A Gradient Analysis of Understory Vegetation in a Sugarberry-Elm Floodplain Forest on the Brazos River

Perry J. Grissom
David B. Wester*
Department of Range, Wildlife, and Fisheries Management
Texas Tech University, Lubbock 79409

ABSTRACT

Relationships between understory vegetation pattern, topography, flooding, and soil properties were studied in a bottomland hardwood forest on the lower Brazos River floodplain. Elevation varied 30 to 70 cm along 220-m transects in 3 study sites. We infer that a microtopographically-induced soil aeration gradient influenced understory vegetation pattern. Swales were flooded from autumn through spring and supported species-poor vegetation dominated by *Panicum gymnocarpon*. Unflooded areas supported more diverse vegetation varying in composition along an elevation gradient: *Carex cherokeensis* characterized lower elevations, with dominance gradually shifting to *Oplismenus hirtellus* on slightly elevated ridges. Vegetation pattern was strongly related to relative elevation and soil water content as well as to abundance of clayey horizons in the soil profile, and soil copper, iron, phosphorous, potassium, and salinity.

KEYWORDS: Floodplain, understory, vegetation pattern, flooding, Brazos River

On river floodplains, duration, frequency, and timing of flooding influence plant distribution (Huenneke, 1982; Bren, 1993). Smith and Linnartz (1980; p. 154) wrote that in the flat terrain of river flood plains, "even slight variations in elevation are associated with considerable differences in soils, drainage conditions, and forest species composition." Even periodically flooded soils develop distinct morphological features that can be used to infer soil saturation (Megonigal et al., 1993). An elevation-induced flooding gradient affects many chemical, physical, and biological factors which in turn influence vegetation pattern (Gauch and Stone, 1979). Jones et al. (1994) indicated that the fine-scale effects of flooding as related to microtopographic relief have only recently been quantified; much of this work has dealt with tree species (e.g., Streng et al., 1989). There is less information on elevation-induced flooding effects on understory vegetation.

This study investigated understory vegetation patterns in a bottomland hardwood forest along the Brazos River, Texas, in relation to microtopography and its effects on flooding regime. We examined hydrologic and edaphic properties in order to correlate variation in hydrology, soils, and vegetation.

This is manuscript no. T-9-785, College of Agricultural Sciences and Natural Resources, Texas Tech University, Lubbock, TX 79409. *Corresponding author.

STUDY AREA

The study site is in the Gulf Coastal Plain Physiographic Province (Thornbury, 1965) on Sienna Plantation, a private land holding of about 3,000 ha in Fort Bend County, Texas (29°30' N, 95°30' W). The plantation, about 32 km southwest of Houston, lies on the east bank of the Brazos River. Elevation on the plantation ranges from 15 to 20 m above mean sea level. The area was settled by Anglo-Americans in about 1822, and by the end of the 1850s the site was part of the largest cotton and sugar plantation in Texas. The plantation was financially destroyed during the Civil War; it was divided and has been farmed and grazed under various landowners since that time (Wharton, 1939; Christensen, 1982).

Climate at Sienna is warm with a long growing season and a frost-free period usually exceeding 280 days. Annual precipitation averages about 110 cm and is distributed evenly throughout the year. Average annual temperature is 22° C, the hottest months being July and August (Mowery et al., 1960; National Oceanic and Atmospheric Administration, 1996).

The study was conducted on the floodplain of the Brazos River. Soils are classified as Miller Clay, although profiles deviate from the Natural Resource Conservation Service (NRCS) description for that series (Mowery et al., 1960). Flats and swales are fine, mixed, thermic Vertic Haplustolls, and ridges are fine, loamy, mixed, thermic Typic Haplustolls (Grissom, 1987). Study sites are level areas of heavy clay alluvium, with coarser horizons often present. Small channels, less than 1 m deep with gently sloping sides, are present within these flats. Still or very slowly moving water is present in these swales generally from autumn through spring. Floodplain deposits have characteristic morphological features created by the movement of a river through sediments and by periodic overbank flows. Standard nomenclature for floodplain features (Putnam et al., 1960; Hosner and Minckler, 1963; Smith and Linnartz, 1980) will be followed here, except that flooded depressions are called swales (instead of sloughs) to indicate their gentle slope, slight elevational variation, and relatively short flood duration. Ridges and flats remained above floodwaters during the period of observation and generally had similar soils and vegetation and are collectively referred to as flats unless otherwise noted.

Flats are dominated by sugarberry (*Celtis laevigata*), green ash (*Fraxinus pensylvanica*), and elm (*Ulmus crassifolia* and *U. rubra*) (scientific nomenclature generally follows Correll and Johnston, 1970). Other common species include pecan (*Carya illinoinensis*), soapberry (*Sapindus saponaria*), and woolly bucket (*Bumelia lanuginosa*). Subcanopy species include deciduous holly (*Ilex decidua*), hawthorn (*Crataegus invisa, C. Marshallii, C. texana*), and rough-leaf dogwood (*Cornus drummondii*). Average tree density is 950 trees/ha, basal area averages 26.5 m^2/ha, and average canopy height is 20 to 23 m. The most common vines are Virginia creeper (*Parthenocissus quinquefolia*) and poison ivy (*Toxicodendron radicans*). Shrubs are uncommon (8.2% frequency) and of small stature, usually less than 0.5 m tall. The most abundant species are small, erect greenbrier (*Smilax* spp.) plants; others include dewberry (*Rubus trivialis*) and coralberry (*Symphoricarpos orbiculatus*). Herbaceous vegetation in unflooded sites is dominated by grasses and sedges (31.7 and 43.1% frequency, respectively), with the most common species being *Carex cherokeensis, C. amphibola,* and *Oplismenus hirtellus.* Forbs have a frequency of 5%; *Ruellia pendunculata, Polygonum virginicum,* and *Sanicula canadensis* are the most common species. Grissom (1987) provides a complete vegetation description.

