Ecology, 84(7), 2003, pp. 1849–1861
© 2003 by the Ecological Society of America

SEEDLING SURVIVAL AND GROWTH OF THREE FOREST TREE SPECIES: THE ROLE OF SPATIAL HETEROGENEITY

BRIAN BECKAGE[1] AND JAMES S. CLARK

University Program in Ecology and Biology Department, Duke University, Durham, North Carolina 27708 USA

Abstract. Spatial heterogeneity in microenvironments may provide unique regeneration niches for trees and may promote forest diversity. We examined how heterogeneity in understory cover, mineral nutrients, and moisture and their interactions with canopy gaps contribute to the coexistence of three common, co-occuring tree species. We measured survival and height growth of 1080 seedlings of *Acer rubrum* (red maple), *Liriodendron tulipifera* (yellow poplar), and *Quercus rubra* (red oak) that were planted in one of five understory treatments: removal of understory vegetation, trenched, trenched plus removal of understory vegetation, fertilization, and a control. Understory treatments were replicated in 12 paired gap and canopy environments.

Survivorship varied among species, with *Q. rubra* having the highest probability of surviving beyond the 1135-day experiment (probability = 0.64), followed by *A. rubrum* (probability = 0.27) and *L. tulipifera* (probability = 0.07). Although canopy gaps and understory treatments had large effects on survivorship, species survival rankings changed little across microenvironments; *Q. rubra* had the highest survival in all microenvironments. In contrast to survival, *L. tulipifera* had a relative growth rate for height that was three times greater than that of *A. rubrum* and *Q. rubra* in high-resource microenvironments. There was broad overlap among species in relative growth rates in the remaining seven microenvironments, with no clear top-ranked species.

Differences in seedling growth and survival across these 10 microenvironments may contribute to the coexistence of two of the three species studied, *L. tulipifera* and *Q. rubra*, but not *A. rubrum*. *Q. rubra* had higher survival than *A. rubrum* and *L. tulipifera* in all microenvironments, but *L. tulipifera* tended to grow faster than *A. rubrum* and *Q. rubra* in high-resource microenvironments. Despite the generally poor performance of *A. rubrum*, it was the only surviving species in some quadrats at the end of the experiment, indicating that stochastic effects, in conjunction with broad niche overlap, may also contribute to species coexistence. The importance of stochastic effects will probably increase when differential fecundity across these three species is considered because the high fecundity of *A. rubrum* offsets survival and growth disadvantages of its seedlings through their greater total abundance.

Key words: Acer rubrum; *canopy gaps; forest dynamics;* Liriodendron tulipifera; Quercus rubra; *regeneration niche; seedling growth; seedling survival; southern Appalachian forests; spatial heterogeneity; species diversity; stochasticity.*

INTRODUCTION

Spatial heterogeneity in environmental conditions that affects the growth and survival of tree seedlings may act as "filters" that differentially affect tree species (Harper 1977). Environments favoring seedlings of particular species might function as regeneration niches that promote species coexistence (Grubb 1977, Pacala and Roughgarden 1982, Huston 1994, Pacala and Tilman 1994, George and Bazzaz 1999*a*, *b*). However, the potential for spatial heterogeneity in microenvironments to maintain forest diversity depends on interactions of different sources of heterogeneity across spatial scales. Fine-scale variability (less than one square meter) in environmental conditions in the forest understory is superimposed on coarse-scale (greater than one square meter) variability represented by canopy gaps and other large disturbances. Canopy gaps, resulting from the death of overstory trees, can increase the levels of light, soil moisture, and nutrients in the forest understory (Pearcy 1983, Canham 1988, Denslow et al. 1990, Pacala et al. 1994), all of which may limit seedling growth and survival. However, the forest understory further modifies resource heterogeneity at the seedling scale (Korstian and Coile 1938, Harmon and Franklin 1989, Veblen 1989, Facelli 1994, Lorimer et al. 1994, Berkowitz et al. 1995, George and Bazzaz 1999*a*, *b*). For example, Beckage et al. (2000) showed that the understory shrub *Rhododendron maximum* L. usurped light resources in canopy gaps, reducing resource heterogeneity at the forest floor and lowering seedling diversity.

Manuscript received 1 May 2002; revised 18 September 2002; accepted 5 October 2002. Corresponding Editor: S. Lavorel.

[1] Present address: Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, Teunessee 37996-1610 USA. E-mail: bb2@duke.edu

Interactions between heterogeneity in the forest overstory (e.g., gap or closed canopy) and understory microenvironments may affect seedling performance, subsequent community composition, and the potential for species coexistence (Beckage et al. 2000, Heinemann et al. 2000). The presence of gap–understory interactions could influence both the seedling competitive environment and the nature of the resource limitation on seedling growth and survival. For example, understory herbs, ferns, and shrubs may increase in response to high light availability in canopy gaps and may compete with tree seedlings. Conversely, microenvironments characterized by high mineral nutrients or soil moisture may have disproportionate effects on seedling performance in high light environments, e.g., canopy gaps, and little effect in light-limited environments, e.g., closed canopy, (Denslow et al. 1998, Fahey et al. 1998, Coomes and Grubb 2000). Tolerance of low light levels may be enhanced by environmental conditions such as increased moisture (Coomes and Grubb 2000).

Despite the fact that gap–understory interactions on resource availability may be common and important, there are few large-scale, long-term experiments that examine the magnitude of these interactions and their impacts on seedling performance under field conditions. We implemented long-term, replicated experiments to determine the interactions in spatial heterogeneity and their effects on demographic rates that may contribute to coexistence. Our three-year study of the dominant species *Acer rubrum* L. (red maple), *Liriodendron tulipifera* L. (yellow poplar), and *Quercus rubra* L. (red oak) in the southern Appalachians involved canopy treatments with superimposed understory manipulations that simulate the primary factors affecting resources for understory seedlings. We monitored the survival and growth of seedlings in contrasting microenvironments created by removal of understory vegetation, trenching, trenching plus removal of understory vegetation, fertilization, and in unmanipulated controls. These fine-scale treatments were replicated in closed-canopy and gap conditions. These treatments allowed us to determine if 10 contrasting microenvironments (five understory treatments × two overstory conditions) provide sufficient heterogeneity to promote coexistence. We asked whether each species outperformed the others in some microenvironment (i.e., some subset of the 10 experimental treatments) as measured by seedling survival or growth.

Study Area

We conducted this study in second-growth forests at the Coweeta Hydrologic Laboratory (35°03′ N degrees latitude, 83°27′ W, elevation 675 m to 1592 m), in the Blue Ridge Physiographic Providence of the southern Appalachians (see Plate 1, top). Average monthly temperatures range from 3°C in January to 19°C in July. Precipitation is abundant, averaging 1800 mm annually, and is distributed evenly throughout the year (Swank and Crossley 1988).

Whittaker (1956) described the regional vegetation in relation to elevation and moisture, including mixed-oak forest, which is the most widespread forest type in the southern Appalachians and is the focus of our analysis. Mixed-oak forest is found at mid-elevations and at moisture levels intermediate between those of cove hardwoods and oak–pine ridges. *Castanea dentata* (Marshall) Borkh. (American chestnut) was abundant in mixed-oak communities before the chestnut blight killed most chestnut trees in the Coweeta basin by 1940. Today, mixed-oak forest is dominated by *Acer rubrum* L. (red maple), *Betula lenta* L. (sweet birch), *Carya* spp. (hickories), *Liriodendron tulipifera* L. (yellow poplar), *Nyssa sylvatica* Marshall (black gum), *Oxydendrum arboreum* (L.) DC. (sourwood), *Quercus coccinea* Münchh. (scarlet oak), *Quercus prinus* L. (chestnut oak), *Q. rubra* L. (northern red oak), *Robinia pseudoacacia* L. (black locust), and *Tsuga canadensis* (L.) Carrière (eastern hemlock).

Methods

Study species

Seedlings of *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra* were used in our experiments because they are dominant elements of southern Appalachian forests, co-occur within our study sites, and represent a range of life history traits including shade tolerance and seed size (Table 1). *A. rubrum*, *Q. rubra*, and *L. tulipifera* are considered tolerant, intermediately tolerant, and intolerant of shade, respectively.

