.* 1981, Wharton *et al.* 1982, Hook 1984, and Theriot 1988, Table 5). Hall and Smith (1955) determined that no tree species along the edge of a Tennessee reservoir was tolerant of repeated surface flooding for more than 54 percent of the growing season. With the exception of *T. distichum* and *N. aquatica* occurring under extreme flooding conditions near the channel, no other species thrived in the Durham Creek floodplain where the surface flooding frequency in the growing season was greater than 56 percent. The flooding regimes associated with the lowest elevations of the downstream stand containing *T. distichum* and *N. aquatica* were often more extreme than indicated due to a lack of sampling at the lowest elevations. In the lowest elevational increments, the flooding frequency gradient in the Durham Creek

floodplain changed so rapidly relative to elevation that a few more plots a few centimeters lower might have suggested a greater frequency of flooding.

Soil fertility of a frequently flooded forest is inseparable from its hydrologic regime due to interaction between the "soil aeration-drainage complex" (Robertson et al. 1978) and the availability of chemical species within the soil (Harms 1973). Since soil moisture regimes and the concentration of exchangeable nutrients are strongly correlated, it is difficult to surmise the temporal scales at which hydrologic and edaphic factors play the most critical roles in determining the response of plant species. Higher locations along the Durham Creek floodplain tended to have sandier soils since alluvial ridges are deposited by large floods of greater flow velocity while bottoms are frequently covered with relatively stagnant water. Lower elevations of frequently flooded areas contain more clay and organic matter and therefore have a greater cation exchange capacity. When the stage is at or above the ground surface in these areas, water does not readily percolate through the soil, especially where the uppermost soil horizon contains a large fraction of colloidal particles that decrease hydraulic conductivity. As a result, leaching of calcium and other essential nutrients should be less in topographically lower positions where movement of the water table is slower. Since stage fluctuations appeared to be slower and less variable in the downstream stand, reduced leaching losses of calcium and magnesium may explain differences in concentrations of those nutrients between the two stands. Increases in calcium and magnesium concentrations and the Ca/Mg ratio with increasing depth of flooding were shown to be an important influence on vegetation in hardwood swamps of north-central Florida (Monk 1966).

Analyses of ordinations suggested that soil fertility exerted a greater influence on vegetation in the upstream stand than in the downstream stand, despite a distinct gradient in percent base saturation over the elevational gradient in the downstream stand. The lower availability of essential basic cations and higher exchangeable acidity in the upstream stand may have facilitated the dominance of *N. sylvatica* var. *biflora*. Harms (1973) demonstrated that *N. sylvatica* var. *biflora* seedlings were much more sensitive to flooding regime than to soil fertility, while the growth of *N. aquatica* seedlings was much more dependent on soil fertility factors. *Nyssa aquatica* did not occur on the relatively acidic soils in the upstream stand. The occurrence of *F. pennsylvanica* in the downstream stand appeared to be linked to an affinity for calcium, a high Ca/Mg ratio, and a very specific moisture regime associated with a narrow range of elevations across the floodplain.

Anthropogenic influences may have created divergent conditions for regeneration in the stands. Although increment cores taken in the stands indicated that many overstory individuals were similar in age (40–50 years), there were considerably more large residual trees in the downstream stand than in the upstream stand. Given the shade intolerance of *T. distichum*, compositional differences between the stands may have been significantly influenced by high grading. Post-harvest hydrologic patterns (magnitude, duration, and timing) may have also played an important role in eliminating the regeneration niche of certain species (Grubb 1977). The potentially disparate disturbance histories of the two stands preclude straightforward interpretation of species occurrences relative to site-specific and stream network scale hydrologic processes.

