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SIXTEEN YEARS OF OLD-FIELD SUCCESSION AND REESTABLISHMENT OF A BOTTOMLAND HARDWOOD FOREST IN THE LOWER MISSISSIPPI ALLUVIAL VALLEY

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Abstract: In the Lower Mississippi Alluvial Valley (LMAV), losses of bottomland hardwood forests have been severe, with less than 30% of the original 10 million ha remaining. Reforestation of abandoned farmland is occurring, but there has been little research on natural reestablishment of these forests. We examined understory succession and tree establishment patterns in a 3.2-ha field in northeast Louisiana, USA, abandoned in 1984. Relative elevation, strongly correlated with flooding depth and frequency, varied by approximately 1m. Ground-layer composition was monitored from 1985 to 1999 in twenty 1-m^2 quadrats stratified along the elevation gradient. In 2000, shrubs and tree saplings were mapped and their relative elevations determined. Ordination of the ground-layer data revealed that the major trends in species composition were related to time-since-abandonment and elevation. Annual species gradually declined, woody perennials became more abundant, and a shrub and young tree layer emerged from beneath the ground layer, but species composition in low and high elevation plots did not converge. Obligate species were more common at lower elevations, while facultative species were more common at upper elevations. By 16 years after abandonment, a total of 16 tree and shrub species had established in the field; eleven of these had potential local seed sources on levees adjacent to the study site. Abundance of dominant species was significantly related to elevation in most cases. In addition, distance to seed source influenced density and spatial distribution of *Celtis laevigata* and *Fraxinus pennsylvanica*. Our study suggests that rate and pattern of secondary succession in LMAV bottomlands are strongly influenced by elevation, dispersal mode of species, and the composition and proximity of forest remnants. Successful restoration of bottomland forests will require an improved understanding of these factors

Key Words: bottomland hardwoods, elevation, floodplain, *Fraxinus pennsylvanica*, Huisman-Olff-Fresco models, hydrologic gradient, Lower Mississippi Alluvial Valley, natural revegetation, old-field, ordination, response curve, succession, wetland forest

INTRODUCTION

The bottomland hardwood forest of the southeastern USA has been called an ''ecosystem in crisis'' (Creasman et al. 1992). Once extensive along streams and rivers, it has been reduced by conversion to agriculture (MacDonald et al. 1979) and more recently urban development (Sharitz and Mitsch 1993). Remaining forests are often highly fragmented (Creasman et al. 1992) (Figure 1), with diminished ecosystem functioning due to hydrologic alteration and invasion of exotic species (Kellison et al. 1998). Historically, the largest extent of this forest type was in the Lower Mississippi Alluvial Valley (LMAV) (Turner et al. 1981), an area with an estimated 72% loss of the original 10 million ha (Hefner and Brown 1985, Sharitz 1992). In this region, the three states that have sustained the heaviest losses, Arkansas, Mississippi, and Louisiana, still retain the majority of remaining forest cover (Dahl 1990, Dahl and Johnson 1991, Hefner et al. 1994, Dahl 2000). Of the three, Louisiana contains the greatest coverage of bottomland forests, but only approximately 30% of the original 6.5 million ha remain (Dahl 1990, Hefner et al. 1994).

These dramatic losses have prompted restoration

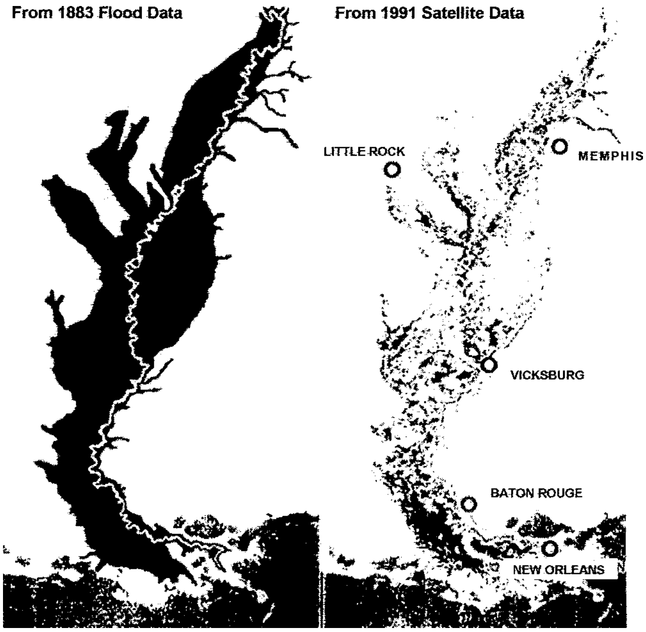

Figure 1. Map of the Lower Mississippi Alluvial Valley (LMAV) showing extent of bottomland hardwood forest fragmentation since 1883. Adapted with permission from The Nature Conservancy of Louisiana.

and conservation efforts (Newling 1990, Sharitz 1992). Many abandoned agricultural areas targeted for restoration are being seeded or planted with seedlings to restore dominance by bottomland species rapidly. Reforestation operations commonly include a limited number of species, mostly oaks, and vary in success (Allen 1990, Allen 1997, Allen et al. 1998, King and Keeland 1999). Some fields have been left fallow, with the expectation that succession will eventually lead to reestablishment of bottomland forest; however, few studies have examined succession (Bonck and Penfound 1945, Hopkins and Wilson 1974, Battaglia et al. 1995) and invasion by tree species in these systems (Allen 1997, Allen et al. 1998). Management decisions would benefit from studies that evaluate natural reestablishment potential. Such studies would also provide information about vegetation development and dynamics in bottomland plant communities.

Paradigms of old-field succession based on upland systems may not apply fully in bottomlands, where hydrology is a primary driver of vegetation dynamics (Robertson et al. 1978, Wharton et al. 1982, Sharitz and Mitsch 1993). Tree regeneration in forested (Jones et al. 1994, Jones and Sharitz 1998, Battaglia et al. 1999) and degraded (DeSteven and Sharitz 1997) floodplains is closely linked to variation in flooding. Thus, the rate and pattern of succession in abandoned bottomlands may differ from upland successions, due, in part, to annual hydrologic fluctuations (Battaglia et al. 1995).

The objectives of this study were 1) to describe patterns of secondary succession along an elevation gradient in a bottomland site, following abandonment of agriculture; 2) to examine patterns of natural tree establishment in relation to elevation and location of seed source; and 3) to highlight aspects of succession that are characteristic of bottomlands in the LMAV.

METHODS

Site Description

This study was conducted in the Ouachita Wildlife Management Area (OWMA), in northeastern Louisiana, USA, at the western edge of the great Mississippi River floodplain. Prior to clearing in the 1960s, this area was covered by bottomland hardwood forest. Until acquisition by the Louisiana Department of Wildlife and Fisheries in 1984, it was planted with sorghum, soybeans, and rice. The landscape is currently a patchwork of small fragments of bottomland forest interspersed with old fields of different times-since-abandonment and restoration stage. After abandonment, some fields were planted with seeds or seedlings of *Carya aquatica*, *C. illinoensis*, *Juglans nigra*, *Quercus laurifolia*, *Q. lyrata*, *Q. michauxii*, *Q. nigra*, *Q. nuttallii*, *Q. phellos*, and *Taxodium distichum* (DePoe and Pritchett 1986). Large saplings of many of these species, particularly the oaks, now dominate these fields (Battaglia, pers. obs.). Nomenclature follows that of Radford et al. (1968). Taxonomic authorities for all names are given in Tables 1 and 4.

A 160 × 200-m study site near Louisiana Highway 15, at 91° 59′ W, 32° 24′ N, was established following abandonment and disking of a soybean field in 1984. The field is periodically inundated following heavy precipitation and backflooding from Bayou Lafourche, a tributary of the Boeuf River, which borders the field on the east. The study site and a buffer zone were left fallow, but the adjacent field was planted with seedlings of native oak species in 1985. See Battaglia et al. (1995) for additional site information.

Field Procedures

A 20 × 20-m grid was established across the field. We used a laser theodolite to measure relative elevation and spatial coordinates at three random points within each grid cell. Repeated measurements showed that elevation and coordinates are accurate to the nearest centimeter. This set of points was used to create a contour map of relative elevation (Figure 2) in SigmaPlot version 4.0 (SPSS Inc. 1997). The elevation range in the field is approximately 1 m.

