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Robert H. Jones, *Auburn University*
Rebecca R. Sharitz, *University of Georgia*
Philip Dixon, *University of Georgia*
Debra S. Segal, *KBN Engineering and Applied Sciences*
Rebecca L. Schneider, *Cornell University*

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Author(s): Robert H. Jones, Rebecca R. Sharitz, Philip M. Dixon, Debra S. Segal and Rebecca L. Schneider
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WOODY PLANT REGENERATION IN FOUR FLOODPLAIN FORESTS[1]

ROBERT H. JONES
School of Forestry, Auburn University, Auburn, Alabama 36849-5418 USA

REBECCA R. SHARITZ
Savannah River Ecology Laboratory, Aiken, South Carolina 29802 USA and
Department of Botany, University of Georgia, Athens, Georgia 30602 USA

PHILIP M. DIXON
Savannah River Ecology Laboratory, Aiken, South Carolina 29802 USA

DEBRA S. SEGAL
KBN Engineering and Applied Sciences, 1034 Northwest 57th Street, Gainesville, Florida 32605 USA

REBECCA L. SCHNEIDER
Department of Ecology, Cornell University, Ithaca, New York 14853 USA

Abstract. Between 1987 and 1990, we estimated seedfall and recorded age, growth, and survival of 10 933 tree and vine seedlings growing in the understories of four bottomland hardwood forests in South Carolina. The forests differed in flood frequency, soils, and vegetation structure but had a number of woody plant species in common.

Several demographic processes were consistent for all four forests as well as for floodplain forests described in other published studies. Smaller seeded species had larger numbers of seeds dispersed, germinants, and established seedlings. Seed size, however, was not clearly related to seedling survival. Published rankings of shade and flood tolerances were also unrelated to survival, at least during the first growing season after germination. Seedling survival rates were least during the first growing season and greater in subsequent years. Within a growing season, early germinants had greater survival. For some species, survival was negatively related to basal area of neighboring conspecific adult trees.

Some aspects of the regeneration process were more site specific. Within species, seedfall densities relative to adult tree abundance differed across forests by an order of magnitude. First-year seedling mortality rates were significantly affected by site and site × species interactions. Mortality in subsequent years was also significantly affected by site. Although the role of flooding in site-specific mortality was not clear, small elevation changes within flooded sites were correlated with changes in germination and survival for some species.

Key words: Acer rubrum; *bottomland hardwood forest; demography; floodplain forests; forest regeneration; life history traits;* Liquidambar styraciflua; Nyssa sylvatica *var.* biflora; *population dynamics;* Quercus *spp.; seed size; seedling recruitment; shade tolerance.*

INTRODUCTION

Tree regeneration by seed is a critical and frequently studied component of forest succession (Grubb 1977, Harcombe et al. 1982, Augspurger 1984, Streng et al. 1989, Schupp 1990, De Steven 1991*a, b,* Gill and Marks 1991). Several distinct phases, seed production and dissemination, germination, and survival, are involved. Each may be a bottleneck that restricts reproduction of a particular species.

In floodplain forest ecosystems, predictions of regeneration success and plant succession are particularly complex due to high species richness and the influence of numerous environmental factors such as flooding, disease, herbivory, root competition, shade, and occasional drought (Walker et al. 1986, Streng et al. 1989). The approach to understand this complexity normally includes an investigation of key plant life history traits and a description of a plant's ability to become established based on these traits. Some of the more commonly studied life history attributes include shade tolerance, seed size, and flood tolerance (Burns and Honkala 1990*a, b,* Prentice and Helmisaari 1991, Young and Young 1992).

Shade tolerance is a concept dating back to the 19th century (Daniel et al. 1979) that explains survival in forest understories based on seedling responses to two stresses: shade and the presence of roots from overstory trees (Toumey and Kienholz 1931, Baker 1949, Daniel et al. 1979, Burns and Honkala 1990*a, b*). The concept that seed size is related to the process of tree regeneration is of more recent vintage (Grime and Jeffrey

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TABLE 1. Environmental data for four floodplain forest sites. Data are means ± 1 SD.

Attribute	Site			
	Small river		Large river	
	Unflooded	Flooded	Unflooded	Flooded
Organic matter in upper 10 cm soil (%)*	11.4	46.9	4.6	3.8
Litter mass (g/m^2)†				
September 1987	510 ± 125	503 ± 271	1014 ± 362	809 ± 370
December 1987	782 ± 240	790 ± 163	976 ± 187	840 ± 265
March 1988	860 ± 458	796 ± 185	1088 ± 269	913 ± 307
Water table depth below soil surface (cm)‡	23.4 ± 13.9	21.8 ± 16.6	153.6 ± 24.1	31.7 ± 26.3
Redox potential at 15 cm soil depth (mV)§	300 ± 79	189 ± 127	567 ± 52	182 ± 146

* Loss on ignition from composite of five samples.

† Organic debris <1 cm diameter and above the mineral soil surface, from 35 systematically located 0.25-m^2 plots; different set of plots for each date.

‡ Measured twice per month between July 1987 and March 1989 in 5 cm diameter, perforated PVC pipes buried to a depth of 2 m, five pipes per site.

§ Measured twice per month between June 1987 and March 1989 using 18 randomly located platinum-tipped redox probes per site (see Patrick and DeLaune 1972).

1965, Streng et al. 1989). In an East Texas floodplain forest, Streng et al. (1989) found that small-seeded species dispersed high numbers of seeds, germinated early in the growing season, had high population flux (i.e., high rates of natality, mortality, or both), and had relatively unstable seedling populations from year to year. Heavy-seeded species germinated later and had more stable seedling populations.

Flood tolerance, its physiological basis, and its consequences in floodplain forest succession, have been widely studied (Hook 1984, Kozlowski et al. 1991). Fine-scale effects of flooding vis-à-vis microtopographic relief, however, have only been recently quantified. Microtopography can affect patterns of seed dispersal, seedling mortality, and consequently, overall seedling establishment (Huenneke and Sharitz 1986, Streng et al. 1989).

Although many greenhouse and manipulative field experiments have been used to reveal autecological characteristics of floodplain forest trees, demographic studies remain one of the strongest approaches for investigating tree seedling regeneration. The work of Walker et al. (1986), Chambers and Henkel (1989), Streng et al. (1989), and similar research on herbaceous plants (Menges and Waller 1983), have documented long-term population dynamics of plants in floodplain forests. Streng et al. (1989), in a particularly thorough study, measured germination rates and seedling flux within and across growing seasons. They determined that timing of germination, and the timing and extent of flooding were strong factors affecting long-term seedling survival. They also revealed the important relationship between seed size and regeneration pattern and corroborated a finding in other studies that conspecific adults can affect seedling survival. Their study, however, was based on observations from a single forest site during one period of time. To determine whether their findings are general or unique, demographic studies in additional forest sites are needed.

The goals of this study were to: (1) quantify aspects of the tree regeneration process, including detailed observations of population dynamics, in shaded forest understories of floodplain forests; (2) identify patterns of regeneration that are consistent across floodplain forests differing in environmental conditions; and (3) determine if the patterns correlate with life history traits such as shade tolerance, seed size, and flood tolerance. The study was conducted in four southeastern U.S. floodplain forests. This ecosystem type is species rich, very productive, and important economically as well as ecologically to the region (Gosselink et al. 1990).

METHODS

Site description

Geographic setting and soils.—The four floodplain forests were located at the Savannah River Site, an 800 km^2 area administered by the U.S. Department of Energy in South Carolina. Two study areas, referred to as the small flooded and small unflooded sites, were within the floodplain of Upper Three Runs Creek, a small stream in the Coastal Plain Province with a mean flow of 7.5 m^3/s. Soils at both small river sites are classified as Johnston series, a Cumulic Humaquept. The surface 75 cm is a black mucky loam with dark grey to brown sandy loam or clay loam below. Two additional sites, referred to as large flooded and large unflooded, were within the floodplain of the Savannah River, a stream with a mean flow of 295 m^3/s and a drainage basin that includes Mountain, Piedmont, and Coastal Plain provinces. Soils at the large flooded site are of the Chewacla series, a Fluvaquentic Dystro-

TABLE 2. Basal area (m^2/ha) of overstory stems (≥ 2.5 cm diameter at 1.3 m height on five 25 × 25 m plots per site in fall 1987. Species are arrayed in order of greatest to least overall basal area.

	Site			
	Small river		Large river	
Species*	Unflooded	Flooded	Unflooded	Flooded
Liquidambar styraciflua	5.05	6.29	4.20	9.76
Quercus laurifolia	1.27	9.52	1.56	11.33
Nyssa sylvatica var. *biflora*	8.74	8.30	0.02	0.14
Quercus nigra	2.29	0.26	10.32	0.02
Acer rubrum	1.98	1.53	0.00	5.72
Fraxinus caroliniana	0.00	6.80	0.00	0.00
Quercus pagoda	0.00	0.00	4.17	0.00
Ilex opaca	3.10	<0.01	0.90	0.03
Magnolia virginiana	4.00	0.00	0.00	0.00
Quercus michauxii	2.78	0.00	0.69	0.42
Pinus spp.	0.00	0.00	3.74	0.00
Taxodium distichum	0.00	3.30	0.00	0.00
Ulmus alata	0.00	0.00	1.76	0.41
Persea borbonia	1.81	0.00	0.00	0.00
Carpinus caroliniana	0.01	0.27	0.82	0.61
Liriodendron tulipifera	1.65	0.00	0.00	0.00
Fagus grandifolia	1.40	0.00	0.00	0.00
Betula nigra	0.09	1.11	0.00	0.00
Ulmus americana	0.00	0.02	0.07	0.88
Fraxinus pennsylvanica	0.00	0.13	0.00	0.77
Quercus lyrata	0.00	0.00	0.00	0.66
Carya aquatica	0.00	0.00	0.00	0.59
Carya cordiformis	0.00	0.00	0.47	0.00
Others	0.04	0.03	0.87	0.89
Total	34.21	37.56	29.61	32.23

* Species and authorities as in Radford et al. (1968).

chrept with a 15-cm brown, loamy A horizon over a 100 cm thick, mottled B horizon ranging from a loam to a sandy clay loam. Soils at the large unflooded site are Buncombe series, a Typic Udipsamment with a 15-cm reddish-brown A horizon over an organically stained C horizon ranging in texture from fine sandy loam near the surface to coarse sand at greater depths. Compared to the large river sites, small river sites have greater organic matter content in the soil surface but less standing litter mass (Table 1).

Flooding and soil moisture.—From late March 1987 through September 1990, a continuously recording water level gauge indicated that flood events (i.e., overland water for a 1–6 d period) occurred 41 times at the small flooded site. Eleven of these floods were deep (>0.5 m above forest floor). Eight of the deep floods occurred during October 1989 through March 1990, and one each occurred in September 1989, July 1990, and August 1990. No deep floods occurred in 1988, a dry year. At the large river flooded site, periodic flooding occurred during winter through spring of each year; however, no evidence of summer or fall flooding was noted. On 20 discrete dates during 1987 through 1990 (i.e., when seedlings were censused as discussed below), an average of 11.1 ± 29.3% (mean ± 1 SD) and 7.3 ± 23.6% of the surface area in seedling census plots was covered by water at the small and large flooded sites, respectively. No floods or floodwater covered seedling plots were observed at either of the unflooded sites. Since the 1940s, overall levels of flooding may have been reduced by the installation of dams constructed on the Savannah River upstream of the study sites (Schneider et al. 1989).

During the study, water table levels were less variable and closer to the surface in the small river sites (Table 1). Soil oxidation/reduction potentials were lower in flooded sites (Table 1), an indication that flooded sites had more soil water and greater likelihood of anoxic conditions.

