THE FERN UNDERSTORY AS AN ECOLOGICAL FILTER: GROWTH AND SURVIVAL OF CANOPY-TREE SEEDLINGS

Lisa O. George and F. A. Bazzaz

*Department of Organismic and Evolutionary Biology, Harvard University, The Biological Laboratories,
16 Divinity Avenue, Cambridge, Massachusetts 02138 USA*

Abstract. We investigated the role of the fern understory of closed-canopy forests as an ecological filter shaping the density, species composition, size structure, and spatial distribution of the seedling bank. In New England deciduous forests we tested the hypothesis that the understory stratum is a selective filter that differentially influences growth and survival of tree-seedling species by comparing performance of *Acer rubrum, Betula alleghaniensis,* and *Quercus rubra* seedlings in plots where the fern understory was undisturbed, partially removed, or completely removed. We related seedling growth and survival to microenvironmental characteristics of experimental plots in order to further explore mechanisms responsible for the filtering capacity of the fern understory.

The presence of a fern understory reduced growth and survival of all seedling species, but the magnitude of the effect differed among species. Mortality resulting from resource limitation in *Quercus* below the fern understory was balanced by mortality resulting from insect herbivory in fern-free areas. Relative biomass growth rates of all species were negatively influenced by the presence of fern cover, whereas relative height growth rates of *Acer* and *Quercus* were uniformly low and insensitive to the presence of fern cover. Growth and survival rates indicate that only *Quercus* seedlings can emerge from the fern stratum in the absence of understory or overstory canopy disturbance. A trade-off between persistence in low light and maximum growth in understory light levels was observed among species. The relative growth rate of *Betula* in terms of biomass and height was more responsive to light levels than were relative growth rates of *Acer* or *Quercus,* and the growth rate of *Betula* was higher than that of *Acer* and *Quercus* in all light levels. However, survival of *Betula* below the fern stratum was lower than survival of *Acer* and *Quercus.*

The fern understory has the capacity to selectively filter tree seedlings as they grow up through it because seedling species respond differentially to the presence of fern cover. The selective filtering of tree seedlings by the fern understory results in a seedling spatial structure that reflects the spatial heterogeneity of the fern stratum. The seedling pool below the fern stratum has a lower seedling density and different species composition and size structure than the seedling pool in fern-free areas.

Key words: Acer rubrum; *advance regeneration;* Betula alleghaniensis; Dennstaedtia punctilobula; *ecological filter; fern understory; forest regeneration; Harvard Forest, Massachusetts, USA;* Osmundia claytonia; Quercus rubra; *seedling bank; tree seedlings, growth and survival.*

INTRODUCTION

Studies that have identified linkages between the overstory canopy and the herbaceous stratum at the landscape level (Gilliam et al. 1995) and studies that have detected associations between tree seedlings and understory plants within communities (Maguire and Forman 1983, Smith and Vankat 1991) suggest that plants of the forest understory may play an important role in structuring the competitive environment of seedlings of potential overstory dominants. In New England forests the fern stratum of the forest understory acts as an ecological filter that shapes the composition and organization of the seedling bank through differentially influencing tree species emergence and establishment (George and Bazzaz 1999). The understory filter may

play an important role in forest regeneration by shaping characteristics of the seedling bank such as density, species composition, size structure, and spatial distribution. In this study we explore how the fern understory filters the seedling bank through its influence on growth and survival of established canopy-tree seedlings.

Seedlings of many non-pioneer or late-successional tree species of temperate and tropical forests germinate and reside in the forest understory for a few to over 100 years (Barden 1983, Whitmore 1984, Canham 1985, 1990). As a result, several cohorts accumulate over time and form a seedling bank, a pool of suppressed seedlings "waiting" for enhanced resource availability to complete their life cycle. Many studies of forest regeneration following canopy gap formation and large-scale disturbances such as wind throw and timber harvest demonstrate that seedlings and saplings

established before disturbance (''advance regeneration'') make a significant, if not dominant, contribution to future stand composition (Brokaw 1985, Ashton 1990, Marquis et al. 1992, Morin 1994). While several studies document the fate of advance regeneration in post-disturbance gap and stand succession (Hibbs 1982a, 1983, Brokaw 1985, Merrens and Peart 1992, Rebertus and Veblen 1993, Peterson and Pickett 1995), a broader understanding of forest regeneration can be gained from studying pre-disturbance processes that shape the starting array of advance regeneration (Brokaw and Scheiner 1989, Connell 1989, Pacala et al. 1996). We predict that the herb and shrub stratum of the forest understory is an ecological filter that has a selective influence on growth and survival rates among species of advance regeneration in the seedling bank, and that the influence of this filter will have far-reaching consequences for regeneration processes and future forest structure and dynamics.

Processes that affect the growth and survival of tree seedlings are known to influence both the population dynamics of individual species and community composition. Several studies have shown that the rate of population increase of trees is very sensitive to changes in juvenile mortality (Hartshorn 1975, Enright and Ogden 1979, Piñero et al. 1984, Alvarez-Buylla and Martinez-Ramos 1992). Clark and Clark (1992) have demonstrated that canopy recruitment in a wet tropical forest is primarily influenced by growth and survival of seedlings and saplings <4 cm in diameter. Additionally, forest modeling studies demonstrate that interspecific differences in juvenile mortality and growth of canopy-tree species have dramatic effects on community composition and dynamics (Pacala et al. 1993, Kobe et al. 1995, Pacala et. al 1996).

We studied tree-seedling growth and survival in forest plots in which the fern understory was left undisturbed, partially removed, or completely removed in order to: (1) determine how the presence of a dense fern understory influences growth and survival of tree seedlings, (2) evaluate the relative importance of aboveground and belowground processes in interactions between the understory and tree seedlings and identify resources that mediate these interactions, (3) assess the importance of the identity of understory species and site factors in dictating the nature of interactions between the understory and tree seedlings. We predicted that the fern understory acts as a selective ecological filter that differentially affects seedling growth and survival rates among canopy-tree species, and that this filter will influence the density, species composition, size structure and spatial distribution of the seedling bank.