Experimental design and sampling

In the summer of 1997, we located 12 natural windthrow gaps that were of recent origin, i.e., the downed trees often had leaves still attached and showed little sign of decay. The gaps were found in mixed-oak communities throughout the Coweeta basin. Most of the trees were uprooted, although some trees had snapped boles. The forest understories were dominated by *Gaylussaccia baccata* (Wangenh.) K. Koch (black huckleberry), typically <1 m in height, but also included scattered individuals of *Rhododendron maximum* (great laurel) and *Kalmia latifolia* L. (mountain laurel), both taller, evergreen shrubs.

We randomly located five 1-m^2 quadrats within each gap. Each quadrat was assigned one of five understory treatments: removal of understory vegetation (Removed, T + R), trenched (Trenched, T), trenched plus removal of understory vegetation (Trenched + Removed), fertilization (Fertilized, F), or control (Control, C). In the removal treatments, we clipped all understory vegetation <2 m in height two to three times during each growing season to increase light availability within the quadrat. The understory vegetation that was initially removed was dried and weighed. We

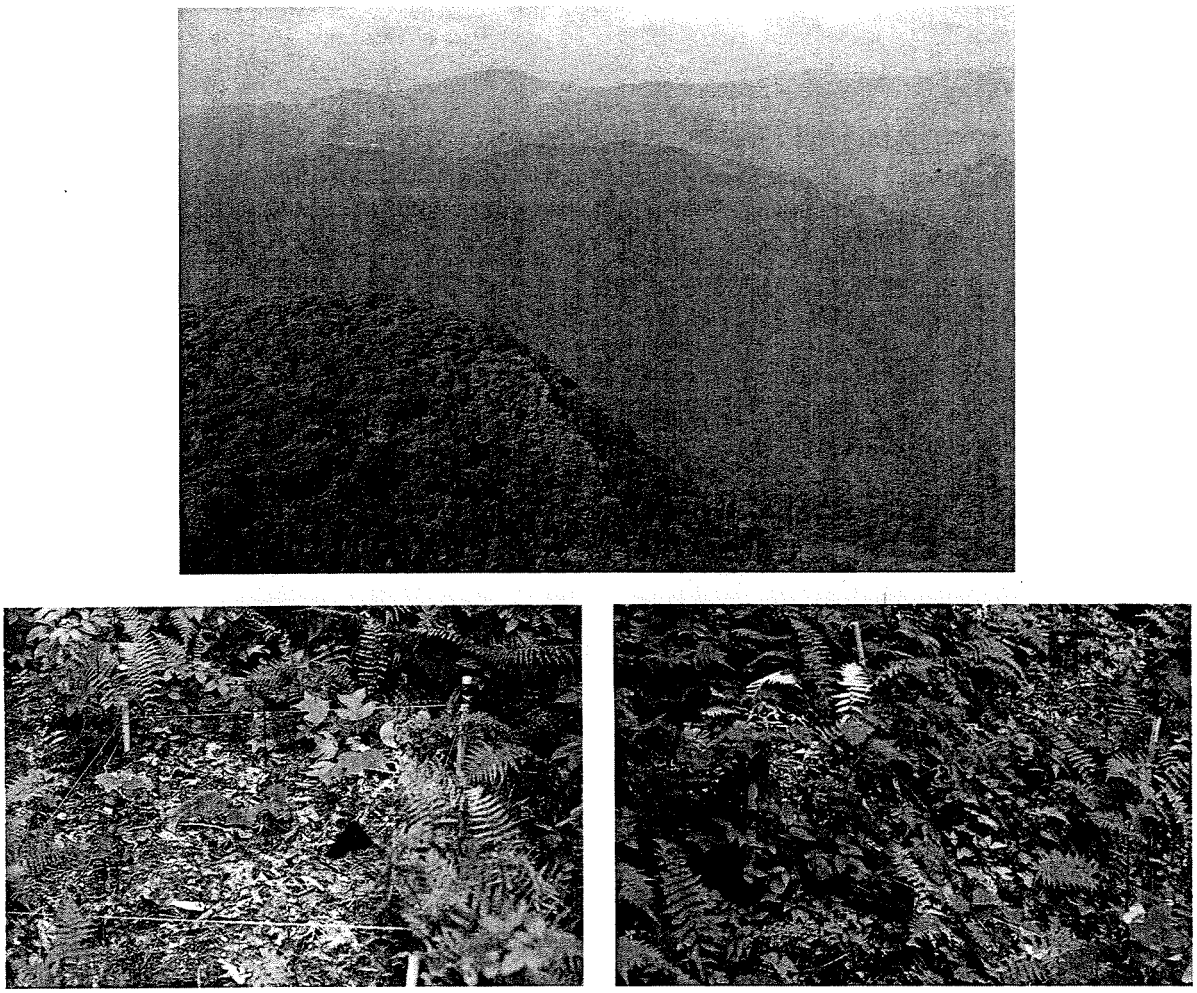

PLATE. 1. (Top) The view from the top of Coweeta basin in western North Carolina. Approximately 60 tree species occur withing the basin. (Bottom left) A study quadrat with the understory vegetation removed and *Liriodendron tulpifera* seedling visible at the rear of the quadrat. (Bottom right) A study quadrat with the herbaceous vegetation intact.

reduced competition with adjacent plants for belowground resources such as water and nutrients by severing roots to a depth of 45 cm around the quadrat perimeter in trenched treatments. Large roots were cut using a handsaw. Trenching to this depth is expected to sever >93% of active roots (Yeakley 1993). The trenches were backfilled and did not contain any barriers to lateral water flow that might have caused drying out of the quadrats. Drying out of the trenched quadrats was also unlikely because of the abundant precipitation and humid climate of the study sites (Swank and Crossley 1988). The Trenched and Trenched + Cleared treatments were trenched again each summer. Trenching and removal of understory vegetation in combination reduced levels of both above- and belowground competition. In the fertilization treatment, we inserted slow-release fertilizer tablets into the soil (~3–5 cm depth) adjacent to the seedlings at the time of planting. The tablets (10 g Agriform planting tablets NPK 20-10-5 plus minors; Grace-Sierra Horticultural Products Company, Milpitas, California, USA) had an expected life of two years and contained a full range of macro- and micronutrients. New tablets were inserted adjacent to surviving seedlings on 19–22 June 1999. The fertilizer treatment was always assigned to the subplot farthest downslope to avoid possible effects on other quadrats. With this exception, treatments were randomly assigned to quadrats.

Within each quadrat, we planted three first-year seedlings of *A. rubrum*, *L. tulipifera*, and *Q. rubra* for a total of nine seedlings per quadrat near the end of the summer growing season (24–27 August 1997). *A. rubrum* and *L. tulipifera* seedlings were collected from within the Coweeta basin. *Q. rubra* seedlings were germinated from acorns purchased from a nearby seed source. Before planting, we recorded initial heights, stem diameters, and numbers of leaves (excluding cotyledons) for each seedling.

We repeated this experimental design beneath the closed canopy adjacent to each gap location. We refer

TABLE 1. Characteristics of the three tree species used in this experiment.

Species	Shade tolerance†	Drought tolerance‡	Low-N tolerance§	Diaspore mass (mg)‖	"Seed" mass (mg)‖
Acer rubrum	2	3¶	1	33.3	29.1
Liriodendron tulipifera	4	2	3	39.8	26.9
Quercus rubra	3	2	1	364#	NA

† Rankings: 1, very tolerant; 2, tolerant; 3, intermediately tolerant; 4, intolerant. Data are after Burns and Honkala (1990).
‡ Rankings: 1, tolerant; 2, intermediately tolerant; 3, intolerant. Data are after Wilde (1958); *Acer rubrum* was not rated.
§ Rankings: 1, tolerant; 2, intermediately tolerant; 3, intolerant. Data are after Mitchell and Chandler (1939).
‖ Data are after De Steven (1991); NA indicates not applicable.
¶ Data are after Barton and Geeson (1996).
# Data are after Young and Young (1992).

to each gap or canopy location as a subplot and each gap/canopy pair as a single plot or replicate. In total, there were 12 plots and 1080 seedlings. Characteristics of the canopy and gap portions of all plots are given in Table 2.