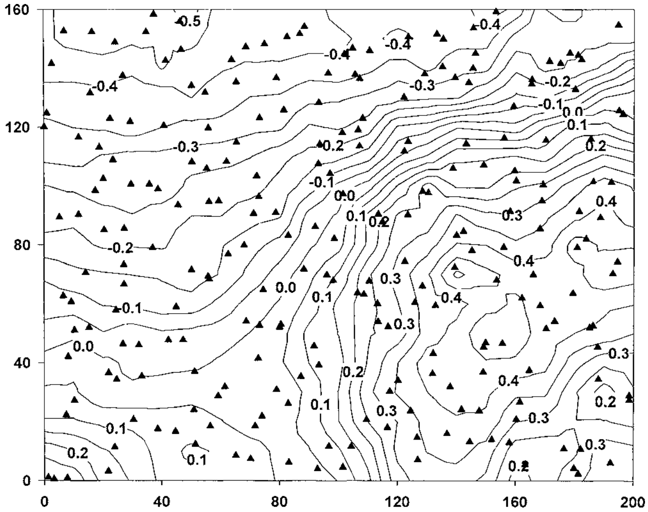

Figure 2. Contour map of the 160 × 200-m study site. Isoclines of relative elevation were generated in SigmaPlot version 4.0 and are based on 240 surveyed points (filled triangles).

Twenty permanent 1-m^2 quadrats, spanning the elevation gradient, were established in 1985 (Year 1) (Battaglia et al. 1995). Relative elevations at the southwest corner of each quadrat ranged from −0.53 to 0.40 m. In August 1985–1989 (Years 1–5), 1994 (Year 10), and 1999 (Year 15), projected foliage cover of each species in these plots was estimated to the nearest 1%. To eliminate variation among observers, estimates were always made by the same person (D. W. P.).

In May–June 2000, individuals ≥1 m in height of all trees and the multi-stemmed shrub, *Cephalanthus occidentalis*, were tagged, identified to species, and mapped using a laser theodolite. The relative ground elevation at the base of each individual sapling or center of each *C. occidentalis* clone was also measured. For tree saplings, we measured height of the tallest foliage and the diameter of each stem at 30 cm above ground. Only height was measured for *C. occidentalis*. The density of *Fraxinus pennsylvanica* was so great that we measured only a sample of the individuals. A stratified random procedure was used to select 379 of the 787 *F. pennsylvanica* saplings (48%) for measurement.

The multi-stemmed shrub, *Baccharis halimifolia*, was too abundant for tagging individual stems and too large and patchily distributed to be adequately sampled in the small permanent plots. In May 2000, we estimated its cover in twenty 100-m^2 circular plots centered on each of the permanent cover quadrats.

The nearest seed sources of tree species were located approximately 10 m from the northern and southern borders, along two small levee systems. The levees are roughly parallel to the site boundaries. We surveyed each levee community in July 2000 and recorded species with at least one large and presumably reproductive individual present.

Data Analyses

To examine trends in species composition in the permanent plots, we used non-metric multidimensional scaling (NMDS), a technique that has been shown to be robust and effective for ordination of community data (Minchin 1987). NMDS finds an ordination of quadrats in a specified number of dimensions, such that the distances among all pairs of quadrats in the ordination are, as far as possible, in rank-order agreement with compositional dissimilarities among the quadrats. Starting from an initial ordination, the positions of quadrats are gradually adjusted in order to minimize ''stress,'' a measure of the badness-of-fit of a rank-order regression of ordination distances on dissimilarities. The percentage cover data were standardized by species maxima, and dissimilarities were calculated using the Bray-Curtis index (Bray and Curtis 1957). This combination of standardization and dissimilarity index is one of the most effective for community ordination (Faith et al. 1987, Sandercock 1997). We performed NMDS in one to six dimensions, in each case using 10 random initial configurations.

Vector fitting (Dargie 1984, Faith and Norris 1989, Kantvilas and Minchin 1989) was used to examine patterns of correlation between the ordination and explanatory variables. Vector fitting is a form of multiple linear regression that finds the direction across the ordination along which sample coordinates have maximum correlation with the fitted variable. Statistical significance of the correlation is tested by randomly permuting the values of the variable among quadrats, simulating the null hypothesis of no trend. Ordinations, vector fitting, and related data manipulations were performed using the DECODA package (Minchin 1989).

Distribution maps were plotted for each of the tree and shrub species surveyed in May–June 2000. Frequency histograms of height and diameter at 30 cm above ground were created for each species. For multistemmed individuals (particularly common in *Ilex decidua* and *Crataegus viridis*), we first computed the total basal area of all stems, then calculated the diameter of an equivalent single stem of the same basal area. Overall density and basal area per hectare were computed for each tree species (density only for the shrub *C. occidentalis*). For *F. pennsylvanica*, mean basal area per individual was computed for those individuals that were measured, and basal area per hectare was calculated by assuming the same mean for the unmeasured individuals.

Response curves of species to elevation were fitted using Huisman-Olff-Fresco (HOF) models (Huisman et al. 1993, Oksanen 1997). HOF models are particularly useful for modeling response curves in that they can accommodate the monotonic, symmetric unimodal, ''plateau'' and skewed unimodal shapes that have been observed in direct gradient studies (Austin and Gaywood 1994). The models were fitted using non-linear maximum likelihood methods with a Poisson error distribution and adjustments for overdispersion. Starting with the ''full'' model, which allows for a skewed unimodal response, backwards elimination was used to determine the appropriate response shape for each species, with the p value for significance of the change in deviance set at 0.05. HOF modeling was conducted using the program by Oksanen (1996).

For tree species, HOF models were fitted for both density and basal area. A density model was also fitted for the shrub *C. occidentalis*. Density and basal area were computed in each 0.1-m elevation class between -0.5 m and 0.5 m. The proportion of surveyed random points falling into each elevation class was used as an estimate of the proportion of the total area of the field in that class. These proportions were then used to adjust raw counts of numbers of individuals or total basal area in each class to density or basal area per hectare.

The spatial distributions of *C. laevigata* and *F. pennsylvanica* suggested that both elevation and distance from closest seed source (the levee systems running parallel to the southern and northern margins of the field) may have influenced their densities. The field was divided into sixteen 10 × 200 m strips parallel to its long axis, and density was tallied for each species in each strip. Prevailing winds are from the southwest, so distance of each strip from the southern edge of the field was estimated for the wind-dispersed *F. pennsylvanica* recruits. Minimum distance of each strip from either the southern or northern edge of the field was estimated for the bird/mammal- dispersed *C. laevigata*. General non-linear modeling software (SAS Institute Inc. 1989: Procedure NLIN) was used to fit models for density as a function of distance. The fitted model for *F. pennsylvanica* was of the form

$$y = ae^{-bx^c} + d$$

where y is density, x is distance from edge, and $a, b, c,$ and d are fitted parameters. For *C. laevigata*, a simpler model was found to be sufficient, leaving out the parameter d.

The wetland indicator status of each species observed in the field was determined using the system developed by the United States Department of Agriculture (United States Department of Agriculture 2001).

RESULTS

Understory Succession

Examination of changes in mean cover among years (Table 1) shows a shift toward dominance by perennial species. The majority of annual taxa attained peak cover during the early years of succession; gradually, they were overtaken by herbaceous and woody perennial species. In the first few years following abandonment, many annual species (*e.g.*, *Digitaria sanguinalis*, *Sesbania macrocarpa*, and *Sida spinosa*) and a few perennial species (*e.g.*, *Amaranthus arenicola* and *Rumex crispus*) peaked in abundance. Most of these early colonists are weed species, considered to be common pests in soybean fields, and had declined or disappeared by Year 5. In Year 5, several herbaceous perennial species became established (*e.g.*, *Andropogon virginicus*, *Cyperus pseudovegetus*, and *Solidago canadensis*) that would persist through Year 15. Most of the early perennial invaders were herbaceous, although *Campsis radicans*, a woody vine, maintained high cover values throughout the study, particularly at higher elevations. By Year 15, woody taxa were more abundant throughout the field. Three tree species (*Crataegus viridis*, *Fraxinus pennsylvanica*, *Ilex decidua*) were recorded in the 1-m^2 permanent plots. The shrub, *Baccharis halimifolia*, gradually increased in cover over the study period.

The two-dimensional NMDS ordination (stress = 0.27, achieved from four of the ten random starts) was accepted as an adequate summary of the permanent quadrat data (Figure 3). Reductions in stress with increasing dimensions were gradual and modest (stress in 3D = 0.20), and additional dimensions had no clear ecological interpretation. Fitted vectors of maximum correlation for year (r = 0.82) and elevation (r = 0.65) were both highly significant ($p < 0.001$), and the angle between the vectors was 89°, so these vectors represent two independent trends in species composition, summarized by Tables 2 and 3.

The year trend (Table 2) corresponds closely with the pattern observed in Table 1 and outlined above. This is to be expected, given the high correlation between this floristic dimension and year. The pattern of change in composition among years was examined by plotting the trajectory of the centroids of the quadrats in each year (Figure 3). This was done separately for the subsets of quadrats at lower elevations (≤0.0 m) and higher elevations (>0.0 m). The trajectories of the subsets are generally parallel and broadly in the direction of the year vector, indicating an overall trend of directional succession in both lower and higher elevation sites, but some anomalies are apparent. In lower elevation quadrats, the directions of change from 1985 to 1986 and from 1986 to 1987 are virtually perpen-

Table 1. Average percent cover of species in 20 permanent 1-m^2 quadrats over a 15-year period following field abandonment in 1984. Cover was estimated in August 1985–1989, 1994, and 1999 and averaged over the 20 plots in each sampling year. Wetland indicator status, where available, is given for each taxon (OBL = obligate wetland; FACW = facultative wetland; FAC = facultative; FACU = facultative upland) (United States Department of Agriculture 2001). Annual, biennial, and perennial growth forms are coded using A, B, and P, respectively. Additionally, grasses, herbs, shrubs, trees, and vines are coded using G, H, S, T, and V, respectively. Generic names are given in cases where neither sexual nor species-specific vegetative structures were found. Voucher specimens are stored in the herbarium at the University of Louisiana—Monroe.