METHODS

Site manipulations and experimental design

Research was conducted at the Harvard Forest in Petersham, Massachusetts, USA (42°30′ N, 72°15′ W),

which is located in the Transition Hardwoods–White Pine–Hemlock forest type (Westveld et al. 1956). Six sites were chosen for study that had a prominent fern stratum composed primarily of *Dennstaedtia punctilobula* (hayscented fern) and *Osmunda claytoniana* (interrupted fern). Sites are abbreviated in the text as PH3A and PH3B (located in Prospect Hill compartment 3), PH4A and PH4B (located in Prospect Hill compartment 4), PH9 (located in Prospect Hill compartment 9), and TS1 (located in Tom Swamp compartment 1). Study sites ranged broadly in overstory composition and age, drainage, soil type, and slope (see George and Bazzaz 1999: Table 1).

In each of the six experimental sites, three types of manipulations were randomly assigned to and implemented in 1-m² plots randomly located within clones of both *Dennstaedtia punctilobula* and *Osmunda claytoniana*. Ferns were left undisturbed in the first manipulation as a control (''fern''). In order to separately investigate belowground interactions between ferns and tree seedlings, a ''shade-free'' manipulation was implemented. Fern fronds were directed toward the edges of plots and pinned down horizontally using wire wickets. Fronds were not bent to the ground but allowed to lie horizontally 5–10 cm above the ground, creating a shade-free area above the fronds while leaving fern roots and rhizomes intact. Ferns were pinned back in a 0.5-m buffer zone around experimental plots to reduce side shading. Ferns were removed from plots in the third manipulation (''fern-free'') by applying glyphosate (Round-up, Monsanto, Saint Louis, Missouri, USA) directly to fern fronds in July 1993 at commercially recommended rates (Grossbard and Atkinson 1985). After herbicide application, dead fern fronds were cut at the base and removed from the plots; dead roots and rhizomes were not removed from plots in order to minimize disturbance. Plots were spaded at the perimeter and weeded to remove new establishment. Each manipulation within each fern species was replicated five times for a total of 30 plots within each site and a total of 180 experimental plots (3 manipulations × 2 fern species × 5 replications × 6 sites = 180 plots).

In each experimental plot, integrated photon flux density was measured at two heights: above the fern canopy (1 m) and below the fern canopy (8 cm), in order to evaluate the amount of light reaching the fern canopy and subsequently the amount of light reaching seedling level as a result of the presence or absence of ferns (George and Bazzaz 1999). Soil water content, soil organic-material content, litter depth, and percentage of exposed soil were also measured in each plot and related to site, fern species, and manipulation (George and Bazzaz 1999). Spring and summer light levels (at 8 cm) were lowest below the fern stratum and equivalent in shade-free and fern-free manipulations. In contrast, soil exposure was highest in fern-free plots but equivalent in shade-free and control plots.

TABLE 1. ANCOVA results of the effects of site, fern species, manipulation, and seedling species for four performance parameters: relative growth rate of total biomass (RGR_B), relative growth rate of total biomass excluding the shade-free manipulation ($RGR_{B(-SF)}$), relative height growth rate (RGR_H), and survival.

Source of variation	df	Relative growth rate			Survival
		RGR_B	$RGR_{B(-SF)}$	RGR_H	
Light (mol·m^{-2}·d^{-1})	1	6.09*	4.41*	0.08	†
Site, S	5	2.39	1.22	1.06	4.41**
Fern species, F	1	1.47	4.25*	0.03	0.80
Manipulation, M	2	79.64****	130.97****	6.56**	25.50****
Seedling species, SS	2	119.79****	76.75****	392.60****	27.52****
S × F	5	4.16**	4.35***	1.49	0.51
S × M	10	1.06	1.29	0.94	1.41
S × SS	10	1.54	1.74	2.05*	3.06**
F × M	2	2.17	0.88	0.47	1.60
F × SS	2	0.65	0.69	0.97	1.06
M × SS	4	11.58****	23.60****	10.09****	6.05***
Error	495				

Notes: Light reaching the level of the fern stratum in each plot, measured as mean daily integrated photon flux density at 1 m height, was used as a covariate in analysis. Interactions between covariates and experimental factors as well as higher order interactions among experimental factors were not significant (data not shown). *F* statistics are reported for analyses of relative growth rates; χ^2 values are reported for survival data, which were analyzed using categorical modeling procedures (SAS Institute 1987 CATMOD procedure). For a description of the calculation of RGRs, see *Methods: Tree-seedling growth and survival measurements.*

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, **** $P \leq 0.0001$.

† Factor not tested.

Litter depth was highest in fern plots, followed by shade-free plots, and lowest in fern-free plots. Soil water content and soil organic material varied by site but not by manipulation. Only May light levels differed between fern species—on average they were lower under the canopy of *Osmunda* because of earlier frond development.

Tree-seedling growth and survival measurements

Seeds of locally collected *Acer rubrum* (red maple), *Betula alleghaniensis* (yellow birch) and *Quercus rubra* (red oak) were germinated in June 1993. Because of unforeseen delays in site preparation, seedlings were stored in flats after germination in an outdoor shade house adjacent to site PH3A. Light was maintained at levels characteristic of the forest understory in the absence of fern cover (i.e., fern-free manipulation). Seedlings were transplanted into plots during the 1st wk of August 1993. Eight seedlings were placed in each plot: two *Quercus,* three *Acer* and three *Betula.* Only one seedling per species per plot was ultimately harvested; however, extra seedlings were planted in order to allow for natural mortality during the course of the experiment. Seedlings were initially monitored for 3 wk, after which those dying of transplant shock were replaced.

