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THE FERN UNDERSTORY AS AN ECOLOGICAL FILTER: EMERGENCE AND ESTABLISHMENT OF CANOPY-TREE SEEDLINGS

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Abstract. We investigated the role of the fern understory as an ecological filter that influences the organization of the seedling bank in New England deciduous forests. Microenvironmental variables—including light levels, litter depth, soil exposure, soil moisture, and soil organic matter content—were quantified in experimental plots where the fern understory was undisturbed, partially removed or completely removed and were related to natural recruitment and 1st-yr survival of *Acer rubrum*, *Betula lenta*, *B. alleghaniensis*, *Fraxinus americana*, *Pinus strobus*, and *Quercus rubra*. We conducted a series of three field emergence experiments to test hypotheses regarding mechanisms of fern interference with seedling emergence.

The fern understory reduced light levels from 3.4% of full sun to 1.1% of full sun beneath its canopy. Soil exposure was lower and litter depth was greater under fern cover, whereas soil moisture and soil organic-matter content were not affected by fern cover. The understory filter differentially influenced tree-seedling emergence. Fern cover decreased emergence of *Betula*, *Pinus*, and *Quercus* but did not affect the emergence of *Acer* or *Fraxinus*. The mechanism of fern interference was species-specific: *Betula* emergence was reduced primarily by low levels of soil exposure, *Pinus* emergence appeared to be related to reduced light levels, and *Quercus* suffered higher levels of seed predation under fern cover. The presence of understory fern cover also differentially influenced 1st-yr survival of natural tree-seedling recruitment. Although seedling survivorship during the first growing season was related to seed size, seedling survivorship below ferns by the end of the 1st yr was independent of seed size. Selectivity of the fern filter is caused by differential response of tree-seedling species to the presence of understory cover and was generally not affected by the species identity of the understory plant. The selectivity of the understory filter can influence the density and species composition of the seedling bank below its canopy and can determine patterns of seedling spatial distribution at the stand level.

Key words: Acer rubrum; Betula alleghaniensis; *competition; fern understory as ecological filter; forest regeneration;* Fraxinus americana; *Harvard Forest, Massachusetts, USA; microenvironments;* Pinus strobus; Quercus rubra; *tree-seedling recruitment; understory.*

INTRODUCTION

Population biologists often view the physical environment as a sieve that filters out individuals from an initial seed population during successive life stages and ultimately determines the success of a seed in producing more seeds (Harper 1977). Through its influence on populations of individual species, the environment can also act as an ecological sieve that structures communities (Van der Valk 1981). An ecological filter ‘‘sifts’’ through the initial seed populations of a whole community and determines emergent community characteristics such as species composition, productivity, and spatial distribution patterns. We propose that the herb and shrub stratum of the forest understory is an important ecological filter in many temperate and tropical communities that influences the composition and structure of the overstory canopy. Seedlings of canopy trees must establish in and grow through the understory herb and shrub stratum in order to reach the overstory canopy. Through differential influence on tree-seedling emergence, growth, and survival, the understory filter may determine which individuals and species will survive in and ultimately penetrate the understory stratum.

Interest in the structure and organization of forests at the community and landscape levels has concentrated on the role of the physical environment (e.g., topography and soils) as determinants of tree recruitment and growth (Collins 1987, 1990, Clark et al. 1995). However, in closed-canopy forests, the physical environment as perceived by tree seeds and seedlings can be highly modified by the biotic environment, particularly the established members of the forest understory. The forest understory stratum is a spatially variable mosaic composed of plants of different species, densities, and degrees of mixture. Because of their clonal nature and ability to resprout after disturbance, many understory herbs and shrubs commonly form dense, monospecific patches that are relatively temporally stable. Clonal plants can be extremely long-lived, with

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TABLE 1. Stand characteristics of six experimental sites in the Harvard Forest (Massachusetts, USA).

Stand characteristic	PH3A	PH3B	PH4A	PH4B
Overstory	*Pinus strobus, Quercus rubra*	*Betula papyrifera, Quercus rubra*	*Quercus rubra, Acer rubrum*	*Quercus rubra, Acer rubrum*
Stand age (yr)	80, mixed	37, even†	50, even	70, mixed
Soil type	Woodbridge fine sandy loam	Canton loam	Newfields fine sandy loam	Woodbridge loam
Drainage	Moderately well	Well	Moderately well	Moderately well
Hard pan	Absent	Absent	Absent	Present
Slope/aspect	0°	7° NW	0°	8° W

Notes: Site overstory is characterized by the two most important species in terms of basal area. Soils information is from Harvard Forest Soil Survey, and stand age was determined from historical records (Harvard Forest Archives).

† Although the overstory canopy is essentially even aged, a few large older individuals remain scattered throughout these sites.

life spans commonly exceeding those of individual trees (Watt 1947, Oinonen 1967*a*, *b*). For example, clones of the fern *Osmunda claytoniana* growing in our study site date from the period of land abandonment in New England and are presently 150–200 yr old (Knight 1964). Populations of clonal plants may be resilient to disturbance and leave strong imprints on patterns of resource heterogeneity in the forest (Halpern 1989, Hughes and Fahey 1991).

Herbs and shrubs of the understory intercept much of the remaining light in a closed-canopy forest, altering light quality and reducing light quantity beneath their canopies (Messier et al. 1989). Germination and establishment of tree species have been shown to be sensitive to temperature and moisture (Fenner 1985, Burton and Bazzaz 1991) and to quantity and quality of litter (Collins 1990, Facelli and Pickett 1991). To the extent that the understory modifies these microenvironmental variables, temperature, soil moisture, and litter distribution may also play an important role in interactions between the understory and tree seedlings. Understory interference with tree-seedling emergence and establishment may occur not only directly through resource competition or modification, but may occur indirectly through the understory's influence on the behavior of seed predators. For example, higher rodent densities and acorn removal rates below understory bamboo cover result in low densities of oak tree seedlings in dense bamboo patches in Japanese temperate forests (Wada 1993).

Interactions between ground vegetation and invading tree species have been well studied in old-field environments (Warner and Harbeck 1982, Burton and Bazzaz 1991, 1995, De Steven 1991), and both positive and negative interactions have been demonstrated to occur. Not only has the presence of ground vegetation been shown to modify the microenvironment of potential establishment sites, but different old-field vegetation types uniquely modify microenvironmental conditions below their respective canopies (Burton and Bazzaz 1995). Herbaceous understory plants have additionally been shown to interfere with regeneration of commercially important species after timber harvest primarily through reduction of light levels and production of potential allelopathic substances (Drew 1988, Horsley 1988, 1993, McWilliams et al. 1995). The importance of interactions among herbs, shrubs, and tree seedlings in open environments suggests that herbs and shrubs of the forest understory may similarly be an important determinant of tree regeneration in closed forest environments.

Because the herb and shrub stratum of the forest understory represents one of the first potential barriers to tree regeneration, it can be viewed as a filter that all tree seedlings must pass through (e.g., Gilliam et al. 1994). The understory filter may be nonspecific and regulate only the density of the seedling bank, or it may differentially influence emergence and survival of tree species, thereby controlling species composition and spatial structure of the seedling bank. The objective of this study was to explore the nature of the fern understory as an ecological filter in New England deciduous forests. We monitored emergence of planted seed, and emergence and establishment of natural tree-seedling recruitment in plots where the fern understory was experimentally manipulated in order to: (1) determine how the presence of a well-developed fern understory influences emergence and establishment of canopy-tree species, (2) assess the importance of the identity of understory species in dictating the nature of interactions between the understory and tree seedlings, (3) relate measurements of microenvironmental conditions associated with or imposed by the understory to emergence and establishment of tree seedlings, and (4) explore the importance of using multiple experimental field sites to the interpretation of the nature of the understory filter. We hypothesize that the fern understory selectively filters tree regeneration by differentially influencing emergence and establishment of tree-seedling species, and that the selectivity of this filter will determine the abundance, relative species composition, and spatial distribution of the seedling bank.