Species	1985	1986	1987	1988	1989	1994	1999	Wetland Status	Growth Form
Alternanthera philoxeroides (Martius) Grisebach	0.35	0.25	0.14	0.05	0.04	0.01	—	OBL	PH
Amaranthus arenicola I. M. Johnston	0.50	0.04	—	—	0.02	—	—	FACU	PH
Ambrosia trifida L.	—	—	—	—	0.10	—	—	FAC	AH
Ampelopsis arborea (L.) Koehne	—	—	—	—	—	0.20	—	FAC+	PV
Andropogon virginicus L.	—	—	—	0.68	4.39	1.83	0.55	FAC−	PG
Aster spp.	0.48	17.63	0.25	0.72	2.38	2.29	1.52	—	AH/PH
Baccharis halimifolia L.	0.30	1.00	0.08	0.26	—	0.35	3.38	FAC	PS
Berchemia scandens (Hill) K. Koch.	—	—	—	—	—	—	0.20	FACW	PV
Brunnichia ovata (Walt.) Shinners	3.18	1.10	3.41	1.24	3.39	7.31	1.52	FACW	PV
Campsis radicans (L.) Seemann	7.85	12.42	16.75	16.55	14.56	14.03	4.43	FAC	PV
Cardiospermum halicacabum L.	0.13	—	—	—	—	0.20	0.10	FAC	AH
Carex verrucosa Muhl.	—	0.34	2.45	0.01	0.08	—	0.35	OBL	PH
Conyza canadensis (L.) Cronq.	0.03	1.70	0.13	—	0.04	0.45	—	FACU	AH
Crataegus viridis L.	—	—	—	—	—	—	0.13	FACW	PT
Cyperus pseudovegetus Steudel.	—	—	—	—	0.01	0.14	0.71	FACW	PH
Desmanthus illinoensis (Michaux) MacM.	0.05	0.70	0.47	3.20	2.47	17.74	6.84	FAC	PH
Digitaria sanguinalis (L.) Scopoli.	—	—	0.14	—	0.03	—	—	FAC−	AG
Diodia virginiana L.	0.01	0.14	—	—	—	—	—	FACW	PH
Eclipta alba (L.) Hasskarl.	—	—	—	0.45	0.02	—	—	FACW−	AH
Elymus virginicus L.	—	—	—	—	—	0.05	0.09	FAC	PG
Euphorbia spp.	1.06	0.34	1.28	0.03	0.08	—	—	—	AH
Fraxinus pennsylvanica Marshall	—	—	—	—	—	—	0.21	FACW	PT
Galium tinctorium L.	—	—	—	—	<0.01	0.05	—	FACW	AH
Gnaphalium purpureum L.	—	0.02	0.30	—	—	—	—	UPL	AH
Ilex decidua Walter	—	—	—	—	—	—	0.02	FACW−	PT
Ipomoea spp.	4.78	0.81	1.49	0.12	0.47	0.09	—	—	AV
Iva annua L.	—	1.18	2.59	9.28	0.69	3.18	1.78	FAC	AH
Juncus spp.	—	—	0.01	0.10	0.46	0.29	0.07	—	PH
Krigia dandelion (L.) Nuttall	—	—	—	0.50	—	0.03	—	FACU	PH
Lathyrus hirsutus L.	—	—	—	—	0.01	0.35	—	?	AV
Leptochloa filiformis (Lam.) Beauvois	0.78	—	0.15	—	—	—	—	FACW	AG
Ludwigia spp.	—	—	—	—	0.08	0.99	—	OBL	AH/PH
Lythrum alatum Pursh.	—	—	—	—	—	0.03	0.16	FACW+	PH
Mimosa strigillosa Torr. and Gray	—	—	—	—	—	—	0.01	FAC	PH
Oenothera biennis L.	0.69	—	—	0.05	—	—	—	FACU	BH
Oenothera laciniata Hill	0.10	—	—	—	—	—	—	FACU	AH

Table 1. Continued.

Species	1985	1986	1987	1988	1989	1994	1999	Wetland Status	Growth Form
Oxalis debilis var. *corymbosa* (DC.) Lourteig	0.04	0.30	0.03	—	0.03	—	—	?	AH
Panicum dichotomum L.	—	—	—	—	—	—	0.08	?	PG
Phalaris caroliniana (Walter)	—	—	—	—	—	0.12	—	FACW	AG
Phyla lanceolata (Michaux) Greene	—	—	—	—	—	0.17	—	FACW+	PH
Polygonum spp.	4.90	—	0.04	0.04	0.15	0.32	0.03	OBL	AH
Portulaca oleracea L.	0.01	—	—	—	—	—	—	FACU	AH
Pyrrhopappus carolinianus (Walter) DC.	—	0.09	0.03	0.11	0.18	0.08	—	?	AH
Ranunculus sardous Crantz	0.14	0.31	2.68	1.68	0.40	0.94	—	FAC+	AH
Rorippa palustris (L.) Bess	0.15	—	—	—	—	—	—	OBL	AH
Rubus trivialis Michaux	—	—	—	—	0.07	0.59	2.53	FAC	PV
Rumex crispus L.	1.03	0.06	—	0.01	0.06	—	—	FAC	PH
Sesbania macrocarpa Muhl. ex Raf.	0.41	0.03	13.45	0.03	0.81	—	0.08	FACW−	AH
Setaria geniculata (Lam.) Beauvois	—	—	—	—	0.06	—	—	FAC	PG
Sida spinosa L.	0.39	1.07	2.30	0.16	1.35	0.02	—	FACU	AH
Smilax bona-nox L.	—	—	—	—	—	—	0.02	FAC	PV
Solanum carolinense L.	0.49	0.30	0.40	0.20	0.14	0.04	—	FACU	PH
Solidago canadensis L.	—	—	—	—	3.84	0.58	0.80	FACU	PH
Sorghum halepense (L.) Persoon	0.21	1.11	0.82	0.18	0.61	0.09	—	FACU	PG
Spermacoce glabra Michaux	—	—	—	—	—	—	0.58	FACW	PH
Spiranthes spp.	—	—	—	—	—	0.02	—	?	PS
Trachelospermum difforme (Walter) Gray	—	—	—	—	—	—	0.10	FACW	PV
Verbena brasiliense Vellozo	—	—	—	—	—	0.04	—	?	PH

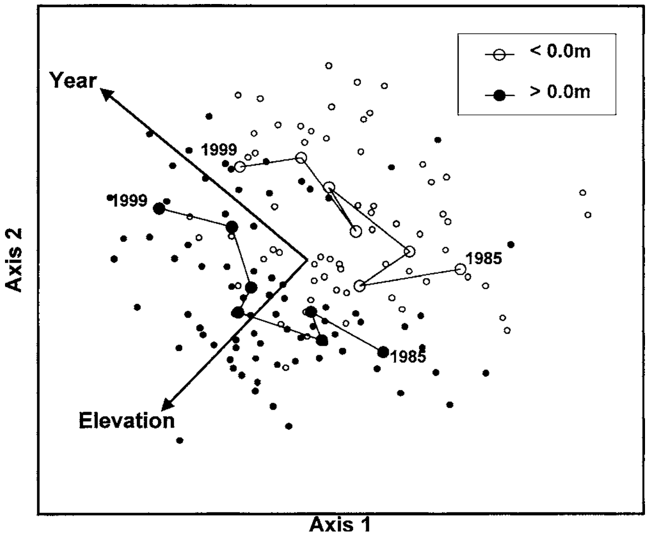

Figure 3. Two-dimensional NMDS ordination (stress = 0.27) of the 20 permanent 1-m^2 quadrats, based on cover data standardized by species maxima and using the Bray-Curtis dissimilarity index. Fitted vectors are shown for year ($r = 0.82$, $p < 0.001$) and elevation ($r = 0.65$, $p < 0.001$). These are virtually perpendicular (angle = 89°). Vector lengths are proportional to correlations. The trends in species composition represented by the vectors are summarized in Tables 2 and 3. Time trajectories are shown separately, using the centroids in each year, for quadrats above (filled circles) and below (hollow circles) 0.0m relative elevation. Centroids are joined in order of sampling year: 1985, 1986, 1987, 1988, 1989, 1994, and 1999. The smaller symbols show the coordinates of individual quadrats in each year.

dicular to the year vector and suggest a shift toward composition more typical of higher elevation sites in 1986, then a reversion toward lower elevation species in 1987. Lower elevation sites seem to have undergone a reversal, relative to the overall trend, between 1988 and 1989. In the upper elevation sites, the degree of change between years is relatively small between 1986 and 1987 and again between 1988 and 1989. The total amount of compositional change (length of trajectory) is similar in lower and higher elevation subsets. In both subsets, succession was more rapid during the first five years than in the final ten years.