Seasonal soil saturation and flooding in low areas occur from fall through spring, a consequence of flat relief and impermeable, heavy clay soils. Additionally, temporary ponded water may be found following heavy rains. The incised nature of the Brazos River within its floodplain has made overbank flow uncommon (Campbell, 1925). Thus, poor internal drainage has probably been the most important factor contributing to site flooding.

METHODS

A 40 x 220 m transect was established in each of three study sites to sample soils and vegetation in topography ranging from flats to swales. Study sites were separated by roads, ditches or natural drainages and thus drained independently. The long axis of each transect was oriented at right angles to swales. Elevation was measured with transit and rod to the nearest 0.03 cm at 2-m intervals along two parallel lines running the length of each transect. Elevation was relativized by subtracting the lowest recording from all other recordings for each transect.

Vegetation and soils were sampled in five macroplots (10 x 40 m) positioned randomly along each transect with the constraint that the plot did not include obvious disturbance caused by windthrow (Mueller-Dombois and Ellenberg, 1974). Each macroplot was oriented with its long axis perpendicular to the transect (and parallel to the swale). Relative elevation was calculated for each macroplot by averaging four elevation readings, two from each surveyed line nearest the intersection of that line and the macroplot main axis.

Vegetation data were collected along four, 40-m lines randomly placed parallel to the long axis in each macroplot. Understory species frequency was recorded along each line in 25 randomly located 10 x 10 cm quadrats. Plot size was determined after preliminary sampling (Greig-Smith, 1983). Species frequency was also recorded at 2-m intervals along each 220-m transect. Vegetation sampling was conducted in transects 1 and 2 in July and August, 1985, and in transect 3 in August, 1986. A canopy photograph was taken during vegetation sampling at each macroplot center with a 150-degree fish-eye lens, and a canopy closure was estimated following Brown (1962).

Water level was recorded at swale macroplot centers monthly from August, 1985 to August, 1986. Water levels of two creeks (Oyster Creek and Cow Bayou) and a ditch (Water's Ditch) (constructed ca. 1850) were also monitored during portions of this period to aid in understanding drainage relationships within the site. Weather data were collected from the nearest recording station approximately 4 km west of the study site.

Soil gravimetric water content (Gardner, 1965) was sampled at four locations in each macroplot of transects 1 and 2 during the driest period of the year (August, 1985), soon after initial flooding of swales (November, 1985), and just before dry-down after swales had been flooded for several months (March, 1986). Soil nutrient status [calcium, copper, iron, magnesium, maganese, nitrogen (NO3), phosphorous, potassium, sodium, zinc], pH, and salinity were determined from five samples taken from random locations in each macroplot of transect 1 in April 1987. Analyses were performed by the Texas A&M Soil Testing Laboratory, Lubbock. Soil samples for nutrient analysies were collected from the A horizon at a 12 to 18 cm depth. Comparisons between swales and flats were made with a student's t test.

Soil pits were dug near the centers of macroplots 1 and 2 (transect 1) and macroplots 25 and 26 (transect 3) for profile description. One 10-cm auger hole, about 150 cm in depth, was placed near the center of each of the 11 remaining macroplots to allow gross examination of the profile. Clay content (as indicated by relative amount of profile made up of clayey horizons) was determined for each soil pit and augur hole.

Vegetation data were collected along each of 4 transects in each macroplot; however, only one recording of relative elevation and clay content was made for each macroplot.

Reciprocal averaging (RA) (Hill, 1973; cf. detrended correspondence analysis, Wartenberg et al., 1987) of vegetation data was used for ordination analyses, with relative elevation and clay content included as supplementary variables (Gauch and Stone, 1979). Canonical correspondence analysis (e.g., ter Braak, 1986; Palmer, 1993) of vegetation data, relative elevation, and clay content was not used because there were more vegetation sampling points (4 transects per macroplot) than sampling points for relative elevation and soil clay content (1 sampling point per macroplot). Standardized principal components analysis of vegetation and soil data was used to establish correlations between soil properties and principal components. Coordinated patterns in these analyses were used to explain vegetation pattern related to soil characteristics and microtopography. Species occurring in only one sample (consisting of 25, 10 x 10 cm quadrats) were deleted (Gauch, 1982). Frequency data recorded at a 2-m intervals along the 220-m transects were ordinated and plotted in a trace diagram using axis I (Whittaker et al., 1979). Trace analysis was strongly influenced by outliers, and species occurring in 2% or less of plots in a transect line were omitted.