All seedlings were subsequently surveyed in October 1997, May, June, and August 1998, June and August 1999, and June and October 2000. During each census, a seedling was recorded as either alive or dead. Seedling heights were initially measured at the time of planting and were remeasured in August 1999.

We quantified the understory light environment using hemispherical photographs taken over the center of each quadrat. Photographs were taken at a height of 1 m on 18–20 August 1999 using a fisheye Nikkor 8 mm f2.8 lens (180° field of view) with Kodak color slide film and a self-leveling gimbal. All photographs were oriented with magnetic north toward the top of the image, allowing superposition of the solar track. Photographs were digitized and analyzed using Hemiview canopy analysis software (Delta-T Devices, Cambridge, UK). The software estimates indirect and direct site factors (ISFs and DSFs), which are defined as the proportion of direct and diffuse radiation received below the canopy as a fraction of that received above the canopy (Rich 1989). Site factors range from 1 (open sky) to 0 (complete obstruction). Cosine-corrected direct and indirect site factors were combined into a global site factor (GSF) using weights that represent the proportion of diffuse vs. direct light at our study site. Weights were calculated based on meteorological data from the Coweeta basin (Bonan 1989, Nikolov and Zeller 1992). We used the GSF values in two ways. For comparison of gap and canopy conditions, an average GSF value was calculated for the gap and canopy portions of each plot (i.e., mean of five quadrats). For modeling of seedling survival and growth, the GSF value associated with each quadrat was used as a covariate.

Analysis

We examined differences in light levels (i.e., GSF values) and biomass of understory vegetation in gap and canopy environments. Comparisons were made using paired t tests, with the alternative hypothesis being that of greater light or understory vegetation in canopy gaps. To avoid psuedoreplication, samples from within gap or canopy subplots were averaged prior to conducting the t tests.

TABLE 2. Characteristics of canopy and gap portions of the overstory of all 12 plots.

Plot no.	Gap area (m^2)	Elevation (m)		Slope (%)		Aspect		Aspect (°)	
		Canopy	Gap	Canopy	Gap	Canopy	Gap	Canopy	Gap
1	1194	1022	1036	21	28	SE	SE	135	138
2	365	1031	1029	28	24	SE	E	126	96
3	262	1014	1009	16	19	E	E	100	89
4	294	969	960	9	18	N	N	7	355
5	267	958	948	25	25	NE	NE	34	36
6	353	943	946	44	35	NW	N	314	350
7	467	913	919	25	14	SE	N	148	350
8	346	991	990	27	25	N	NE	22	35
9	390	731	724	20	22	NW	W	331	275
10	473	723	717	21	24	NE	W	33	260
11	286	873	867	35	24	N	N	356	354
12	179	959	969	28	22	N	NW	5	331

Notes: Gap areas are the expanded definition (Runkle 1981). Slope and aspect were estimated using an inclinometer and compass, respectively.

The analysis of the seedling survival data is based on the survival function. The survival function $S(t)$ is the probability that an individual survives beyond age t, i.e., $\Pr(T > t)$, where T is a continuous random variable representing the age at death. We calculated both nonparametric and parametric survival functions. The nonparametric survival functions do not require any distributional assumptions, whereas the parametric survival functions allowed for a regression analysis with explanatory variables.

We estimated nonparametric survivor functions using an algorithm from Klein and Moeschberger (1999) that is based on Turnbull (1976). Our survival data were interval- and right-censored because a seedling can die between two censuses or it can survive beyond the last census. The algorithm iteratively estimates the survival function using the product-limit (Kaplan-Meier) estimator:

$$\hat{S}(t) = \begin{cases} \prod_{t_i \le t} \left(1 - \frac{d_i}{Y_i}\right) & t_1 < t \quad \text{or} \\ 1 & t < t_1 \end{cases}$$

where d_i is the number of deaths that occur in the interval t_i, and Y_i is the number of seedlings at risk (i.e., alive at the beginning of the interval) in t_i. We coded the algorithm in S-PLUS (Insightful, Seattle, Washington, USA). Intermediate quantities estimated by this algorithm suggested an analog to the log rank test (Klein and Moeschberger 1999), which we used to compare pairs of survival functions.

For inference and formal comparison of treatment effects, we fit parametric survival models to the data. The models were accelerated time models of the form

$$\text{f(seedling lifetime)} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{w} + \sigma\varepsilon$$

where f() is either an identity or a natural log link (model dependent), $\mathbf{X}$ is the design matrix for fixed effects, $\boldsymbol{\beta}$ is a vector of fixed-effects coefficients, $\mathbf{Z}$ is the design matrix for random effects, $\mathbf{w}$ is the vector of random-effects coefficients, σ is the scale parameter (either scalar or vector, depending on the model), and ε is the model-dependent error distribution (Klein and Moeschberger 1999, Venables and Ripley 1999). We modeled $\mathbf{w}$ as realizations from a $N(0, \sigma_r^2)$. We explored models in which ε was distributed as Weibull, exponential, lognormal, log-logistic, normal, and logistic. The first four models have a natural log link, whereas the latter two have an identity link.

The "best" model of seedling survival was selected from the large number of potential models that included six different error distributions and the following covariates (fixed effects): seedling species ("species"), understory treatment ("understory"), gap or canopy conditions ("overstory"), light levels (GSF), slope, aspect, and elevation. Elevation was centered at 0 because values were large. Slope and aspect entered the model as a vector of three components:

$$\mathbf{B} = \begin{bmatrix} \cos\theta & \sin\varphi \\ \sin\theta & \sin\varphi \\ & \cos\varphi \end{bmatrix}$$

where θ is the aspect (radians) and φ is slope (radians). The aspect effect is described by the first two parameters, $\mathbf{B}[1]$ and $\mathbf{B}[2]$, and the slope effect is described by $\mathbf{B}[3]$ (Clark 1990*a*, *b*). Allometric measurements were recorded at the time of planting, including the number of true leaves (not cotyledons, "L.nc"), stem diameter (D), and stem height (H). Plots and subplots were included in the model as random effects.

Model selection proceeded using an automated stepwise procedure that retained model terms based on Akaike's Information Criterion (AIC), so that the "best" model was the most parsimonious model as judged by AIC. Likelihood ratio tests were used to calculate P values for the inclusion or exclusion of model terms, whereas AIC was used to compare models that assumed different probability densities. The probability density selected in the final model was the Weibull; this was convenient as it has a proportional hazards (i.e., relative risk) interpretation in addition to an accelerated time interpretation (Klein and Moeschberger 1999). We report the parameter estimates as well as the relative risk and accelerated time interpretations of the treatment effects. Relative risk compares the relative mortality risk with vs. without a particular treatment (for factor variables). In the case of continuous covariates, the interpretation is the relative risk associated with a one-unit increase in the covariate. The accelerated time interpretations reflect the amount by which time until death is accelerated by a factor variable or a one-unit increase in a continuous covariate.