The correlation of the other dimension of the ordination with elevation underlines the importance of ecological factors associated with elevation in determining the species composition of the vegetation within years. Throughout the study, a clear trend in composition was evident along the elevation gradient (Figure 3). Species appeared, disappeared, and some species distributions shifted, expanded, or contracted with time, so that beta diversity along the elevation gradient varied among years. In general, obligate and facultative-wetland species were more common at lower el-

Table 2. Mean cover of species in 10 segments along the fitted vector for year in the NMDS ordination. The data were standardized by species maxima and rounded into 10 classes, with upper limits of 0.1, 0.2, 0.3, . . . , 0.9 and 1.0 (represented by X). Dashes (--) indicate absence. The species are ordered according to their weighted mean coordinates along the year vector. The table summarizes the compositional trend represented by the year vector.

Portulaca oleracea	X---------
Oenothera laciniata	X---------
Oenothera biennis	X-----1---
Rorippa palustris	-X--------
Rumex crispus	X612111---
Alternanthera philoxeroides	X-8---11--
Amaranthus arenicola	XX3511----
Leptochloa filiformis	4X23------
Polygonum spp.	X91411111-
Ipomoea spp.	9X631111--
Carex verrucosa	X1-1111111
Euphorbia spp.	44X41111--
Sesbania macrocarpa	1X6421-1--
Diodia virginiana	--XX------
Digitaria sanguinalis	-XX55-----
Solanum carolinense	-X13311-1-
Sida spinosa	25X5611---
Sorghum halepense	71X862211-
Aster spp.	-1XX761242
Krigia dandelion	----X-11--
Conyza canadensis	--X25414--
Ranunculus sardous	1422X2231-
Setaria geniculata	----XX----
Gnaphalium purpureum	----X1----
Oxalis debilis	-5--1X1---
Campsis radicans	--286X5211
Pyrrhopappus carolinianus	6--X55249-
Brunnichia ovata	-71525X521
Cardiospermum halicacabum	-X--1-39--
Juncus spp.	---13X4834
Iva annua	--1133X644
Eclipta alba	----11X1--
Andropogon virginicus	---113X343
Ludwigia spp.	----118X--
Phalaris caroliniana	------X14-
Ampelopsis arborea	-----28X--
Galium tinctorium	-----36X--
Rubus trivialis	----1812X2
Phyla lanceolata	------5X--
Fraxinus pennyslvanica	-----4--X1
Desmanthus illinoensis	-11-116X21
Solidago canadensis	----112X61
Baccharis halimifolia	-2211114X
Lathyrus hirsutus	----1--2X-
Cyperus pseudovegetus	----1-13X2
Elymus virginicus	------25-X
Lythrum alatum	-------92X
Verbena brasiliense	--------X-
Berchemia scandens	--------X-
Crataegus viridis	--------X-
Spermacoce glabra	-----1-1-X
Panicum dichotomum	---------X
Trachelospermum difforme	---------X
Ilex decidua	---------X
Mimosa strigillosa	---------X

Table 3. Mean cover of species in 10 segments along the fitted vector for elevation in the NMDS ordination. The data were standardized by species maxima and rounded into 10 classes, with upper limits of 0.1, 0.2, 0.3, . . . , 0.9 and 1.0 (represented by X). Dashes (-) indicate absence. The species are ordered according to their weighted mean coordinates along the year vector. The table summarizes the compositional trend represented by the elevation vector.

Rorippa palustris	X---------
Gnaphalium purpureum	X--1------
Eclipta alba	X3-1-1----
Setaria geniculata	-X-6------
Ludwigia spp.	X161-111--
Amaranthus arenicola	615X------
Leptochloa filiformis	X1X--12-11
Iva annua	X733211111
Sesbania macrocarpa	1XX111111-
Ampelopsis arborea	-X6-22-2--
Polygonum spp.	X2321111-4
Digitaria sanguinalis	X96-84-3--
Cardiospermum halicacabum	3X9-2-512-
Ranunculus sardous	1X31231211
Juncus spp.	1X42124111
Sida spinosa	1XX3354211
Brunnichia ovata	6X36257111
Cyperus pseudovegetus	--X541214-
Spermacoce glabra	--1X-3-2--
Ipomoea spp.	1X36355111
Phalaris caroliniana	2-1-X1-4--
Desmanthus illinoensis	1185X44661
Euphorbia spp.	-54156X411
Conyza canadensis	62142412X2
Carex verrucosa	-1311x3112
Andropogon virginicus	--2X322135
Rumex crispus	---53X62-1
Aster spp.	1117958X62
Elymus virginicus	----4XXX--
Baccharis halimifolia	142131-X41
Pyrrhopappus carolinianus	---262X882
Campsis radicans	1111146X76
Solanum carolinense	-1---3919X
Rubus trivialis	----12326X
Solidago canadensis	---211213X
Sorghum halepense	11-1111-3X
Fraxinus pennsylvanica	-------1X8
Ambrosia trifida	---------X
Crataegus viridis	---------X
Krigia dandelion	----11-1-X

evations, while facultative and facultative-upland species were more common at upper elevations. *Cyperus pseudovegetus*, a facultative-wetland species that was absent in 1985–1988, established in the lowest elevation plot in 1989. By 1994, it had expanded to five low- to mid-elevation plots and one high-elevation plot. In 1999, we recorded this species in 12 plots spanning most of the elevation gradient. In the first few years of succession, occurrence of *Desmanthus illinoensis*, a facultative legume, was limited to a few plots of intermediate elevation. Over time, it expanded toward both lower and higher elevations; it was observed in seven plots in 1989, 16 in 1994, and 18 in 1999. *Rubus trivialis*, a facultative vine species absent in the first four years, had established in three upper elevation plots by 1989 and four in 1994. By 1999, its abundance was high, and it had expanded into a total of seven upper elevation plots. In 1994, lower elevation plots were dominated by *Brunnichia ovata* and contained a mixture of herbaceous taxa with low abundance (*e.g.*, *Ludwigia* spp. and *Iva annua*). *Campsis radicans* was abundant throughout the gradient. Several species, including *Andropogon virginicus*, *Rubus trivialis*, and *Solidago canadensis*, were restricted to higher elevations. By 1999, the vines, *B. ovata* and *C. radicans*, had decreased in abundance, and *A. virginicus* occupied most sections of the gradient. *Baccharis halimifolia*, *R. trivialis*, *S. canadensis*, and seedling establishment of tree species (*F. pennsylvanica*, *C. viridis*, *I. decidua*) were limited to the upper elevation plots. In general, these shifts in species composition along the elevation gradient were gradual, and there were no clear community discontinuities.

Dissimilarity between lower and higher elevation plots was lowest in 1986. Rainfall data from the University of Louisiana at Monroe station showed that 1986 was the driest year in which we sampled the permanent plots (National Oceanic and Atmospheric Administration 2001). The decrease in dissimilarity was driven primarily by changes in the distribution of *Aster* spp., a taxon typically more abundant in upper elevation areas (Table 3). In 1986, however, it also dominated the lower plots and occurred in 19 of the 20 plots, contributing to its overall peak in this dry year. This expansion was temporary, as *Aster* spp. occurred in only four plots in 1987. Its frequency increased again in 1988–1989. By 1994, its abundance had increased, and it was found in 15 plots. By 1999, it had reoccupied the lower plots, but unlike in 1986, low and high elevation plots did not become more similar due to their discrimination at that time by other species.

Woody Species Establishment

By May 2000, a total of sixteen species of trees and shrubs had established in the field. Eleven of these had potential local seed sources on one or both of the levee systems that parallel the southern and northern edges of the study site (Table 4).

Total density of all tree species and the shrub *Cephalanthus occidentalis* was 497 ha^{-1}. The total basal area of all tree species was 0.71 m^2 ha^{-1} (Table 5).

Table 4. Primary dispersal mechanisms and occurrence of shrub and tree species in the study site and adjacent levee communities (Radford et al. 1965, McKnight et al. 1981). "B" = bird, "G" = gravity, "M" = mammal, and "W" = wind; "+" = present and "−" = absent. Presence of each species on the levees is noted only if large and presumably reproductive individuals are present.