Vegetation.—In fall 1987, the four sites had many overstory and understory species in common; however, overall stand structure was dissimilar, especially in the sapling, woody seedling, and herbaceous layers (Tables 2–3; Figs. 1–2; Jones and Sharitz 1991). Overstory species abundant in two or more sites included *Liquidambar styraciflua, Quercus laurifolia, Nyssa sylvatica* var. *biflora, Q. nigra,* and *Acer rubrum* (Table 2). Sites differed in total overstory basal area by no more than 27%. Sapling, seedling, and herbaceous layer densities, however, varied by 1–2 orders of magnitude (Table 3, Fig. 1). Saplings were most abundant in the small unflooded site while herbaceous cover was greatest in the small flooded site (Fig. 1). Sapling canopies were dominated by two life forms: shrubs such as *Itea virginica* and *Vaccinium elliotii,* and small tree species such as *Fraxinus caroliniana* and *Persea borbonia* (Fig. 2). Tree species, such as *Quercus laurifolia* and *Liquidambar styraciflua,* comprised 30% or less of the

TABLE 3. Density of seedlings (stems <1 m tall) estimated from 35 (flooded sites) or 75 (unflooded sites) 1-m² plots per site in fall 1987. Species are arrayed in order of greatest to least overall density.

	Site			
	Small river		Large river	
Species	Unflooded	Flooded	Unflooded	Flooded
Acer rubrum	0.05	15.23	0.00	7.37
Liquidambar styraciflua	1.23	8.60	0.63	8.86
Quercus laurifolia	0.43	5.97	0.05	0.06
Nyssa sylvatica var. *biflora*	0.05	3.74	0.00	0.06
Rhus radicans	0.01	0.09	1.27	2.26
Quercus nigra	3.03	0.00	0.07	0.06
Persea borbonia	2.77	0.00	0.00	0.00
Berchemia scandens	0.00	0.00	1.59	1.06
Ulmus spp.	0.00	0.00	0.08	2.20
Itea virginica	0.03	2.11	0.00	0.00
Crataegus marshallii	0.00	0.00	1.67	0.00
Ilex opaca	1.16	0.00	0.35	0.14
Vitis spp.	0.05	0.00	0.45	0.74
Lyonia lucida	0.93	0.00	0.00	0.00
Ampelopsis arborea	0.00	0.46	0.00	0.43
Parthenocissus quinquefolia	0.01	0.03	0.47	0.37
Carpinus caroliniana	0.01	0.46	0.07	0.11
Fraxinus caroliniana	0.00	0.51	0.00	0.00
Vaccinium elliottii	0.01	0.29	0.20	0.00
Betula nigra	0.00	0.46	0.01	0.00
Quercus michauxii	0.45	0.00	0.00	0.00
Anisostichus capreolata	0.11	0.17	0.13	0.00
Pinus spp.	0.03	0.00	0.36	0.00
Ilex decidua	0.00	0.00	0.12	0.26
Magnolia virginiana	0.32	0.00	0.00	0.00
Others	0.72	0.20	0.83	0.59
Total	11.40	38.32	8.35	24.57

sapling layer stems. Seedlings were abundant in all sites, especially flooded ones (Table 3). In all but the large unflooded site, woody seedling communities were dominated by tree life forms; however, vines were abundant in both large river sites (Fig. 2).

The four study sites are second-growth forests. Plant community structure has been influenced by more than one episode of partial timber harvests in the past century. The most recent harvests took place prior to federal acquisition of the land in 1950. Since then, no overstory trees have been cut.

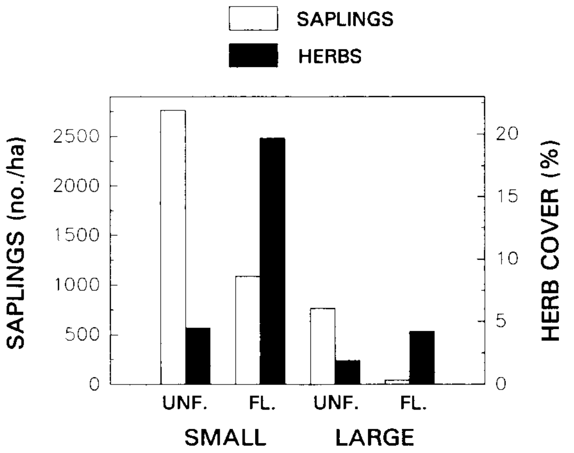

FIG. 1. Density of saplings (stems >1 m tall and <2.5 cm dbh) on five 25 × 25 m plots per site, and cover of herbaceous plants (nonwoody plants plus vegetatively produced vine stems plus all stems of *Smilax* spp.) on seedling census plots at the four study sites in fall 1987.

Field methods

Five randomly located 25 × 25 m quadrats were established in each small river site during summer 1985 and each large river site during spring 1987. All trees and shrubs in each quadrat were counted in summer through fall 1987. Seedfall collectors and seedling measurement plots were established in each quadrat as described below.

Seedfall.—Seedfall was collected in plastic buckets, each 0.11 m² in horizontal cross section. The buckets were mounted on styrofoam for flotation during flooding, and covered by wire mesh (2.5 cm openings) to minimize frugivory by small mammals. Seven buckets per quadrat were systematically located in the small river sites during October 1985, and in the large river sites during early spring 1987. Seed was collected monthly starting October 1985 (small river sites) or early July 1987 (large river sites) and ending 30 June 1990. For each collection, we recorded numbers of full, potentially viable seed by species or species group for some taxa difficult to identify to species.

Monthly seedfall data were combined into "seed years," each corresponding to midsummer of the previous year through spring of the current year (July–June). These dates were chosen to match germination in each year with the seedfall that potentially contributed to that germination (i.e., seed falling from the previous July through the end of the current June). The June–July cut-off fell within a period of naturally low seedfall; seedfall peaked in autumn and spring of each year. Because seed buckets were not located immediately adjacent to individual seedling plots, seedfall, germination, and seedling establishment data were combined for each quadrat before relationships between seedfall and germination were explored through correlation analysis.

Seedling dynamics.—To record seedling dynamics, we randomly located square 1-m^2 plots in each quadrat at each site. Prior to spring 1987, we established 7 seedling plots per quadrat in the large flooded, small flooded, and small unflooded sites (35 seedling plots per site). At the large unflooded site, where seedling densities were relatively low, we established 15 seedling plots per quadrat (total of 75). At the end of summer 1987, when it was clear that the small unflooded site also had low seedling densities, we installed eight more seedling plots per quadrat at that site. By fall 1987, the study had a total of 220 seedling plots.

Prior to new seedling germination in spring 1987, we attached a 2 × 3.5 cm aluminum tag to the base of each woody plant seedling (stems <1 m tall) in each seedling plot. Tags were loose enough to avoid damage to the seedling; however, a small percentage ($<10\%$) of the tags floated away or were otherwise missing between some of the surveys. In all but very few cases, these seedlings were easily re-identified due to carefully maintained notes on species, size, and condition of each plant. Woody stems obviously belonging to a population of interconnected ramets, and stems of *Smilax* spp., which often sprout periodically from bulbs, were not tagged; however, many of the vines we tagged in spring 1987 were probably produced vegetatively by runners or layering. Although vegetatively produced stems are important for regeneration of some species, especially vines and some shrubs, we avoided the assessment of clonal plant survival because mortality of a genet is difficult to determine in the field without destructive sampling.

When germination began in spring 1987 and spring 1988, we initiated periodic surveys to tag as many of the new germinants as possible. During the first part of the 1987 and 1988 growing seasons, we surveyed all plots every 2–3 wk. Later in the 1987 and 1988 growing seasons, when new germinants were rare, intervals between surveys were increased to 4–5 wk. No surveys were made during the leafless period (i.e., late November through early March).

In 1989 and 1990, we surveyed seedlings once in spring and once in fall. During these spring surveys, only previously tagged seedlings were inventoried; new germinants were not tagged. In the fall 1989 and 1990 surveys, we censused all tagged seedlings and tagged all surviving 1989 or 1990 germinants, respectively.

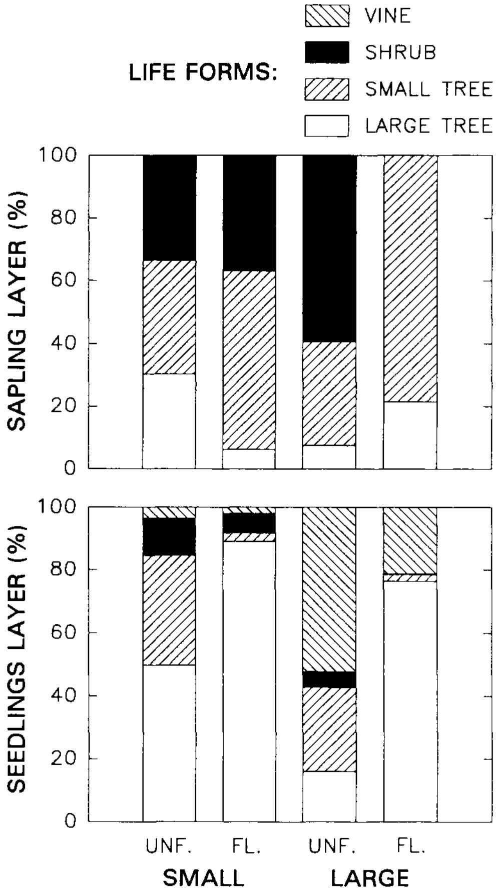

FIG. 2. Life form distribution of sapling and seedling layers in fall 1987.

For each tagged seedling, we recorded species and total height. During each survey, we assigned the survey date as a date of mortality for any seedling having an obviously dead shoot and root system. For most new germinants, mortality was obvious. However, in many cases, seedling mortality was uncertain because we could not determine the health of the root system, or we could not find the seedling. When mortality was uncertain, the seedling was declared dead if it remained missing or without new shoot development for three successive surveys. In the latter case, we used the first date that the seedling was missing or without a living shoot as the date of mortality.

During the 1987 growing season, one seedling plot at both the large flooded and large unflooded sites had too many new seedlings to tag without damaging some seedlings (i.e., the tags could not fit between seedlings). At the large flooded plot, ≈200 *Liquidambar styraciflua* were not tagged; at the unflooded plot, ≈30 *Crataegus marshallii* and 50 *Berchemia scandens* were not tagged. Thus, seedling densities at these two sites were slightly underestimated through fall 1988. By fall 1988,

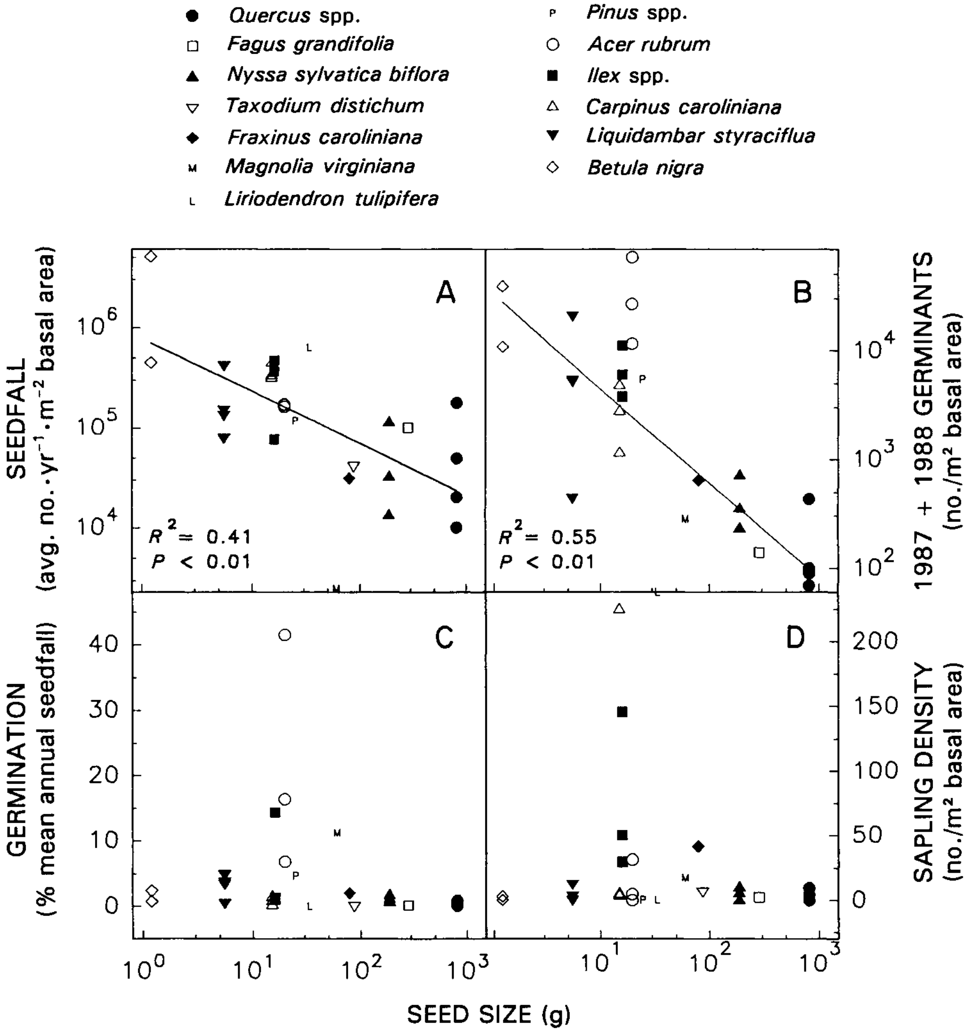

FIG. 3. Mean annual seedfall (A), mean annual germination (B, C), and 1987 sapling densities (D); each point represents one forest site. Only species–site combinations where ≥50 seeds were collected are shown. Seed size is from Schopmeyer (1974). Percent germination is mean annual germination as a percent of mean annual seedfall. Lines are linear regressions.