IMPLICATIONS FOR RESTORATION AND CREATION OF ALLUVIAL SWAMP FORESTS

The marked differences in flooding regime occurring over a few centimeters in alluvial swamp forests make precise prediction, planning, or design of species-site interactions very challenging. Sites with similar surface flooding regimes may show markedly different subsurface drainage characteristics due to differences in soil physical properties, vegetation, and local watershed influences. The two forest stands studied had almost identical annual flooding frequency distributions, soils in the same series, and were similar in age. Yet, the stands were dissimilar in a number of hydrologic and edaphic characteristics. Which would have been the better reference ecosystem for a restoration project in the region? Clearly, the use of both stands augmented with detailed analyses of additional stands to establish a detailed database of abiotic characteristics and a range of successional trajectories for such systems in the region would be the best approach. Westman (1985) advocated developing reference ecosystem databases, and the U.S. Army Corps of Engineers and the U.S. Environmental Protection Agency have initiated such an effort as part of their plan to implement the hydrogeomorphic approach to wetland functional assessment (Smith et al. 1995). The use of hydrogeomorphic assessments to develop performance goals for compensatory mitigation projects is a laudable objective, but performance goals are of limited value without specific, quantitative design standards for obtaining them. Although this study was limited in its geographic scope, our work and that of others have demonstrated the importance of balancing qualitative regional studies with more detailed quantitative analyses of swamp forest hydrology and related soil characteristics at the microtopographic scale (10^{-1} m).

A number of studies of mitigation projects find a lack of technical ability to create or restore wetland functions (Kusler and Kentula 1990, Confer and Niering 1992, Pfeifer and Kaiser 1995, Geratz 1999). Despite efforts to evaluate the success of wetland creation and restoration projects in terms of ecological functions, most projects constructed for compensatory mitigation are assessed according to a regulatory hydrologic criterion and survival of plantings after a few years (*e.g.*, U.S. Army Corps of Engineers Wilmington District Compensatory Hardwood Mitigation Guidelines, 12/8/93). After conducting this research and evaluating many unsuccessful swamp forest restoration efforts in the eastern U.S., our view is that swamp forest restoration efforts should focus on repairing soil and establishing a quasi-natural hydrologic regime that is accurately matched to a desired assemblage of species. The direct gradient analysis and hydrologic results of this study indicate that achieving the minimum hydroperiod associated with jurisdictional wetland status (Sipple 1987) does not fulfill this objective, particularly for the most flood tolerant species associated with frequent flooding in the growing season (see also Geratz 1999).

A sound strategy for swamp forest restoration is to design for resilience by combining the appropriate hydrologic regime and soil conditions in the proper geomorphic position with judicious planting of non-opportunistic tree species in topographic distributions defined by regional databases, previous studies (Table 5), and fairly detailed hydrologic modeling. Intentionally creating microtopography might also improve recruitment by providing a variety of sites favorable for seed germination and establishment of different plant species (Harper et al. 1965, Titus 1990). A reasonable alternative to planting 1200 trees/ha is to restore microtopography with a small modified plow and plant only 120 trees/ha of heavy-seeded tree species that are slow to invade, as light-seeded species will adequately invade most sites (Shear et al. 1996, Shear et al. 2000). This will leave a soil surface much more amenable to the full suite of species found across microsites in a bottomland forest.

ACKNOWLEDGMENTS

We are grateful to PCS Phosphate Company, Inc., in Aurora, N.C. for funding this study. Professor Thomas Wentworth, Botany Dept., North Carolina State University provided invaluable guidance in vegetation data analyses. Field work was accomplished with assistance from Kate Piatek and Carlos Wilson.

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Appendix Table 1a. Direct gradient analyses of downstream stand. Relative density and relative basal area of tree and shrub species ≥ 1 m height in elevational increments of 0.15 m and 0.30 m above datum. Zero indicates present in numbers < 0.49 . For each data pair, relative density is listed on the left and relative basal area on the right. Elevation data include \pm one standard deviation.