Species	Dispersal Agent	Present in Site	South Levee	North Levee
Acer negundo L.	B, M, W	−	+	−
Acer rubrum L.	B, M, W[1]	+	−	−
Baccharis halimifolia L.	W	+	−	−
Carya aquatica (Michaux f.) Nuttall	B, G, M[1]	+	+	+
Celtis laevigata Willd.	B, M[1]	+	+	+
Cephalanthus occidentalis L.	W[1]	+	+	+
Crataegus viridis L.	B, M	+	+	+
Diospyros virginiana L.	B, M	+	+	+
Forestiera acuminata (Michaux) Poiret	B[1]	−	+	+
Fraxinus pennsylvanica Marshall	W[1]	+	+	−
Gleditsia triacanthos L.	B, M, W[1]	+	+	+
Ilex decidua Walter	B, M	+	+	+
Liquidambar styraciflua L.	W	+	−	−
Planera aquatica Walter ex J. F. Gmelin	B, M[1]	−	−	+
Populus deltoides Marshall	W[1]	−	+	−
Quercus lyrata Walter	B, G, M[1]	−	+	+
Quercus nigra L.	B, G, M[1]	+	−	−
Quercus phellos L.	B, G, M[1]	−	+	−
Salix nigra Marshall	W[1]	+	+	+
Sideroxylon lycioides L.	B	+	−	−
Ulmus crassifolia Nuttall	W[1]	+	+	−
Ulmus americana L.	W[1]	+	+	−
Ulmus rubra Muhl.	W[1]	−	+	−

[1] May be secondarily dispersed by water.

Table 5. Mean height, density, and basal area of invading shrub and tree species in OWMA study site. Total density = 497 ha^{-1}. Total basal area = 0.71 m^2 ha^{-1}. The shrub *Baccharis halimifolia* is not included in these data.

Species	Mean Height ± s.d. (m)	Density (ha^{-1})	Basal Area (m^2 ha^{-1})
Acer rubrum	1.30*	0.31	0.00002
Carya aquatica	5.73 ± 1.52	1.56	0.034
Celtis laevigata	2.56 ± 1.12	36.25	0.042
Cephalanthus occidentalis	2.39 ± 0.71	57.19	—†
Crataegus viridis	2.23 ± 0.84	32.81	0.028
Diospyros virginiana	2.32 ± 0.96	17.81	0.017
Fraxinus pennsylvanica	2.97 ± 1.48	245.00	0.390
Gleditsia triacanthos	1.90 ± 0.92	5.00	0.0023
Ilex decidua	2.84 ± 0.83	50.63	0.076
Liquidambar styraciflua	0.85 ± 0.57	0.63	0.00059
Quercus nigra	3.12 ± 0.14	0.94	0.00141
Salix nigra	3.50*	0.31	0.00030
Sideroxylon lycioides	3.20*	0.31	0.00039
Ulmus crassifolia	3.08 ± 0.78	40.00	0.095
Ulmus americana	2.96 ± 1.97	7.19	0.018

* Only one individual recorded.
† Diameters not measured.

Fraxinus pennsylvanica was by far the most dominant tree species, both in terms of density and basal area, and accounted for approximately half of all stems and more than half of the total basal area in the field. Its abundance was over four times greater than that of *C. occidentalis*, the species with the second greatest density, and *Ulmus crassifolia*, the species with the second greatest basal area. Other species, abundant in either or both density and basal area, included *Ilex decidua*, *Celtis laevigata*, *Crataegus viridis*, *Ulmus americana*, *Diospyros virginiana*, *Gleditsia triacanthos*, and *Carya aquatica* (Table 5).

Distribution patterns in the field varied by species (Figure 4). Although abundant, *F. pennsylvanica* was not ubiquitous. This wind-dispersed tree was most common along the southern edge of the site and was sparse in the interior part of the field, particularly at higher elevations. *Celtis laevigata*, a species dispersed by birds and small mammals, showed a similar pattern of greater density near the southern edge of the site and also had a relatively high density along the northern edge. *Crataegus viridis* and *Ilex decidua*, both primarily bird-dispersed species, spanned the field from north to south but were concentrated in the eastern half, *I. decidua* being particularly dense in the southeastern corner. *Diospyros virginiana*, which has large

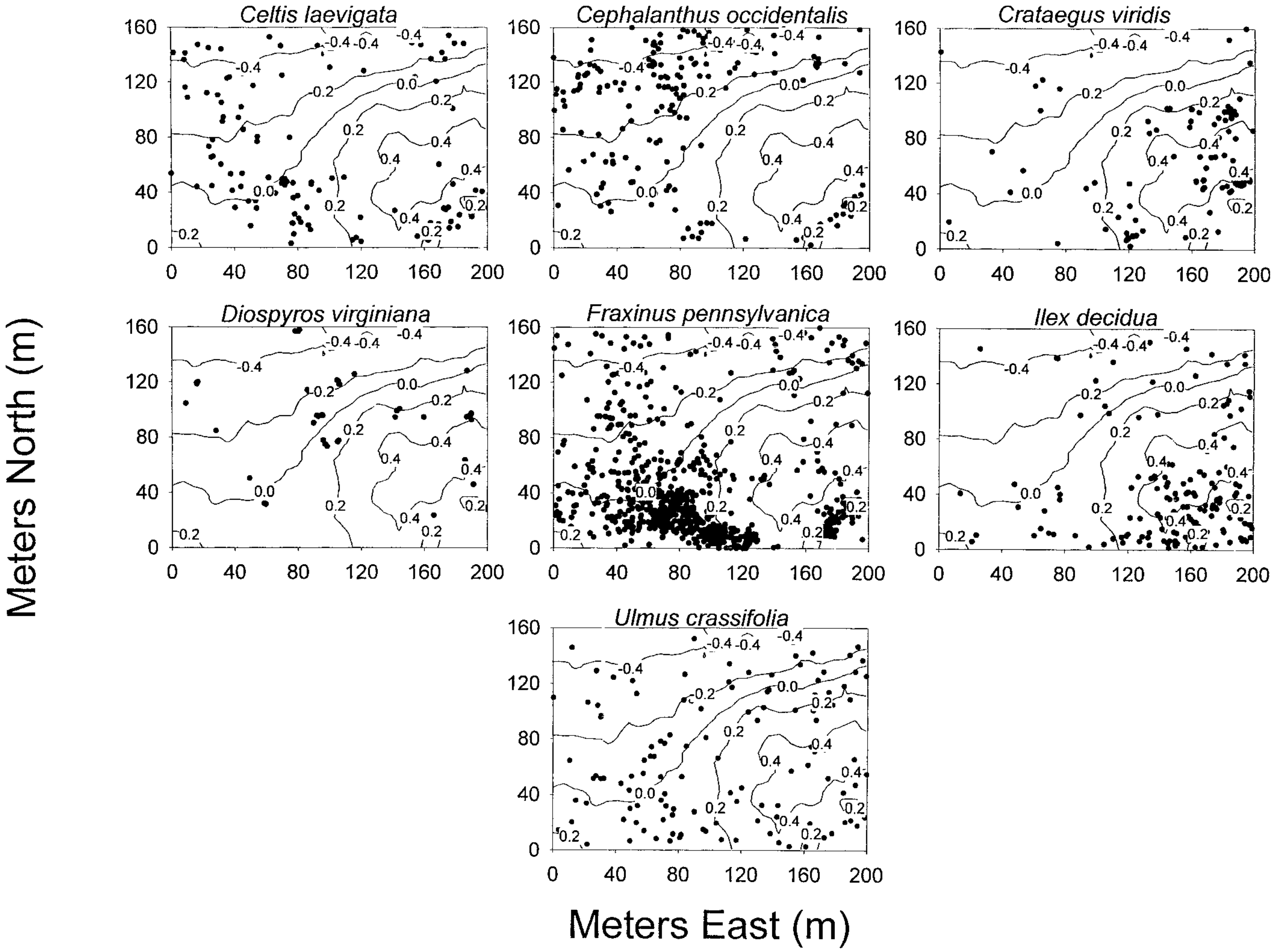

Figure 4. Maps of all individuals of six dominant tree species and *Cephalanthus occidentalis*.

fleshy fruits, occurred in the central portion of the field, usually in small clusters. *Ulmus crassifolia*, a light-seeded wind-dispersed species, was found throughout the field. The shrub *Cephalanthus occidentalis* was largely confined to areas lower than 0.2 m relative elevation.

The shrub *Baccharis halimifolia*, a wind-dispersed species in the *Asteraceae* (not included in Figure 4), was present in the seven highest elevation 100-m^2 plots of the 20 established in 1999. Across these plots, its percent cover averaged 22% and ranged from 2 to 75%. Patches of this species corresponded with sparser regions in the distributions of *F. pennsylvanica* and *C. laevigata* but overlapped with large portions of *C. viridis* and *I. decidua* distributions.

We have no data on natality, growth, mortality, or age structure of these populations, so inferences about the population dynamics based on height and diameter class distributions of individuals ≥ 1 m in height are based on several assumptions. First, we assume that age and size are closely related. Second, we assume that mortality of individuals ≥ 1 m in height is negligible and constant across size classes and years. Observations made during annual visits to the field suggest that this is a reasonable assumption. If these assumptions are accepted, then the main source of variation is in annual recruitment to the ≥ 1 m height class. The combination of variable germination, seedling survival, and growth among years is incorporated into this rate.