Experimental tree seedlings were censused for survival at the beginning and end of the two subsequent growing seasons (May and September 1994, May and September 1995). Remains of dead seedlings were examined to determine the cause of death when possible. Cause of mortality was assigned to one of four categories: physical damage (damage from falling debris), insect herbivory (herbivory removing >75% of total leaf area), predation by rodents (seedlings uprooted, broken, or eaten), or possible resource limitation (all other dying seedlings).

Seedling height, basal diameter, and leaf lengths were measured on newly transplanted seedlings, and regressions using extra seedlings were used to obtain estimates of initial total biomass as well as biomass of roots, stems, and leaves. All regressions were highly significant ($P < 0.0001$) and predicted biomass well ($R^2 = 0.92$–0.94). Initial biomass (mean ± 1 SE) of *Quercus, Acer,* and *Betula* seedlings was 0.777 ± 0.011 g, 0.084 ± 0.002 g, and 0.085 ± 0.004 g, respectively. Initial height (mean ± 1 SE) of *Quercus, Acer,* and *Betula* seedlings was 12.8 ± 0.21 cm, 7.2 ± 0.11 cm, and 4.4 ± 0.11 cm, respectively. Initial height of experimental *Quercus* and *Acer* seedlings reflected their height at establishment because no additional height growth occured after the first leaf flush of the season. *Betula* seedlings were quite small at establishment, ~1 cm tall, and grew continuously in height throughout the growing season.

One seedling of each species was randomly chosen among surviving seedlings in each experimental plot and harvested during the 1st wk of September 1995. Seedlings were separated into root, stem, and leaf components, dried at 70°C for 48 h, and weighed. Relative growth rates (RGR) in terms of biomass and height were calculated as $RGR = [\ln(y_{i+1}) - \ln(y_1)]/yr$, where y_{i+1} is final height or biomass, y_1 is initial height or biomass, and yr is the length of the experiment in years.

Relative growth rates of height and biomass were analyzed using four-factor ANCOVA with site, fern species, experimental manipulation, and tree-seedling species as main effects. Light measurements made above the fern canopy (1-m height) were incorporated

as a covariate in the model. Interactions between the covariate and main effects were not significant. Interactions among main effects higher than two-way interactions were not significant and were thus pooled with error variance. Relative biomass growth rate was analyzed a second time after removing the shade-free manipulation from the analysis. This was done to assure that detectable manipulation effects and interactions resulted from the presence of a fern understory rather than the shade-free manipulation that was designed primarily to explore the mechanisms underlying interactions between ferns and tree seedlings. Microenvironmental measurements of integrated photon flux density (at 8 cm height), soil water content, soil organic-material content, litter depth, and percentage exposed soil were related to RGR of seedlings using multiple-regression techniques. Forward stepwise regression and backwards elimination of variables yielded the same results.

Seedling survivorship was analyzed as a categorical variable using a four-factor ANOVA design (SAS Institute 1987: CATMOD procedure). Cause of seedling mortality among manipulations was compared using chi-square analysis for each seedling species. For chi-square analysis, mortality data were pooled over all plots within each manipulation and seedling species. Projected seedling densities after four years of the combined 1994 and 1995 seedling cohorts of *Acer, Betula,* and *Quercus* were calculated by multiplying 1994 recruitment values of each species by first-year survivorship (data from George and Bazzaz 1999) and by annual survivorship for three years using survivorship values obtained from the present experiment. To this value was added the contribution of 1995 cohorts after three years, which was obtained by multiplying 1995 natural recruitment by first-year survivorship (data from George and Bazzaz 1999) and annual survivorship for two years using data from the present experiment.

RESULTS

Seedling biomass growth

The presence of a fern understory significantly reduced the relative growth rates in terms of total biomass (RGR_B) of all tree-seedling species (Fig. 1A). Because RGR_B of *Acer* and *Quercus* were equivalent in the shade-free and fern-free manipulations, reduced light levels are interpreted to be the primary factor responsible for reduction of RGR_B under ferns. Although RGR_B of *Betula* was also lowest under the fern understory, RGR_B in the shade-free manipulation was also slightly lower than RGR_B in the fern-free manipulation suggesting possible belowground effects.

Although the fern understory had a negative effect on RGR_B of all species, the severity of that reduction differed among seedling species as indicated by the highly significant interaction between manipulation and seedling species when all manipulations were an-
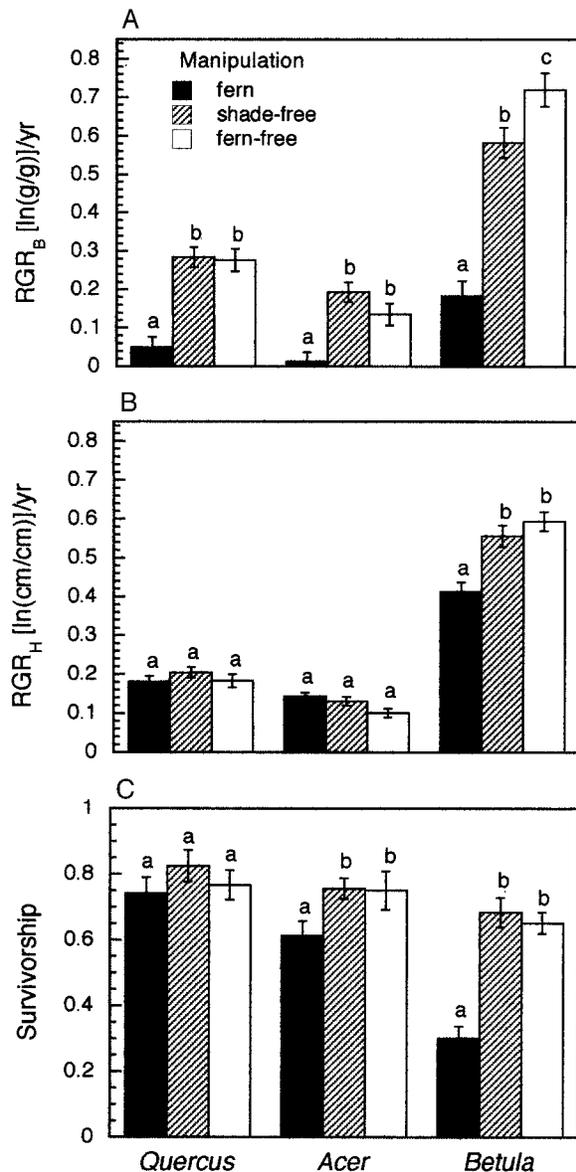