all living, previously untagged seedlings in these two plots were tagged; however, because specific dates of origin were unknown, these seedlings were not included in within-year survival analyses.

Presence of conspecific adults.—During February 1990 we estimated basal area of trees that had the potential for competing with or affecting seedlings on the 1-m^2 seedling plots. A 10-factor English-unit prism was used to tally trees whose diameters were at least 33 times their distance from the seedling plot center (plotless sampling; Grosenbaugh 1952). This is, in effect, a distance and size-weighted method for assessing a plant's competitive neighborhood (Zeide 1985). Past studies have shown that as tree basal area increases, understory seedling densities decline, presumably due to competition (Zeide 1985, Kittredge and Ashton 1990). We assumed that competition from overstory trees is proportional to the basal area of trees counted by the prism.

Survival analysis

We analyzed survival rates within years using within-year cohorts, and between years using annual cohorts. Within-year cohorts correspond to all seedlings germinating within a 3–5 wk period during the 1987 or 1988 growing seasons. Thus, for either 1987 or 1988 seedlings, within-year cohorts differ in age by weeks, or at most, by several months. In contrast, annual cohorts are seedlings that germinate any time during the growing season and survive to the last survey of that growing season. Annual cohorts differ in age by one or more years.

We analyzed survival of within-year cohorts by a parametric approach. First, survival (in days) was cal-

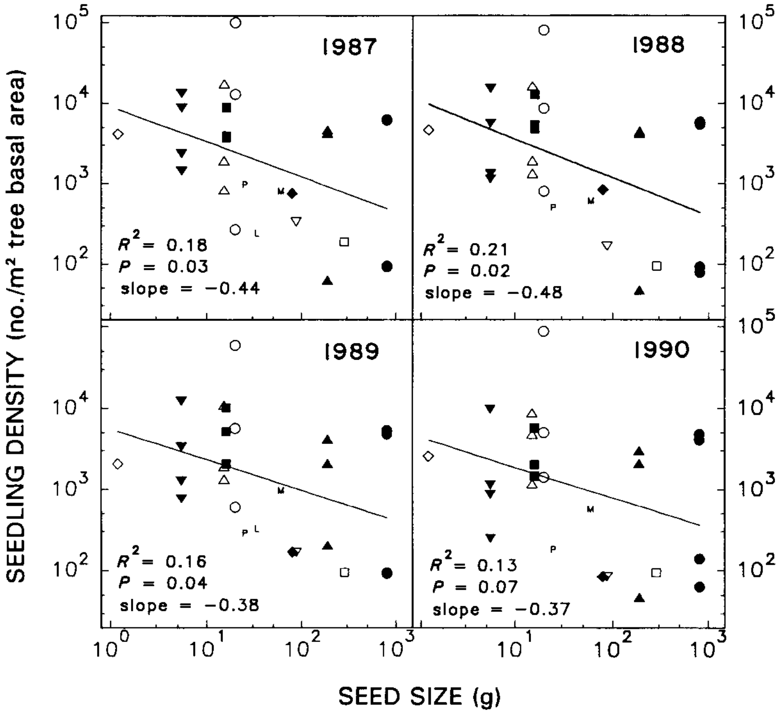

FIG. 4. Seedling density in fall of 1987–1990; each point represents one forest site. Only species–site combinations where ≥50 seeds were collected are shown. Seed size is from Schopmeyer (1974). Lines are linear regressions. For each year, one or two outliers in seedling density (zero density) are not plotted or included in the regression.

culated for each seedling in its first growing season. These data included both interval- and right-censored values. They were interval censored because the exact date of mortality was unknown; mortality occurred between two censuses. Observations were right censored if the seedling survived until the end of the growing season. Second, a log-logistic model was fit to the survival data to determine the effects of cohort, site, species, and all two-way interactions on survival (PROC LIFEREG; SAS 1988). We selected the log-logistic model over Weibull and lognormal models on the basis of a better fit and the ability to obtain numeric solutions to parameter estimates. Because some of the cohorts had few seedlings, it was necessary to delete all but the four largest cohorts in each year before analysis. Each year was analyzed separately. Daily hazard curves were calculated by substituting parameter estimates into the equation for a log-logistic hazard (SAS 1985).

For annual cohorts, numerical solutions to parametric model fits were not possible; thus a nonparametric approach was used. Before analysis, we calculated survival in days since the first survey. The first survey for the pre-1987 annual cohort (all seedlings germinating prior to 1987) was spring 1987. The first survey for each of the 1987, 1988, 1989, and 1990 cohorts was the fall of each respective year. Because the survival times were interval and right censored (as described above for the within-year cohorts), we used the Kaplan-Meier product limit method to estimate survival. This method accommodates unequal time intervals between survey dates and allows for estimation of approximate standard errors and confidence intervals of survival (SAS 1985, Fox 1989). A log-rank test (Lee 1980) was used to determine if cohort, site, and species main effects were statistically significant. Because of potential interactions (e.g., differences in species composition may affect whether sites are different), each main effect was tested while holding the other two main effects constant.

Effects of conspecific adult basal area and elevation on regeneration were analyzed by plotting or correlating seedfall, tree basal area, density of living seedlings, and seedling population flux against basal area and elevation. Two measures of flux were calculated: total number of germinants and total seedling mortality between spring 1987 and fall 1990. Correlations of either flux measure with other variables were virtually identical no matter which was used; thus, only the latter (total mortality) is reported in this paper. Because most seedlings die within weeks of germination, both measures more or less reflect natality and mortality, and both are therefore an index of population turnover rate.

RESULTS AND DISCUSSION

Seedfall, germination, and establishment

To compare data among species and across sites, the densities of seeds, seedlings, and saplings were first

TABLE 4. Correlation of seedfall in seed years 1987 and 1988 with number of germinants in 1987 and 1988 (all sites combined).

Species or species group*	n†	r	P
Vitaceae	21	0.86	<0.01
Pinus spp.	20	0.81	<0.01
Rhus radicans	23	0.73	<0.01
Berchemia scandens	13	0.62	0.02
Betula nigra	11	0.62	0.04
Liquidambar styraciflua	28	0.49	0.01
Acer rubrum	29	0.44	0.02
Nyssa sylvatica var. *biflora*	23	0.22	0.30
Carpinus caroliniana	21	0.21	0.34
Ilex spp.	23	0.20	0.35
Quercus spp.	18	−0.23	0.35

* Species and authorities as in Radford et al. (1968).

† n = number of observations, each observation is one quadrat (7-15 1-m^2 seedling plots and 7 0.1 1-m^2 seedfall buckets) in one seed year; for each species, quadrats with no seedfall and no germinants were excluded from analysis.

relativized to basal area of conspecific adult trees. The relativized data reflect the reproductive power of a species per unit of adult tree basal area and therefore do not reflect mere differences in the abundances of adult trees.

Relative seedfall and total numbers of germinants were significantly related to seed size according to regression analysis (Fig. 3). In addition, seedfall and germinant density were correlated, especially for small-seeded species (Table 4). Streng et al. (1989) also reported that smaller seeded species have more seeds and germinants, and that seedfall and germination are correlated. The close correspondence of the two studies is further illustrated by comparing correlation coefficients in Table 4 with those in Streng et al.'s (1989) Table 11. Coefficients for *Acer rubrum, Liquidambar styraciflua, Ilex* spp., and *Quercus* spp. were not significantly different ($P > 0.05$), although those for *Carpinus caroliniana* and *Nyssa sylvatica* var. *biflora* were significantly smaller ($P < 0.05$) in our study. The relatively weak correlations noted for heavier seeded plants in Table 4 may have been the result of redistribution of seeds by water prior to germination (Schneider and Sharitz 1988), the tendency for delayed germination and seedbank formation (e.g., in *Ilex* spp.; Schopmeyer 1974), and animal dispersal or frugivory (e.g., in *Quercus* spp.). The inverse relationship between seed size and numbers of seed makes sense based on theoretical and observed studies of flowering plant reproduction. Limits on allocation to reproduction constrain plants to produce either fewer larger seeds or more smaller seeds (Harper 1977).

Relativized seedling densities were also related to seed size (Fig. 4). Here again is a strong similarity with results of Streng et al. (1989). In their study, however, periodic floods substantially reduced seedling densities of small-seeded species while densities of large-seeded species were less affected. In our study, small-seeded species maintained an overwhelming dominance from 1987 through 1990 (Fig. 4), even when unflooded sites were removed from the analysis (data not shown). Two explanations for weaker flood effects in our study are: (1) less physical damage to seedlings during flooding and (2) greater within-species flood tolerance. Growing-season flood water moved very slowly in our study, causing little physical damage to seedlings whereas in Streng et al. (1989), floods damaged many seedlings by smothering them with silt or debris. Because growing-season floods in both studies were of brief duration and therefore unlikely to kill many seedlings outright, differences in floodwater energy may be the key. Variation in flood tolerance within a species is common, especially for the two species most abundant in our study: *Liquidambar styraciflua* and *Acer rubrum* (Hook 1984). Differences between the two studies point out the need for additional work on fundamental relationships between flood tolerance, floodwater energy, and seedling survival.

Although seed size was on the whole related to relative density of seeds, germinants, and seedlings, large differences between sites, some an order of magnitude or more, occurred within species (Figs. 3 and 4). Large within-species differences in percent germination and sapling densities also occurred (Fig. 3). No site consistently had the greatest relative density of seeds, number

TABLE 5. Seedfall, germination, and seedling densities of common vines.

Species or species group	Site*	Annual seedfall (no./m^2)	1987 + 1988 germinants (no./m^2)	Percent germination	Density in fall 1990 (no./m^2)
Berchemia scandens	LU	23.0	3.21	14.0	0.75
	LF	8.1	1.47	18.1	0.37
Campsis radicans	LF	6.9	0.23	3.3	0.26
Rhus radicans	LU	23.5	1.43	6.1	0.85
	LF	82.9	2.74	3.3	1.46
Vitaceae†	SU	4.5	0.24	5.3	0.05
	LU	8.2	1.19	14.5	0.52
	LF	16.9	2.16	12.8	0.86

* LF = large flooded, LU = large unflooded, SU = small unflooded.