Size class distributions of *F. pennsylvanica*, *C. laevigata*, *D. virginiana*, and *C. viridis* (Figures 5 and 6) suggest that recruitment rates were initially low and have been increasing gradually. In these populations, most individuals are in the smaller size classes. Distributions of *I. decidua*, *U. crassifolia*, and *C. occidentalis* indicate initially low recruitment rates, a peak, and a return to lower levels. The largest tree in the field was an *Ulmus americana* with a height of 9.25 m and diameter of 21.1 cm at 30 cm above the ground. We do not know when this individual established.

The relationships of density and basal area per hect-

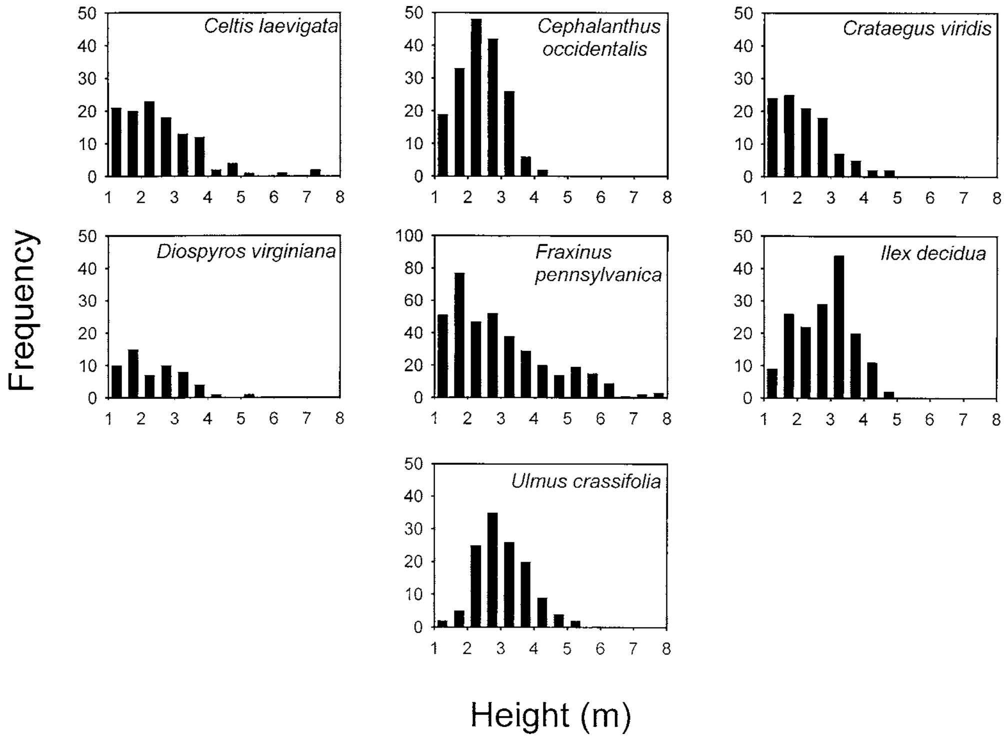

Figure 5. Height class distributions of six dominant tree species and *Cephalanthus occidentalis*.

are with relative elevation varied by species. Densities of *F. pennsylvanica*, *U. crassifolia*, and *U. americana* had symmetric, unimodal response curves along the gradient. Density of *C. occidentalis* increased monotonically toward lower elevations, while *C. viridis* and *I. decidua* showed monotonic increases in density toward higher elevations (Figure 7). *Fraxinus pennsylvanica*, *U. crassifolia*, and *U. americana* also displayed symmetric, unimodal responses for basal area, while *C. laevigata* required a skewed, unimodal curve. The basal area response of *I. decidua* was monotonic toward higher elevations (Figure 8). All of these response curves were statistically significant ($p < 0.05$), based on F-tests for change in deviance.

Celtis laevigata showed no significant trend in density in relation to elevation, mainly due to an unusually high value in the lowest elevation class. No significant trend in basal area was observed for *C. viridis*. The

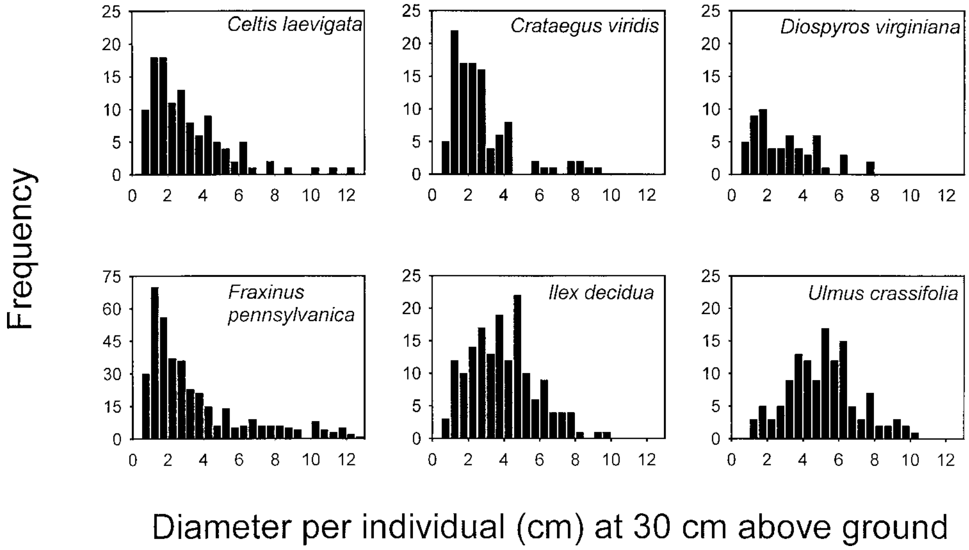

Figure 6. Diameter class distributions of six dominant tree species.

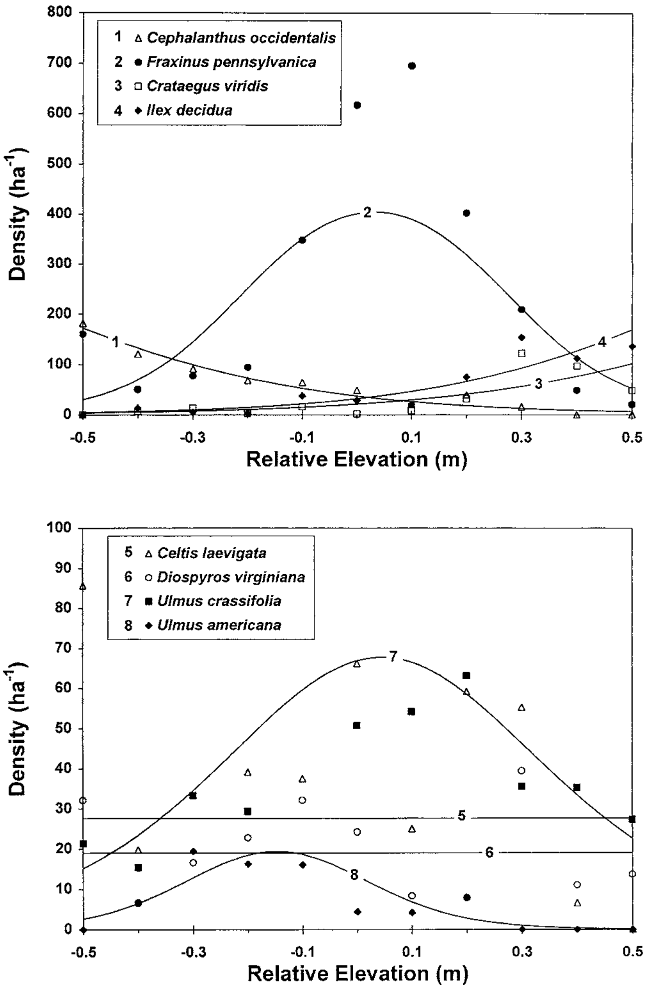

Figure 7. HOF models for density in relation to elevation. Except for *Celtis laevigata* and *Diospyros virginiana*, all models are significant ($p < 0.05$), based on F-tests for the change in deviance.