FIG. 1. Variation in relative growth rates (RGR) for (A) total biomass (RGR_B), and (B) height (RGR_H), and (C) variation in seedling survivorship through two growing seasons in experimental understory manipulations. Histogram bars represent the mean (± 1 SE) of the manipulation. Sample sizes for RGRs, was $n = 60$ seedlings for each manipulation for all species. For survivorship in each manipulation, $n = 120$ seedlings for *Quercus,* and $n = 180$ seedlings for *Acer* and *Betula.* Bars with the same lowercase letters are not significantly different among manipulations within seedling species at $P < 0.05$ (Fisher's Protected LSD). See *Methods: Tree seedling growth and survival measurements* for explanation of how RGR values were calculated.

alyzed or when only fern and fern-free plots were analyzed (Table 1). The severity of growth-rate reduction was inversely related to growth rate attained in fern-free areas (Fig. 1). Relative growth rate of *Betula* was reduced by 75% under ferns with respect to fern-free
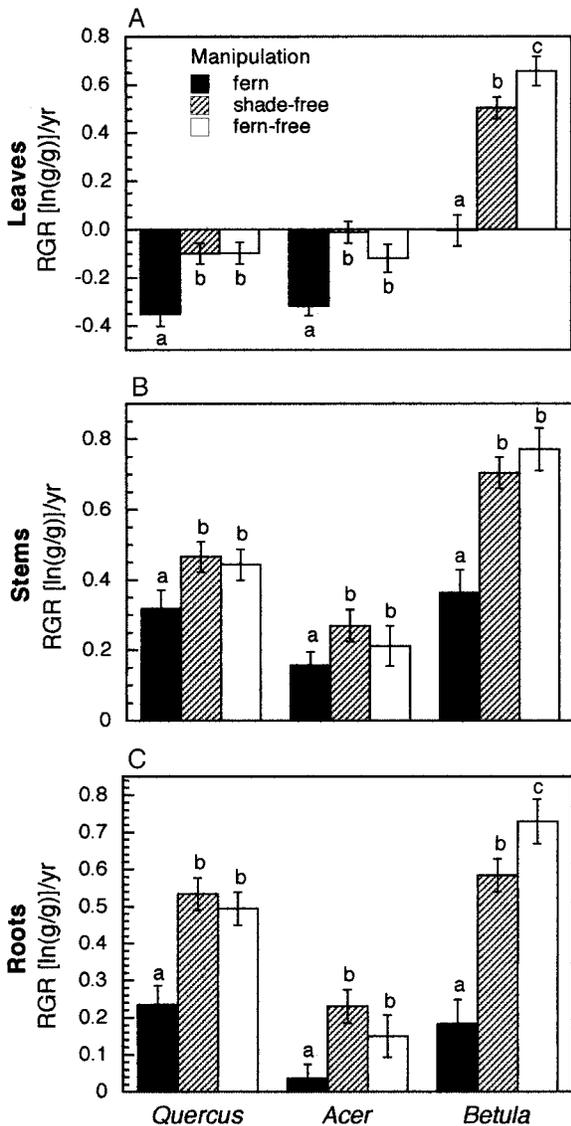
FIG. 2. Variation in relative growth rate (RGR) in terms of biomass of (A) leaves, (B) stems, and (C) roots among experimental manipulations for three tree-seedling species. Each bar represents the mean of the manipulation (± 1 SE, n = 60 seedlings). Bars with the same lowercase letters are not significantly different among manipulations within seedling species at $P < 0.05$ (Fisher's Protected LSD).

the lowest leaf, stem, and root biomass for all species. The negative effect of the fern understory was dampened in the case of stem biomass, because stems represented a higher proportion of total biomass for all species in fern plots than in the shade-free or fern-free plots. In *Quercus* and *Acer,* relative growth rates of leaves, stems, and roots in terms of biomass in the shade-free manipulation were equivalent to those in the fern-free manipulation, and in *Betula* the shade-free manipulation yielded slightly lower leaf and root RGR_B than the fern-free manipulation. Although relative growth rates in terms of total biomass increased over time for all species in all experimental manipulations, leaf biomass decreased over time in all manipulations for *Quercus* and *Acer.*

On average, the species of fern had no effect on seedling RGR_B; however, there was a significant site $\times$ fern species interaction (Table 1). At site PH4B, a site with a soil hard pan and high soil moisture levels, RGR_B across all seedling species and manipulations was lower in *Dennstaedtia* plots than *Osmunda* plots. The effect of the presence or absence of understory cover on the relative biomass growth rates of seedlings remained consistent over the six study sites (no significant site $\times$ manipulation interaction).

Seedling height growth

The fern understory also differentially influenced RGR in terms of seedling height (RGR_H) as indicated by the significant interaction between manipulation and seedling species (Table 1). In contrast with the results for biomass, only *Betula* RGR_H was higher in shade-free and fern-free manipulations than under fern cover (Fig. 1B). *Quercus* and *Acer* RGR_H were not affected by experimental manipulation of the fern understory. Biomass of *Quercus* and *Acer* seedlings in the shade-free and fern-free manipulations was substantially higher than in fern plots, which may enhance survivorship; however, these species only grew minimally in height regardless of understory environment and thus may never reach canopy height in a closed-canopy forest. Relative height growth of *Betula* was greater than that of *Quercus* or *Acer* in all experimental manipulations at all sites. Relative height growth rate of *Quercus* was greater than that of *Acer* at sites PH3B and PH4B but equivalent to that of *Acer* at all other sites (significant site $\times$ seedling species effect, Table 1). In general, seedling height among species under the fern understory is more uniform than seedling height in open areas.