Seedling height growth

We analyzed the relative growth rate for seedling height in response to our experimental treatments using mixed linear models. Relative growth rates (RGR) for surviving seedlings were calculated as

$$\text{RGR} = \frac{\log\left(\frac{H_T}{H_0}\right)}{T}$$

where H_T was the height of the seedling in the August 1999 census, H_0 was the initial height of the seedling, and T was the elapsed time in days. Within each quadrat (corresponding to one of five understory treatments), a mean RGR was calculated across surviving seedlings of each species. The Box-Cox method indicated that a transformation was not required to normalize these data (Weisberg 1985). A linear mixed model was fit to the mean RGRs with plots, subplots within plots, and quadrats within subplots all considered random effects. The set of covariates described for the survival analysis was also used in this analysis, with the exception of the

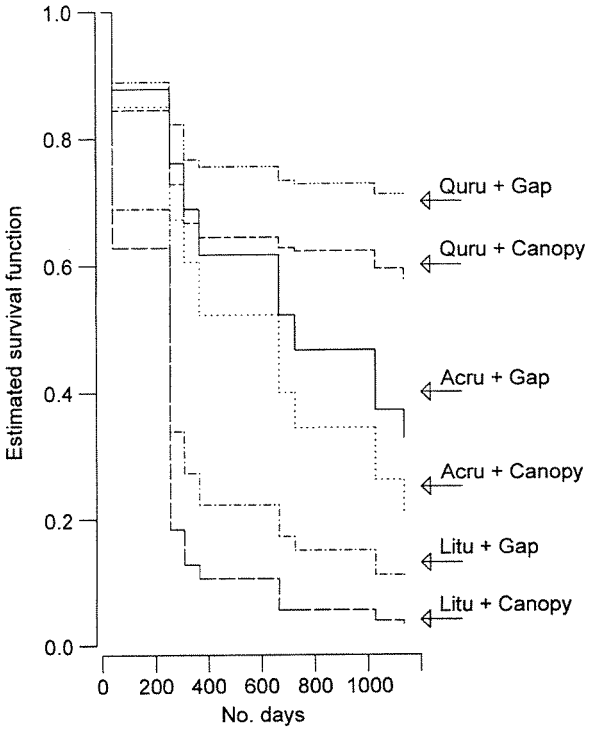

FIG. 1. Seedling survival of *Quercus rubra* (Quru), *Acer rubrum* (Acru), and *Liriodendron tulipifera* (Litu) under canopy gap and closed-canopy conditions. Canopy gaps uniformly increased survival across species. The survival functions are nonparametric Kaplan-Meier estimates marginalized over understory treatments.

allometric measurements on individual seedlings (because we analyzed mean species responses within quadrats). RGR data were necessarily unbalanced because mortality differed among plots and treatments. The model fitting procedure is robust to unbalanced data (Pinheiro and Bates 2000). We tested differences among species RGRs with the 10 treatment combinations by constructing single-degree-of-freedom contrasts within the context of the fitted model (Steel et al. 1997).

RESULTS

Light levels were 7.3 ± 1.7% (mean ± 1 SE) greater in canopy gaps than beneath closed canopy ($P < 0.001$). GSF (global site factor) values ranged from 0.048 beneath closed canopies to 0.34 in some gaps. The biomass of understory vegetation was 66% greater in canopy gaps than under closed canopies ($P < 0.001$): 180.1 ± 12.9 g/m^2 in canopy gaps vs. 108.4 ± 16.1 g/m^2 beneath closed canopy.

Seedling survival differed among species (Fig. 1, Table 3, $P < 0.001$), with *Quercus rubra* having the highest survival beyond the 1135 days of the experiment ($S[1135] = 0.64$), followed by *Acer rubrum* ($S[1135] = 0.27$) and *Liriodendron tulipifera* ($S[1135] = 0.07$). The risk of mortality for *Q. rubra* was 0.44 that of *A. rubrum*, whereas *L. tulipifera* had a risk 4.4 times greater than that of *A. rubrum* (Table 4). Overstory condition had a large effect on survivorship (Table 3; $P < 0.001$); the risk of mortality was 1.57 times greater for a seedling beneath closed canopy than for a seedling in a canopy gap. Absence of a species × overstory ($P = 0.58$) interaction indicates that all species benefited similarly from canopy gaps (Fig. 1). Understory treatments influenced survival as well (Table 3; $P < 0.001$): Removed, Trenched + Removed, Trenched, and Fertilized treatments all increased seedling survival compared to the Control (Fig. 2, Table 4; P from 0.017 to <0.001) and corresponded to reduced mortality risks of 0.76, 0.47, 0.52, and 0.54 relative to seedlings in the Control. Although an understory × overstory interaction was suggested by the reordering of treatment effects in gap and canopy conditions (Fig. 2), the interaction was not significant ($P = 0.11$). In addition, there were neither understory × species ($P = 0.72$) nor understory × overstory × species ($P = 0.27$) interactions. Thus, the ordering of seedling survival was maintained across all microsites; *Q. rubra* had highest survival, followed by *A. rubrum* and *L. tulipifera*.

Spatial variability in seedling survival was large, even after accounting for covariates (frailty term; Table 3). The variance of the random subplot effect on seedling survival was 0.31 (1 SD = 0.56); effects of individual subplots ranged from −1.39 to 1.01. These were of the same magnitude as the fixed effects.

The results from the nonparametric analysis of seedling survival were similar to those for the parametric model; species rankings of seedling survival did not change across treatments (Fig. 3), with *Q. rubra* having the highest survival in all microenvironments. The survival of *Q. rubra* was significantly greater than that of *L. tulipifera* in all 10 treatments and than that of *A. rubrum* in eight treatments ($P > 0.05$ in Fig. 3E, F) based on the log rank test. The slight differences in these results compared with those from the parametric model stem from the fact that the log rank test is nonparametric, is not global in scope (because each test is based on a subset of all the data), and thus has lower power.

Seedling relative growth rates (RGR) varied substantially among species, overstory condition, and un-

TABLE 3. ANOVA table of Weibull survival model.

Term	df	Deviance	Pr(Chi)
Species	2.0	359.6	<0.001
Understory	4.0	47.8	<0.001
Overstory	1.0	29.7	<0.001
Stem diameter, *D*	1.0	2.5	0.111
Frailty(Subplot)†	16.5	102.4	<0.001
Species × *D*	2.1	4.6	0.108

Note: Terms were added sequentially and are order dependent.

† The frailty(Subplot) term represents the Subplot random effect.

TABLE 4. Parameter estimates for the seedling survival model as well as relative risk and accelerated time interpretations of model coefficients. Estimates are for levels of a given factor, e.g., "Species (*Liriodendron*)" is the level of the factor Species for *Liriodendron tulipifera*.

Term	Mean	1 SE	z	P	Relative risk†	Accelerated time‡
Intercept	6.44	0.29	22.60	<0.001	0.01	0.00
Species (*Liriodendron*)	−2.15	0.30	−7.28	<0.001	4.42	8.62
Species (*Quercus*)	1.19	0.36	3.36	0.001	0.44	0.30
Understory (R)	0.40	0.17	2.39	0.017	0.76	0.67
Understory (T + R)	1.10	0.18	6.26	<0.001	0.47	0.33
Understory (T)	0.95	0.17	5.55	<0.001	0.52	0.39
Understory (F)	0.89	0.17	5.14	<0.001	0.54	0.41
Overstory (canopy)	−0.66	0.25	−2.60	0.009	1.57	1.93
Diameter	−0.07	0.15	−0.47	0.636	1.05	1.07
Liriodendron × diameter	0.46	0.22	2.14	0.032	0.73	0.63
Quercus × diameter	0.21	0.25	0.83	0.409	0.87	0.81

Notes: Species are *Acer rubrum, Liriodendron tulipifera*, and *Quercus rubra*. Treatments are: R, removal of understory vegetation; T + R, trenching plus removal; T, trenching; and F, fertilization. Diameter is the initial diameter of the seedling.

† Relative risk compares the relative mortality risk with vs. without a particular treatment (for factor variables). In the case of continuous covariates, the interpretation is the relative risk associated with a one-unit increase in the covariate.

‡ The accelerated time interpretations reflect the amount by which time is accelerated by a factor variable or a one-unit increase in a covariate.

derstory treatments (Table 5, Fig. 4). *L. tulipifera* had relative growth rates as much as 283% greater than those of *Q. rubrum* and 380% greater than those of *A. rubrum*. Canopy gaps increased relative growth rates, but the effect varied across species (Table 5; main effect $P = 0.011$, interaction $P < 0.001$). The understory treatments tended to increase relative growth rates compared to Controls (Table 6), although only the Fertilization treatment was statistically significant ($P = 0.011$). The overstory and understory treatment effects were largely driven by the strong response of *L. tulipifera* to canopy gaps (Table 6; $P = 0.001$) and to Removed, Trenched, and Trenched + Removed treatments (Table 6; $P = 0.049$, 0.008, and 0.002 respectively) coupled with the failure of *Q. rubra* to respond to these same treatments (Table 6). The variability in relative growth rates associated with the random effects term was generally an order of magnitude less than the fixed effects, but the unbalanced nature of the data led to low precision of these estimates.