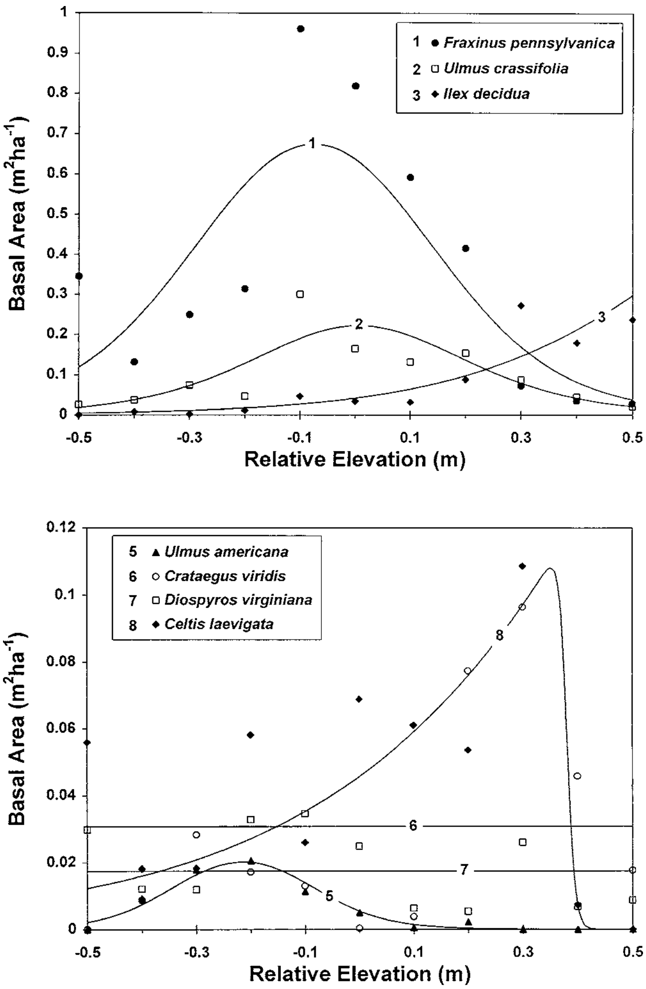

Figure 8. HOF models for basal area in relation to elevation. Except for *Crataegus viridis* and *Diospyros virginiana*, all models are significant ($p < 0.05$), based on F-tests for the change in deviance. The multi-stemmed shrub, *Cephalanthus occidentalis*, is omitted, since we did not measure its stem diameters.

data points suggest a bimodal response (Figure 8), which cannot be accommodated by HOF models. For *D. virginiana*, neither measure of abundance showed a significant trend with elevation.

The density of *F. pennsylvanica* also showed a clear relationship with distance from the southern edge of the site (Figure 9a), decreasing from a mean of about 800 ha^{-1} within 10 m of the southern edge to about 70 ha^{-1} at 80 m from the edge. This is consistent with wind dispersal from mature individuals on the southern levee system (Table 4). *Celtis laevigata* density decreased monotonically with distance from either edge of the field (Figure 9b), from a mean of about 45 ha^{-1} within 10 m of either edge to about 10 ha^{-1} at 80 m from the nearest edge. This species has small fleshy fruits that are dispersed by birds and mammals; mature individuals are present on both the southern and northern levee systems (Table 4).

DISCUSSION

Succession and the Hydrologic Gradient

Successional changes occurred in the ground layer vegetation over the 15-year period covered by the permanent quadrat data. This was evident from the strong correlation between time-since-abandonment and one of the two principal trends in species composition revealed by ordination. The time trend coincided with gradual shifts in dominance by annuals to herbaceous perennials during the first five years of succession (Battaglia et al. 1995), followed by loss of most annual species and increasing abundance of woody perennials over the subsequent ten years (1994–1999). The woody vine *Campsis radicans* was an exception to this pattern in that it was a dominant species throughout the 15-year period. By Year 16, a shrub and young

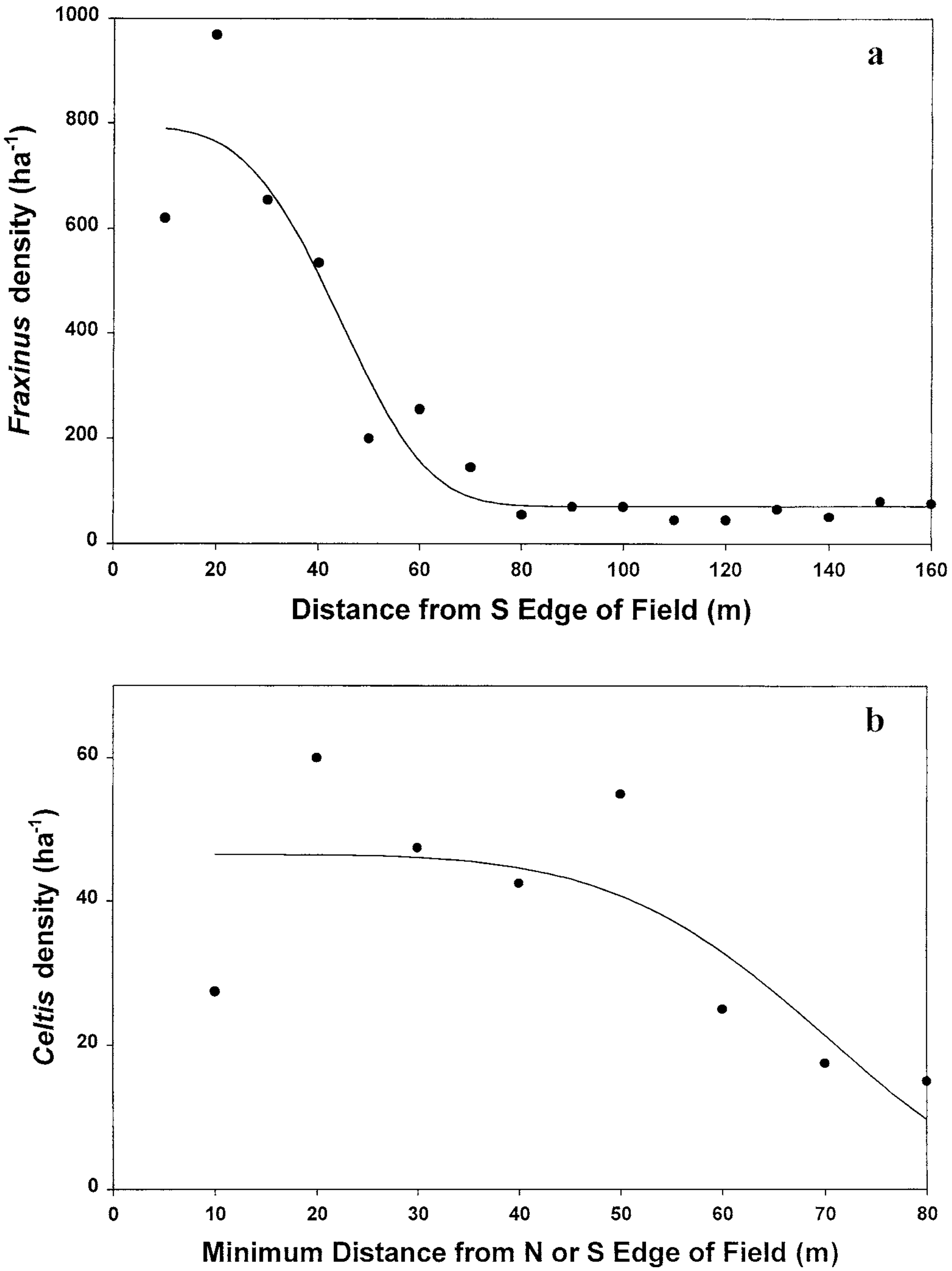

Figure 9. a) Exponential model for density of *Fraxinus pennsylvanica* in relation to distance from the southern edge of the site ($F_{4,12} = 45.5$, $p < 0.0001$). b) Exponential model for density of *Celtis laevigata* in relation to minimum distance from either the southern or northern edge of the site ($F_{3,5} = 22.7$, $p = 0.0024$).

tree layer had emerged from beneath the thick ground layer of vegetation. This recent shift indicates that a transition phase between old-field and young forest communities has begun (Bonck and Penfound 1945, Hopkins and Wilson 1974).

Compositional changes over time indicated an overall trend of directional succession, but the pattern was not uniform throughout the field. The second major compositional trend, approximately perpendicular to that of time-since-abandonment, was significantly correlated with elevation, although the identity of species present and beta diversity along the elevation gradient varied among years. It is likely that annual variation in precipitation and local flooding from Bayou Lafourche (Battaglia et al. 1995), as well as increasing establishment and survival of perennial species through time, contributed to inter-annual differences in the pattern along the elevation gradient. The most pronounced shift in our study occurred in 1986, the year with the lowest cumulative rainfall in the pre-growing season (November–April). Beta diversity was lowest along the gradient and corresponded to species typical of higher elevations in wetter years colonizing lower sites. Ours is not the first study to report annual variation in compositional trends along environmental gradients in old-field communities. For example, in a classic study of old-field succession in the North Carolina Piedmont, Keever (1950) described an early successional field with a slight slope (*i.e.*, moisture gradient) in which *Aster* spp. dominated in one year but was replaced by broomsedge (*Andropogon virginicus*) in the following year. This replacement occurred throughout the field, except in the lower, wetter corner. In contrast to our results, convergence did occur in her study site, as *Aster* spp. was eventually replaced by *A. virginicus*, even in the wetter corner.