METHODS

Study area

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

TABLE 1. Extended.

PH9	TS1
Betula lenta, *Pinus strobus*	*Quercus rubra,* *Acer rubrum*
33, even†	90+, mixed
Scituate loam	Paxton fine sandy loam
Moderately well	Well
Absent	Absent
3° N	5° NW

located in the Transition Hardwoods–White Pine–Hemlock forest type (Westveld et al. 1956). *Acer rubrum* L. (red maple) and *Quercus rubra* L. (northern red oak) are the most widespread and abundant overstory species in this region. *Betula alleghaniensis* Britt. (yellow birch), *B. lenta* L. (black birch), *B. papyrifera* Marsh. (white birch), *Fraxinus americana* L. (white ash), *Pinus strobus* L. (white pine), and *Tsuga canadensis* (L.) Carr. (eastern hemlock) are locally abundant. Clonal ferns such as *Dennstaedtia punctilobula* (Michx.) Moore (hayscented fern), *Osmunda claytoniana* L. (interrupted fern), *Osmunda cinnamomea* L. (cinnamon fern) and *Thelypteris noveboracensis* (L.) Nieuwl. (New York fern) commonly form a dense stratum near the forest floor.

Six sites, in which the herb/shrub stratum was dominated by the clonal ferns *Dennstaedtia punctilobula* and *Osmunda claytoniana*, were randomly located within Harvard Forest property. These sites are abbreviated and named in the text after the Harvard Forest compartment in which they are located: PH3A and PH3B (Prospect Hill compartment 3), PH4A and PH4B (Prospect Hill compartment 4), PH9 (Prospect Hill compartment 9), and TS1 (Tom Swamp compartment 1). While these sites were chosen for similar understory composition, they varied in overstory composition and age, drainage, soil type, and slope (Table 1).

Experimental manipulations

In the following experiments, three types of experimental treatments were implemented within naturally occurring clones of both *Dennstaedtia* and *Osmunda*. In one treatment, ferns were left undisturbed as a control (''fern''), and in another ferns were removed from plots (''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). Treatments were implemented in 1-m^2 study plots and in a 0.5-m-wide buffer zone around the perimeter of each study plot. In order to conserve an intact litter layer and soil horizons, dead fern fronds were cut at the base and removed from the plots; dead roots and rhizomes were not removed from plots. Plots were spaded at the perimeter to restrict horizontal in-growth and were periodically weeded to remove new establishment. Additionally, a ''shade-free'' manipulation was implemented by pinning fern fronds down horizontally using wire wickets. This method allowed fronds to lie horizontally 5–10 cm above the ground, creating a shade-free area above the fronds while leaving fern roots and rhizomes intact. Shade-free conditions could not be maintained at ground level over the entire area of 1-m^2 plots. However, fronds could be directed away from target areas within plots, thus creating relatively ''shade-free'' conditions at ground level in smaller zones. Five replicate plots of each fern × manipulation treatment were established in each of the six study sites (3 manipulations × 2 fern species × 5 replications × 6 sites = 180 plots).

Microsite descriptions

Microenvironmental conditions associated with experimental manipulations implemented within the two fern species were measured in all or a subset of all study plots. Before implementation of experimental treatments, fern canopy height and percentage cover were also measured in each experimental plot in order to characterize the two fern species. Fern canopy height was sampled in four locations within each plot with a meter stick, and percentage cover was estimated using a partitioned sample quadrat placed over the plot.

After treatment implementation, integrated photon flux density (PFD) was evaluated using photosensitive-paper light sensors (Friend 1961, Wayne and Bazzaz 1993) during the growing season from 7 to 14 July 1994 and from 11 to 17 August 1995 and during canopy leaf-out from 25 May to 1 June 1 1995. Light readings in July and August were similar in magnitude and were combined in analysis to present more integrated values of mid-summer light levels. Two light sensors per measurement period were placed in a random location at two heights within each experimental plot: one at 1 m to measure light above the fern canopy and one at 8 cm to measure light at the approximate height of 1-yr-old tree seedlings beneath the fern canopy. The 8-cm height was above the level of the restrained ferns fronds in the shade-free manipulation. Paper light sensor readings were calibrated with measurements of instantaneous photosynthetically active radiation ($R^2 = 0.982$–0.994) obtained concurrently using a LI-COR quantum sensor (LI-190SA, LI-COR, Lincoln, Nebraska, USA).

Soil samples (0–10 cm depth) were collected from each experimental plot on 1 July 1995. Soil water content was measured gravimetrically by weighing fresh samples, oven-drying them at 70°C for 48 h, and reweighing dry samples. Soil water content (SWC) is expressed as grams of soil water per unit dry mass of soil. The percentage of exposed soil (no litter cover) in experimental plots was estimated by placing a transect through the plot and scoring 10 random points along the transect as exposed or not exposed. Litter depth was measured with a ruler to the nearest millimeter at nine random points in a subset of experimental plots ($n = 108$ plots). Three-factor ANOVA was used to test whether these microenvironmental measurements varied among sites, fern species, and experimental manipulations. Soil water and organic-matter content measurements were ln-transformed and soil exposure measurements were square-root transformed to reduce heteroscedasticity.

Natural recruitment of tree seedlings

Natural recruitment of seedlings of *Acer rubrum*, *Fraxinus americana*, *Pinus strobus*, and *Quercus rubra* into fern and fern-free plots was recorded during the 1994 and 1995 growing seasons (2 manipulations × 2 fern species × 5 replications × 6 sites = 120 plots). Recruitment of *Betula alleghaniensis* and *B. lenta* was recorded together as *Betula* because the species are indistinguishable at emergence. Natural recruitment data were gathered on a plot-level basis, therefore natural recruitment in shade-free plots was not recorded because the entire area of the plot at ground level, where seedlings were emerging, was not shade-free. Emergence was scored as the visibility of cotyledons or leaves above the litter layer. Seedlings were tagged during the initial survey during the last week of May and new births were tagged at two more subsequent dates during the growing season.

Three-factor ANOVA was performed in order to test the effects of site, fern species, and understory manipulation on the emergence of each tree-seedling species. Because of the severe nonnormality of the data, significance levels of factor effects and interactions were determined using randomization procedures (Manly 1996). Seedling survivorship of the 1994 cohort was monitored until September 1994 (survivorship through the first growing season) and again in June 1995 (survivorship through the first year). Data from all plots of each fern manipulation (fern vs. fern-free) were pooled across fern species and sites ($n = 60$ plots; 10 plots per site × 6 sites), and chi-square tests were used to determine whether survivorship depended on fern manipulation. A second chi-square analysis, in which plots were pooled across manipulation and sites, tested whether survivorship depended on fern species.

In order to explore possible microenvironmental factors responsible for the influence of the fern understory on seedling emergence, Spearman correlation coefficients were calculated between density of emergent seedlings and plot microenvironmental variables. The first correlation analysis was performed using data from both fern and fern-free plots. A second analysis tested correlations between microenvironmental variables and density of emergent seedlings in fern and fern-free plots separately. In species exhibiting an effect of fern manipulation, we wished to more narrowly examine which microenvironmental variables exhibited correlations strong enough to be detected over the natural range of microenvironmental variability within fern manipulations.

Emergence experiments

In order to further explore factors responsible for differential response of tree species to understory manipulation, several field experiments were conducted to test hypotheses generated from known natural-history characteristics of the species and observed patterns of recruitment in the field. ''Fern,'' ''shade-free,'' and ''fern-free'' manipulations were implemented in plots measuring 20 × 30 cm (3 manipulations × 2 fern species × 3 replications × 6 sites = 108 plots) that were located adjacent to a subset of the plots used for measuring microenvironmental conditions and natural recruitment patterns. Planting depth was determined by observing naturally overwintering seed. All seed was planted under the most recent season's litter layer at the interface between the coarse litter and decomposing humus. Greenhouse germination trials were run concurrently to estimate potential emergence of planted seed.