L. tulipifera had the highest relative growth rates in three microenvironments (Fig. 5F, H, J; $P < 0.05$) where it benefited from reduced levels of competition and increased resource levels: Removed, Trenched, and Trenched + Removed treatments in gap environments. No single species was clearly the best performer in the remaining treatments (all $P > 0.05$).

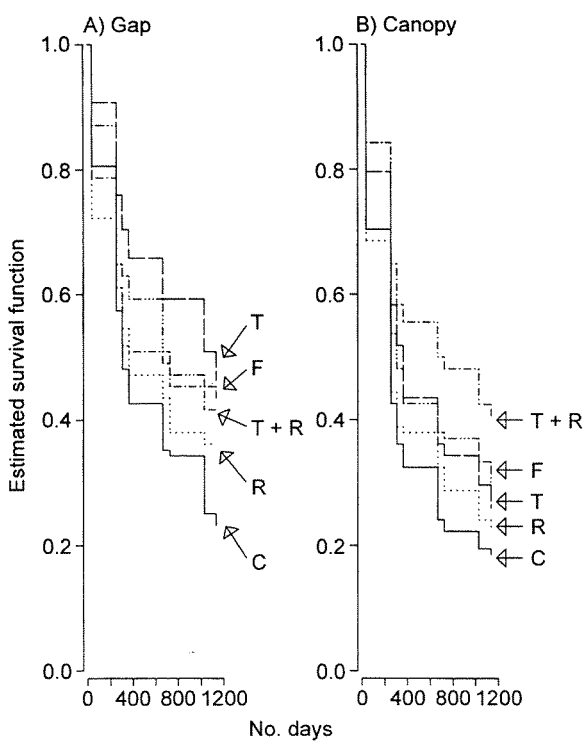

FIG. 2. The effect of understory treatments (R, removal of understory vegetation; T, trenched; T + R, trenched plus removal of understory vegetation; F, fertilization; and C, control) on seedling survival in (A) gap and (B) canopy conditions. There was not a statistically significant overstory × understory treatment interaction ($P = 0.11$). The survival functions are nonparametric Kaplan-Meier estimates, marginalized over overstory treatments and species.

DISCUSSION

In our three-year experiment, we found evidence that spatial heterogeneity in microenvironmental conditions might contribute to the coexistence of only two of the three tree species studied. *Quercus rubra* had higher seedling survival than either *Acer rubrum* or *Lirioden-*

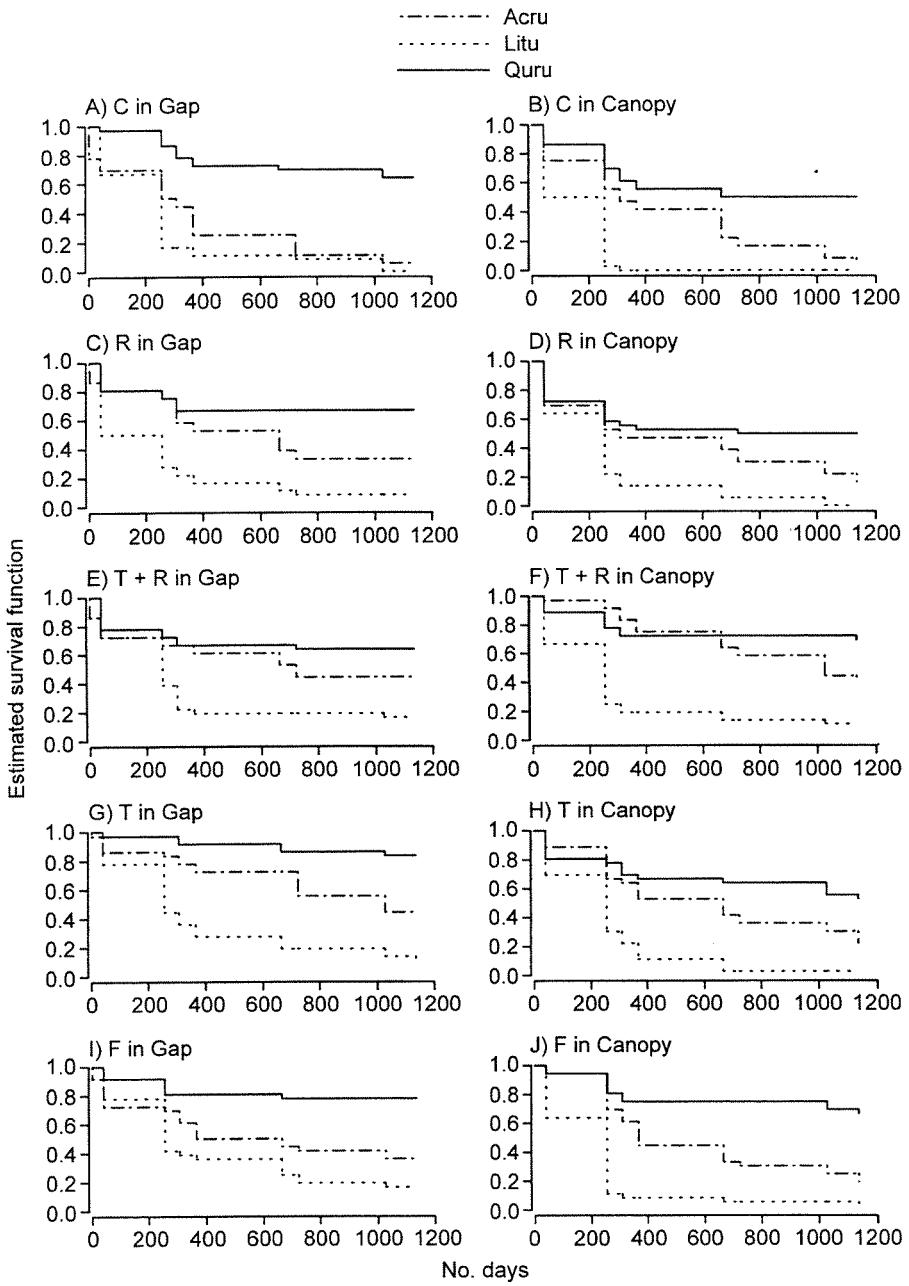

FIG. 3. Seedling survival in all 10 treatment combinations for *Acer rubrum* (Acru), *Liriodendron tulipifera* (Litu), and *Quercus rubra* (Quru) seedlings. The survival functions are nonparametric Kaplan-Meier estimates. *Q. rubra* had higher survival than *L. tulipifera* in all 10 treatments and higher survival than *A. rubrum* in all treatments except E and F (all $P > 0.05$). The left and right columns represent overstory gap and canopy conditions, respectively. Treatments are as in Fig. 2.

dron tulipifera in all microenvironments, whereas *L. tulipifera* had the highest growth rates in three high-resource environments. Species overlapped broadly (in their relative growth rates) in the remaining seven treatments, with no clear best performer. The simplest interpretation of these results is that *Q. rubra* would outsurvive *A. rubrum* and *L. tulipifera* in all microenvironments, but that the occasional surviving *L. tulipifera* seedling would outgrow *Q. rubra* in some high-resource environments. The third species, *A. rubrum*, was not top-ranked in terms of survival or growth in any microenvironment.

Although seedling survival and growth varied across species and microenvironment, this led to only two of the three study species (e.g., *L. tulipifera* and *Q. rubra*) being top-ranked in one of the 10 treatments. Regeneration niches may thus help promote coexistence of two, but probably not all three of these species. The

TABLE 5. ANOVA table of model of relative growth rate for seedling height.