† Includes *Vitis* spp., *Ampelopsis arborea,* and *Parthenocissus quinquefolia.*

TABLE 6. Seedling density, recruitment, and mortality in pig-rooted and nonrooted plots in the large river system (no. seedlings/m^2). Pig rooting occurred primarily between summers 1989 and 1990. Data are means ± 1 SE.

Year of survey	Rooted plots (n = 31)			Nonrooted plots (n = 79)		
		Current to next year			Current to next year	
	Fall population	Mortality	Recruitment	Fall population	Mortality	Recruitment
1987	12.5 ± 2.2	5.0 ± 1.0	3.9 ± 1.3	13.9 ± 2.2	5.0 ± 0.9	3.7 ± 0.5
1988	11.4 ± 1.9	3.7 ± 0.8	1.2 ± 0.4	12.6 ± 1.7	4.3 ± 0.7	0.9 ± 0.1
1989	8.9 ± 1.4	6.1 ± 1.1	2.0 ± 0.5	9.2 ± 1.1	5.1 ± 0.9	1.8 ± 0.3
1990	4.8 ± 0.7			5.9 ± 0.6		

of germinants, or percent germination. The large site differences may reflect differences in forest structure. For example, if a species has the same basal area in two sites, one site may have fewer, larger trees with large seed-bearing crowns, while the other site may have more, smaller trees with very small crowns and therefore low seed production. For seedlings and saplings, greatest within-species densities occurred in the small flooded site, an indication that this site may have had the best conditions for long-term survival.

Vines had high percent germination when compared to tree life forms (Table 5). Apparently, many of the vine species native to the southeastern U.S. are well adapted for germination in the shaded understory environment of a floodplain forest.

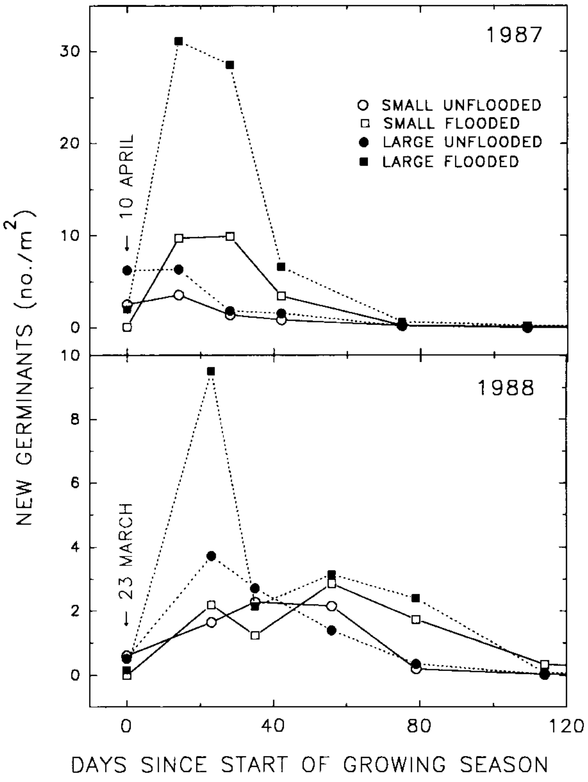

FIG. 5. Number of new germinants on seedling plots during 1987 and 1988 growing seasons.

Seedling survival

General causes of mortality.—Because of the time between surveys (3 wk minimum), we were unable to determine precise causes of mortality. Approximately 75% of all dead plants were listed as missing (no evidence of the plant found), the rest were wilted. Missing plants may have been eaten; however, they may have succumbed to other causes and then rotted or floated away. The wilted plants could have succumbed to pathogens, root herbivory, drought, or stem girdling. Streng et al. (1989), who used weekly surveys, reported similar difficulties in determining precise causes of mortality. They were able to observe only two direct causes in the field: damping-off (disease) and flooding. We noted many cases of *Acer rubrum* mortality due to damping-off in low elevation plots at the large unflooded site in summer 1987. However, we were unable to observe direct effects of inundation since no significant summer flooding occurred during the intensive sampling periods of our study (early summer of 1987 and 1988).

Beginning in summer 1989 and ending by spring 1990, 31 plots in the large river sites were rooted by feral pigs, resulting in substantial disturbance to 25% or more of the forest floor. Remarkably, this had no apparent effect on seedling population densities, mortality rates, or new seedling recruitment (Table 6). The overall densities were not different between rooted and unrooted plots. Severe effects of repeated pig rooting

TABLE 7. Significance of main and interaction effects in the within-year log-logistic regression models.

Year	Effect	−2 × log-likelihood	df	P
1987	Species	499.6	14	<0.0001
	Cohort	675.2	3	<0.0001
	Site	68.2	3	<0.0001
	Species × cohort	74.8	38	0.0003
	Species × site	36.8	25	0.0603
	Cohort × site	28.0	9	0.0009
1988	Species	329.2	14	<0.0001
	Cohort	53.0	3	<0.0001
	Site	70.0	3	<0.0001
	Species × cohort	56.6	34	0.0088
	Species × site	61.6	24	<0.0001
	Cohort × site	49.4	9	<0.0001

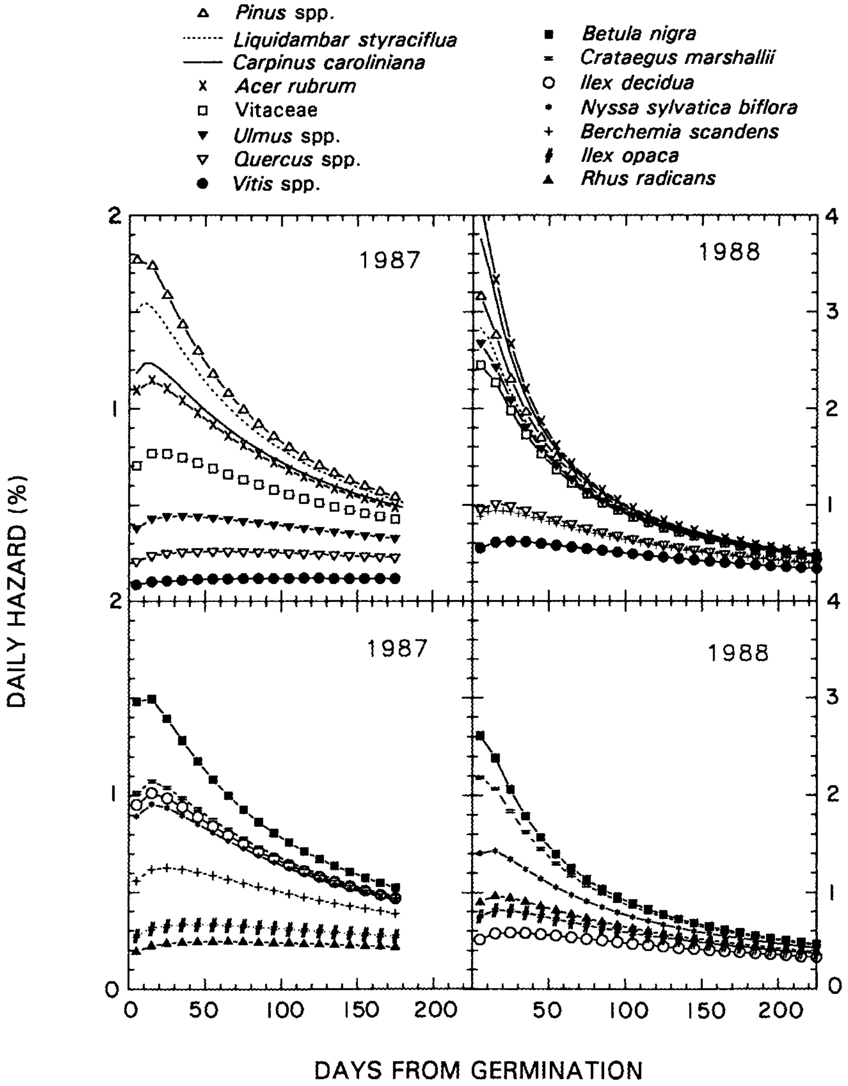

FIG. 6. Mortality of seedlings during the first growing season predicted by log-logistic model: species patterns.

have been noted in other North American hardwood forests (Singer et al. 1984); however, in the present study, this disturbance was a single occurrence.

Within-year dynamics.—During the 1987 and 1988 growing seasons, germination began in early April and late March, respectively. Total germination was much greater in 1987 than in 1988 (Fig. 5). In both years, the large flooded site had many more germinants than did the other three sites.

At each site, the timing of germination was affected by species composition. For example, *Liquidambar styraciflua* had a study-wide peak in germination 2 wk before *Acer rubrum* in 1987 and 5 wk before in 1988. Thus, sites with many *Liquidambar styraciflua* and few *Acer rubrum* (large unflooded site in 1987) tended to have an earlier peak compared to those with more *Acer rubrum* and fewer *Liquidambar styraciflua* (small flooded site in 1987). Streng et al. (1989) reported similar patterns in a Texas floodplain forest where germination was concentrated in the early half of the growing season and the peak of *Acer rubrum* germination was well after that of most other species. Additional variation in germination timing was caused by within-species patterns. For example, peak 1988 germination of *Acer rubrum* at the small unflooded site occurred 2 wk after that for the large flooded site.

Within-year survival patterns differed according to species, cohort, and site. To make this determination, we had to remove small cohorts and uncommon species from analysis; solutions for parameter estimates were not possible if all data were included. Out of eight cohorts and 47 species in 1987 and nine cohorts and 43 species in 1988, four cohorts per year and 15 species common in both years were used for analysis. All interaction effects between site, species, and cohort were significant ($P < 0.05$) in both years except for species

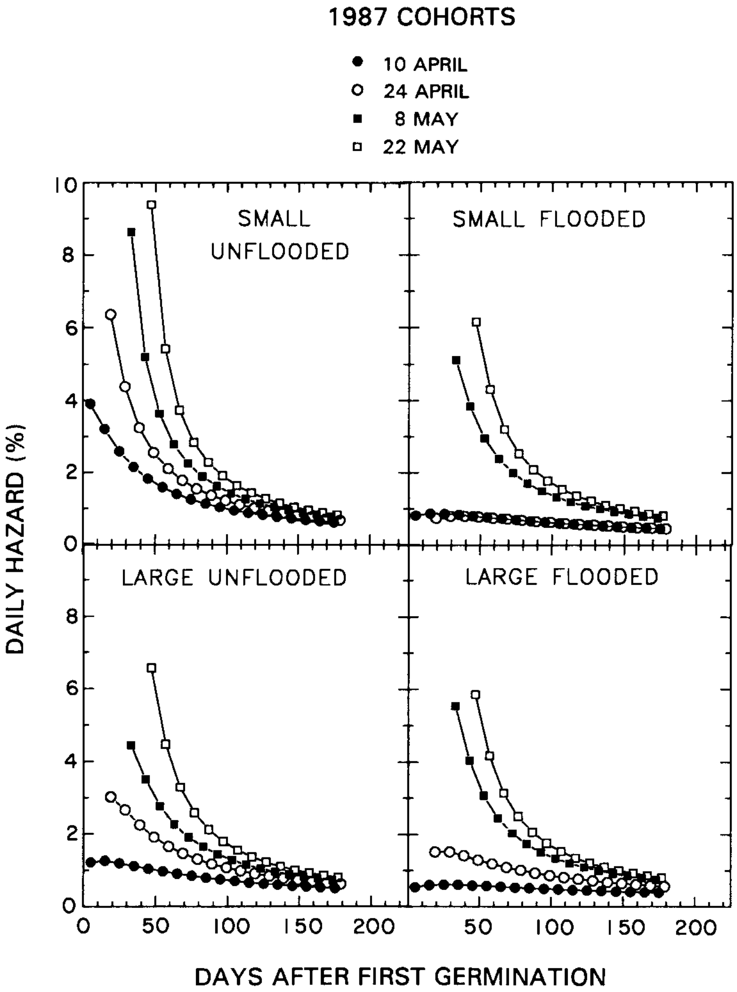

FIG. 7. Mortality of seedlings during the first growing season predicted by log-logistic model: 1987 cohort patterns at the four sites.