Species	N	Mean Elevation	Elevational Increment																		
			2.46	2.61	2.76	2.92	3.07	3.37	3.68	4.14	4.59										
<i>Taxodium distichum</i>	45	2.72 \pm 0.12	24	77	12	42		3	16												
<i>Fraxinus caroliniana</i>	121	2.74 \pm 0.09	44	5	32	5	16	2	4	1											
<i>Ulmus americana</i>	3	2.81 \pm 0.01					1	1													
<i>Quercus laurifolia</i>	3	2.83 \pm 0.10			1	0	1	1													
<i>Nyssa aquatica</i>	36	2.83 \pm 0.17	9	18	7	11	5	7	5	10	2	7	1	3							
<i>Fraxinus pennsylvanica</i>	20	2.89 \pm 0.18			3	9	3	17	3	21	3	28									
<i>Leucothoe racemosa</i>	22	2.92 \pm 0.30			6	0	2	0		2	0	1	0	1	0						
<i>Ligustrum sinense</i>	2	2.95 \pm 0.18					0	0	1	0											
<i>Acer rubrum</i>	305	3.04 \pm 0.44	18	1	30	17	43	18	45	22	37	23	19	12	23	26	8	4	9	0	
<i>Carpinus caroliniana</i>	4	3.07 \pm 0.12							3	0	2	0									
<i>Liquidambar styraciflua</i>	70	3.16 \pm 0.62			4	7	9	8	11	10	11	21	9	18	5	18	3	3	4	0	
<i>Cyrilla racemiflora</i>	20	3.22 \pm 0.41			1	0	2	0	3	0	2	0	7	0	4	0					
<i>Nyssa sylvatica</i> var. <i>biflora</i>	49	3.24 \pm 0.53			3	10	6	26	5	20	4	18	17	67	1	12	7	0	2	0	
<i>Itea virginica</i>	6	3.31 \pm 0.24							3	0		6	0								
<i>Clethra alnifolia</i>	37	3.43 \pm 0.50	3	0	1	0	3	0			2	0	12	0	16	0	2	0			
<i>Ilex opaca</i>	78	3.53 \pm 0.77			1	0	3	0	10	0	30	3	12	0			15	2	13	2	
<i>Magnolia virginiana</i>	11	3.64 \pm 0.62			1	0					2	0			5	1	5	0			
<i>Persea borbonia</i>	31	3.69 \pm 0.43					0	0	4	0	2	0	10	0	13	0	10	2			
<i>Quercus nigra</i>	5	3.95 \pm 0.25											1	0	2	14	3	1			
<i>Vaccinium</i> spp.	13	4.08 \pm 0.46											1	0	8	0	2	0	6	0	
<i>Quercus michauxii</i>	7	4.14 \pm 0.65									3	0	2		2				6	27	
<i>Liriodendron tulipifera</i>	11	4.37 \pm 0.49													5	25	7	24	6	49	
<i>Leucothoe axillaris</i>	2	4.39 \pm 0.19															3	0			
<i>Hamamelis virginiana</i>	5	4.46 \pm 0.10															7	0	2	0	
<i>Pinus taeda</i>	5	4.64 \pm 0.28															5	63	4	13	
<i>Symplocos tinctoria</i>	35	4.69 \pm 0.77													12	0	16	0	28	0	
<i>Oxydendrum arboreum</i>	13	5.09 \pm 0.86															8	0	15	1	
<i>Cornus florida</i>	2	5.44 \pm 0.02																		4	0
% annual flooding frequency:			61		29		7		1		<0.1		0		0		0		0		
% growing season flooding frequency:			56		27		8		1		<0.1		0		0		0		0		
number observed in increment:			34		180		289		73		122		69		82		61		54		
species richness:			6		13		15		13		13		13		13		13		15		14

Appendix Table 1c. Continued.