Quercus rubra.—We placed red oak acorns into fern plots, shade-free plots, and fern-free plots after fern canopy development to test the hypotheses that differential *Quercus* emergence was related to light levels and/or seed predation. In April 1994 naturally stratified *Quercus* acorns were collected from locations adjacent to experimental sites. Two acorns were placed into each plot, and emergence, decay, and predation of acorns was monitored through the growing season and analyzed using categorical modeling procedures (CATMOD, SAS Institute 1987).

Acer rubrum.—Because *Acer rubrum* is the only dominant tree species in the study sites that disperses in spring and can germinate immediately during the current growing season, we wished to evaluate and contrast the effects of the fern understory on germination and emergence of the spring (overwintering) and summer (non-overwintering) seedling cohorts. The majority of the spring cohort of *Acer* emerges in April and May before fern leaf-out, and the summer cohort emerges after fern leaf-out. The contrast in timing of emergence with respect to fern leaf-out provided a way to test the importance of light reduction by ferns to *Acer* emergence. In June 1994, 50 recently fallen *Acer* samaras were planted into each emergence plot. Summer emergence was monitored during 1994 and early spring emergence of the same seed cohort was monitored the following year.

Betula alleghaniensis.—This experiment was designed to test the importance of both light and litter cover in *Betula* emergence. Because litter cover was expected to exert a strong influence on *Betula* emergence, two emergence subplots were created within each fern, shade-free, and fern-free experimental plot, one in which litter was undisturbed (''litter'') and one in which coarse litter cover had been removed (''litter removal''). In April 1994 the *Betula* seeds that had been collected from the Harvard Forest and placed in cold storage were planted in *Betula* emergence plots (40

TABLE 2. Summary of means for microenvironmental variables by site.

Variable	Site					
	PH3A	PH3B	PH4A	PH4B	PH9	TS1
Fern height (cm)	53.3^{b}	49.6^{b}	58.8^{c}	52.1^{b}	42.1^{a}	53.2^{b}
Fern cover (%)	65.7^{b}	63.7^{b}	67.7^{b}	62.3^{b}	55.5^{a}	64.8^{b}
May light (mol·m^{-2}·d^{-1})†	3.86^{b}	$4.37^{b,c}$	5.21^{c}	$4.33^{b,c}$	2.73^{a}	4.00^{b}
Midsummer light (mol·m^{-2}·d^{-1})†	1.18^{c}	1.00^{b}	1.18^{c}	$1.10^{b,c}$	0.72^{a}	1.23^{c}
SWC (g water/g dry soil)	0.497^{a}	0.506^{a}	0.599^{a}	1.057^{b}	0.641^{a}	0.577^{a}
SOM (g organic matter/g dry soil)	0.125^{b}	0.130^{b}	0.145^{b}	0.262^{c}	0.156^{b}	0.088^{a}
Litter depth (cm)‡	2.33^{c}	1.62^{a}	$1.86^{a,b}$	1.52^{a}	1.62^{a}	$1.98^{b,c}$
Soil exposure (%)§	$0.9^{a,b}$	$16.3^{c,d}$	$3.9^{a,b}$	28.8^{d}	0.1^{a}	$5.1^{b,c}$

Notes: Means are averaged across fern species and understory manipulations ($n = 30$ plots for each site) unless otherwise noted. Means sharing the same lowercase superscript letter are not significantly different at $P < 0.05$ (Fisher's protected LSD). SWC = soil water content; SOM = soil organic matter.

† Measured at 1 m above the forest floor.

‡ For litter depth, $n = 18$ plots for each site.

§ Soil exposure values are back-transformed means for fern-free plots only ($n = 10$ plots for each site); soil exposure did not significantly differ among sites in fern plots.

seeds/plot). Seedling emergence was monitored through the 1994 growing season. The influence of understory manipulation on both *Acer* and *Betula* emergence was analyzed using nonparametric Kruskal-Wallis χ^2 tests.

RESULTS

Microsite descriptions

Fern cover and fern height, measured before implementation of experimental manipulations, varied by fern species and by site. Mean fern cover was higher in *Osmunda* plots (66%) than in *Dennstaedtia* plots (60%) ($F = 13.18$, df = 1, 168, $P < 0.001$), and *Osmunda* was significantly taller (64 cm) than *Dennstaedtia* (39 cm) ($F = 442.13$, df = 1, 168, $P < 0.0001$). Fern height and fern cover were lower at site PH9 than all other sites, whereas fern height was greater at site PH4A than all other sites (Table 2).

Midsummer (July–August) light levels below the fern understory (8-cm height) differed among experimental manipulations (Table 3, Fig. 1a). Light levels at 8 cm in plots where fern fronds had been pinned back to create a shade-free area were comparable to light levels at 8 cm in plots where ferns had been removed. Midsummer light levels beneath ferns were ~32% of light levels in shade-free or fern-free plots. During the growing season when the overstory was fully leafed out, light in the forest at 1 m was 3.4% that of full sun, whereas light below ferns was only 1.1% full sun (1.03 mol·m^{-2}·d^{-1} vs. 0.33 mol·m^{-2}·d^{-1}, respectively).

Midsummer light levels measured above the fern canopy at 1 m did not vary with manipulation or fern species (Table 3), which indicates that *Osmunda* and *Dennstaedtia* are found in similar light environments. Midsummer light levels below the fern understory did not differ between fern species, indicating that *Osmunda* and *Dennstaedtia* reduce light to equivalent levels beneath their canopies. However, because *Osmunda* initiates and completes frond development earlier than *Dennstaedtia*, light levels in late May, a period when tree seedlings have leafed out but the overstory has not yet completely leafed out, were lower under *Osmunda* (2.22 mol·m^{-2}·d^{-1}) than under *Dennstaedtia* (3.08 mol·m^{-2}·d^{-1}) (significant fern × manipulation effect, Table 3). Light levels in late May at 1-m height were on average greater (3.93 mol·m^{-2}·d^{-1}) than during the growing season (1.03 mol·m^{-2}·d^{-1}). Although the dif-

TABLE 3. Table of F values for analysis of variance of the effects of site (S), fern species (F), and understory manipulation (M) on microenvironmental variables.

		ANOVA F values							
		Summer light		May light					
Factor	df	1-m height	8-cm height	1-m height	8-cm height	Soil exposure	Litter depth	SWC	SOM
S	5	12.12***	9.67***	11.76***	11.66***	12.76***	5.77***	11.41***	19.06***
F	1	0.001	0.31	0.63	5.25*	0.51	1.22	1.01	0.051
M	2	0.61	142.89***	0.35	43.77***	44.97***	24.37***	0.54	2.92
S × F	5	1.00	1.20	0.59	0.40	0.36	0.34	2.39*	0.85
S × M	10	0.68	2.19*	0.81	0.48	3.85***	1.64	0.7	0.60
F × M	2	1.21	0.82	0.049	4.43*	1.35	1.70	0.17	0.67
S × F × M	10	1.36	1.09	0.80	0.20	2.31*	1.21	0.82	1.35
Error	144†								

Note: SWC = soil water content; SOM = soil organic matter.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† Error df = 144 for all variables except litter depth for which error df = 72.