× site in 1987 (Table 7). Analysis of all 120 species interactions (60 each for species × site and species × cohort) was prohibitive and would have been partially artificial since not all species actually occurred in all sites and cohorts. Therefore, we removed species interactions from the model and then made two comparisons: (1) species as a main effect and (2) cohorts within sites. In each case we plotted the daily hazard function: the probability that individuals alive at the beginning of a day will die that day (Lee 1980). For both types of plots, the hazard function curves can be compared directly. For example, curves for each species in Fig. 6 represent averages over all cohorts and sites.

Hazard functions for the 15 species reveal a continuum of responses (Fig. 6). At one extreme were species that had a constantly low risk of mortality (e.g., *Vitis* spp., *Quercus* spp., *Rhus radicans,* and *Ilex opaca*). At the other extreme were species with high early mortality followed by reduced risk of death over time (e.g., *Pinus* spp., *Acer rubrum, Liquidambar styraciflua, Carpinus caroliniana, Betula nigra,* and *Crataegus marshallii*). Hazards were generally higher in 1988 than in 1987 (note scale in Fig. 6); however, the pattern among species remained relatively similar from year to year.

The pattern of high mortality early in the growing season followed by reduced absolute mortality was expected since the youngest seedlings are probably the most susceptible to pathogens, herbivory, drought stress, and flooding damage (Augspurger 1984, Streng et al. 1989, De Steven 1991*b*). Even those species with relatively low overall hazards often had a small peak in their estimated hazard function corresponding to the early part of the growing season (Fig. 6).

Survival patterns were not significantly correlated with shade or flood tolerance rankings in 1987 or 1988 (Spearman's rank correlations of cumulative hazard and tolerance; $P > 0.10$) despite the apparently low daily risk of mortality noted for several of the shade-tolerant species (Table 8). This apparent lack of cor-

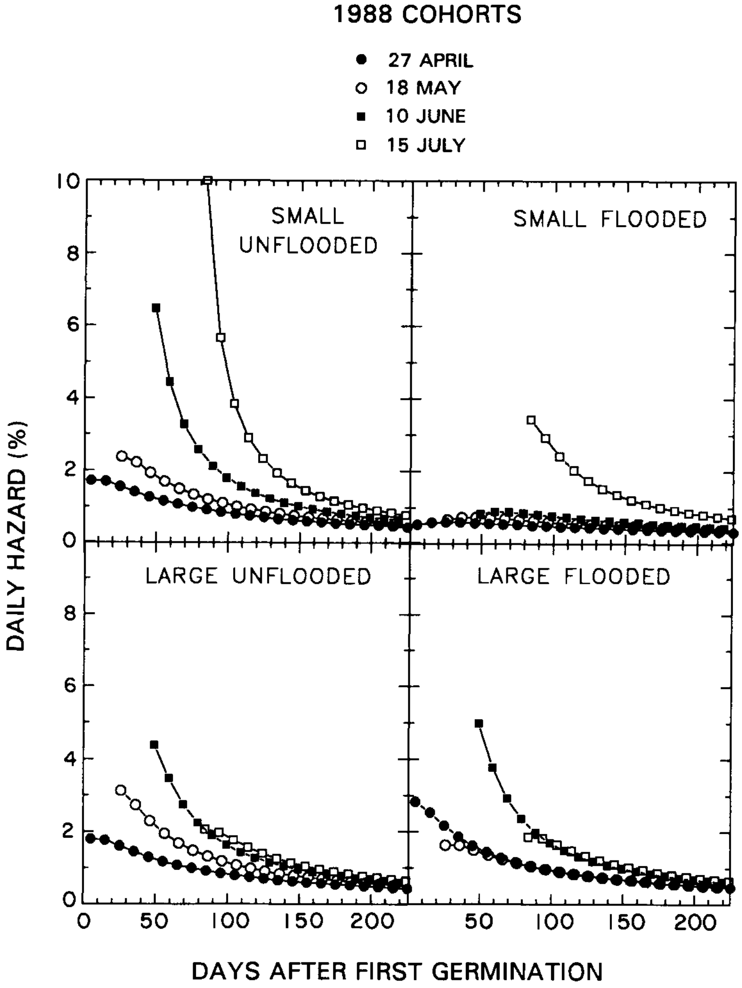

FIG. 8. Mortality of seedlings during the first growing season predicted by log-logistic model: 1988 cohort patterns at the four sites.

relation is not surprising since, for some species, actual shade and flood tolerance changes over time (Daniel et al. 1979, Hook 1984). Tolerance ratings used in the rank correlation test probably relate to persistence of seedlings and saplings over periods of years and not necessarily to survival during the first growing season.

Seed size was also unrelated to the pattern of mortality. Although *Quercus* spp., the largest seeded group by far, had relatively low hazards, so did *Berchemia scandens*, a species with very small seeds. Rank orders of seed size and cumulative hazard were not significantly correlated in 1987 or 1988 (Spearman's rank correlations; $P > 0.10$). Streng et al. (1989) also reported a nonsignificant rank correlation between 1st-yr survival and seed size. When they adjusted their data to remove the significant influence of emergence time, however, they did find that heavier seeded species had significantly greater survival for seedlings of the same emergence date. The effect of emergence time in our study, however, was removed before hazards were calculated (Fig. 6). Thus, our results and those of Streng et al. (1989) differ with respect to seed size and survival relationships.

When all 15 species were combined, a consistent pattern of lower hazards for early cohorts occurred in all sites in both years (Figs. 7 and 8). The pattern was most pronounced at the small river unflooded site, which also had the highest overall hazards. Greater survival of earlier germinants, although rarely documented, is apparently a major component of seedling dynamics in forests (Trimble and Tryon 1969, Streng et al. 1989). Streng et al. (1989) found that date of emergence had a stronger effect on seedling mortality than did flooding or light levels. Hypotheses to explain this effect include better growing conditions (e.g., more light) during the early part of the growing season, a correlation between emergence time and seed vigor, and lower pathogen loads during cooler spring weather (Jones and Sharitz 1989, Streng et al. 1989, St. Clair and Adams 1991). No experimental evidence exists to date to determine which of these alternatives is most plausible.

Table 8. Within-year hazard ranks, seed size ranks, and shade tolerance classification from Burns and Honkala (1990*a*, *b*) for common tree species and species groups.

Species or species group	Within-year hazard rank*		Seed size rank	Shade tolerance
	1987	1988		
Vitis spp.	1	2	3	unknown
Quercus spp.	2	4	1	intermediate
Ilex opaca	3	3	7	very tolerant
Ulmus spp.	4	8	10	intermediate
Nyssa sylvatica var. *biflora*	5	5	2	intolerant
Ilex decidua	6	1	9	unknown
Crataegus spp.	7	6	5	unknown
Acer rubrum	8	12	6	tolerant
Carpinus caroliniana	9	11	8	very tolerant
Betula nigra	10	7	12	intolerant
Liquidambar styraciflua	11	9	11	intolerant
Pinus spp.	12	10	4	intolerant

* Lower numbers are lower hazards and therefore higher survival in shade.

Between-year dynamics.—Fall seedling populations (all seedlings combined) declined slightly over the duration of the study (Fig. 9). Annual mortality of established seedlings was between 15 and 60% (Fig. 9). Mortality was consistently greater at the large vs. the small river; however, differences between flooded and unflooded sites within river types were relatively minor. Annual natality ranged between 1 and 40% (Fig. 9). Natality was temporally variable, with no two sites having the same pattern. The less predictable nature of natality compared with mortality may have resulted from: (1) the highly variable nature of seed production and dispersal and (2) greater sensitivity of seedlings to environmental conditions during the germination period (≈60 d). A small spike in mortality caused by a single environmental event may have a large impact on natality if it occurs during the first 2 mo of the growing season. On the other hand, a similar spike may be buffered by other mortality events during a full year and thus annual mortality may be less strongly affected. Taken together, data from this study and from Streng et al. (1989) show that annual mortality may be easier to predict than natality.

Over the study period, seedlings grew very little. Most remained <25 cm tall and only 12 of the 10 933 tagged seedlings grew into the sapling class (i.e., reached ≥1 m tall) during the 3.5-yr study period. Slow growth of established woody plant seedlings in shaded understories is a consistent phenomenon in floodplain forests as well as other forest types (Streng et al. 1989, and citations therein).

After we removed potential effects of site and seedling age on annual survival, large species differences in survival pattern were evident (Figs. 10 and 11). In eight log-rank tests, each with 4–8 species included, the species' survival curves were significantly different ($P \leq 0.013$). In most cases, shrub, vine or small tree life forms had relatively greater survival than did large tree life forms (Figs. 10 and 11). Exceptions included the large tree *Quercus laurifolia*, which had the highest survival for the pre-1987 cohort in the small flooded site (Fig. 10), and the small tree *Ilex opaca*, which had relatively low survival (Fig. 11).

Survival was not related to seed size. In each of the eight survival comparisons (Figs. 10 and 11), no correlations of survival rank and seed size rank were sig-

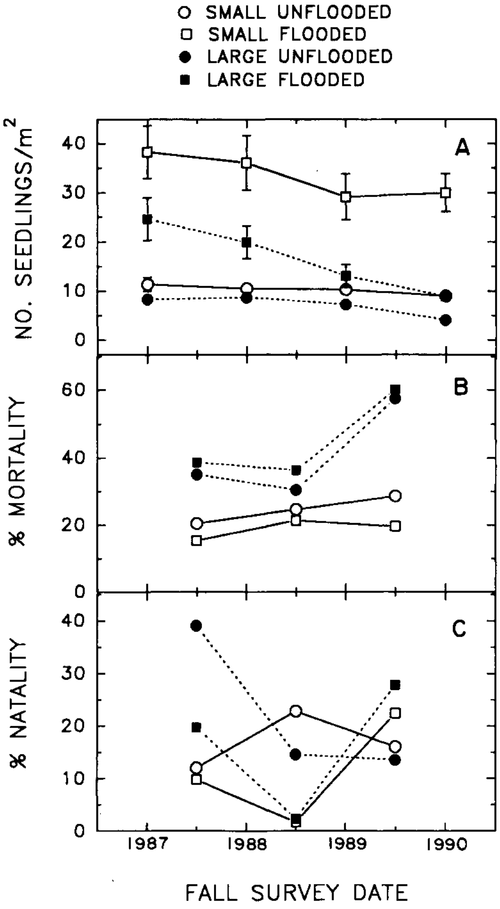

Fig. 9. Fall seedling populations (A), and mortality (B) and natality (C) of seedlings between fall surveys; data are means ± 1 se.