Species	N	Mean Elevation	Elevational Increment											
			4.11	4.27	4.42	4.57	4.72	5.03	5.33	5.64	5.94			
<i>Symplocos tinctoria</i>	22	5.03 ± 0.92	1 0	4 7	3 4	5 0				1 1	2 7	1 2		
<i>Fagus grandifolia</i>	3	5.03 ± 0.92				5 1				1 0				
<i>Quercus michauxii</i>	12	5.05 ± 0.29			1 0	2 0		6 0						
<i>Persea borbonia</i>	74	5.14 ± 0.79	1 0	3 7	6 2	10 3	7 9	4 0	6 4	11 5	10 3			
<i>Rhus radicans</i>	26	5.17 ± 0.48		1 0	1 0	3 0	2 0	5 0	6 1	4 0	1 0			
<i>Mitchella repens</i>	21	5.17 ± 0.58	0 0	1 0	1 0	2 0			7 1	5 0	1 0			
<i>Gelsemium sempervirens</i>	2	5.17 ± 0.72				1 0				2 0				
<i>Quercus laurifolia</i>	19	5.30 ± 0.93	0 0	2 0	1 0			1 0	1 1		5 0			
<i>Anisostichus capreolata</i>	18	5.34 ± 0.65	0 0	0 0	1 0			4 0	3 1		3 0			
<i>Leucothoe axillaris</i>	146	5.34 ± 0.82	0 0	4 23	8 37	14 65	20 74	16 85	14 67	20 63	21 89			
<i>Vitis</i> spp.	32	5.37 ± 0.87		0 0	3 0	3 1	7 2	2 0	6 7	4 4	4 0			
<i>Quercus alba</i>	6	5.41 ± 0.11						1 0	3 1					
<i>Euonymus americana</i>	6	5.42 ± 0.61						1 0		4 0	1 0			
<i>Magnolia virginiana</i>	2	5.50 ± 1.00					2 0				1 0			
<i>Rosa palustris</i>	1	5.54							1 0					
<i>Ilex verticillata</i>	1	5.68								2 1				
<i>Ilex coriacea</i>	6	5.83 ± 1.01					5 3			4 0	1 0			
<i>Lonicera japonica</i>	19	5.85 ± 0.38						2 0	3 1	2 0	8 0			
<i>Lonicera sempervirens</i>	22	6.09 ± 0.23							1 0	4 0	12 1			
<i>Quercus nigra</i>	8	6.24 ± 0.37							1 0		5 0			
<i>Arundinaria gigantea</i>	5	6.26 ± 0.09									3 1			
% annual flooding frequency:			61	30	7	1	<0.1	0	0	0	0	0		
% growing season flooding frequency:			48	19	5	1	<0.1	0	0	0	0	0		
number of quadrats in increment:			68	46	43	27	9	28	24	11	35			
species richness:			20	27	30	25	16	21	23	19	22			

Appendix Table 1d. Relative frequency and relative percent cover of understory species (<1 m height) of downstream stand in elevational increments of 0.15 m and 0.30 m above datum. Zero indicates presence in numbers <0.49. For each data pair, relative density is listed on the left and relative basal area on the right. Mean elevation data include ± 1 standard deviation.