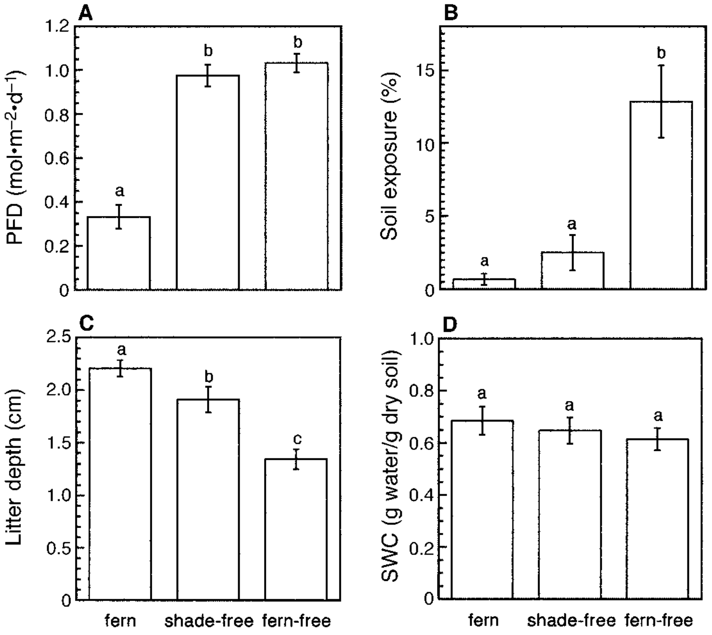

FIG. 1. Microenvironmental characterization of experimental plots: (A) photon flux density (PFD) measured 8 cm above the forest floor, (B) soil exposure, (C) litter depth, and (D) soil water content (SWC). Each bar represents the mean level of the microenvironmental variable (±1 SE). Sample size per manipulation for all variables is $n = 60$ plots, with the exception of litter depth for which $n = 36$ plots. Bars with the same lowercase letters did not differ significantly among understory manipulations at $P < 0.05$ (Fisher's protected LSD).

ference between ferns disappears after the canopies of both ferns are fully developed, the lag in development may allow tree seedlings below *Dennstaedtia* to accumulate more carbon during a critical period of relatively high light.

Midsummer light levels above and below the fern canopy varied by site (Table 3) and were particularly low at PH9 (Table 2). At site PH9, light levels in shade-free and fern-free manipulations were lower than all other sites, but below ferns the light levels were comparable with all other sites (significant site × manipulation effect, Table 3). Site PH9 had less light reaching the level of the fern canopy. However, the fern canopy was less well developed at this site (i.e., lower in height and percentage cover, Table 2) and therefore removed proportionally less light than the fern stratum of other sites. May light levels also varied by site at 1-m height and at 8-cm height (Table 3) and were relatively high at PH4A and relatively low at PH9 (Table 2).

Averaged across all sites, there was a significant understory manipulation effect on soil exposure (Table 3, Fig. 1B): soil exposure was greater in fern-free plots than in either shade-free or fern plots. However, the effect of understory manipulation depended on the site (significant site × manipulation effect, Table 3). Soil exposure was greater in the fern-free manipulation only at sites PH4B, PH3B, TS1, and PH4A. In fern-free plots at these sites, there was no vegetation to hold litter in place against wind, which resulted in large areas of soil exposure in fern-free plots. In fern and shade-free plots, intact fern fronds held litter in place at their bases, resulting in low amounts of soil exposure. The most sloped sites (PH4B and PH3B) had particularly high levels of soil exposure in fern-free plots. At sites PH9 and PH3A soil exposure was equivalent among understory manipulations. These sites, in addition to being relatively less exposed (PH9: base of a sheltered cove; PH3A: no slope), also differed from other sites in the structure and dominant species in the litter layer, which may help explain their resistance to soil exposure. Litter at site PH3A was composed of a deep layer of pine needles, and litter at site PH9 was composed of a high proportion of matted birch leaves, in contrast to the dominantly oak and maple litter of other sites.

Litter depth varied with understory manipulation and by site (Table 3). Litter depth was highest in fern plots, followed by shade-free plots, and was lowest in fern-free plots (Fig. 1C). Average litter depth was particularly high at site PH3A, where the litter layer was composed of a high proportion of pine needles, and at site TS1 where the litter layer was composed of a high proportion of relatively slowly decomposing oak leaves (Table 2).

Soil water content was not influenced by experimental manipulation (Fig. 1D) but did differ among sites (Table 3). Similarly, soil organic-matter content varied only by site (Table 3). Site PH4B had higher soil water content and soil organic material than all other sites, presumably because of the occurrence of a hard pan not present at other sites (Table 2). Site TS1 had lower soil organic material than all other sites.

Microenvironmental variables generally did not differ by fern species (Table 3). However, at site PH9, which is located near a stream at the base of a cove, soil water content was higher in *Osmunda* plots than in *Dennstaedtia* plots (significant site × fern effect, Table 3). Soil water content was higher in plots where *Osmunda* was removed as well as in plots where *Os-*

TABLE 4. Table of *F* values for analysis of variance of the effects of site (S), fern species (F), and understory manipulation (M) on field emergence of five tree species at six sites in Harvard Forest (Massachusetts, USA).

		ANOVA *F* values							
		Quercus	*Fraxinus*		*Acer*		*Pinus*	*Betula*	
Factor	df	1994	1994	1995	1994	1995	1994	1994	1995
S	5	10.59***	13.15***	16.38***	3.82**	4.30***	23.24***	12.15***	5.70**
F	1	0.89	0.17	4.80*	0.16	0.24	0.33	1.64	0.47
M	1	5.14*	0.04	0.15	0.32	0.13	12.26***	38.83***	24.38***
S × F	5	0.40	0.03	3.55**	3.81**	1.86	0.44	1.56	1.00
S × M	5	0.89	0.82	0.02	0.73	0.24	3.46**	10.17***	4.82**
F × M	1	0.57	0.005	0.41	0.28	0.13	1.62	2.58	0.70
S × F × M	5	0.55	0.62	0.13	0.22	0.23	2.00	2.11	1.09
Error	84								

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

munda was left intact, which indicates that *Osmunda* occupies moister microsites than *Dennstaedtia* at this site. This was the only other case where fern species was significantly related to any microenvironmental variable in addition to May light levels.

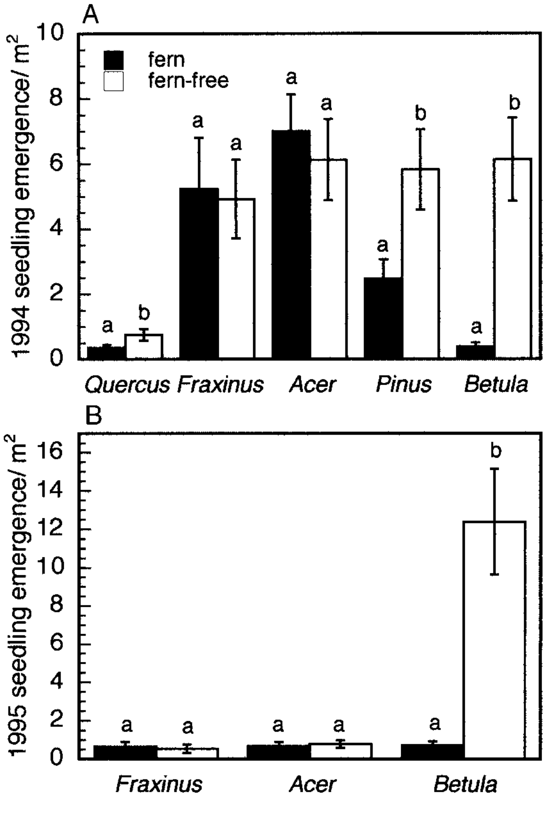

FIG. 2. Density of emergent natural recruitment in fern and fern-free experimental plots in (A) 1994 and (B) 1995. Each bar represents mean (±1 SE) seedling emergence per square meter across all sites ($n = 60$ plots). Bars with the same lowercase letter did not differ significantly between treatment means within seedling species at $P < 0.01$ (Fisher's protected LSD). Tree-seedling species are arranged from left to right in order of decreasing seed size; mean seed size of *Acer* and *Pinus* did not significantly differ.

Natural recruitment of tree seedlings

The density of emergent seedlings of each species varied by site (Table 4) and presumably was at least partially related to differences in site overstory composition and thus to differential seed input. Density of emergent seedlings of each tree species also varied between 1994 and 1995. No emergence of *Quercus* or *Pinus* was observed in 1995 due to lack of a seed crop the previous year, and no summer recruitment of *Acer* was observed in 1994 or 1995. Total *Betula* recruitment in 1995 was approximately double the value observed in 1994.