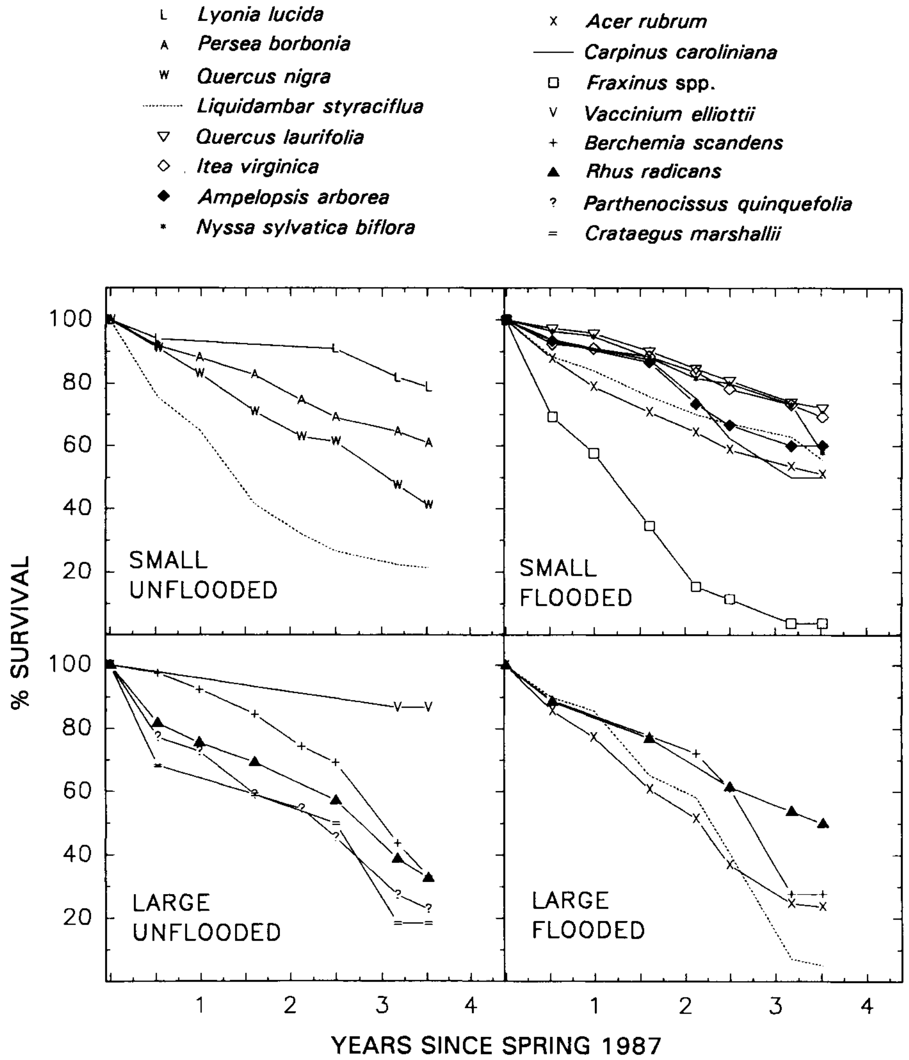

FIG. 10. Survival of the pre-1987 annual seedling cohort, comparing species within sites. Curve shapes are significantly different according to log-rank tests ($P < 0.001$).

nificant (Spearman rank order tests; $P \geq 0.20$). Although Streng et al. (1989) also found no significant correlation, they did find that average 5-yr survival was greatest for two species with relatively large seeds (*Quercus nigra* and *Sebastiana fruticosa*). In our study, *Quercus laurifolia* and *Quercus nigra* had by far the largest seeds among the species compared in Figs. 10 and 11. Although *Quercus laurifolia* had the greatest survival among the species with which it was compared, *Quercus nigra* did not (Fig. 10). Further, some of the smallest seeded species had the greatest survival rates in Figs. 10 and 11 as well as in the analyses of within-year survival (Fig. 6). Thus, both within-year and between-year survival patterns in our study failed to reveal an underlying relationship with seed size.

Many of the species in Figs. 10 and 11 have no published shade or flood tolerance ranks. The data from these two figures may be useful, therefore, for posing new tolerance rankings based on survival after the first growing season. For example, three understory shrubs (*Lyonia lucida, Vaccinium elliottii,* and *Itea virginica*) were especially shade tolerant according to this criterion (Fig. 10). All three tended to spread vegetatively and maintain belowground physical connections. Their clonal nature may have buffered individual stems against environmental stresses (Abrahamson 1979, Cook 1985). Vines were the next most shade-tolerant group. Both older vines, many of which were produced vegetatively (Fig. 10), and vines of younger seedling origin (Fig. 11) had high rates of survival in shade. *Campsis radicans,* however, was an exception. Although seeds of this vine were collected in the study, percent germination was low compared to that for other vine species, and few seedlings of *Campsis radicans* survived to the end of their first growing season (Table 5). *Vitis* spp. had lower survival (both absolute and

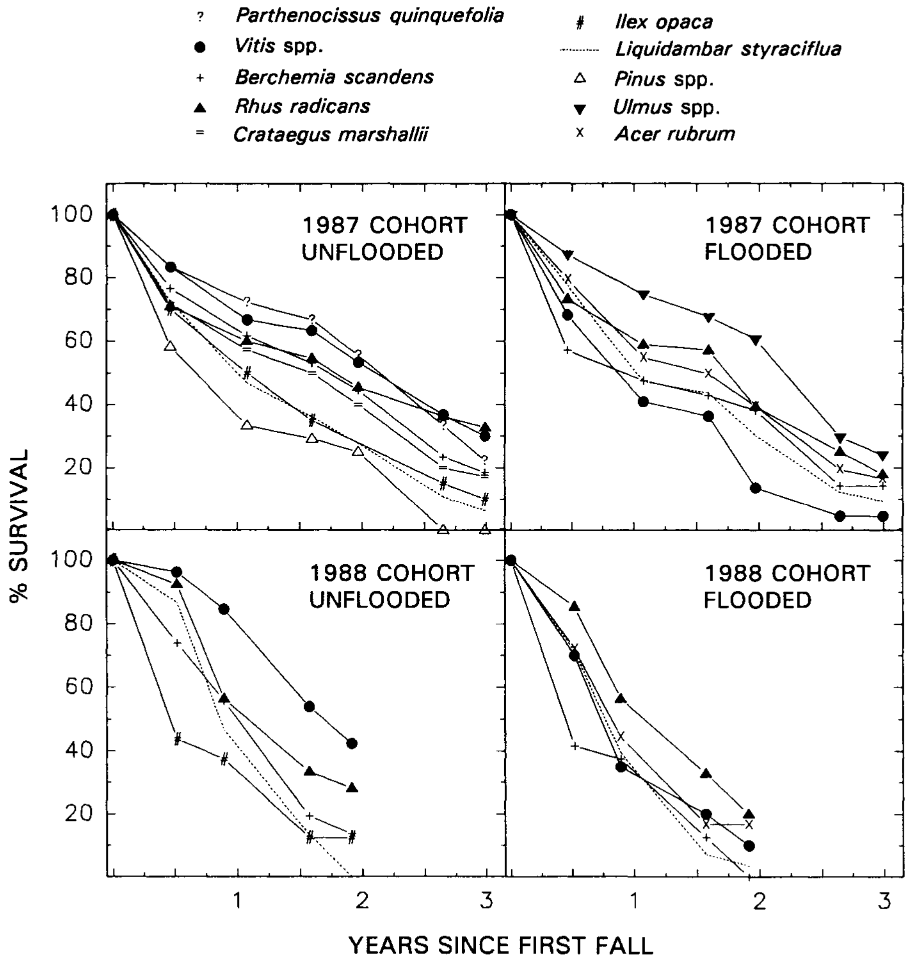

FIG. 11. Survival of 1987 and 1988 annual seedling cohorts, comparing species within large river sites. Curve shapes are significantly different according to log-rank tests ($P < 0.001$).

relative to other species) in flooded than in unflooded sites (Fig. 11), an indication that this vine group is relatively intolerant of flooding in the seedling stage. Among tree species, *Ulmus* spp. and *Quercus laurifolia* were usually tolerant relative to co-occurring species of the same cohort, while *Acer rubrum* and *Carpinus caroliniana* were intermediate. *Liquidambar styraciflua* and *Pinus taeda* often had the poorest survival, an indication that these two species were the least tolerant of the species tested.

To explore effects of seedling age on mortality, we first tested survival curves of various annual cohorts within the same species growing at the same site. Out of 12 tests, significant differences ($P < 0.05$) among survival curves were found 11 times. Four representative tests, shown in Fig. 12, indicate greater survival rates for older seedlings. In this analysis, two factors could have led to lower survival in younger cohorts: (1) an inherent increase in survival as seedlings became older and (2) changes in climate from 1987 through 1990 (Pyke and Thompson 1986). To remove the potential effect of the latter factor, we reanalyzed the data by comparing seedlings of three annual cohorts (pre-1987, 1987, and 1988) over the same period of time (fall 1988 through fall 1990). Out of nine such tests, seven were significant ($P < 0.05$); the two nonsignificant cases were the only ones where pre-1987 seedlings were not included (due to small sample size). Thus, even after controlling for differences in annual environmental fluctuations, a general pattern of greater survival for older seedlings again emerged (Fig. 13), although the pattern was not as consistent as in Fig. 12. Decreased mortality over time has been previously noted for tree seedlings, including those in forest understories (Hett and Loucks 1971, 1976, Streng et al. 1989) and in more open conditions (Uhl et al. 1988, De Steven 1991*b*).

Mean monthly mortality for each annual cohort was greatest in winter months (Table 9). This was possibly a result of flooding stresses, although trees are more tolerant of flooding during the dormant than during the growing season (Hook 1984).

To investigate site effects, we held species and cohort constant and compared curves associated with sites.

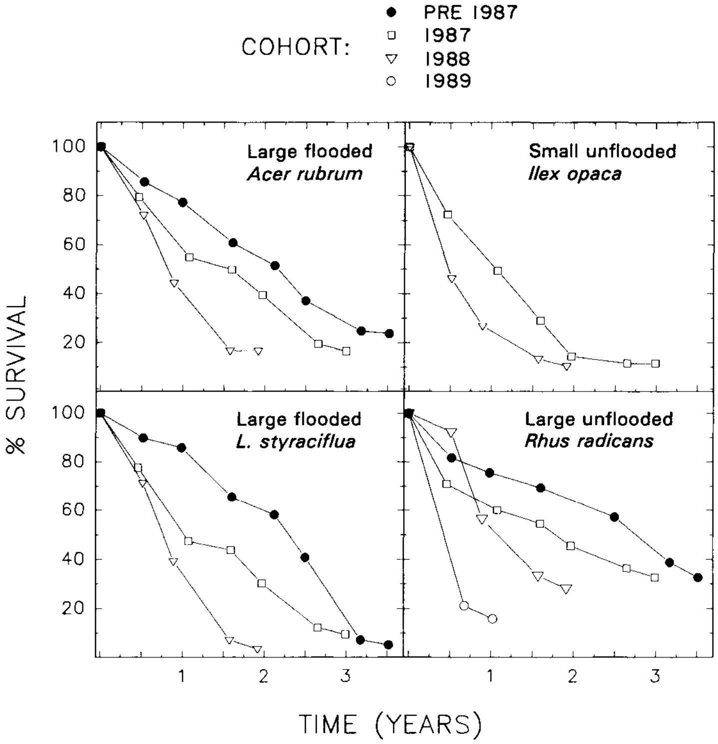

FIG. 12. Representative survival of annual seedling cohorts, comparing cohorts while species and site are held constant; data for 1987–1990 included. Within each panel, curve shapes are significantly different according to log-rank tests ($P < 0.001$).

Out of 13 such comparisons, only 5 were significant ($P < 0.05$). Four of the five significant differences occurred when the small flooded site was included. Survival tended to be greater at that site (Fig. 14). For example, in the pre-1987 *Liquidambar styraciflua* cohort, 150 out of 337 (44.5%) seedlings died between fall 1987 and fall 1990 at the small flooded site while 63 out of 67 (94.0%) died at the large flooded site during that same period (Fig. 14).

Relationship with conspecific adults

When seedlings were compared to basal area of conspecific overstory trees, a weak pattern emerged. Seedling flux and conspecific tree basal area were significantly, positively correlated in only three instances (Table 10). Positive correlations would be expected since seed rain is highest near the adult trees. When density of seedlings alive in fall 1990 was compared to conspecific tree basal area, however, correlations were more negative, an indication that seedling survival may be affected negatively by the proximity of conspecific adults. Correlations of conspecific tree basal area with actual survival estimates were even more negative (Table 10). Negative associations between adults and conspecific seedling survival or sapling density have been previously reported for Southern Coastal Plain floodplain forests (Streng et al. 1989), other temperate forests (Woods 1979), and tropical forests (Augspurger 1984). Potential explanations for this phenomenon include density-dependent mortality, increased herbivory, more pathogens, or other factors (Janzen 1970, Hubbell 1980, Streng et al. 1989).