Similarity of macroplots was quantified in paired comparisons of presence-absence data using a coefficient of community (Whittaker, 1975). Pearson's correlation coefficient was used to examine relations between water levels and weather data.

RESULTS

Site Flooding Regime

Elevation varied most on transect 1, with a vertical difference of 71.9 cm over a 220-m distance; transects 2 and 3 were flatter (Table 1). Swales in transects 1 and 2 were flooded during January, March, and as late as the end of May, 1985 (pers. obs.). Swales (marcroplots 2, 4, and 8) were flooded in November, 1985 and retained standing water until March, 1986 (Table 1). Macroplot 8 had very little water in March 1986 and by April had no standing water. Macroplots 2 and 4 had relatively deep water in March, but were drying rapidly with water levels dropping 3.2 and 1.3 cm, respectively, in 3 days. In April, only scattered puddles remained in macroplots 2 and 4, and by May they had drained, although the soil was still moist.

Water levels in swales and major drainages were strongly negatively correlated with seasonal variation in temperature; correlations between water levels and mean monthly precipitation were weaker (Table 2). Poor correlation between water levels and precipitation may be partly related to differences in rain received at the weather station (4 km distant) and rain received at the site.

Table 1. Topographic, edaphic, and hydrologic data from study plots. Clay in profile is the relative amount of the top150 cm of the soil profile made up of clayey horizons.

				Vertical distance above water level (cm)							Gravimetric water content (%)		
Tran-sect	Macro-plot	Relative elevation (cm)	Clay in profile (%)	Aug-Oct 1985	Nov. 1985	Dec. 1985	Jan. 1986	Feb. 1986	Mar. 1986	Apr-Aug. 1986	Aug. 1985	Nov. 1985	Mar. 1986
1	1	65.5	53.3	-[1]	54.6	49.4		50.6	57.0	-	23.8	34.5	29.2
	2*[2]	3.1	100.0	-	-8.2	-13.4	(not	-12.2	-5.8	-	32.9	55.8	54.5
	3	52.1	46.7	-	39.6	37.3	mea-	32.6	35.1	-	25.1	36.7	37.5
	4*[3]	21.0	96.7	-	8.5	6.1	sured)	1.5	4.0	-	28.2	49.5	48.5
	5	37.5	76.7	-	25.0	22.6		18.0	20.4	-	27.1	40.7	38.2
2	6	25.3	100.0	-	13.7	11.3	13.1	13.4	-	-	29.6	52.3	45.0
	7	23.5	100.0	-	11.9	9.5	10.1	11.6	-	-	29.7	48.2	46.8
	8*	3.7	100.0	-	-0.9	-3.4	-1.5	-1.2	-	-	34.9	60.5	60.1
	9	18.6	100.0	-	7.0	4.6	6.4	6.7	-	-	29.4	49.5	46.2
	10	22.0	100.0	-	10.4	7.9	9.8	10.1	-	-	29.0	48.4	46.6
3	24	22.0	86.7										
	25	17.7	81.7										
	26*	4.9	100.0				(not measured)						
	27	20.7	86.7										
	28	18.9	86.7										

[1] Dash indicates that transect was not flooded.
[2] An asterisk indicates that the macroplot was located in a swale.
[3] Macroplot was flooded even though average plot elevation exceeded elevation of standing water.

Topo-edaphic Parameters

The soil profile on ridges of transect 1 was made up of very fine sandy loam horizons alternating with clays or silt loams (Table 1; see Grissom, 1987 for complete profile descriptions). Similar clay horizons were present in a swale 40 m away; however, coarser horizons were absent. The absence of coarse horizons, regardless of topographic position, distinguished soils on transect 2 from those of transects 1 and 3.

Soil water content was higher in swales than in adjacent flats during dry periods (August, 1985) and with "normal" flooding (November, 1985 and March, 1986) (Table 1). Soil pH was slightly alkaline. Soil Ca, Mg, Mn, N, Na, and Zn exhibited as much variability within macroplots as between macroplots of swales and flats. Soil Cu, Fe, P, K, and salinity were much higher in swales than in flats (Table 3). Flooding-induced accumulation of organic matter was noted at the soil surface in swales (see Ponnamperuma, 1984). Soil structure of clayey horizons was similar in swales and flats.

Table 2. Correlation of weather and water levels of macroplots and other drainages on study site.

	Current Month		Previous Month	
Location	Temp.	Precip.	Temp.	Precip.
Plot 2	-0.80 [1]	-0.01	-0.52	0.37
	0.0032 [2]	0.9834	0.1044	0.2684
Plot 4	-0.71	-0.51	-0.81	-0.29
	0.0144	0.1090	0.0023	0.3895
Plot 8	-0.74	0.01	-0.36	0.62
	0.0061	0.9997	0.2571	0.0309
Oyster Creek	-0.71	0.46	-0.27	0.44
	0.0317	0.2114	0.4785	0.2306
Cow Bayou	-0.95	-0.69	-0.91	0.37
	0.0130	0.1959	0.0305	0.5357
Water's Ditch	-0.60	-0.42	-0.62	-0.05
	0.2846	0.4804	0.2674	0.9323

[1] Correlation coefficient.
[2] Significance level.