Tree species responded differently to understory manipulation, thus providing evidence for selectivity of the fern filter. There was no effect of the presence of a fern understory on the emergence of *Acer* or *Fraxinus* seedlings in 1994 or 1995 (Fig. 2). Average emergence across all sites of *Quercus*, *Pinus*, and *Betula* in 1994 and 1995 was lower in fern plots compared to fern-free plots (Fig. 2).

The effect of understory manipulation on *Pinus* and *Betula* emergence depended on the site (Table 4). *Pinus* emergence was only higher in fern-free plots at sites PH3A, PH4A, and PH9; emergence was negligible in both manipulations at sites TS1, PH4B, and PH3B (Fig. 3A). This pattern appears related to expected seed input based on basal area of *Pinus* in the overstory canopy. Sites TS1 and PH3B have no overstory pine in the stand, and site PH4B has only a few individuals, so little seed input was expected in these sites. In contrast, PH3A, which has a dominantly pine overstory, had the highest emergence in fern and fern-free plots compared to all other sites. The contrast between the manipulations increased with overall expected seed input to the site.

Betula emergence was only higher in fern-free plots at sites PH4B and PH3B in 1994 and additionally at TS1 in 1995 (Fig. 3B). *Betula* emergence patterns differ from *Pinus* in that they do not bear a clear relationship with stand basal area of *Betula* (Fig. 3B). Under the fern canopy *Betula* emergence was nearly completely

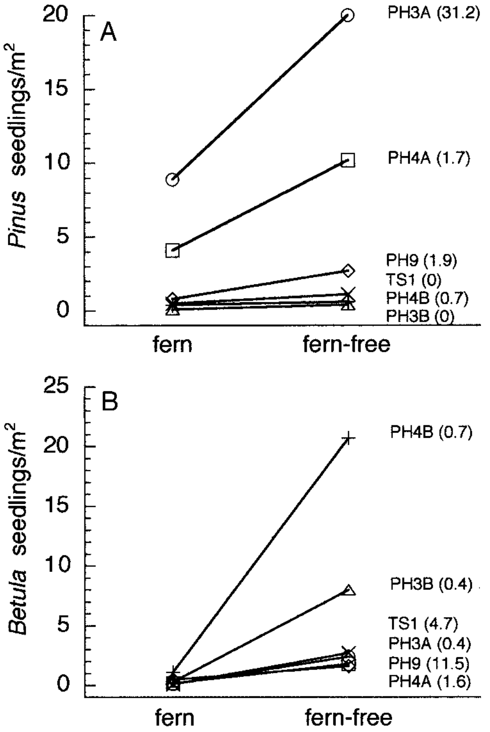

FIG. 3. Mean density of emergent natural recruitment of (A) *Pinus* and (B) *Betula* in fern and fern-free experimental plots in 1994 at six sites in Harvard Forest (Massachusetts, USA). Overstory basal area (m²/ha) is in parentheses.

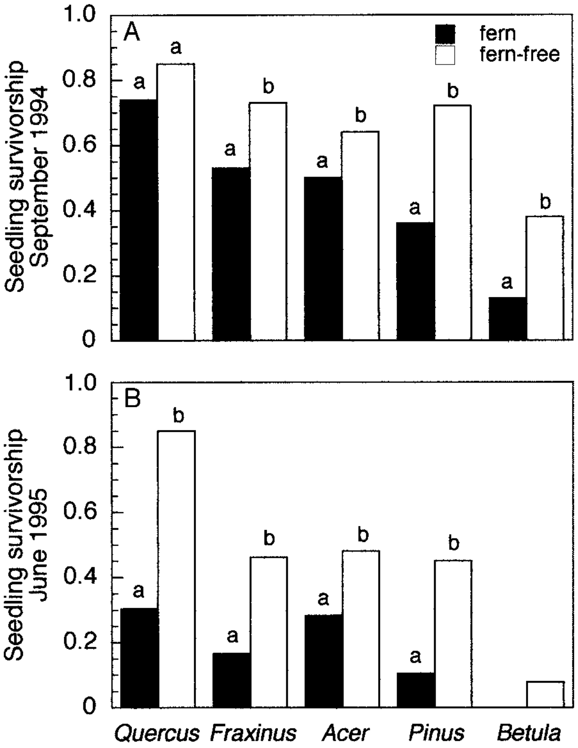

FIG. 4. Total proportion of 1994 seedlings cohorts surviving in fern and fern-free experimental plots until (A) September 1994 and (B) June 1995. Bars with the same lowercase letter did not differ significantly between fern manipulations in survivorship of each species (χ^2 test, $P < 0.05$). No *Betula* seedlings had survived under ferns by 1995. Tree-seedling species are arranged from left to right in order of decreasing seed size; mean seed size of *Acer* and *Pinus* did not significantly differ.

precluded in all sites regardless of expected seed input. *Betula* emergence in fern-free plots closely follows the pattern of soil exposure: highest at PH4B followed by PH3B followed by TS1 and all other sites (Table 2). Emergent seedlings within plots were visibly concentrated in areas of soil exposure. Sites with little or no soil exposure in fern-free plots showed no significant differences in *Betula* emergence among manipulations.

Survivorship of tree-seedling natural recruitment through the 1994 growing season in *Quercus*, the largest-seeded species, was comparable between fern and fern-free plots (Table 5). All of the smaller-seeded species exhibited lower survivorship below ferns. The magnitude of the difference in survivorship between understory manipulations increased with decreasing seed size (Fig. 4A). By the beginning of the second growing season, survivorship of all seedling species was lower below ferns (Table 5). Survivorship in fern-free plots reflected trends in seed size (highest survi-

TABLE 5. Values of χ^2 for comparisons of 1994 seedling cohort survivorship in fern and fern-free plots (fern manipulation) and for comparisons of survivorship in *Dennstaedtia* and *Osmunda* plots (fern species) through the first growing season (September 1994) and through the first year (June 1995).

	Quercus	*Fraxinus*	*Acer*	*Pinus*	*Betula*
Fern manipulation					
Sep 1994	1.46	28.87***	16.23***	62.07***	5.93*
Jun 1995	24.00***	65.46***	34.92***	60.28***	N.T.†
Fern species					
Sep 1994	0.03	14.70***	0.001	0.65	0.39
Jun 1995	0.74	24.24***	4.07*	0.63	0.31

Note: Sample sizes vary among species: *Quercus* $n = 84$ seedlings, *Fraxinus* $n = 645$ seedlings, *Acer* $n = 836$ seedlings, *Pinus* $n = 545$ seedlings, *Betula* $n = 402$ seedlings; for all comparisons df = 1.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† N.T. = not tested; expected values of *Betula* survivorship did not meet assumptions required for chi-square analysis.

TABLE 6. Spearman correlation coefficients for correlations between density of natural recruitment into experimental plots and microenvironmental variables.

Microenvironmental variable	*Quercus* 1994	*Pinus* 1994	*Betula* 1994	*Betula* 1995
Fern and fern-free plots				
Light (May)†	0.218*	0.163	0.265*	0.163
Light (summer)†	0.153	0.217*	0.216*	0.278*
Litter depth	0.078	0.045	−0.456**	−0.342**
Soil exposure	0.055	−0.143	0.507**	0.541**
Soil moisture	−0.057	−0.139	0.273*	0.272*
Fern-free plots				
Light (May)†	0.335*	0.184	0.079	−0.028
Light (summer)†	0.228*	0.213*	−0.037	0.011
Litter depth	0.225	0.398*	−0.302	−0.244
Soil exposure	−0.052	−0.371*	0.506**	0.435**
Soil moisture	−0.011	−0.195	0.501**	0.473**

Notes: Correlations were first calculated using fern and fern-free plots together ($n = 120$ plots) and then calculated separately for fern and fern-free plots ($n = 60$ plots). No significant correlations were found when fern plots alone were tested (data not shown).