Environmental correlates of seedling growth

In multiple-regression models, light level at 8 cm above the forest floor was the only microenvironmental variable that explained a significant amount of the variation in seedling relative growth rates in terms of biomass (RGR_B; Table 2, Fig. 3). All other microenvironmental variables (soil moisture, soil organic material,

areas; *Quercus* RGR_B was reduced by 82% and *Acer* RGR by 90%. *Acer,* which exhibits the lowest RGR_B in open plots, suffered the greatest percentage reduction of RGR_B under ferns. Where ferns were absent, *Betula* RGR_B was greater than *Quercus* RGR_B, which was greater than *Acer* RGR_B. Under fern cover, RGR_B of *Quercus* and *Acer* were equivalent yet significantly less than RGR_B of *Betula.*

Patterns of RGR of leaf, stem, and root biomass generally reflected the pattern of RGR of total biomass, indicating that all plant tissues responded similarly to experimental manipulations (Fig. 2). Fern plots yielded

TABLE 2. Linear regression relationships between relative growth rate in terms of total biomass (RGR_B) and height (RGR_H) and light level (in moles per square meter per day) measured 8 cm above the forest floor.

Dependent variable	Species	R^2	P	Slope value	Intercept value
RGR_B	*Quercus*	0.24	<0.0001	0.275	−0.014
	Acer	0.16	<0.0001	0.195	−0.037
	Betula	0.26	<0.0001	0.463	0.145
RGR_H	*Quercus*	⋯	NS	⋯	0.177
	Acer	⋯	NS	⋯	0.145
	Betula	0.09	<0.0001	0.154	0.404

Notes: Analysis of residuals indicated the appropriateness of a linear model. NS = nonsignificant.

litter depth, and soil exposure) did not explain any additional variation. Light level was also correlated with relative height growth rate (RGR_h) of *Betula* but not of *Acer* or *Quercus.* No other microenvironmental variables explained any additional variation in seedling relative height growth. The slope of the relationship between light level and *Betula* RGR_B was steeper than that of *Quercus* or *Acer* ($P < 0.01$), indicating that *Betula*'s growth rate was more responsive to increasing light levels (Fig. 3). *Betula* RGR_B was higher than that of *Quercus* and *Acer* even at the lowest light levels encountered in this field experiment.

Seedling survivorship

The fern understory selectively influenced the survivorship of tree species (significant manipulation × seedling species interaction, Table 1). Survivorship was reduced by the presence of a fern understory in *Acer* and *Betula* but not *Quercus* (Fig. 1C). Although survivorship after 2 yr (September 1993–September 1995) was equivalent among species in shade-free and fern-free plots, survivorship under ferns was highest for *Quercus* (74%), followed by *Acer* (61%) and *Betula* (30%). A significant site × seedling species interaction (Table 1) was caused by particularly high predation rates for *Acer* at site PH4A and for *Quercus* at site TS1.

Generally, survivorship declined steadily over the course of the experiment (Fig. 3). Projected residence time in the seedling bank (which assumes a constant mortality rate) for each species in fern and fern-free areas is presented in Table 3. In fern-free plots, *Quercus* and *Acer* have the longest projected residence time, followed by *Betula*. In fern plots, *Acer* has the longest projected residence time, followed by *Quercus*. *Betula* does not maintain a seedling bank under ferns.

Inferred resource limitation accounted for the highest proportion of mortality across all species and manipulations (Fig. 4). Mortality from insect herbivory and predation by rodents was most substantial in *Quercus* seedlings, but predation by rodents was also an important source of mortality for *Acer* seedlings grown in fern-free areas. Mortality from physical damage was generally low and was equivalent across manipulations
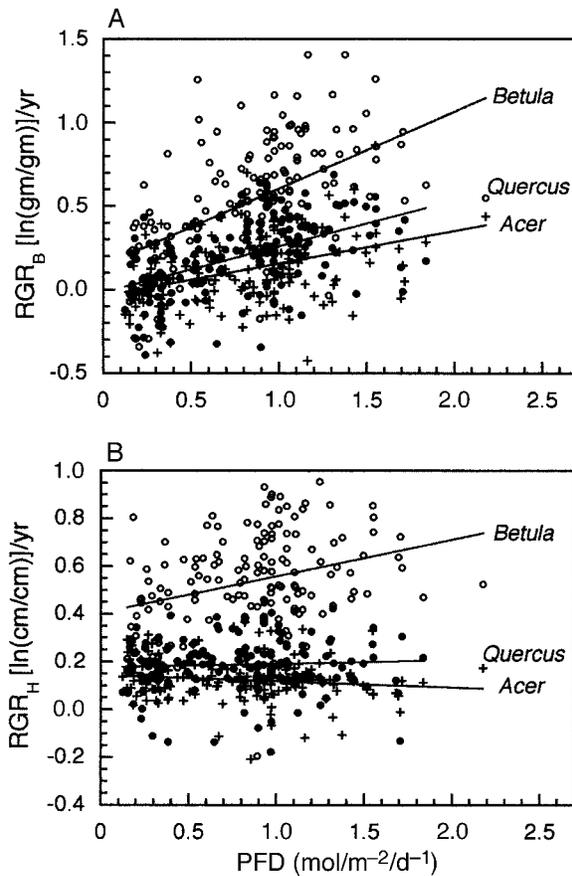
FIG. 3. Relationship between daily integrated photon flux density (PFD) measured 8 cm above the forest floor and seedling relative growth rate in terms of (A) total biomass (RGR_B) and (B) height (RGR_H) for three tree-seedling species (+ = *Acer*, ○ = *Betula*, ● = *Quercus*).

within each species. Cause of seedling mortality was associated with experimental manipulation for *Quercus* and *Acer* but not for *Betula*. Although total mortality in *Quercus* was equivalent across manipulations, mortality resulting from resource limitation was higher in fern plots than in the shade-free or fern-free manipulations ($\chi^2 = 9.19$, df = 2, $P \le 0.01$, $n = 80$ seedlings). Although predation by rodents was equivalent across manipulations for *Quercus,* it was a substantial cause of mortality for *Acer* only in the fern-free manipulation ($\chi^2 = 25.76$, df = 2, $P \le 0.0001$, $n = 159$ seedlings).