Principal components analysis of data from transect 1 was used to estimate correlations between soil nutrients and principal components. Relative elevation, soil water content, clay (%), and soil Cu, Fe, P, K, and salinity were strongly related to principal component 1 (Table 4), which was interpreted as an elevation-induced soil aeration gradient (see below).

Table 3. Mean (standard deviation) of soil properties in study plots. Nutrients are expressed in parts per million. Gravimetric water content (GWC) is expressed as a percentage.

Soil Property	Flats		Swales	
pH	7.72	(0.19)	7.62	(0.11)
N	4.5	(3.7)	5.1	(4.3)
P	39.5	(10.6)	60.9	(11.1)
K	580	(119)	766	(78)
Ca	24,320	(7,899)	26,248	(6,019)
Mg	1,053	(202)	1,070	(59)
Salinity	427	(43)	508	(60)
Zn	0.91	(0.26)	1.07	(0.20)
Fe	23.9	(4.6)	45.4	(13.5)
Mn	13.0	(3.6)	15.3	(3.1)
Cu	2.2	(0.4)	3.4	(1.3)
Na	96	(25)	112	(17)
August GWC	25.3	(2.2)	30.6	(2.8)
November GWC	37.3	(3.0)	52.6	(6.9)
March GWC	34.9	(4.9)	51.5	(4.4)

Table 4. Correlation of environmental variables with principal component 1 from an analysis of environmental and vegetation data.

Variable	r
Salinity (ppm)	0.9895
Nov. water content (%)	0.9739
Clay (%)	0.9716
P (ppm)	0.9651
K (ppm)	0.9608
Fe (ppm)	0.9606
Relative elevation (cm)	-0.9550
March water content (%)	0.9405
Cu (ppm)	0.9395
Aug. water content (%)	0.8954
Zn (ppm)	0.6517
Na (ppm)	0.6001
Ca (ppm)	0.3746
Mg (ppm)	0.3086

Vegetation

Reciprocal averaging ordination showed clear trends in plot and species ordinations related to topography. Frequency lines from swales were on the positive end of axis I, whereas those of flats were on the negative end of this axis and aligned along axis II (Fig. 1). In addition, the alignment of frequency lines from flats along axis II roughly paralleled changes in relative elevation, with frequency lines of macroplot 1 having the highest relative elevation and those of macroplot 25 the lowest. Relative elevation was ordinated among transects 1 and 2 (with the highest macroplot elevation), and clay was plotted to the right toward swales.

Little overlap between different transects was due principally to occurrence of stand-specific species. Species characteristic of swales (e.g., *Cardamine bulbosa, Panicum gymnocarpon, Leersia lenticularis*) were on the positive end of axis I (Fig. 1, right). Species common in flats (e.g., *Oplismenus hirtellus, Smilax* spp., *Carex cherokeensis*) were aligned parallel to axis II in order of their abundance along a relative elevation gradient (also see Fig. 2). Species common to both flats and swales (e.g., *Celtis laevigata* seedlings, *Carex tribuloides*) were ordinated between species of flats and swales. The transition from swale to flat was quite distinct in the ordination, and few species were shared between the two types.

Reciprocal averaging can be used as a divisive technique to examine relations within subsets of data (Gauch, 1982). When plots located in swales were removed prior to analysis, frequency lines (Fig. 3, left) and species (Fig. 3, right) were arranged along axis I in very nearly the same order as they were arranged along axis II in the ordination of the full data set (Fig. 1). The arch effect exhibited in Fig. 3 often indicates that there is only one major direction of variation in these data (e.g., Werger et al., 1978). Similarities in ordination results between Fig. 1 (complete data set) and Fig. 3 (excluding swales) shows how little effect the removal of species common to swales had on ordination of species of flats, suggesting that the two habitats each support distinct vegetation.

Ordination of frequency plots placed along the 220-m transect lines also suggested the existence of 2 distinct vegetation types (Fig. 4). Within swales, RA scores were similar and quite different from scores in higher, unflooded flats. Depth of a swale appears of little importance in determining vegetation type: both shallow and deep swales were inhabited by *Panicum gymnocarpon* with few other species present. Continuous variation of species distributions within flats, as well as the lack of overlap between swales and flats, contributed to a noticeable separation of RA scores along axis I.

Mean of similarity comparisons using coefficient of community was 0.645 among flats and 0.357 among swales. Plots in flats generally had a consistent group of core species (e.g., *Carex cherokeensis, Oplismenus hirtellus, Ruellia pedunculata, Leersia virginica*) which is reflected in relatively high coefficient of community. Swales were characterized by one ubiquitous dominant (*Panicum gymnocarpon*) and a small set of relatively uncommon species whose sporadic occurrence lowered the coefficient of community. The mean of flat/swale comparisons was 0.18, indicating little floristic overlap and supporting ordination results suggesting the existence of two relatively distinct herbaceous communities.

Species richness tended to increase with relative elevation (Fig. 5). This may be caused in part by an exchange of dominants along the gradient from flooded swales to more droughty flats and ridges (Table 1; Whittaker, 1972; Prach, 1986).