* $P \leq 0.05$; ** $P \leq 0.01$.

† Daily integrated photon flux density ($\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$) measured 8 cm above the forest floor.

vorship in large-seeded *Quercus*, intermediate survivorship in species of intermediate seed size, and lowest survivorship in small-seeded *Betula*), but survivorship beneath ferns no longer reflected seed size (Fig. 4B).

Survivorship differences in *Fraxinus* seedlings were exhibited between *Dennstaedtia* and *Osmunda* plots (Table 5). Not only was higher survivorship observed in plots where *Osmunda* was left intact compared to where *Dennstaedtia* was left intact, but survivorship was higher in *Osmunda* plots where ferns had been removed in comparison to *Dennstaedtia*-removal plots. Half of the total *Fraxinus* seedlings observed were found at site PH9, the site where *Osmunda* plots exhibited higher soil moisture values than did *Dennstaedtia* plots. When seedlings from PH9 were analyzed separately, higher seedling survivorship was found in *Osmunda* plots at PH9 (September 1994: $\chi^2 = 45.03$, df = 1, $P < 0.001$; June 1995: $\chi^2 = 67.40$, df = 1, $P < 0.001$, $n = 371$ seedlings), but no survivorship differences were found between *Dennstaedtia* and *Osmunda* plots at all other sites (September 1994: $\chi^2 = 1.89$, $P > 0.05$, df = 1; June 1995: $\chi^2 = 0.90$, $P > 0.05$, df = 1, $n = 374$ seedlings). By the beginning of the second growing season a difference in *Acer* survivorship was observed between *Dennstaedtia* and *Osmunda* plots (Table 5). Because survivorship was lower than expected in *Osmunda* fern-removal plots compared to *Dennstaedtia* fern-removal plots, we attribute this survivorship difference to undetected environmental factors or perhaps residual factors (e.g., allelopathic substances) rather than to a direct detrimental result of the presence of *Osmunda*.

With the exception of *Quercus* emergence, the majority of tree-seedling emergence occurred before complete leaf-out of the fern canopy, which suggests that factors in addition to light reduction by the fern canopy were important in producing emergence patterns observed for these species. Ninety percent of *Fraxinus* and 87% of *Acer* had germinated and emerged above the litter in April and May before complete leaf-out of the fern canopy. By the time of full fern-canopy development, 83% of *Pinus* seedling emergence and 75% of *Betula* emergence was complete. Although all *Quercus* seeds had germinated and their radicles were actively growing, only 35% of *Quercus* seedlings' shoot systems had emerged above the litter by the time of complete fern-canopy development.

Correlations between seedling emergence and microenvironmental variables for species responding to understory manipulation indicate that tree species may be responding to different environmental factors (Table 6). *Quercus* and *Pinus* emergence were correlated with light levels during and subsequent to fern canopy development. *Betula* emergence was also positively correlated with light levels, soil exposure, and soil moisture, and was negatively correlated with litter depth. When environmental correlations were examined in fern-free plots alone, *Quercus* and *Pinus* emergence retained a correlation with light levels and *Betula* exhibited a strong positive correlation with soil exposure and soil moisture. No correlations were found between seedling emergence and microenvironmental variables in fern plots alone.

Experimental studies of seedling emergence

Quercus emergence depended on manipulation of the fern understory ($\chi^2 = 9.60$, df = 2, $P < 0.01$, Fig. 5A). As in the natural recruitment study, emergence was lower in fern plots than in fern-free plots. However, seedling emergence in shade-free plots was more equivalent to emergence in fern plots, which indicates that reduced light was not the cause of lower emergence under ferns. Seedling predation also varied with fern manipulation ($\chi^2 = 7.00$, df = 2, $P < 0.05$). Predation

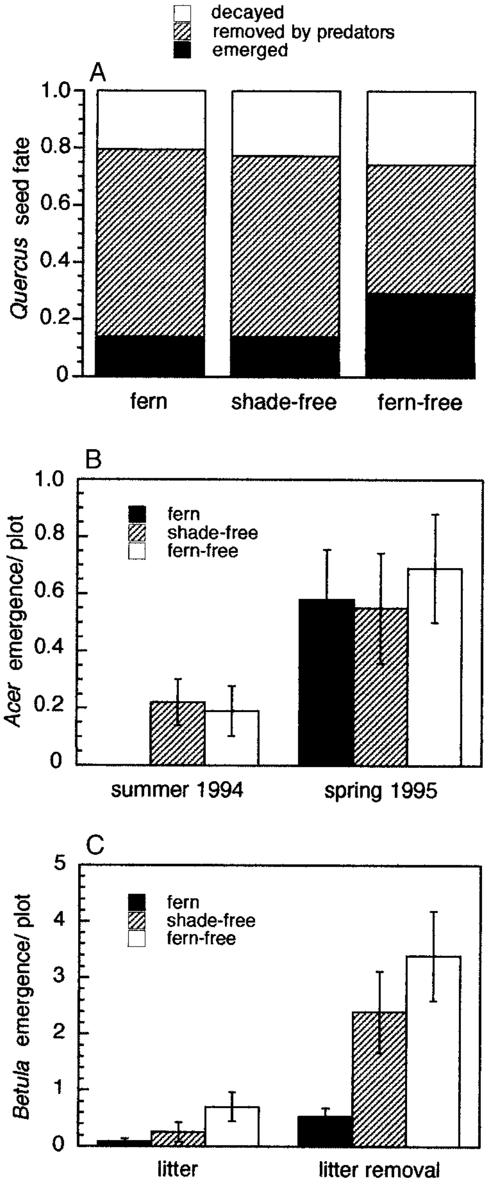

FIG. 5. Results of seedling emergence experiments: (A) proportion of *Quercus* acorns that emerged as seedlings, were removed by predators, or had decayed in fern, shade-free, and fern-free plots during 1994; (B) number of emergent seedlings of *Acer rubrum* in fern, shade-free, and fern-free plots during the summer of 1994 and the following spring of 1995 (means ± 1 SE); (C) number of emergent seedlings of *Betula alleghaniensis* in fern, shade-free, and fern-free plots during 1994 (means ± 1 SE). Mean potential emergence as evaluated in greenhouse trials was 22 seedlings/plot for *Acer* and 25 seedlings/plot for *Betula.*

was lower in the fern-free manipulation than under fern cover and in the shade-free manipulation. Seedling predation also varied by site ($\chi^2 = 19.68$, df = 5, $P < 0.01$) from a low of 25% of all acorns at site PH3a to a high of 78% at site PH9. Numbers of decayed acorns were comparable among understory manipulations; decay appeared to be the result of infection of the radicle, leading to failure of the newly germinated seedling to emerge above the litter layer.

Summer emergence of *Acer* differed among experimental manipulations of the fern understory (Kruskal-Wallis $\chi^2 = 7.14$, df = 2, $P < 0.05$). No emergence of planted seed was observed in fern plots, while emergence in shade-free and fern-free plots was comparable (Fig. 5B), indicating sensitivity of *Acer* summer emergence to reduced light levels under ferns. Although emergence of experimental *Acer* seed in greenhouse trials was 44%, total experimental emergence in the field was very low (0–4%), which suggests that field conditions were not conducive to summer emergence of *Acer* in 1994. Planted seed was allowed to overwinter and germinate the following spring. Emergence the following spring was equivalent in all three understory manipulations (Fig. 5B), which reflects the natural pattern of spring recruitment of *Acer.*

Where litter was undisturbed, *Betula* emergence differed among experimental manipulations (Kruskal-Wallis $\chi^2 = 6.32$, df = 2, $P < 0.05$, Fig. 5C). Emergence was higher in fern-free plots than in fern plots, which reflects natural recruitment patterns. Emergence in shade-free plots was more equivalent to emergence in fern plots, which suggests that soil exposure and litter depth were more important to *Betula* emergence than was the distribution of light levels among manipulations. Where litter cover was removed, overall emergence of *Betula* improved. Emergence differed among experimental manipulations (Kruskal-Wallis $\chi^2 = 21.57$, df = 2, $P < 0.0001$) and was again lowest in fern plots (Fig. 5C). In contrast to undisturbed litter treatments, emergence was more equivalent in shade-free and fern-free plots. Although litter cover appeared to be the primary impediment to *Betula* emergence, in areas where litter cover was not a factor, *Betula* emergence was also reduced by low light levels under the fern understory.