Term	Numerator df	Denominator df	F	P
Intercept	1	94	5.046	0.027
Species	2	94	6.710	0.002
Understory	4	85	2.152	0.081
Overstory	1	11	9.380	0.011
Species × understory	8	94	2.769	0.009
Species × overstory	2	94	8.925	<0.001

Note: Terms are order independent.

failure to find microenvironments where seedlings of each species clearly outperformed the others could result from a failure to examine a wide enough array of microenvironments or from sample sizes that were inadequate to detect small differences among the three species in each of the 10 treatments. We consider the former concern unwarranted because we examined a wide array of understory environments crossed with contrasting gap/closed canopy conditions. These are major axes of environmental variability in forests. The latter concern about sample size is necessarily true when statistically significant differences are not found in field experiments such as ours (i.e., we would not expect any two species to have precisely the same performance, given large enough replication). However, our study represents one of the best replicated manipulative field experiments of which we are aware. Instead, our results are most likely representative of only limited niche partitioning by seedlings, with broad overlap across species (Brokaw and Busing 2000, Clark et al. 2003) and is consistent with other studies of seedling recruitment that have found only ambiguous evidence of environmental partitioning, niche differentiation, or microhabitat specialization (Maguire and Forman 1983, Collins and Good 1987, Collins 1990, Latham 1992, Sipe and Bazzaz 1995, Ashton and Larson 1996, Gray and Spies 1997, Broncano et al., 1998, Carlton and Bazzaz 1998, van der Meer et al. 1998, Webb and Peart 2000). Alternatively, the residual variability in seedling performance (i.e., random effects) across species could represent additional underlying spatial structure that we failed to measure, for example, species-specific interactions with spatially variable soil biota (Klironomos 2002).

Broad overlap in species performance and demographic stochasticity ensured that seedlings of all three species captured some sites. For example, although *Q. rubra* had the highest survival in all treatments, both *A. rubrum* and *L. tulipifera* were the sole surviving species in some quadrats at the end of our experiment. The importance of such unlikely events will only increase when fecundity differences across species are considered, because the rankings of seedling survival were the opposite of fecundity. *L. tulipifera* and *A. rubrum* have low seedling survival but produce many seeds, whereas *Q. rubra* has much higher survival but produces fewer seeds (Clark et al. 1998). The greater fecundity of *A. rubrum* and *L. tulipifera* will result in more instances of these species capturing a site, despite a low probability of this occurring on a per seedling basis. For example, if instead of planting equal numbers of seedlings in each quadrat, we had weighted the number of seedlings by species-specific fecundity, then there would be many more instances of *A. rubrum* and *L. tulipifera* capturing sites.

Interactions of understory and overstory heterogeneity

We found little evidence that heterogeneity associated with the canopy overstory or understory was interacting in a manner other than additive. Although there was increased understory biomass in canopy

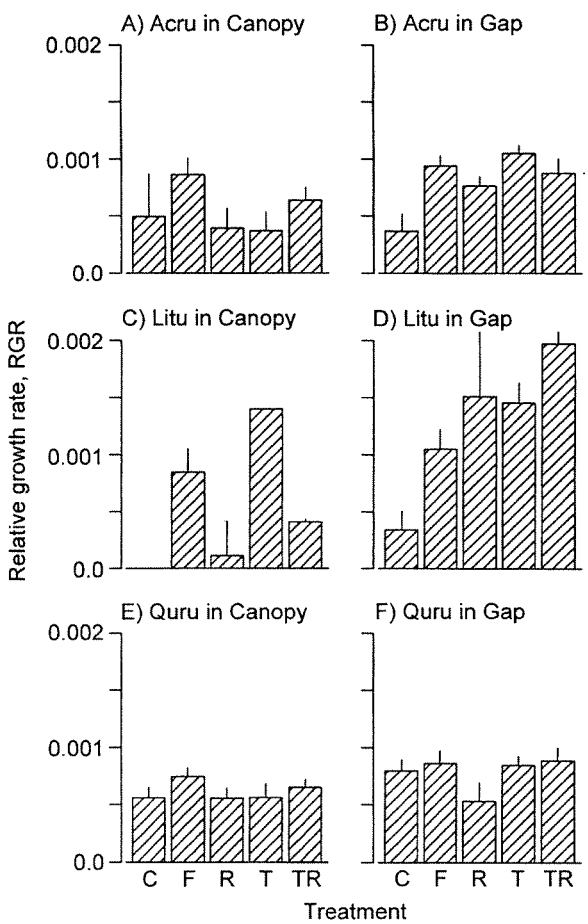

FIG. 4. Overstory and understory treatment effects on relative growth rates, RGR (mean + 1 SE) for *Acer rubrum* (Acru), *Liriodendron tulipifera* (Litu), and *Quercus rubra* (Quru) seedlings. *L. tulipifera* responded most strongly to high-resource treatments, whereas *Q. rubra* maintained similar growth rates across treatments. The response of *A. rubrum* to increased resource levels was intermediate between those of *L. tulipifera* and *Q. rubra*. Understory treatments are as in Fig. 2.

TABLE 6. Parameter estimates for model of relative growth rate for seedling height.

Term†	Mean ($\times 10^4$)	1 SE ($\times 10^4$)	df	t	P
Intercept	3.156	1.405	94	2.246	0.027
Liriodendron	−9.131	3.552	94	−2.571	0.012
Quercus	2.783	1.674	94	1.663	0.100
F	4.257	1.632	85	2.609	0.011
R	1.239	1.727	85	0.717	0.475
T	2.631	1.599	85	1.645	0.104
T + R	2.957	1.609	85	1.837	0.070
Gap	2.943	0.961	11	3.063	0.011
Liriodendron × F	4.650	3.566	94	1.304	0.195
Quercus × F	−3.013	2.010	94	−1.499	0.137
Liriodendron × R	7.878	3.951	94	1.994	0.049
Quercus × R	−2.660	2.102	94	−1.266	0.209
Liriodendron × T	10.05	3.723	94	2.698	0.008
Quercus × T	2.281	2.002	94	−1.140	0.257
Liriodendron × T + R	11.03	3.508	94	3.144	0.002
Quercus × T + R	−2.090	2.014	94	−1.038	0.302
Liriodendron × gap	6.463	1.888	94	3.423	0.001
Quercus × gap	−1.259	1.170	94	−1.076	0.285

Note: Values in columns 2 and 3 have been multiplied by 10^4.
† Abbreviations are as in Table 4.

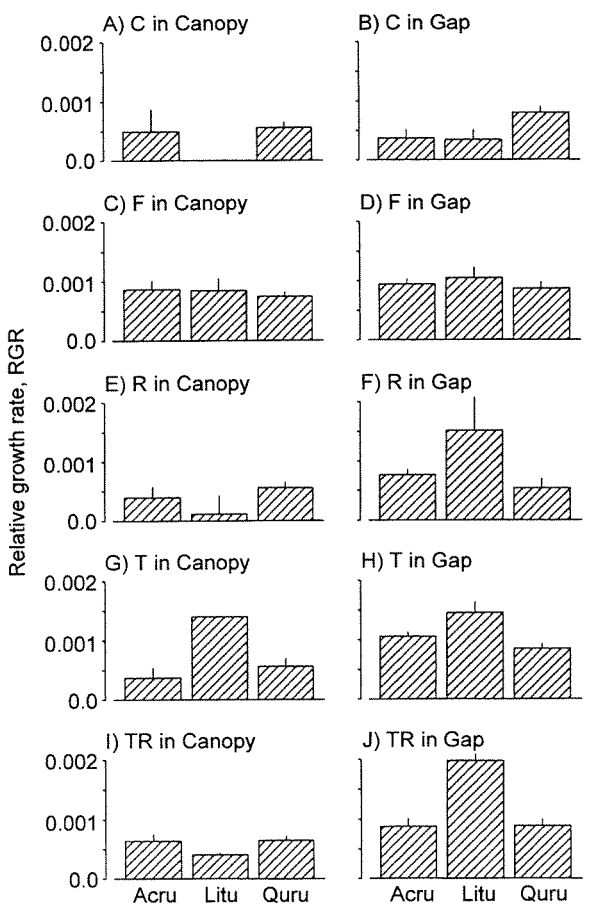

FIG. 5. Comparison of relative growth rates, RGR (mean + 1 SE), for *Acer rubrum* (Acru), *Liriodendron tulipifera* (Litu), and *Quercus rubra* (Quru) seedlings in all 10 treatment combinations. *L. tulipifera* was top-ranked in panels F, H, and J (all $P < 0.05$) with no clear best performing species in the remaining seven treatments (all $P > 0.05$). Understory treatments are as in Fig. 2.

gaps, the effects of understory treatments did not appear to be dependent on the overstory condition, e.g., overstory × understory interactions were not statistically significant for either growth or survival. These results appear to contrast with hypotheses suggesting, for example, that moisture availability would disproportionately favor the shade-intolerant *L. tulipifera* beneath closed canopy or that nutrient addition would disfavor it (Coomes and Grubb 2000). Similarly, trenching had a positive effect on seedling survival and growth in these nutrient-rich, moist forests, contrary to previous hypotheses, and the effect did not depend on overstory condition (Coomes and Grubb 2000).