Our study illustrates that variation in species composition along the elevation gradient persists as succession proceeds, in accordance with the climax pattern concept of Whittaker (1967). Lower and higher elevation plots were moving in the same general direction in the ordination, and there did not appear to be a long- term trend toward divergence or convergence between the two groups. Further, based on the significant responses of most species in the emerging tree layer to elevation, there is no indication that convergence will occur in the developing forest community. This pattern is consistent with those found in mature bottomland hardwood forests where small changes in elevation and flooding frequency parallel shifts in community composition (Wharton et al. 1982, Huenneke and Sharitz 1986, Titus 1990, Sharitz and Mitsch 1993, Jones et al. 1994, Allen and Sharitz 1999, Battaglia et al. 1999).

The influence of microtopography on successional patterns has not been emphasized in studies of bottomland old fields (Bonck and Penfound 1945, Hopkins and Wilson 1974, Allen 1997, but see Battaglia et al. 1995). We believe that it is important to take into account the hydrologic gradient associated with microtopography. Allen et al. (1998) report higher seedling densities in undisked versus disked fields and attribute this, in part, to the remaining elevated planting surfaces in undisked fields that provide safe sites for seedling establishment. Retention, restoration, or enhancement of microtopographic variation may be key to restoring a template that can support diverse assemblages of floodplain species.

Invasion Patterns of Woody Species and Emergence of a Young Tree Layer

Early forest development and composition were influenced primarily by the local seed source and elevation (hydrology) in the study site. Invasion by woody species soon after abandonment has been documented in other bottomlands (Bonck and Penfound 1945, Hopkins and Wilson 1974, Clewell 1981, Allen 1997). Indeed, 13 of the 16 woody tree and shrub species found in 2000 in our study were recorded in the first five years of succession during floristic surveys throughout the study site (Battaglia 1991). We have no data on the distribution and demography of small seedlings below the thick ground layer of old-field vegetation, so we can only speculate about their turnover and survival. We began to observe seedlings overtopping the ground layer in 1994. By 2000, tree seedlings and saplings were very abundant and conspicuous, and the field was in a transitional stage between old-field and young forest. This stage is characterized by a rich mixture of old-field vegetation, including forbs, grasses, vines, and shrub and tree species that have emerged to varying degrees above the ground layer. Eleven of the latter species are capable of becoming canopy trees. Eleven of the 16 species of trees and shrubs had potential local seed sources on one or both of the levee systems that parallel the southern and northern edges of the study site, underscoring the influence of nearby forest fragments on species composition.

The current distribution of species is a manifestation of past dispersal events and establishment conditions. In secondary vegetation, both time-since-abandonment and environmental gradients can influence community composition (Pascarella et al. 2000). Assuming that size and age are closely related, size-class distributions indicate that recruitment rates to the ≥ 1 m height class of the seven dominant species in this study were low initially and then gradually improved. It appears that the recruitment window is still open and that populations of *F. pennsylvanica*, *C. laevigata*, *D. virginiana*, and *C. viridis* are still increasing. In contrast, distributions of *I. decidua*, *U. crassifolia*, and *C. occidentalis* suggest that recruitment levels peaked and then decreased substantially. We suspect that this pattern reflects episodic recruitment in *U. crassifolia* and a decreasing population of the shrub *C. occidentalis*. The majority of the larger individuals of *C. occidentalis* have high vine cover and stem mortality (unpublished data). Recruitment of *I. decidua* may have decreased, but the population is not in danger of senescing, as many of the stems in the field are now reproductively mature. Size-class distributions and relative abundance of species are expected to shift as succession continues and canopy closure occurs.

It is unknown whether propagule deficiency, unfavorable environmental conditions in the recently abandoned field, or a combination of the two contributed to low levels of seedling recruitment early in succession. Many of the trees along the levees have become reproductively mature during the course of the study, so influx of seeds has likely increased with time. Also, cover of herbaceous species and development of the shrub layer in recent years may have facilitated establishment of some tree species. Distribution of the shrub, *Baccharis halimifolia*, which is largely confined to higher elevations, overlaps widely with those of *C. viridis* and *I. decidua*, two species primarily dispersed by birds. Clumping of bird-dispersed species in association with shrubs has been reported in other old fields (Foster and Gross 1999), and there are several possible reasons why shrubs may be recruitment foci for tree species at our site. First, dispersal may be greater in shrub patches because birds use them as perches (Holl et al. 2000), and they provide a haven for dispersers from their predators (Jordano and Schupp 2000). Second, seedling densities may be greater due to lower seed predation and improved microsite suitability for germination and seedling establishment (Callaway 1992). Finally, mature shrubs may reduce the cover of herbaceous species that would otherwise compete with tree seedlings (Posada et al. 2000).

While shrubs may influence pattern and rate of tree establishment (Callaway 1992), the effects of shrubs are not necessarily constant and positive due to changes in shrub cover through time. It is possible that previously sparse cover of *B. halimifolia* was suitable for *I. decidua* establishment and seedling growth, but increasingly dense shrub cover may be limiting further recruitment in those patches. Shrubs may also have different effects among tree species (Callaway 1992), and mortality under shrubs may vary (Kollmann and Grubb 1999). Spatial distributions of *F. pennsylvanica*, *C. occidentalis*, and C. *laevigata* were negatively associated with areas of high *B. halimifolia* cover, yet they have invaded elsewhere in the old field.

As in many studies of bottomland forests, abundance patterns of most of the dominant species were significantly related to the elevation (hydrology) gradient (Titus 1990, Sharitz and Mitsch 1993, Jones et al. 1994). Without experiments, however, it is impossible to isolate effects of biotic from abiotic filters. Since *B. halimifolia* is confined to the higher elevations, we cannot determine whether *C. viridis* and *I. decidua* are most abundant in the eastern portion of the field and *C. occidentalis* is absent there due to suitability of environmental conditions, presence of *B. halimifolia*, or both. Nevertheless, the hydrologic gradient is underlying these patterns and may influence intensity of biotic interactions (Budelsky and Galatowitsch 2000). Elevation does not account for the spatial distribution of *Diospyros virginiana*, a species with large fleshy fruits. This species had a low overall abundance and was found at a wide range of elevations at the maximum distance from seed source (the middle of the field), indicating that it can be dispersed great distances and may not be particularly sensitive to the gradient.

Species richness in the emerging tree layer corresponds with values reported for other abandoned bottomland sites with nearby seed sources (Allen 1997), and they are approaching those reported for mature forests in the area (Huffman 1980, Devall 1990). It remains unclear, however, whether composition of mature communities that have developed through natural invasion of abandoned fields will closely resemble that of old-growth forests.

The extent to which individual species present in nearby forest patches are represented in the overall composition of the target site depends on proximity to the seed source, which can influence rate of seedling establishment, abundance, and spatial distribution of individual species (Golley et al. 1994, Pinder et al. 1995, Brunet et al. 2000). Distance to seed source seems to be an important filter on establishment of *F. pennsylvanica and C. laevigata*, but we cannot conclusively separate effects of this factor from those discussed above. Both species were low in density in the center of the site, a pattern typical of larger fields (Pinder et al. 1995). Sharply decreasing densities of these species suggest some dispersal limitation between 60 and 80 m from the edge of the field, a threshold similar to that reported by Allen (1997). It is probable that species have different dispersal limitation thresholds and that the thresholds become less critical with time since abandonment (Allen 1997, Brunet et al. 2000). *Quercus* spp. are scarce or absent in our study site although abundant on the adjacent levees. This may be due to the initial low abundance of the necessary animal dispersers. In addition, seed predation may limit the establishment of large-seeded species such as *Quercus* spp. and *Carya* spp. (DeSteven 1991).

The combination of factors leading to successful reforestation in this study does not occur everywhere. The potential for natural reestablishment in abandoned bottomlands must be assessed on a case-by-case basis. If the distance to nearest seed source exceeds 60–80 m, natural invasion of some woody species may be delayed indefinitely (Allen 1997, Allen et al. 1998). Supplemental plantings may then be necessary to improve similarity to reference sites (Aide et al. 2000, Pascarella et al. 2000). The composition of propagule sources must also be evaluated carefully. If they are depauperate in species or if they lack desirable species, intervention by managers may be warranted, possibly including seeding or planting. Finally, the source species must be well-matched to the target site conditions, particularly in terms of flood tolerance (Stanturf et al.

2000), which requires some information about the hydrologic range and variation within the site.

Restoring ecosystem connectivity and functioning in this highly disturbed system will require scaling up from individual sites and building a network of abandoned old fields linked with forest fragments. Organizations such as the Louisiana Department of Wildlife and Fisheries and The Nature Conservancy of Louisiana have already begun building these linkages; however, the legacy of extensive and intensive hydrologic modification and agricultural use in the LMAV landscape presents a formidable challenge. Ultimately, the degree to which separate sites are restored and interconnected will be determined by land managers balancing local management goals, costs, and feasibility of restoration in a highly disturbed and increasingly urbanized setting. Successfully restoring, reforesting, and reconnecting portions of the great floodplain of the Mississippi River in the LMAV will require a refined and improved understanding of succession and reestablishment of bottomland hardwood forest in agricultural fields that are dominant features in the current landscape.

ACKNOWLEDGMENTS

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