Elevation effects

In flooded sites, elevation was a significant predictor of seedling flux and seedling density (Fig. 15). Regressions (linear or quadratic) of flux and density on elevation were significant for all species combined. At both sites, peak population densities occurred at higher elevations than did peak flux (Fig. 15). Streng et al. (1989) reported similar results: greater numbers of germinants and population flux on wetter sites but larger densities of surviving seedlings on somewhat higher elevations. Greater flux in lower sites may reflect more seeds deposited through hydrochory (Schneider and Sharitz 1988), better conditions for germination, or both. Individual species at the small flooded site followed the pattern for all species combined; however, at the large flooded site, differences among species were evident. For example, in low elevations at that site, both *Acer rubrum* and *Liquidambar styraciflua* had relatively high tree density but low seedling survival (Fig. 16). Yet seedling flux for *Acer rubrum* greatly exceeded flux for *Liquidambar styraciflua*. This pattern reflects a difference in the timing of germination. *Acer rubrum* sheds seed in spring; its seeds are sometimes

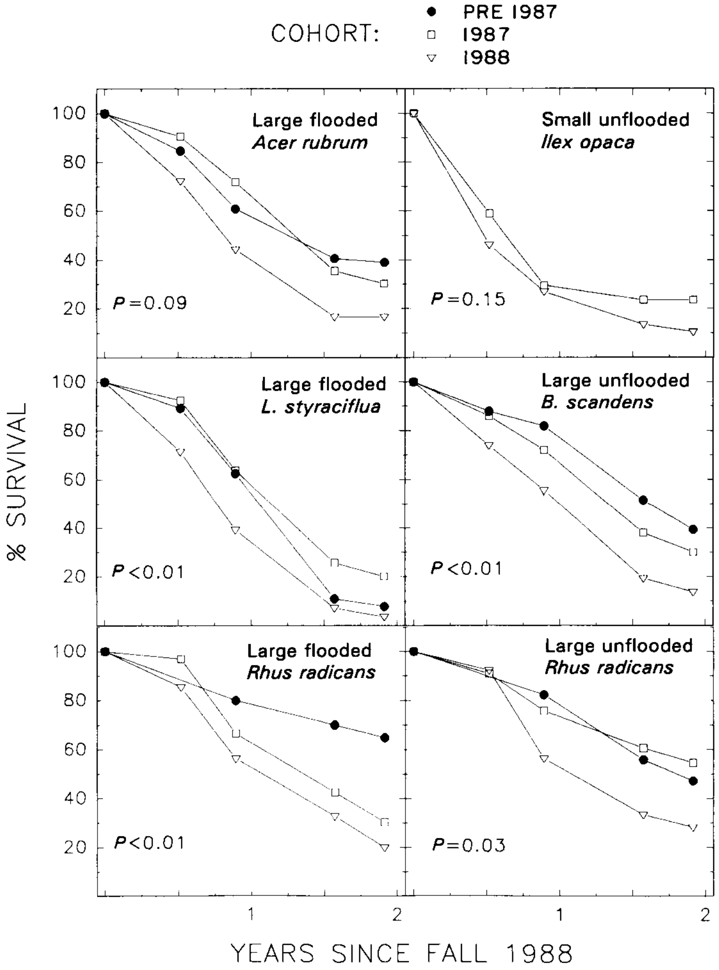

FIG. 13. Representative survival of annual seedling cohorts, comparing cohorts while species and site are held constant; data for 1988–1990 only.

released while spring flooding is occurring. *Acer rubrum* seeds may float on water, deposit when the waters subside, and then germinate. *Liquidambar styraciflua* sheds seeds in the fall and the seeds remain submerged by winter floods until flooding subsides. This submergence may exert a physiological stress on the seeds that results in low germination.

TABLE 9. Monthly mortality of annual seedling cohorts subsequent to first growing season, all species and sites combined.

	Mean monthly mortality after first summer					
	First year		Second year		Third year	
Annual cohort	Winter*	Summer*	Winter	Summer	Winter	Summer
1989	5.94	1.72	···	···	···	···
1988	5.09	4.35	2.76	1.69	···	···
1987	3.89	2.53	1.28	2.56	1.98	0.89

* Winter is time between last fall survey and first spring survey, summer is between first spring and last fall surveys.

In unflooded forests, seedling flux and survival for all species combined were not predictable on the basis of elevation (Fig. 17). However, for some individual species at the large unflooded site, seedling flux, seedling survival, tree basal area, and seedfall were apparently related to elevation. *Pinus* spp. had an affinity for higher elevations and *Liquidambar styraciflua* for lower (Fig. 18). In contrast with the flooded sites, this elevation effect may reflect a broad-scale soil moisture gradient that influences species composition of both the seedling and tree canopies.

Saplings

Sapling densities for *Quercus* spp., *Nyssa sylvatica* var. *biflora, Acer rubrum, Liquidambar styraciflua* (and to a lesser extent *Ilex* spp. and *Carpinus caroliniana*), were nonexistent at the two large river sites compared to the small river locations (Table 2). This was true despite abundant seedfall and germination in the large river sites. Robertson et al. (1978) noted a similar paucity of saplings in a Mississippi River bottomland hard-

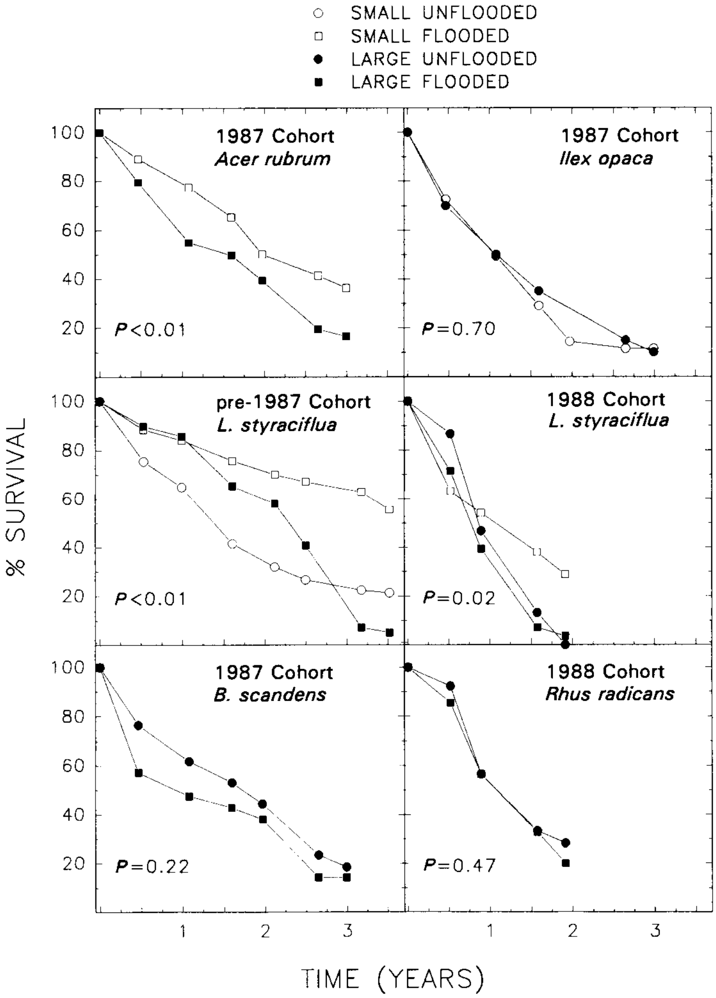

FIG. 14. Representative survival of annual seedling cohorts, comparing sites while species and cohort are held constant.

wood forest located in southern Illinois. Three explanations for this phenomenon are: (1) extended but infrequent flood events in the large river that kill seedlings and young saplings; (2) infrequent droughts, which when combined with the major difference in soil organic matter, stress saplings in the large river but not the small river floodplain; and (3) greater densities of large herbivores in the large river system.

CONCLUSIONS

A detailed examination of seedling establishment in these four closed-canopied floodplain forests, and comparisons with other published studies, have shown that many elements of the tree regeneration process are similar from forest to forest and across a broad range of environments. The most consistent patterns were: (1) more seeds and germinants for smaller seeded species; (2) greater survival rates for earlier germinants within a growing season; (3) increased survival rate for seedlings during the first several years after germination; (4) reduced survival rate for seedlings growing near conspecific adults, at least for some species; and (5) slow growth of seedlings resulting in the establishment of dense understory seedling pools.

Shade and flood tolerance rankings were not strong predictors of survival during the first growing season after germination. Tolerance rankings may have been correlated with long-term seedling survival; however, a scarcity of published tolerances for nontree species prevented us from testing this contention. It appears that seedling populations go through two filters: one during the first few months after germination where shade and flood stresses are relatively unimportant or only secondary factors affecting seedling survival and the other during subsequent years where survival may be increasingly linked to the ability to withstand flooding, deep shade, and intense root competition. An alternative explanation is that relative shade and flood tolerances of the species studied change as seedlings grow older. Regardless of which explanation is correct, the presence of the two filters supports Grubb's (1977) argument that plant community diversity is strongly

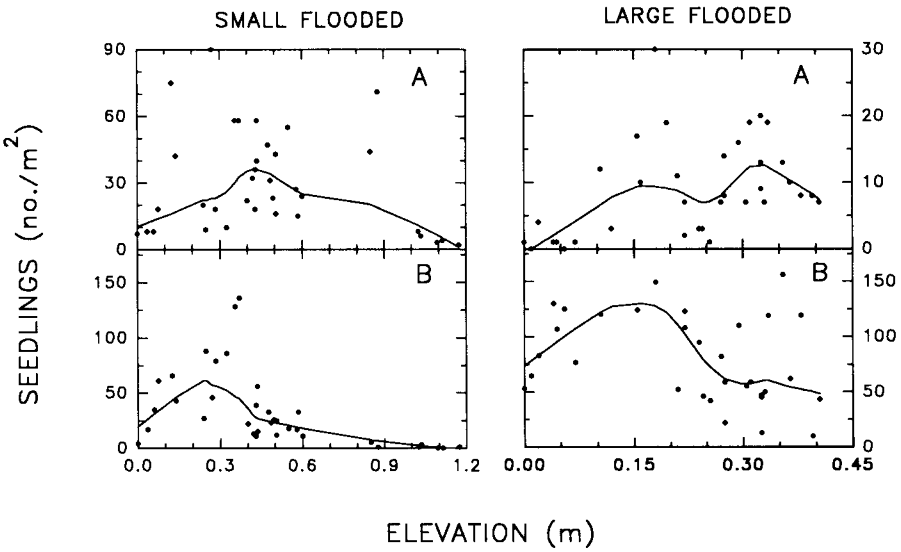

FIG. 15. Seedling densities plotted over elevation at flooded sites; (A) number of seedlings alive in fall 1990; (B) population flux (number of seedlings dying between 1987 and 1990). Lines represent a locally weighted regression, $f = 0.5$ (Cleveland 1979, Statistical Sciences 1991). Each panel had a significant ($P < 0.05$) first- or second-order regression. Elevations determined by Dumpy level in fall 1990.

affected by: (1) multiple environmental filters during the regeneration phase and (2) differences among species in their ability to pass through the various filters.

Although several aspects of seedling demography were qualitatively similar across floodplains, the sampled communities differed in species composition, especially in the seedling and sapling layers (Table 3, Figs. 1 and 2). These structural differences highlight the importance of site-specific aspects of the regeneration process, which were found in both the seed and seedling stages. For example, despite the general trend that small-seeded species had large numbers of seeds, seedfall densities within a species often differed by an order of magnitude across study sites (Fig. 3). Also,

TABLE 10. Correlations between tree basal area and three seedling population parameters (sample sizes ≥10 seedling plots or prism sample points only). Numbers in bold are significant at $P < 0.05$; numbers in parentheses are sample sizes.