DISCUSSION

The presence of a well-developed fern understory influences the forest-floor microenvironment in ways that lead to differential reduction of tree-seedling species emergence and establishment. This differential reduction represents a mechanism by which the fern understory may act as a selective filter that influences future forest composition through reducing density, altering species composition, and determining spatial distribution of the seedling bank. Fern cover reduced emergence of *Betula, Pinus,* and *Quercus* as well as summer emergence of *Acer,* but had no effect on spring emergence of *Acer* and *Fraxinus.* The degree to which seedling density was reduced under fern cover also differed among tree species. Seedling densities of *Pinus* and *Quercus* were reduced slightly more than 50%, whereas *Betula* seedling density was reduced by 94%

under ferns and no summer emergence of *Acer* was observed at all under fern cover.

The herb and shrub stratum of the forest understory modifies the abiotic and biotic environment of the forest floor in several ways. Ferns reduce light levels below their canopies to 32% of the already low light levels existing below the overstory canopy (3.4% full sun) and severely reduce red/far red ratios below their canopies (Horsley 1993). The understory of Asian forests (characterized by a bamboo stratum) and Appalachian forests (characterized by high rhododendron cover) may reduce light levels transmitted through the overstory canopy to even lower percentages (10–12% by bamboo, Nakashizuka 1987, Taylor et al. 1995; 14–35% by rhododendron, Clinton et al. 1994). The litter layer below ferns is deeper compared to fern-free areas and may act as a more impenetrable mechanical barrier for seeds reaching the soil and for seedlings emerging from below the litter mat, particularly small-seeded species. Light levels under the litter mat decrease exponentially as the amount of litter increases (Facelli and Pickett 1991). The lack of herbaceous or woody structure to trap and to hold litter results in greater areas of soil exposure in fern-free areas in sloped sites. Removal of the insulating litter layer also contributes to elevated soil-surface temperatures (Facelli and Pickett 1991). In contrast to the significant effects of the fern understory on light and litter structure, fern cover did not affect soil water content or soil organic matter in this study or other studies of the fern stratum (Horsley 1993, Carlton and Bazzaz 1998). *Dennstaedtia* cover does not affect rates of ammonium or nitrate production, soil ammonium and soil nitrate concentrations, or availability of soil nitrogen (Horsley 1993). In terms of the biotic environment, a dense herb/shrub stratum provides habitat and shelter for both seed and seedling predators, which can lead to reduced seedling densities in both forests (Wada 1993) and old fields (Gill and Marks 1991, Reader 1991).

The mechanism by which fern cover reduced emergence was not uniform among tree species. Summer emergence of *Acer* and emergence of *Pinus* was primarily affected by reduced light levels under ferns. Emergence of *Betula* was also sensitive to light levels, but was primarily inhibited by litter cover below the fern understory. *Quercus* emergence was lower beneath the fern understory due to higher levels of predation. Because of the species-specific nature of fern interference with emergence, the ultimate effect of the fern filter on species composition of the seedling bank cannot be predicted based only on the relative shade tolerances of tree species.

In contrast to the generally strong and clear effects of the presence of understory cover on the microenvironment and seedling emergence patterns, effects of the species identity of understory vegetation were more subtle and complex. Light levels were lower below *Osmunda* than below *Dennstaedtia* for approximately a 2-wk period in May because of earlier frond development in *Osmunda*. However, this phenological difference between fern species did not lead to a detectable effect of fern species on tree-seedling emergence. In Illinois old fields, more distinctive patterns of microenvironmental variation in terms of temperature, soil moisture, and litter depth have been found among patches of different herbaceous and woody species, which resulted in differential tree-seedling emergence among patch types (Burton and Bazzaz 1995). The two fern species did not segregate along measured environmental gradients such as light or soil moisture, except at the cove site (PH9) where *Osmunda* was found in moister plots than *Dennstaedtia*. Higher seedling emergence of *Fraxinus* was correlated with the higher soil moister in *Osmunda* plots, but this pattern was not the effect of the specific presence of *Osmunda*. In systems where dominant understory species occupy different microsites, the activity of an understory filter must be interpreted in the context of this environmental heterogeneity.

Although they were bounded by the natural distribution of *Dennstaedtia* and *Osmunda*, our six study sites varied in canopy composition and multiple edaphic factors. The extent to which the activity of the fern filter was consistent across sites illustrates the strength and predictable nature of interactions between the understory and tree seedlings. Low light levels at site PH9 and high soil moisture at site PH4B did not qualitatively affect the activity of the fern filter. Other site-specific factors such as slope and overstory composition influenced the strength of the contrast between tree-seedling emergence in fern and fern-free plots. As illustrated by patterns of *Pinus* emergence, the contrast between seedling density in fern and fern-free areas was strongest at sites with the highest expected seed rain. Emergence of *Betula* was correlated with soil exposure, and exhibited high values in fern-free plots at sloped sites with a high incidence of soil exposure. The fern filter severely reduced potential *Betula* emergence at these sites, but had little effect at sites where litter structure already impeded *Betula* emergence. Generally, the fern filter may cause its most notable effects in terms of proportional reduction of seedling emergence at sites where potential seedling emergence is high, as a result of high seed input or favorable environmental conditions.

The fern understory differentially influenced 1st-yr survival among tree-seedling species, thus representing another mechanism by which the understory may selectively filter tree seedlings and influence forest composition. The fern filter had a different effect on each seedling species at the emergence and at the establishment stages, which reflects different critical abiotic and biotic mediators at each stage. Survival through the first growing season of all species except *Quercus* was reduced under fern cover. The magnitude of that reduction increased with decreasing seed size and was greatest for small-seeded *Betula.* A positive relationship between seed size and 1st-yr seedling survival in shade has been documented for North American temperate trees (Grime and Jeffrey 1965). The establishment of smaller-seeded species may be more sensitive to understory cover because they face reduced resource levels under ferns sooner as they exhaust their maternal reserves. Trees that are initiated as sprouts may be even more tolerant of the competitive effects of the fern understory for longer periods than seedlings, particularly if large reserves are available to them. By the beginning of the second growing season, seedling survivorship in fern-free plots still reflected seed size, but seedling survivorship below ferns did not. Similarly, for tree seedlings invading patches of old-field vegetation, large-seeded species were more tolerant of competition during the 1st yr of establishment than smaller-seeded tree species; however, in subsequent years tolerance of competition was independent of seed size (Bazzaz 1996).

The selectivity of the fern filter with respect to both seedling emergence and establishment shows that the fern understory has the capacity to influence the density and species composition of the seedling bank. These factors in turn influence the spatial structure of the seedling bank and initially define a seedling's competitive and genetic neighborhoods (Bazzaz 1983, 1996). The selectivity of the fern filter results in *Betula* seedlings being highly concentrated in fern-free areas relative to areas with fern cover. *Quercus* and *Pinus* seedlings are more common in fern-free areas, and *Acer* and *Fraxinus* exhibit a nearly random spatial distribution with respect to fern cover. In terms of absolute seedling numbers in the 1994 and 1995 cohorts, recruitment in fern-free areas was dominated by *Betula,* and recruitment under fern cover was dominated by *Acer* and *Fraxinus.* The spatial structure of the forest will significantly impact a variety of forest processes such as competitive and reproductive dynamics (Bazzaz 1983, 1996). The spatial aggregation of species into monospecific competitive neighborhoods may lead to coexistence of species at the community level and impact forest diversity (Hibbs 1982, Pacala 1986, Silvertown and Law 1987, Pacala et al. 1993).