TABLE 3. Projected seedling-bank residence time (in years) for cohorts of three seedling species in fern and fern-free areas.

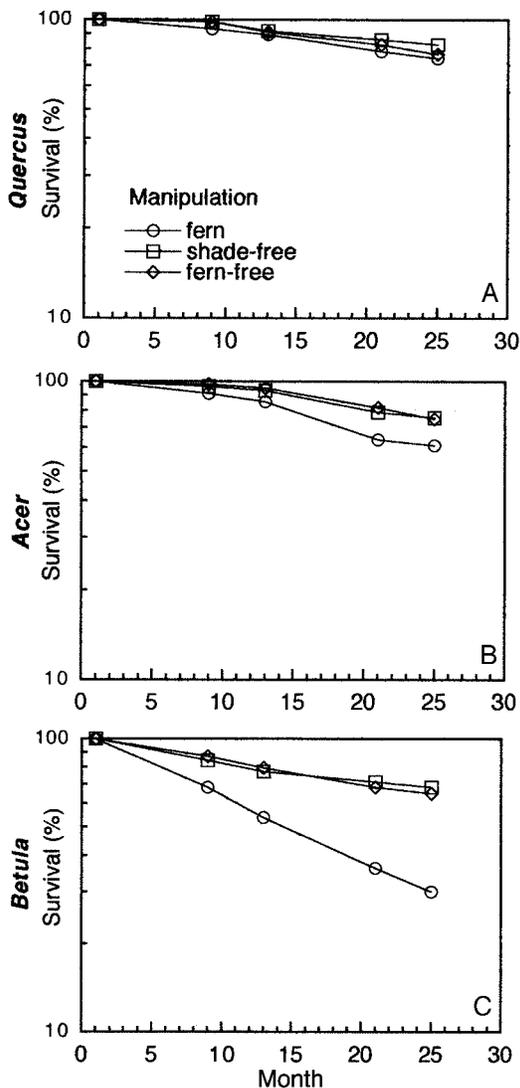| Cohort survival	*Quercus*		*Acer*		*Betula*	
	Fern	Fern-free	Fern	Fern-free	Fern	Fern-free
10% of cohort surviving	6	13	8	17	<1	1
5% of cohort surviving	9	18	12	23	<1	4
1% of cohort surviving	17	30	23	34	<1	15

FIG. 4. Seedling survivorship of (A) *Quercus,* (B) *Acer,* and (C) *Betula* among experimental manipulations over time. Note $\log_{10}$ scale on *y* axis.

However, these cases were a result of uprooting and no tissues ever appeared to have been consumed.

Integrating emergence, growth, and survival

Projected tree-seedling density and species composition, calculated for combined seedling cohorts of *Acer, Betula,* and *Quercus* in the presence and absence of a fern understory is presented in Table 4. Total seedling density of the study cohorts after 4 yr is nearly four times greater in fern-free areas (21 769 seedlings/ha) compared to areas with a dense fern understory (5682 seedlings/ha). Although more *Acer* seedlings are found in fern-free plots compared to fern plots, *Acer* dominates the seedling bank under the fern understory in terms of relative species composition. In contrast, *Betula* seedlings are essentially absent under ferns, but

are codominant with *Acer* in fern-free areas. *Quercus* seedlings are more abundant in fern-free areas compared to areas under the fern understory, but contribute roughly the same percentage to the species composition of each area.

The differential effect of the understory filter on species height growth rates results in different size structures in the seedling bank below the fern canopy compared to the seedling bank in fern-free areas. The initial size of seedlings upon establishment in the field is largely a function of seed size: *Quercus* seedlings are larger and taller (13 cm) than *Acer* seedlings (7 cm), which are taller than *Betula* seedlings (1 cm). Using conservative annual height growth rates observed in this experiment, *Betula* seedlings in fern-free areas surpass *Acer* seedlings of the same cohort in height after 2 yr, and they surpass *Quercus* seedlings in height after 5 yr. Under the fern stratum, *Betula* seedlings do not approach the height of *Acer* or *Quercus* in their estimated residence time in the seedling pool. In fern-free areas, *Betula* seedlings become the tallest seedlings of a given cohort, whereas *Quercus* retains its height advantage under the fern stratum.

The seedling bank is constantly being replenished with new recruitment, and therefore some seedlings of all species exist in the seedling bank under the fern understory at all times. However, only *Quercus* can be expected to survive long enough to grow and emerge from the fern stratum. Using the annual seedling height growth rate under fern cover, *Quercus* seedlings may exceed the height of the *Dennstaedtia* canopy (39 cm) in 10 yr, at which time 4.6% of the original cohort of established seedlings still survive; *Quercus* seedlings may exceed the height of the *Osmunda* canopy (64 cm) in 19 yr at which time 0.76% of the original cohort of established seedlings still survive. *Acer* and *Betula* seedlings may exceed the height of the *Dennstaedtia* canopy in 27 yr and 11 yr, respectively. The percentage survival of an original cohort in that amount of time is 0.60% for *Acer* and 0.0002% for *Betula.* The time that it potentially takes these species to exceed the height of the *Osmunda* canopy basically exceeds their residence time in the seedling bank.