Table 5. Species abbreviations used in reciprocal averaging ordination diagrams (Figs.1, 2, and 3).

Abbreviation	Scientific name	Common name
An	*Acer negunda*	Box elder
Ap	*Asclepias perennis*	Swamp milkweed
Br	*Bignonia radicans*	Trumpet-creeper
Ca1	*Carex amphibola*	Sedge
Ca2	*Carex* sp.	Sedge
Cb	*Cardamine bulbosa*	Spring-cress
Cc	*Carex cherokeensis*	Sedge
Cl	*Celtis laevigata*	Texas sugarberry
Ct	*Carex tribuloides*	Sedge
Db	*Dicliptera brachiata*	
Di	*Dichondra* sp.	Pony's foot
Dl	*Dicanthelium lindheimeri*	Lindheimer panic
Dt	*Desmodium tortuosum*	Tick-clover
Ec	*Elepantopus carolinianus*	Elephant's foot
El	*Eleocharis* sp.	Spikerush
Ev	*Elymus virginicus*	Virginia wildrye
Fp	*Fraxinus pensylvanica*	Green ash
Jl	*Justicia lanceolata*	Lance-leaved willow-water
Ll	*Leersia lenticularis*	Catchfly grass
Lv	*Leersia virginica*	White grass
Ma	*Malvaviscus arboreus*	Turk's cap
Mm	*Melica mutica*	Two-flower melic
Ms	*Muhlenbergia schreberi*	Nimblewill muhly
Oh	*Oplismenus hirtellus*	Basketgrass
Pg	*Panicum gymnocarpon*	Beaked panic
Pl1	*Paspalum langei*	Rustyseed paspalum
Pl2	*Phyla lanceolata*	Northern frog-fruit
Pq	*Parthenocissus quinquefolia*	Virginia creeper
Pv	*Polygonum virginicum*	Jump-seed
Rp	*Ruellia pedunculata*	
Rt	*Rubus trivialis*	Southern dewberry
Sc	*Sanicula canadensis*	Black snake-root
Sm	*Smilax* sp.	Green-brier
So1	*Solidago* sp.	Goldenrod
So2	*Symphoricarpos orbiculatus*	Coral-berry
Ss	Sapindus saponaria	Soapberry
Tr	*Toxicodendron radicans*	Poison Ivy
Ul	*Ulmus* sp.	

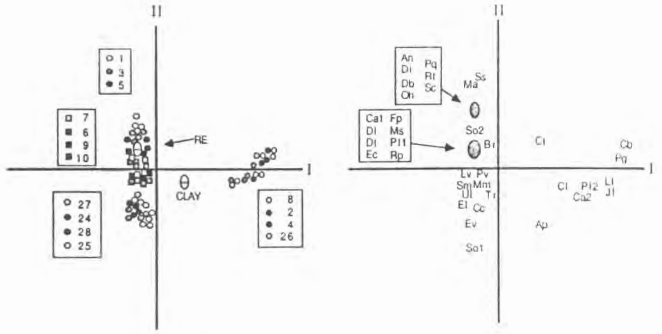

Figure 1. Reciprocal averaging ordination of transects 1, 2, and 3. Left: macroplot ordination; environmental variables are relative elevation (RE) and relative clay content of profile. Right: species ordination; species abbrevations are listed in Table 5.

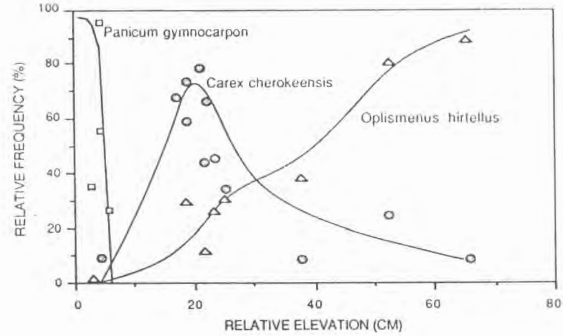

Figure 2. Abundance of 3 common herbaceous species in relation to relative elevation. Abundance is expressed as frequency by macroplot (1 set of 4 frequency lines). Curves are drawn free hand.

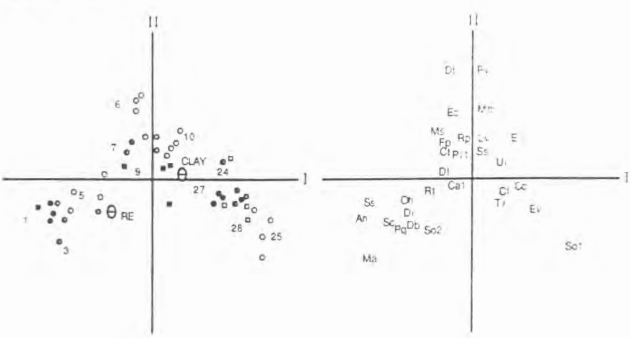

Figure 3. Reciprocal averaging ordination of plots from flats of transects 1, 2, and 3. Left: plot ordination; environmental parameters are relative elevation (RE) and relative clay content of profile. Right: species ordination; species abbreviations are listed in Table 5.