Seedling performance was affected both by overstory and understory conditions (Figs. 2 and 4, Tables 4 and 6). Seedling survival increased in canopy gaps, with removal of understory vegetation, with trenching, and with fertilization. These effects were additive; seedling survival benefited most from a simultaneous reduction in both above- and belowground competition. Previous studies examining the relative effects of forest overstory and understory competition have produced mixed results. Some studies have found large effects of trenching or removal of understory vegetation on seedling performance (Horn 1985, Christy 1986, Lorimer et al. 1994, Jaderlund et al. 1997, Coomes and Grubb 1998), whereas others have not (Jones et al. 1997, Buckley et al. 1998, Pinard et al. 1998). In relatively open, coniferous forests, trenching has resulted in greater increases in sapling growth than has overstory removal (Christy 1986, Riegel et al. 1992). Only a handful of studies have examined the effect of both forest overstory and understory on seedling performance in broadleaved forests; these have generally found overstory removal to have a greater effect on seedling performance than trenching or understory re-

moval (Horn 1985, Buckley et al. 1998, Coomes and Grubb 1998). In northeastern hardwood forests, Pacala et al. (1994) and Finzi and Canham (2000) found that sapling growth beneath closed canopies was limited by light but not by moisture or nitrogen. In contrast, the large effects of understory treatments (including fertilization) on seedling performance in our study suggest that light is not the only resource limiting seedling performance in southern Appalachian forests. This may result from the nature of these forests; they are second growth, with relatively high light levels even beneath closed canopies (Beckage et al. 2000). However, other studies in undisturbed tropical forests have also found resources other than light to limit seedling growth (Lewis and Tanner 2000).

Seedling survival responses to heterogeneity

The ranking of seedling survival varied greatly across species and corresponded to relative seed size (Fig. 1, Table 1). The large-seeded *Q. rubra* had half of the mortality risk of the smaller seeded *A. rubrum* and one-tenth that of the smallest seeded *L. tulipifera* (Table 4). We do not claim to demonstrate a positive relationship between seed size and survivorship using only three species, but only point out that these results are consistent with this relationship as found by others (Aizen and Patterson 1990, Aizen and Woodcock 1996, Bonfil 1998, Kormanik et al. 1998, George and Bazzaz 1999*a*). Although energy reserves associated with large seeds would be expected to increase seedling survival through the first year (Bonfil 1998), after which they would be largely exhausted, our survival differences persisted through the three years of this experiment.

Treatments that increased resource availability also increased seedling survivorship. Canopy gaps increased seedling survival relative to closed-canopy conditions (Fig. 1). Understory treatments (Removal of understory vegetation, Trenching, Trenching + Removal, and Fertilization) increased seedling survival relative to Controls (Fig. 2). Species benefited from these increased resources uniformly; there were neither overstory × species nor understory × species interactions. Thus, differential survival across microenvironments does not follow the simplest pattern that could promote coexistence.

Growth responses to heterogeneity

Seedling growth responses contrasted with seedling survival. *L. tulipifera*, which had lower survivorship than the other species, had growth rates 280% to 380% greater than those of *Q. rubra* and *A. rubrum* in high-resource environments (Fig. 5). In contrast, the growth rates for the large-seeded *Q. rubra*, which had the highest survival, were less responsive to microenvironmental conditions (Fig. 4E, F) compared to the smaller seeded *A. rubrum* and *L. tulipifera*. This may reflect the buffering effect of energy reserves from a large seed (Grime and Jeffrey 1965), together with a reduced ability to capitalize on favorable growth conditions (Milberg et al. 1998). Other studies have also found a negative correlation between seed mass and relative growth rate (Agboola 1996, Cornelissen et al. 1996).

Relative growth rates of all species were increased by fertilization and canopy gaps (Fig. 4, Table 6). *L. tulipifera* was particularly responsive to understory and overstory treatments that increased resource availability, which is consistent with its classification as a gap obligate species (Burns and Honkala 1990). These same treatments also tended to disproportionately benefit growth rates of *A. rubrum* relative to *Q. rubra*, although differences were not statistically significant. This pattern is consistent with a reported trade-off between growth rates of forest trees in resource-rich environments vs. low survival in resource-poor environments in northeastern forests (Pacala et al. 1994, 1996, Kobe et al. 1995), and may reflect differential sensitivity to resource availability. The shade-intolerant species *L. tulipifera* was able to capitalize on opportunities in high-resource environments, but performed poorly in competitive environments. *Q. rubra*, on the other hand, was relatively insensitive to its competitive environment and tended to perform consistently across microenvironments (Kolb and Steiner 1990). *A. rubrum* was between these two extremes. George and Bazzaz (1999*b*) found a similar result for *Q. rubra*, *A. rubrum*, and *Betula alleghaniensis* Britt. (a small-seeded, shade-intolerant tree species ecologically similar to *L. tulipifera*) in forest understories: *Q. rubra* and *A. rubrum* had higher persistence in fern understories, but *B. alleghaniensis* had much higher growth rates in favorable conditions. Although this may be a transient phenomenon related to the initial seed size of each species, the persistence of the survival advantage for *Q. rubra* through three years in our study suggests otherwise.

Conclusions

We found large differences in growth and survival of *Acer rubrum*, *Liriodendron tulipifera*, and *Quercus rubra* seedlings in response to spatial heterogeneity in microenvironmental conditions. However, only *Q. rubra* and *L. tulipifera* were clearly favored in some microenvironments, indicating the potential for regeneration niches to contribute to the coexistence of only two of the three species studied. *A. rubrum* was not favored in any microenvironment. Nevertheless, broad species overlap and demographic stochasticity led to capture of some sites by *A. rubrum*. The importance of stochastic processes may increase when interspecific differences in fecundity are considered, and suggest that stochastic processes in conjunction with species niche overlap may also contribute to species coexistence.

Acknowledgments

We would like to thank Phil Camill, Brenda Cleveland, Janneke HilleRisLambers, Ines Ibanez, Jason Lynch, J. Mclachlan, Heather Passmore, Jackie Mohan, Tom Phillipi,

Sharon Taylor, and Pete Wyckoff. We also are grateful for the helpful comments of Sandra Lavorel, Jean-François Molino, and two anonymous reviewers. This research was supported by NSF Grant DEB 9632854.

Literature Cited

Agboola, D. A. 1996. The effect of seed size on germination and seedling growth of three tropical tree species. Journal of Tropical Forest Science **9**(1):44–51.

Aizen, M. A., and W. A. Patterson III. 1990. Acorn size and geographical range in the North American oaks (*Quercus* L.). Journal of Biogeography **17**:327–332.

Aizen, M. A., and H. Woodcock. 1996. Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze. Canadian Journal of Botany **74**:308–314.

Ashton, M. S., and B. C. Larson. 1996. Germination and seedling growth of *Quercus* (section Erythrobalanus) across openings in a mixed-deciduous forest of southern New England, USA. Forest Ecology and Management **80**: 81–94.

Barton, A. M., and S. K. Gleeson. 1996. Ecophysiology of seedlings of oaks and red maple across a topographic gradient in eastern Kentucky. Forest Science **42**:335–342.

Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research **30**:1617–1631.

Berkowitz, A. R., C. D. Canham, and V. R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology **76**: 1156–1168.

Bonan, G. B. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecological Modeling **45**:25–306.

Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). American Journal of Botany **85**:79–87.

Brokaw, N., and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology and Evolution **15**:183–188.