DISCUSSION

The environment is often viewed as a sieve that sifts genotypes from an initial seed population and determines which individuals will contribute to the next generation of seeds (Harper 1977). We have focused on aspects of the biotic environment as an ecological sieve that selectively discriminates among seedling species and structures emergent community characteristics such as composition, productivity, diversity, and spatial structure. We have specifically focused on the fern stratum of the forest understory and have demonstrated that this filter differentially influences growth and survival rates of established seedlings of canopy-tree species. With minor exception, the activity of the
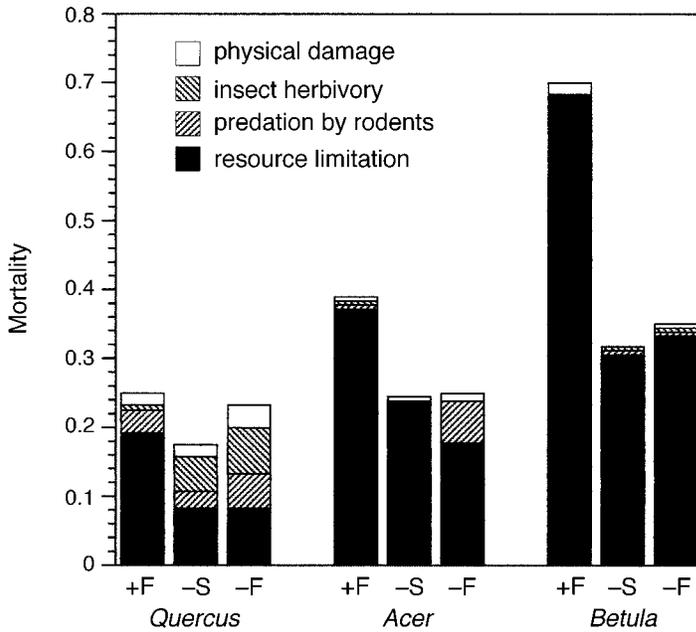
Fig. 5. Relationship between cause of seedling mortality and experimental manipulation for three tree-seedling species. Seedling mortality data are pooled over all replicate plots and sites within manipulations and seedling species. Manipulations: fern (+F), shade-free (−S), fern-free (−F).

fern filter is strong and consistent across sites that vary in overstory composition and multiple edaphic factors. Because the seedling bank represents the starting capital for forest regeneration, pre-disturbance interactions between the understory and tree seedlings that shape the nature of the seedling bank will influence the rate and trajectory of post-disturbance forest regeneration (Brokaw and Scheiner 1989, Connell 1989).

The negative or neutral effect of the fern understory on both tree-seedling survival and recruitment leads to a significantly lower total seedling density beneath ferns than in fern-free areas. As a result of the selectivity of the fern filter, species composition of the seedling pool below ferns is dominated by *Acer,* whereas dominance of the seedling pool in fern-free areas of the forest is shared by *Betula* and *Acer*. If a forest is spatially patchy with respect to understory cover, then the seedling bank will also have a strong spatial structure. In communities with this type of spatial structure, intraspecific competition will predominate within neighborhoods (Bazzaz 1983), and spatial aggregation

into monospecific competitive neighborhoods may lead to coexistence of species at the community level (Hibbs 1982*b*, Pacala 1986, Silvertown and Law 1987, Pacala et al. 1993).

The dampening effect of the fern understory on growth of all tree-seedling species leads to a relatively more uniform seedling bank in terms of plant height in areas of high fern cover. Size similarity among tree-seedling species has been noted in other forests with a prominent fern stratum (Bowersox and McCormick 1987) and may contribute to more similar competitive status among individuals and species when the canopy opens and conditions are more favorable for growth to the overstory. Because the fern understory maintains the initial size ranking of seedlings imposed primarily by seed size, *Quercus* seedlings remain the tallest seedlings of a cohort and are the only species capable of emerging from the fern canopy in substantial numbers. Other species must be released by either disturbance in the overstory or understory canopy in order to exceed the height of the fern stratum. In areas of sparse understory growth, higher survival rates magnify differences in growth and lead to a more uneven seedling size structure. In these areas, the tallest seedlings, most commonly *Betula* in our sites, may have a competitive advantage over their seedling neighbors in post-disturbance competition (Barden 1979, Canham 1988, Connell 1989).

Light availability is the primary factor limiting tree-seedling growth and survival beneath the fern stratum, although *Betula* growth appears to be moderately affected by belowground interactions with ferns. This finding agrees with Pacala et al. (1994, 1996) who found field growth and survival of saplings in the forest

TABLE 4. Projected values of seedling density (no./ha) of combined 1994 and 1995 tree-seedling cohorts after 4-yr growth (3 yr for 1995 cohort) in fern and fern-free areas. The relative contribution to total species composition appears in parentheses.

	Seedling density (no./ha)	
Species	Fern area	Fern-free area
Quercus	332 (0.06)	2029 (0.09)
Acer	5347 (0.94)	10 998 (0.51)
Betula	3 (0.0005)	8742 (0.40)
Total	5682	21 769

understory, including *Acer rubrum, Betula alleghaniensis,* and *Quercus rubra,* and seven other tree species, to be a function of light availability but not of soil moisture or nitrogen mineralization rates. Similarly, survival of *Prunus serotina* was reduced by aboveground interference but not belowground interference from *Dennstaedtia punctilobula* (Horsley 1993). Belowground interference did not contribute to mortality of *Inga* seedlings under a palm and cyclanth understory in Costa Rican tropical forests (Denslow et al. 1991). Studies that have identified a relatively more important role for belowground interference between ground vegetation and tree seedlings have all taken place in open site conditions such as old fields or clearcuts where background levels of light are relatively high (Gill and Marks 1991, Putz and Canham 1992, Lyon 1995). In closed forest environments, it appears that aboveground interference between the understory and tree seedlings predominates in importance.