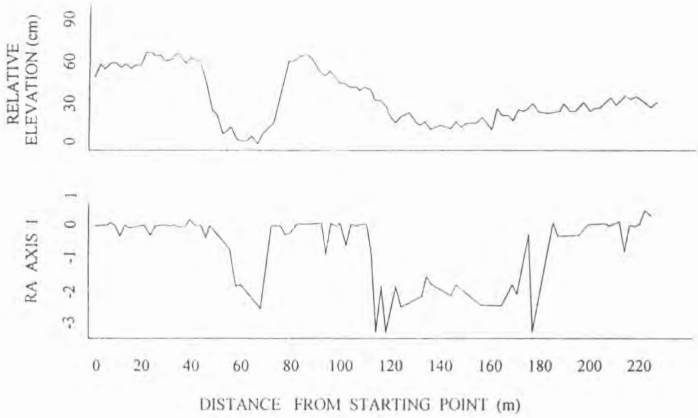

Figure 4. Bottom: trace diagram of frequency plots from transect line of transect 1. Reciprocal averaging (RA) score for axis I is plotted by plot location. Top: relative elevation along transect line.

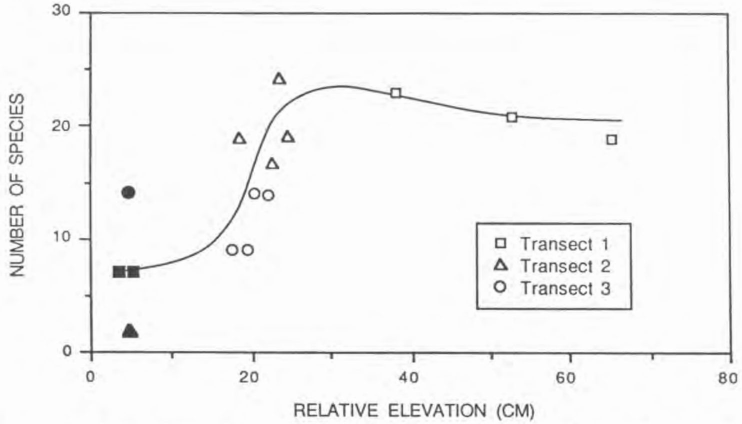

Figure 5. Understory vegetation richness as affected by relative elevation. Richness is express as the number of species occurring within one macroplot (1 set of 4 frequency lines).

Changes of abundance of three common species (*Panicum gymnocarpon, Carex cherokeensis,* and *Oplismenus hirtellus*) as a function of relative elevation (Fig. 2) suggests differential species response to a soil aeration gradient (Table 1). A mixture of species occupied flats with dominance gradually shifting with changing relative elevation. In contrast, swales were dominated by one species (*Panicum gymnocarpon*) whose distribution was confined to seasonally flooded areas.

Herb species diversity and canopy closure (which varied less than 9%) were uncorrelated (Grissom, 1987). Similar results were found by Collins and Pickett (1982, 1987) and Moore and Vankat (1986). The small and widely spaced gaps in our study area probably had little effect on large-scale understory vegetation pattern, and although small patches of understory vegetation may be greatly influenced by these gaps, our sampling was not designed to detect such an effect.

DISCUSSION AND CONCLUSIONS

Floodplain microtopography and edaphic characteristics are products of flooding history. Initial alluvial landscape affects speed and distribution of subsequent floodwaters and, therefore, sediment deposition. Resulting variation in topography and soils produces a mosaic of differentially aerated sites (Wolman and Leopold, 1957; Allen, 1965) which may strongly affect patterns of plant growth (Ewing, 1996) and survival (Robertson et al., 1978; Huenneke, 1982). Thus, seasonal flooding along rivers is an important regulating influence of species richness (Nilsson et al., 1997).

Two basic types of environment, the result of landscape and flooding history, are manifested in the microtopography of our study site and are reflected in edaphic properties and vegetation patterns. Flats and ridges are elevated above standing water and often have coarse-textured horizons interspersed with clayey-textured horizons. Swales hold water during cooler months, have higher soil water content during most of the year, and have soils composed entirely of clays. Swales also had higher concentrations of soil Fe, Cu, P, and K, and were more saline than flats. Vegetation patterns are attributed to microtopographically-induced variation in flooding frequency and duration and its impacts on soil (see Robertson et al., 1978; Gauch and Stone, 1979). Topographic, edaphic, and hydrologic factors are interrelated, and it is difficult to separate and define the nature and magnitude of their individual influences (Struik and Curtis, 1962; Anderson et al., 1969; Bratton, 1976).

Floodplain vegetation has been related to elevation-induced differences in flooding regime and to changes in soil pH, Ca, Mg, and N (Parsons and Ware, 1982; Dunn and Stearns, 1987a, b). Gauch and Stone (1979) found pH, Ca, Mg, Mn, and K related to flooding. These soil parameters appeared to vary independently of elevation and flooding on Sienna and were not related to vegetation pattern. Different climate, soils, parent material, biota, and hydrologic regime, as well as temporal variation, may contribute to the difference in results between other sites and Sienna.