Broncano, M. J., M. Riba, and J. Retana. 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. Plant Ecology **138**:17–26.

Buckley, D. S., T. L. Sharik, and J. G. Isebrands. 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. Ecology **79**:65–78.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Volume 2. Hardwoods. U.S. Department of Agricultute, Washington, D.C., USA.

Canham, C. D. 1988. Growth and canopy architecture of shade tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy gaps. Ecology **69**:786–795.

Carlton, G. C., and F. A. Bazzaz. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecological Monographs **68**:99–120.

Christy, E. J. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). Vegetatio **65**:21–28.

Clark, J. S. 1990*a*. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecological Monographs **60**:135–159.

Clark, J. S. 1990*b*. Landscape interactions among nitrogen mineralization, species composition, and long-term disturbance. Biogeochemisty **11**:1–22.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs **68**:213–235.

Clark, J. S., J. Mohan, M. Dietz, and I. Ibanez. 2003. Coexistence: how to identify trophic trade-offs. Ecology **84**: 17–31.

Collins, B. S., and R. E. Good. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak–pine forest. Oikos **48**:89–98.

Collins, S. L. 1990. Habitat relationships and survivorship of tree seedlings in hemlock–hardwood forest. Canadian Journal of Botany **68**:790–797.

Coomes, D. A., and P. J. Grubb. 1998. Responses of juvenlile trees to above- and belowground competition in nutrient-starved Amazonian rain forest. Ecology **79**:768–782.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs **70**: 171–207.

Cornelissen, J. H. C., P. Casto Diez, and R. Hunt. 1996. Seedling growth, allocation, and leaf attributes in a wide range of woody plant species and types. Journal of Ecology **84**: 755–765.

Denslow, J. S., A. M. Ellison, and R. E. Sanford. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. Journal of Ecology **86**:597–609.

Denslow, J. S., J. C. Schultz, P. M. Vitousek, and B. R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology **71**:165–179.

De Steven, D. 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology **72**:1066–1075.

Facelli, J. M. 1994. Muliple indirect effects of plant litter affect the establishment of woody seedlings in old fields. Ecology **75**:1727–1735.

Fahey, T. J., J. J. Battles, and G. F. Wilson. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. Ecological Monographs **68**:183–212.

Finzi, A. C., and C. D. Canham. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. Forest Ecology and Management **131**: 153–165.

George, L. O., and F. A. Bazzaz. 1999*a*. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology **80**:833–845.

George, L. O., and F. A. Bazzaz. 1999*b*. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology **80**:846–856.

Gray, A. N., and T. A. Spies. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology **78**:2458–2473.

Grime, J. P., and D. W. Jeffrey. 1965. Seedling establishment in vertical gradients of sunlight. Journal of Ecology **53**: 621–642.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review **52**:107–145.

Harmon, M. E., and J. F. Franklin. 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology **70**:48–59.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Heinemann, K., T. Kitzberger, and T. T. Veblen. 2000. Influence of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Canadian Journal of Forest Research **30**:25–31.

Horn, J. C. 1985. Responses of understory tree seedlings to trenching. American Midland Naturalist **114**:252–258.

Huston, M. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.

Jaderlund, A., O. Zackrisson, A. Dahlberg, and M. Nilsson. 1997. Interference of *Vaccinium myrtillus* on establishment, growth, and nutrition of *Picea abies* seedlings in a northern boreal site. Canadian Journal of Forest Research **27**:2017–2025.

Jones, R. H., B. P. Allen, and R. R. Sharitz. 1997. Why do early-emerging tree seedlings have survival advantages?: a test using *Acer rubrum* (Aceraceae). American Journal of Botany **84**:714–1718.

Klein, J. P., and M. L. Moeschberger. 1999. Survival analysis: techniques for censored and truncated data. Springer-Verlag, New York, New York, USA.

Klironomos, J. N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. Nature **417**:67–70.

Kobe, R. K., S. W. Pacala, J. A. Silander, Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications **5**:517–532.

Kolb, T. E., and K. C. Steiner. 1990. Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: effects of shading and grass root competition. Forest Science **36**(1):34–44.

Kormanik, P. P., S. S. Sung, T. L. Kormanik, S. E. Schlarbaum, and S. J. Zarnoch. 1998. Effect of acorn size on development of northern red oak 1–0 seedlings. Canadian Journal of Forest Research **28**:1805–1813.

Korstian, C. F., and T. S. Coile. 1938. Plant competition in forest stands. Duke University School of Forestry Bulletin 3, Durham, North Carolina, USA.

Latham, R. E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology **73**:2129–2144.

Lewis, S. L., and E. V. J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. Ecology **81**:2525–2538.

Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology **82**:227–237.

Maguire, D. A., and R. T. T. Forman. 1983. Herb cover effects on tree seedling patterns in a mature hemlock–hardwood forest. Ecology **64**:1367–1380.

Milberg, P., M. A. Perez-Fernandez, and B. B. Lamont. 1998. Seedling growth response to added nutrients depends on seed size in three woody genera. Journal of Ecology **86**: 624–632.

Mitchell, H. L., and R. F. Chandler, Jr. 1939. The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. Black Rock Forest Bulletin **11**:1–94.

Nikolov, N. T., and K. F. Zeller. 1992. A solar radiation algorithm for ecosystem dynamic models. Ecological Modelling **61**:149–168.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs **66**:1–43.

Pacala, S. W., C. D. Canham, J. A. Silander, Jr., and R. K. Kobe. 1994. Sapling growth as a function of resources in a north temperate forest. Canadian Journal of Forest Research **24**:2172–2183.

Pacala, S. W., and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. Theoretical Population Biology **31**:92–113.

Pacala, S. W., and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist **143**:222–257.

Pearcy, R. W. 1983. The light environment and growth of C3 and C4 tree species in the understory of a Hawaiian forest. Oecologia **58**:19–25.

Pinard, M. A., D. W. Davidson, and A. Ganing. 1998. Effects of trenching on growth and survival of planted *Shorea parivfolia* seedlings under pioneer stands in a logged-over forest. Journal of Tropical Forest Science **10**:505–515.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and Splus. Springer-Verlag, New York, New York, USA. 528.

Rich, P. M. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory, LA-11733-M, Los Alamos, New Mexico, USA.

Riegel, G. M., R. F. Miller, and W. C. Krueger. 1992. Competition for resources between understory vegetation and overstory *Pinus pondersosa* in northeastern Oregon. Ecological Applications **2**:71–85.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology **62**:1041–1051.

Sipe, T. W., and F. A. Bazzaz. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. Ecology **76**:1587–1602.

Steel, R. G. D., J. H. Torrie, and D. A. Dickey. 1997. Principles and procedures of statistics, a biometrical approach. Third edition. McGraw-Hill, New York, New York, USA.

Swank, W. T., and D. A. Crossley. 1988. Introduction and site description. Pages 3–16 *in* W. T. Swank and D. A. Crossley, editors. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York, New York, USA.

Turnbull, B. W. 1976. The empirical distribution function with arbitrarily grouped, censored and truncated data. Journal of the Royal Statistical Association B **38**:290–295.

van der Meer, P. J., F. J. Sterck, and F. Bongers. 1998. Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French Guiana. Journal of Tropical Ecology **14**:119–137.

Veblen, T. T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology **70**:541–543.

Venables, W. N., and B. D. Ripley. 1999. Modern applied statistics with S-PLUS. Third edition. Springer-Verlag, New York, New York, USA.

Webb, C. O., and W. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. Journal of Ecology **88**:464–478.

Weisberg, S. 1985. Applied linear regression. John Wiley, New York,.New York, USA.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs **26**:1–80.

Wilde, S. A. 1958. Forest soils; their properties and relation to silviculture. Ronald Press, New York, New York, USA.

Yeakley, J. A. 1993. Hillslope soil moisture gradients in an upland forested watershed. Dissertation. University of Virginia, Charlottesville, Virginia, USA.

Young, J. A., and C. G. Young. 1992. Seeds of woody plants in North America. Dioscorides Press, Portland, Oregon, USA.