Pre-disturbance interactions between tree seedlings and the understory shape the nature of the seedling bank, which is the starting capital available for future forest regeneration occurring after small- and large-scale canopy disturbance. After disturbance, herbs and shrubs of the understory stratum (if present) may continue to filter the seedling bank, although it may operate differently in the context of new resource flux (e.g., Horsley and Marquis 1983, Drew 1988, 1990). Tree growth after disturbance enters a more rapid phase, and particularly after emergence from dense understory cover, tree-to-tree competition becomes intense (Bormann and Likens 1979, Oliver 1981). However, post-disturbance tree–tree competition may still be influenced by the legacy of the understory. Relative seedling and sapling size as influenced by understory conditions can affect the outcome of tree competition and canopy replacement after release (Canham 1988). The outcome of plant competition depends also on the density and identity of competitors (Bazzaz 1996), features of a seedling's competitive neighborhood that may also be shaped by the understory filter.

Pre-disturbance interactions among tree seedlings and herbaceous and woody understory plants may have far-reaching consequences for the dynamics and trajectory of future forest regeneration. The herb and shrub stratum of the forest understory is an ecological filter that filters tree recruitment from the earliest stages of seedling emergence and establishment. The selectivity of the understory filter results from individual tree-species response to the biotic and abiotic microenvironment imposed by the understory stratum. In order to more precisely understand the effects of the understory filter on the density, species composition, size structure, and spatial distribution of the seedling bank, understory effects on emergence and establishment must be integrated with effects on seedling growth and survival in subsequent years. The contribution of the understory to future forest composition must then be interpreted in the context of pre-disturbance as well as post-disturbance processes.

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LITERATURE CITED

Bazzaz, F. A. 1983. Characterizations of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259–277 *in* H. A. Mooney and M. Godron, editors. Disturbance and ecosystems—components of response. Springer-Verlag, Berlin, Germany.

———. 1996. Plants in changing environments. Linking physiological, population, and community ecology. Cambridge University Press, Cambridge, UK.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Burton, P. J., and F. A. Bazzaz. 1991. Tree seedling emergence on interactive temperature and moisture gradients in patches of old-field vegetation. American Journal of Botany **78**:131–149.

Burton, P. J., and F. A. Bazzaz. 1995. Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. Journal of Ecology **83**:99–112.

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

Carlton, G. C., and F. A. Bazzaz. 1998. Resource congruance and forest regeneration following an experimental hurricane blowdown. Ecology **79**:1305–1319.

Clark, D. A., D. B. Clark, R. M. Sandoval, and M. V. Castro. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. Ecology **76**:2581–2594.

Clinton, B. D., L. R. Boring, and W. T. Swank. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the Southern Appalachians: influences of topographic position and evergreen understory. American Midland Naturalist **132**:308–319.

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

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

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

Drew, A. P. 1988. Interference of black cherry by ground flora of the Allegheny uplands. Canadian Journal of Forest Research **18**:652–656.

———. 1990. Fern and aster effects on black cherry shelterwood regeneration. Canadian Journal of Forest Research **20**:1513–1514.

Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical Review **57**:1–32.

Fenner, M. 1985. Seed ecology. Chapman & Hall, New York, New York, USA.

Friend, D. T. C. 1961. A simple method of measuring integrated light values in the field. Ecology **42**:577–580.

Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs **61**:183–205.

Gilliam, F. S., N. L. Turrill, S. D. Aulick, D. K. Evans, and M. B. Adams. 1994. Herbaceous layer and soil response to experimental acidification in a central Appalachian hardwood forest. Journal of Environmental Quality **23**:835–844.

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

Grossbard, E., and D. Atkinson. 1985. The herbicide glyphosate. Butterworth, London, UK.

Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology **70**:704–720.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

Hibbs, D. E. 1982. White pine in the transition hardwood forest. Canadian Journal of Botany **60**:2046–2053.

Horsley, S. B. 1988. How vegetation can influence regeneration. Pages 38–55 *in* H. C. Smith, A. W. Perkey, and W. E. Kidd, editors. Guidelines for regenerating Appalachian hardwood stands. United States Department of Agriculture, Forest Service, Morgantown, West Virginia, USA.

———. 1993. Mechanisms of interference between hay-scented fern and black cherry. Canadian Journal of Forest Research **23**:2059–2069.

Horsley, S. B., and D. A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Canadian Journal of Forest Research **13**:61–69.

Hughes, J. W., and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology **79**:605–616.

Knight, G. J. 1964. Distribution of *Osmunda cinnamomea* L. and *Osmunda claytoniana* L. in relation to natural soil drainage. Thesis. Harvard University, Cambridge, Massachusetts, USA.

Manly, B. F. J. 1996. RT—a program for randomization testing, version 2.0. The Centre for Applications of Statistics and Mathematics, University of Otago, Dunedin, New Zealand.

McWilliams, W. H., S. L. Stout, T. W. Bowersox, and L. H. McCormick. 1995. Adequacy of advance tree-seedling regeneration in Pennsylvania's forests. Northern Journal of Applied Forestry **12**:187–191.

Messier, C., T. W. Honer, and J. P. Kimmins. 1989. Photosynthetic photon flux density, red:far-red ratio, and minimum requirement for survival of *Gaultheria shallon* in western red cedar–western hemlock stands in coastal British Columbia. Canadian Journal of Forest Research **19**: 1470–1477.

Nakashizuka, T. 1987. Regeneration dynamics of beech forests in Japan. Vegetatio **69**:169–175.

Oinonen, E. 1967*a*. Sporal regeneration of bracken (*Pteridium aquilinium* (L.) Kuhn.) in Finland in light of the dimensions and the age of its clones. Acta Forestalia Fennica **83**(1):1–96.

———. 1967*b*. Sporal regeneration of ground pine (*Lycopodium complanatum* L.) in southern Finland in the light of the size and the age of its clones. Acta Forestalia Fennica **83**(3):76–85.

Oliver, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management **3**:153–168.

Pacala, S. W. 1986. Neighborhood models of plant population dynamics. II. Multi-species models of annuals. Theoretical Population Biology **29**:262–292.

Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements. I. The design of a northeastern forest simulator. Canadian Journal of Forest Research **23**:1980–1988.

Reader, R. J. 1991. Control of seedling emergence by ground cover: a potential mechanism involving seed predation. Canadian Journal of Botany **69**:2084–2087.

SAS Institute. 1987. SAS/STAT guide for personal computers. Version 6 edition.SAS Institute, Cary, North Carolina, USA.

Silvertown, J., and R. Law. 1987. Do plants need niches? Some recent developments in plant community ecology. Trends in Ecology and Evolution **2**:24–26.

Taylor, A. H., Z. Qin, and J. Liu. 1995. Tree regeneration in an *Abies faxoniana* forest after bamboo dieback, Wang Lang Natural Reserve, China. Canadian Journal of Forest Research **25**:2034–2039.

Van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology **62**:688–696.

Wada, N. 1993. Dwarf bamboos affect the regeneration of zoochorous trees by providing habitats to acorn-feeding rodents. Oecologia **94**:403–407.

Warner, P. A., and A. M. Harbeck. 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. American Midland Naturalist **108**: 124–132.

Watt, A. S. 1947. Contributions to the ecology of bracken (*Pteridium aquilinium*). IV. The structure of the community. New Phytologist **46**:97–121.

Wayne, P. M., and F. A. Bazzaz. 1993. Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. Ecology **74**:1500–1515.

Westveld, M., R. I. Ashman, H. I. Baldwin, R. P. Holdsworth, R. S. Johnson, J. H. Lambert, H. J. Lutz, L. Swain, and M. Standish. 1956. Natural forest vegetation zones of New England. Journal of Forestry **54**:332–338.