Flooding has been observed to reduce tree, shrub, and herbaceous richness (Bell 1974; Frye and Quinn, 1979; Robertson et al., 1978). In contrast, Nilsson et al. (1997) have recently shown that impounding rivers and decreasing flooding frequency can reduce species diversity. Herbs may be less sensitive to microhabitat differences than trees (Collins and Pickett, 1982; Huenneke, 1982), and thus plant strata within a community may sometimes exhibit different responses to the same gradient.

Understory vegetation on Sienna showed strong spatial patterns related to microtopography. *Panicum gymnocarpon* dominated species-poor swales. Leaves and stems of this species growing above normal water levels may diffuse oxygen downward from aerial to submerged plant parts (e.g., Armstrong, 1978; Hook, 1984). Additionally, the ability to root at nodes improves flooding tolerance by concentrating roots in better-aerated surface soil. These adaptations are shared by other species as well, for example *Leersia lenticularis.* Ruderal strategy was exhibited by *Solidago* sp., *Cardamine bulbosa, Justicia lanceolata,* and *Phyla lanceolata,* all of which colonized swales in summer after floodwaters disappeared. The latter species are perennials, but acted as annuals in this case, similar to floodplain perennials studied by Rogers (1982). Thus, although species richness increased during periods of drawdown, *Panicum gymnocarpon* was a predictable dominant in these habitats, and its success may be attributable to longevity and morphological features promoting flooding tolerance. In the context of vegetation dynamics, composition of swales is, therefore, generally predictable throughout the cyclic course of seasonal flooding and drawdown (van der Valk, 1981).

Flats, unaffected by seasonal flooding, supported more diverse vegetation than swales. Sedges and grasses dominated, but many forb, vine, and shrub species were also present. This vegetation reflected a soil moisture gradient. This transition, however, was spatially more gradual than that between swales and flats. Species composition shifted gradually from low flats dominated by *Carex cherokeensis* to ridges dominated by *Oplismentus hirtellus.*

Understory species richness is an important aspect of vegetation pattern and is influenced by both environment and biota (Whittaker, 1965; Robertson et al., 1978; Prach, 1986). Severe and unstable conditions usually lower diversity with few species being adapted to such harsh environments. Whittaker (1972; p. 237) wrote that extreme conditions act as a "filter, demanding adaptations for which not all genetic lines have the potentiality." In this bottomland hardwood forest, herbaceous vegetation formed two separate types in response to flooding: (1) a simple, species-poor type in swales where few species were able to tolerate the stressful and unstable conditions associated with seasonal and annual variation common in the flooding of these minor drainages; and (2) a species-rich type in unflooded areas, in which species showed relatively continuous distributions along a moisture gradient from low flats to ridges.

ACKNOWLEDGMENTS

We wish to thank the Johnson Corporation, Houston, Texas and the State of Texas for funding. B.L. Allen and R.E. Zartman described soils. Many others provided vital assistance during various phases of this study, and special thanks are due C. Britton, L. Brown, M. Henschen, G. McPherson, R. Sosebee, J. Weigel, R. Wickwire, D. Williams, J. Wipff, and the employees of Fuqua Industries.

REFERENCES

Allen, J.R.L. 1965. A review of the origin and characteristics of recent alluvial sediments. Sedimentology, 5:89-191.

Anderson, R.C., O.L. Loucks, and A.M. Swain. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. Ecology, 50:255-263.

Armstrong, W. 1978. Root aeration in wetland conditions, p. 269-297. *In:* D.E. Hook and R.M.M. Crawford (eds.). Plant life in anaerobic environments. Ann Arbor Science, Ann Arbor, Michigan.

Bell, D.T. 1974. Studies on the ecology of a streamside forest: composition and distribution of vegetation beneath the tree canopy. Bull. Torrey Bot. Club, 101:14-20.

Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. Am. Nat., 110:679-693.

Bren, L.J. 1993. Riparian zone, stream, and floodplain issues. J. Hydrol. 150:277-299.

Brown, H.E. 1962. The canopy camera. U.S. For. Serv., Rocky Mtn. For. Range Expt. Sta., Sta. Pap. 72. 22 p.

Campbell, E.G. 1925. Plant relations in Brazos County, Texas, with special reference to eastern and western types. Ecology, 6:163-170.

Christensen, R. 1982. Historic, romantic Richmond: 1822-1982. Nortex Press, Burnet, Texas. 175 p.

Collins, B.S. and S.T.A. Pickett. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwood forest. Vegetatio, 70:3-10.

Correll, D.S. and M.C. Johnston. 1970. Manual of the vascular plant of Texas. Texas Research Foundation, Renner, Texas. 1881 p.

Dunn, C.P. and F. Stearns. 1987a. Relationship of vegetation layers to soils in southeastern Wisconsin forested wetlands. Am. Midl. Nat., 118:366-374.

Dunn, C.P. and F. Stearns. 1987b. A comparison of vegetation and soils in floodplain and basin forested wetlands of southeastern Wisconsin. Am. Midl. Nat., 118:375-384.

Ewing, K. 1996. Tolerance of four wetland plant species to flooding and sediment production. Env. and Exp. Bot. 36:131-146.

Frye, R.J. and J.A. Quinn. 1979. Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. Bull. Torrey Bot. Club, 106:334-335.