Species	N	Mean Elevation	Elevational Increment												
			2.46	2.61	2.76	2.92	3.07	3.37	3.68	4.14	4.59				
<i>Lyonia lucida</i>	4	2.69 \pm 0.05		1 0											
Liverworts	38	2.71 \pm 0.09	8 2	5 2	2 1										
<i>Saururus cernuus</i>	34	2.72 \pm 0.09	4 0	4 3	3 1										
<i>Itea virginica</i>	22	2.74 \pm 0.11	7 0	2 1	1 3	1 0									
<i>Hypericum</i> spp. L.	23	2.75 \pm 0.06		4 0	2 0										
<i>Boehmeria cylindrica</i> (L.) Swartz	14	2.78 \pm 0.22	4 0	1 0	1 0				1 0						
<i>Fraxinus</i> spp.	99	2.79 \pm 0.12	9 0	8 1	8 2	6 0	2 0								
<i>Nyssa</i> spp.	34	2.79 \pm 0.19	3 0	5 0	1 0	1 0	2 0								
<i>Taxodium distichum</i>	22	2.81 \pm 0.08	1 0	1	4 0										
Mosses	141	2.84 \pm 0.30	11 3	17 14	7 21	6 8	5 2	6 3	3 0	1 6					
<i>Decumaria barbara</i>	50	2.86 \pm 0.24		0 0	3 2	9 17	12 2	1 0							
<i>Campsis radicans</i> (L.) Seemann	23	2.87 \pm 0.12		1 0	2 0	4 6	1 0								
<i>Osmundia regalis</i> var. <i>spectabilis</i>	26	2.89 \pm 0.25		1 1	3 4	1 3									
<i>Cyrilla racemiflora</i>	7	2.94 \pm 0.36		0 0	1 0										
<i>Liquidambar styraciflua</i>	102	2.95 \pm 0.54	16 1	6 0	8 1	7 1	3 0	1 0		1 0				4 36	
<i>Woodwardia areolata</i>	232	2.96 \pm 0.39	20 92	17 71	13 25	14 51	19 58	17 43	10 11	1 0				3 0	
<i>Rubus hispidus</i>	8	2.98 \pm 0.18		0		2 0	2 0								
<i>Pinus taeda</i>	13	2.98 \pm 0.50		1 0	1 0	1 0	1 0			1 0					
<i>Carpinus caroliniana</i>	11	3.00 \pm 0.15			1 0	2 0	2 0								
<i>Smilax</i> spp.	142	3.11 \pm 0.60	14 1	8 2	8 1	9 0	11 5	8 3	8 2	7 1				7 2	
<i>Acer rubrum</i>	136	3.11 \pm 0.69	1 0	9 0	11 1	6 1	3 0	8 1	7 1	5 0				10 1	
<i>Rhus radicans</i>	109	3.12 \pm 0.59		3 2	8 9	13 8	11 9	8 3	3 0	2 0				7 1	
<i>Parthenocissus quinquefolia</i>	41	3.16 \pm 0.58		0 1	4 1	3 0	2 0	4 1	2 0	1 0				3 0	
<i>Euonymus americana</i>	10	3.18 \pm 0.39		0 0	0 0	2 0	1 0	1 0							
<i>Athyrium asplenoides</i>	1	3.19					1 1								
<i>Panicum</i> spp. L.	2	3.19 \pm 0.86	1 0												
<i>Viburnum nudum</i> L.	1	3.36													
<i>Ilex opaca</i>	8	3.45 \pm 0.62			0 0	1 0	2 0			1 0					
<i>Persea borbonia</i>	42	3.47 \pm 0.71		1 0	2 0	1 2	5 13	4 1	6 2	7 3				1 2	
<i>Leucothoe racemosa</i>	6	3.49 \pm 0.71		0 0	0 0		1 0	1 1	1 0	1 0					
<i>Osmundia cinnamomea</i>	9	3.51 \pm 0.69		0 0			2 3		1 4	2 0					
<i>Vaccinium</i> spp.	3	3.54 \pm 0.64			0 0				1 5						
<i>Quercus laurifolia</i>	1	3.70													
<i>Clethra alnifolia</i>	25	3.79 \pm 0.66				1 1	4 1	7 23	6 14	3 2				3 5	
<i>Mitchella repens</i>	74	3.84 \pm 0.82		1 0	1 0	5 0	4 3	14 8	13 10	15 2				14 2	
<i>Magnolia virginiana</i>	4	3.87 \pm 0.79			0 0				1 0	2 1					
<i>Gelsemium sempervirens</i>	3	3.98 \pm 0.29							1 0	1 0					
<i>Liriodendron tulipifera</i>	4	4.00 \pm 0.99			0 0				1 0	1 0				1 0	
<i>Vitis</i> spp.	24	4.03 \pm 0.72				2 0	2 1	1 0	2 1	10 5				6 20	

Appendix Table 1d. Continued.