A trade-off between traits that enhance persistence in low light and traits that promote maximum growth response with increasing light levels has been recognized between early and late-successional species (Bazzaz 1979, 1996, Pacala et al. 1994, Kobe et al. 1995). A similar trade-off has been observed within this group of species that are relatively similar in successional status. *Acer* and *Quercus* exhibit relatively high persistence under the fern stratum as well as in fern-free areas, whereas *Betula* suffers high mortality under the fern stratum. Biomass growth rates of all seedling species in terms of biomass increase with increasing light levels; however, the rate of that response is greatest for *Betula.* Height growth of *Acer* and *Quercus* do not respond to increasing light level, while *Betula* height growth dramatically increases with increasing light level.

Although *Dennstaedtia* and *Osmunda* differ in growth habit and morphology, the species of fern did not differentially affect growth or survival of tree seedlings, perhaps because both fern species reduce light under their canopies to similar levels (George and Bazzaz 1999). Belowground effects of the two fern species were also similar. Soil moisture differences between the fern species habitats at site PH9 (George and Bazzaz 1999) did not significantly affect seedling growth or survival rates. However, seedling RGR_B was lower in *Dennstaedtia* than *Osmunda* plots across all understory manipulations at the only site with a soil hard pan, site PH4B. An explanation for this result is not obvious, but perhaps in moist sites *Dennstaedtia* grows in microsites less favorable to seedling growth than *Osmunda,* or it is possible that an inhibitory factor responsible for reduced RGR_B under *Dennstaedtia* may still have been present after fern removal (e.g., altered soil chemistry, allelopathic compounds).

Although seedling growth and survival rates do not differ between *Dennstaedtia* and *Osmunda* understories on an annual basis, *Osmunda* understories may ulti-

mately have a more detrimental effect on tree-seedling growth and survival because seedlings will be subjected to a longer period of reduced light beneath the taller *Osmunda* canopy. Berkowitz et al. (1995) found no differences in tree-seedling annual survival and growth among eight different community types dominated by ferns, grasses, or shrubs. However, the compounding of annual growth and survival rates over a longer number of years in community types of tall stature (i.e., shrubs) appears to have led to differences in naturally occurring seedling densities found among community types (Hill et al. 1994).

The fern understory also regulates seedling growth and survival indirectly by influencing the activity of insect herbivores and predators. However, the outcome of their activity on seed and seedling survival will depend specifically upon the identity and behavior of the herbivores or predators involved. The fern understory appears to have protected *Quercus* leaves from intense insect defoliation observed in plots without fern cover. Protection from defoliation balanced the detrimental effects of limited resources below the fern stratum, leading to a net neutral effect of ferns on *Quercus* survival. Uprooting of *Acer* seedlings observed in fern-free plots is a behavior noted for meadow voles, possibly to clear foraging pathways or to search for seed caches (Gill and Marks 1991). Rodent predators equally consumed or disturbed *Quercus* seedlings in fern and fern-free environments, but seed predation of *Quercus* was higher under the fern understory (George and Bazzaz 1999). Predation by rodents is frequently higher under ground vegetation in old fields, presumably because rodents are less likely to forage in areas where they are exposed to predators (Gill and Marks 1991, Ostfeld and Canham 1993). Understory vegetation can also reduce seedling visibility to larger predators such as deer, and protect them from browsing (Horsley and Marquis 1983, De Steven 1991).

The understory filter will continue to influence tree growth and survival after canopy disturbance, but the nature of that influence will depend on changing understory dynamics as well as altered flux in resource levels created by disturbance. *Dennstaedtia* canopies increase in height and density with response to small canopy-gap openings (Hill 1996) as do other species implicated in regeneration problems such as understory bamboos (Taylor and Qin 1992) and understory palms (Piñero et al. 1986). In contrast, the growth rate of *Kalmia latifolia,* a species that interferes with tree regeneration in the Southern Appalachians, is only minimally increased in response to canopy opening (O'Keefe et al. 1982). Cover of the South American bamboo, *Chusquea tenuiflora,* decreases in canopy gaps because of higher snow accumulation and greater frequency of summer frosts (Veblen 1982).

The ability of seedlings beneath the understory canopy to utilize increased light levels in canopy gaps will depend on whether the physiological attributes and

population dynamics of understory plants result in the preemption of increased resource levels such as light. Ferns reduce light levels in areas at the Harvard Forest where the overstory canopy has been removed from 21 $mol \cdot m^{-2} \cdot d^{-1}$ to 2–3 $mol \cdot ^{-2} \cdot d^{-1}$ (Carlton and Bazzaz 1998), which is still higher than light under fern cover in closed-canopy forests (0.33 $mol \cdot m^{-2} \cdot d^{-1}$). In the forest understory an increase in light availability of this magnitude (1–2% full sun) can trigger strong release response in shade-tolerant tree seedlings (Canham 1989). Our findings suggest that *Betula, Acer,* and *Quercus* could realize substantial increases in biomass growth rate and that *Betula* could realize a substantial gain in height growth under these conditions.

The results of our study have demonstrated that the understory filter shapes the abundance, species composition, size structure, and spatial distribution of the community of advanced regeneration that is available for post-disturbance growth. Density of advanced regeneration influences the rate of forest regeneration (Nakashizuka 1987, Taylor and Qin 1992, McWilliams et al. 1995). The species composition as well as the density of the seedling bank will influence the trajectory of regeneration directly by determining which species are available for post-disturbance release and indirectly by determining the competitive environment for species that seed in after disturbance (Veblen 1982, Taylor and Qin 1988, Peterson and Pickett 1995). The filtering activity of the understory organizes the spatial distribution of species within the forest, which in turn influences competitive and reproductive dynamics and levels of diversity. Understory influence continues through post-disturbance forest regeneration, but the nature of that influence is governed by the type and intensity of disturbance and the response of the understory to that disturbance.

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