Gardner, W.H. 1965. Water content, p. 82-101. *In:* C.A. Black (ed.).Methods of soil analysis. Am. Soc. Agronomy, Inc., Publ., Madison, Wisconsin.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge. 298 p.

Gauch, H.G. and E.L. Stone. 1979. Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. Am. Midl. Nat., 102:332-345.

Greig-Smith, P. 1983. Quantitative plant ecology, 3rd ed. Univ. Calif. Press, Berkely. 359 p.

Grissom, P.J. 1987. Effect of microtopography on composition and structure of vegetation in an elm-hackberry forest. M.S. thesis, Texas Tech Univ., Lubbock. 159 p. Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol., 61:237-247.

Hook, D.D. 1984. Adaptations to flooding with freshwater, p. 265-294. *In:* T.T. Kozlowski (ed.). Flooding and plant growth. Academic Press, Inc., Orlando, Florida.

Hosner, J.F. and L.S. Minckler. 1963. Bottomland hardwood forests of souther Illinois--regeneration and succession. Ecology, 44:29-41.

Huenneke, L.F. 1982. Wetland forests of Tomkins County, New York. Bull. Torrey Bot. Club, 109:51-63.

Jones, R.H., R.R. Sharitz, P.M. Dixon, D.S. Segal, and R.L. Schneider. 1994. Woody plant regeneration in four floodplain forests. Ecol. Monogr. 64:345-367.

Megonigal, J.P., W.H. Patrick, and S.P. Faulkner. 1993. Wetland identification in seasonally flooded forest soils: soil morphology and redox potential. Soil Sci. Soc. Amer. J.

57:140-149.
Moore, M.R. and J.L. Vankat. 1986. Response of the herb layer to the gap dynamics of a mature beech-maple forest. Am. Midl. Nat., 115:337-347.
Mowery, I.C., G. S. McKee, F. Matanzo, and E. Francis. 1960. Soil survey of Fort Bend County, Texas. U.S. Soil Cons. Serv., Washington, D.C. 53 p.
Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. Wiley and Sons, New York, N.Y. 547 p.
National Oceanic and Atmospheric Administration. 1996. Climatological data--Texas. Natl. Climatic Center, Asheville, N.C.
Nilsson, C., R. Jansson, and U. Zinko. 1997. Long-term responses of river-margin vegetation to water-level regulation. Science, 276:798-800.
Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology, 74:2215-2230.
Parsons, S.E. and S. Ware. 1982. Edaphic factors and vegetation in Virginia coastal plain swamps. Bull. Torr. Bot. Club., 109:365-370.
Ponnamperuma, F.N. 1984. Effects of flooding on soils, p. 10-45. *In:* T.T. Kozlowski (ed.). Flooding and plant growth. Academic Press, Inc., Orlando, Florida.
Prach, K. 1986. Succession across an environmental gradient. Ecologia (CSSR), 5:425-429.
Putnam, J.A., G.M. Furnival, and J.S. McKnight. 1960. Management and inventory of southern hardwoods. U.S. Dept. Agric. (For. Serv.), Agric. Handbk. 181. 102 p.
Robertson, P.A., G.T. Weaver, and J.A. Cavanaugh. 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. Ecol. Monogr., 48:249-267.
Rogers, R.S. 1982. Early spring herb communities in mesophytic forests of the Great Lakes Region. Ecology, 63:1050-1063.
Smith, D.W. and N.E. Linnartz. 1980. The southern hardwood region, p. 145-230. *In:* J.W. Barrett (ed.). Regional silviculture of the United States, 2nd ed. Wiley and Sons, New York, N.Y.
Streng, D.R., J.S. Glitzenstein, and P.A. Harcombe. 1989. Woody seedling dynamics in an east Texas floodplain forest. Ecol. Monogr., 59:177-204.
Struik, G.J. and J.T. Curtis. 1962. Herb distribution in an Acer saccharum forest. Am. Midl. Nat., 68:285-296.
ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology, 67:1167-1179.
Thornbury, W.D. 1965. Regional geomorphology of the U.S. Wiley and Sons, New York, N.Y. 609 p.
van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. Ecology, 62:688-696.
Wartenberg, S. Ferson, and F.J. Rohlf. 1987. Putting things in order: a critique of detrended correspondence analysis. Amer. Nat. 129:434-448.
Werger, M.J.A., H. Wild, and B.R. Drummond. 1978. Vegetation structure and substrate of the northern part of the Great Dyuke, Rhodesia: Gradient analysis anddominance-diversity relations. Vegetatio, 37:151-161.
Wharton, C.R. 1939. History of Fort Bend County. Naylor Co., San Antonio, Texas. 250 p.
Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science, 147:250-260.
Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, 21:213-

251.
Whittaker, R.H. 1975. Communities and ecosystems. MacMillan Publ. Co., Inc., New York, N.Y. 385 p.
Whittaker, R.H., L.E. Gilbert, and J.H. Connell. 1979. Analysis of two-phase pattern in a mesquite grassland, Texas. J. Ecol., 67:935-952.
Wolman, M.G. and L.B. Leopold. 1957. River floodplains: some observations on their-formation. U.S. Geolog. Survey Prof. Pap., 282(C):87-107.