Species	N	Mean Elevation	Elevational Increment														
			2.46	2.61	2.76	2.92	3.07	3.37	3.68	4.14	4.59						
<i>Anisostichus capreolata</i>	17	4.09 ± 0.69		0	0	0	0	1	0			4	1	5	1	6	0
<i>Quercus</i> spp.	18	4.18 ± 0.94			0	0		1	0			1	0	3	0	6	0
<i>Leucothoe axillaris</i>	27	4.26 ± 0.43										1	5	16	74	3	10
<i>Quercus michauxii</i>	11	4.42 ± 0.78						1	0					2	0	4	1
<i>Symplocos tinctoria</i>	14	4.50 ± 0.84										1	0	4	3	6	7
<i>Hexastylis virginica</i> (L.) Small	2	4.51 ± 0.02												2	0		
<i>Hexastylis arifolia</i>	4	4.80 ± 0.58												2	0		
<i>Asimina triloba</i>	5	4.81 ± 0.92												1	0		
<i>Hamamelis virginiana</i> L.	4	5.35 ± 0.36															
% annual flooding frequency:			61	29	7	1	1	<0.1	0	0	0	0	0	0	0	0	0
% growing season flooding frequency:			56	27	8	1	1	<0.1	0	0	0	0	0	0	0	0	0
number of quadrats in increment:			20	92	66	25	31	12	18	15	12	18	29	26	26	20	20
species richness:			13	28	31	22	26	21	29	26	21	29	29	26	26	20	20

Appendix Table 2. Selected environmental characteristics of segments derived from detrended correspondence analysis. Data are means followed by the standard deviation. For Stand, B = plots from both stands, U from upstream stand, D from downstream stand.

Environmental Variable	Detrended Correspondence Analysis Group			Stand
	Wet	Transitional	Mesic	
% sand in the A horizon		62.7 (8.4)	73.1 (4.4)	B
		63.3 (9.0)	73.3 (4.1)	U
	53.3 (14.5)	60.8 (7.6)	72.5 (7.1)	D
% clay in the A horizon		19.8 (5.4)	13.4 (2.7)	B
		20.6 (5.7)	14.2 (1.3)	U
	26.9 (9.6)	17.5 (4.3)	11.3 (5.3)	D
% sand in the B horizon		65.6 (8.6)	72.8 (7.3)	B
		65.8 (9.8)	73.8 (8.3)	U
	66.1 (3.8)	65.0 (4.3)	70.0 (0.0)	D
% clay in the B horizon		21.0 (4.9)	16.6 (5.5)	B
		20.8 (5.0)	17.1 (6.4)	U
	18.3 (3.3)	21.7 (5.8)	15.0 (0.0)	D
% organic matter		3.8 (1.1)	3.0 (0.9)	B
		3.8 (1.0)	3.2 (0.9)	U
	2.7 (1.5)	4.1 (1.4)	2.4 (0.9)	D
pH		3.8 (0.2)	3.9 (0.3)	B
		3.7 (0.1)	3.9 (0.2)	U
	4.3 (0.2)	4.1 (0.1)	4.1 (0.6)	D
Cation exchange capacity, cmol _c /kg		10.0 (5.3)	5.5 (1.4)	B
		11.3 (5.6)	5.7 (0.9)	U
	10.3 (2.9)	6.1 (1.0)	4.9 (2.8)	D
Exchangable acidity, cmol _c /kg		8.2 (4.2)	4.8 (1.3)	B
		9.3 (4.4)	5.0 (1.0)	U
	6.3 (2.2)	4.9 (0.9)	4.2 (2.6)	D
% base saturation		18.1 (3.4)	14.0 (5.2)	B
		17.7 (3.7)	13.5 (5.6)	U
	39.0 (10.1)	19.3 (2.3)	15.5 (5.0)	D
Calcium, cmol _c /kg		0.8 (0.4)	0.4 (0.1)	B
		0.9 (0.4)	0.4 (0.2)	U
	2.2 (1.0)	0.6 (0.1)	0.4 (0.1)	D
Magnesium, cmol _c /kg		0.3 (0.2)	0.2 (0.1)	B
		0.4 (0.2)	0.2 (0.1)	U
	0.6 (0.3)	0.3 (0.0)	0.2 (0.0)	D
% flooding in the growing season		11.2 (11.5)	0.1 (0.1)	B
		15.0 (10.9)	0.1 (0.1)	U
	14.2 (9.2)	0.0 (0.0)	0.0 (0.0)	D