Species	Site*	Conspecific seedling flux†	Seedling density fall 1990	Survival of pre-1987 annual cohort from fall 1987 to fall 1990
Acer rubrum	SU	**0.59** (12)	0.26 (12)	‡
	SF	−0.34 (12)	0.26 (12)	†
	LF	**0.72** (24)	−0.22 (24)	**−0.69** (11)
Fraxinus caroliniana	SF	0.31 (14)	0.41 (14)	‡
Ilex opaca	SU	0.24 (22)	−0.20 (22)	‡
Liquidambar styraciflua	SU	−0.15 (16)	−0.21 (16)	‡
	SF	0.05 (28)	−0.29 (28)	**−0.60** (25)
	LU	0.05 (15)	−0.24 (15)	‡
	LF	0.28 (30)	−0.18 (30)	−0.44 (14)
Nyssa sylvatica var. *biflora*	SU	**0.54** (18)	‡ (18)	‡
	SF	0.10 (21)	0.00 (21)	−0.11 (17)
Persea borbonia	SU	0.25 (17)	0.27 (17)	−0.30 (15)
Quercus laurifolia	SF	−0.07 (31)	**−0.39** (31)	−0.25 (29)
Quercus nigra	SU	0.18 (12)	0.07 (12)	−0.53 (10)
Ulmus spp.	LF	**0.64** (11)	0.38 (11)	‡
Pinus spp.	LU	−0.04 (19)	−0.22 (19)	‡

* LF = large flooded, LU = large unflooded, SF = small flooded, SU = small unflooded.
† Seedlings dying between spring 1987 and fall 1990.
‡ All seedlings dead or $n < 10$.

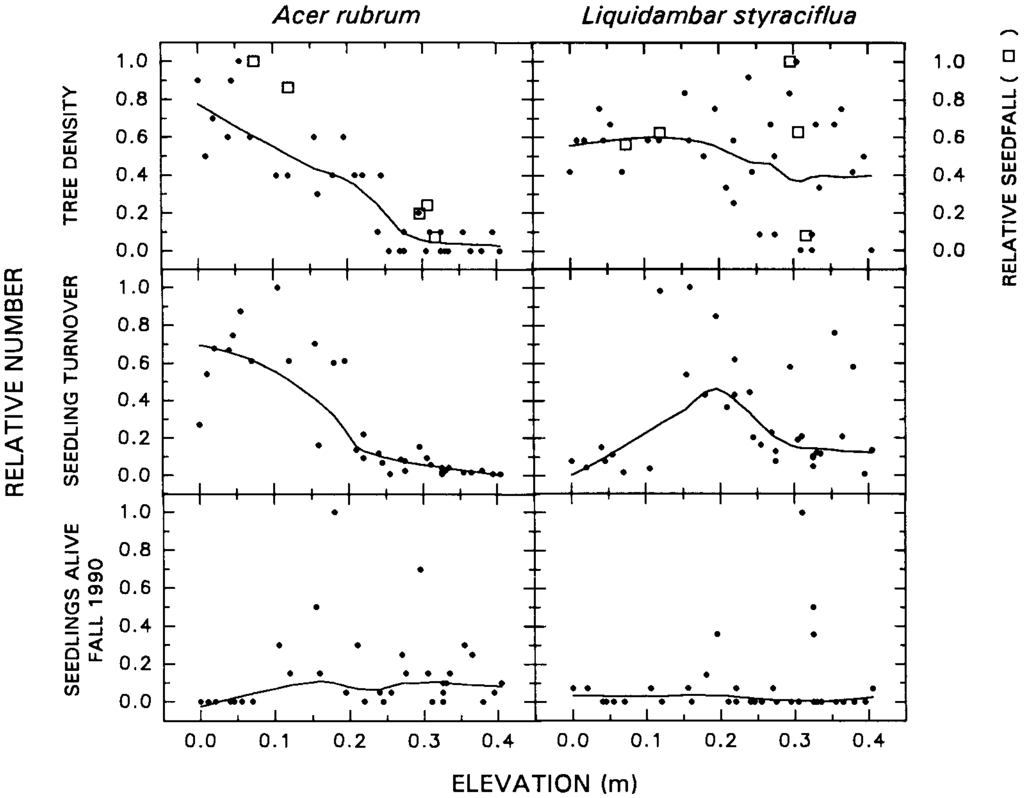

FIG. 16. Tree density (basal area determined by prism sample), seedling flux (seedlings dying between 1987 and 1990), mean annual seedfall and density of seedlings alive in fall 1990 relativized to maxima for *A. rubrum* and *L. styraciflua* and plotted over elevation at the flooded large river site. Lines represent a locally weighted regression, $f = 0.5$.

seedling survival during the first growing season was significantly affected by site and site-species interaction effects (Table 7). Weaker but still significant site effects were found for survival in subsequent years (Fig. 14).

Flooding may have contributed to some of the site differences in regeneration. Yet the precise effects of flooding on seedling survival, whether positive or negative, were hard to discern when flooded forests were

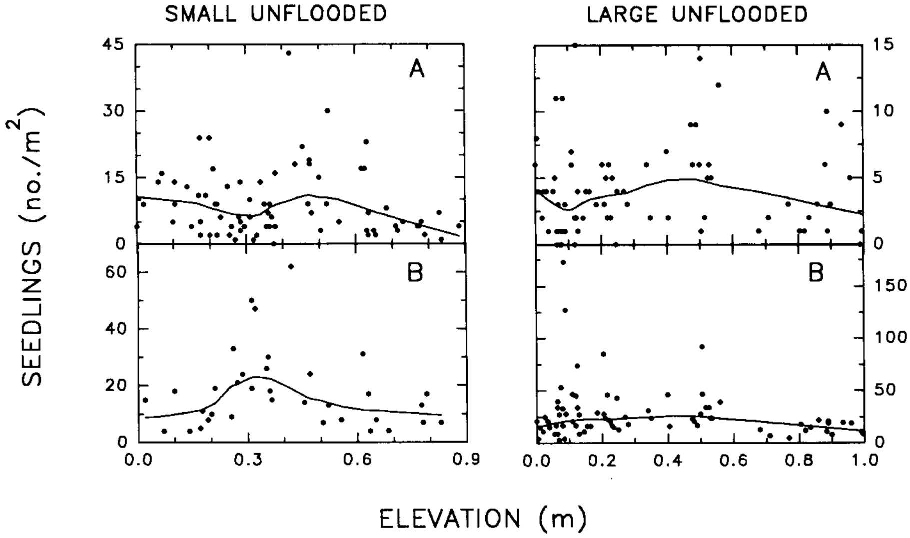

FIG. 17. Seedling densities plotted over elevation at unflooded sites; (A) number of seedlings alive in fall 1990; (B) seedling flux (number of seedlings dying between 1987 and 1990). Lines represent a locally weighted regression, $f = 0.5$.

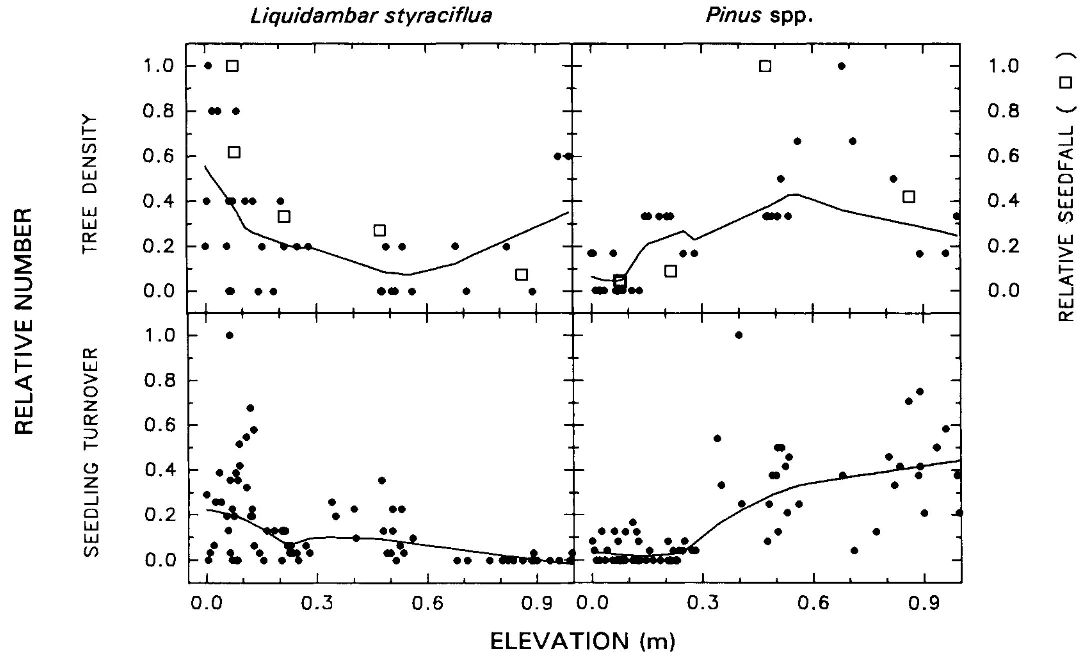

FIG. 18. Tree density (basal area determined by prism sample), seedling flux (seedlings dying between 1987 and 1990), mean annual seedfall and density of seedlings alive in fall 1990 relativized to maxima for *L. styraciflua* and *Pinus* spp. at the unflooded large river site. Lines represent a locally weighted regression, $f = 0.5$.

compared to unflooded forests. For example, the greatest seedling survival rates were found in the small flooded forest despite an expectation of low survival due to growing season floods. Effects of flooding were somewhat easier to see within flooded forests where small differences in elevation led to changes in germination and seedling survival (Figs. 15 and 16). Part of the difficulty in measuring flood impacts in the field relates to the complexity of flood–plant interactions. Responses to flooding depend on the species, life stage, size, and vigor of tree seedlings as well as the type, timing, and duration of the flood (Kozlowski 1984). Thus, to better explore flood effects in the field, detailed flood histories for each seedling or manipulations of flood levels in forest understories may be needed. Understanding the influences of flooding may be particularly important in view of the consistent and strong pattern of greater long-term survival for early germinants. Floods are more frequent in the early part of the growing season in southeastern U.S. floodplain ecosystems. Thus, early germination may have both costs and benefits, the evolutionary consequences of which have been inadequately explored.

The dynamic nature of early growing season seedling populations has important ramifications for sampling. Since seedling populations were relatively stable (i.e., low rates of germination and mortality) during all but the first part of the growing season, the best period for a one-time annual census may be late summer or early fall when leaves are still present. Further, because net population densities remained stable from fall to fall (despite substantial turnover), a survey in fall of one year would have been a good approximation of understory seedling populations in these study sites for some years afterward. Good and Good (1972) reported similarly high stability of understory seedling populations in a New Jersey upland hardwood forest. Streng et al. (1989), on the other hand, found that fall seedling densities ranged between 6.15 and 18.12 individuals/m^2 over a 5-yr period.

In all forests, seedling layers (i.e., seedling pools) differed in composition from their respective overstories. For example, *Liquidambar styraciflua* was well represented in the overstory of all four forests (Table 2) but was far more prevalent in the seedling layer of flooded than unflooded forests (Table 3). For *Acer rubrum*, overstory trees were well represented, but seedlings were nearly absent from the small unflooded site. *Quercus* spp. occurred in the overstory of all sites, but were rare in the seedling pool of large river sites. These findings suggest that species composition of the overstory will likely change in the near future. However, the postdisturbance (or postmortality) replacement of upper canopy trees is a process that is only partially influenced by the composition and density of predisturbance seedling pools. Understory saplings, seedlings of herbaceous and woody species that establish after disturbance, and sprouts from root systems of damaged trees are also important as either sources of new canopy trees or potential competitors. Although many studies have quantified aspects of postdisturbance regeneration in floodplain forests (DeBell et al. 1968, Bowling and Kellison 1983, Gresham 1985, Francis 1987, Janzen and Hodges 1987, Chambers and Henckel 1989, Golden and Loewenstein 1991), the precise role of understory seedling pools remains unclear. Demographic analyses such as those of this study and Streng et al. (1989), if applied in forests undergoing gap formation or major disturbance, would be a useful approach for determining seedling pool contributions to long-term overstory dynamics.

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