

# The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands

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## Summary

**1** When a species influences conditions at a site to promote recruitment of conspecifics, the community may remain dominated by that species until the next major disturbance. We examined the occurrence of possible mechanisms for such a positive feedback in one community where it may be important: forests dominated by eastern hemlock (*Tsuga canadensis*).

**2** Intact soil divots were collected from a hemlock stand in central Massachusetts, USA, and placed in shade-houses at either 1.5% or 60% full sun. Soil was amended with nitrogen ( $5 \text{ g m}^{-2} \text{ year}^{-1}$ ), lime ( $1 \text{ kg m}^{-2} \text{ year}^{-1}$ ; to increase soil pH) or left untreated. Emergence, survival and growth of seedlings arising from the soil seed bank were subsequently monitored.

**3** Light availability had a very large influence on seedling regeneration dynamics. Birch (*Betula* spp.) seedlings were most sensitive of all species to light availability, with low light reducing emergence by 43% and substantially decreasing seedling growth (by 99%) and survival (by 94%). In contrast, light treatments had smaller effects on performance of other species [hemlock and white pine (*Pinus strobus*)]. Birch survival was also increased by nitrogen addition, but only in low light. Liming had only marginal effects on seedling performance.

**4** Differential seedling responses to resource availability led to dominance of final seedling communities by hemlock in low light, unamended soils (i.e., under conditions naturally found in hemlock stands), but by birch in high light, as well as in low light, nitrogen-amended soils.

**5** Positive feedbacks in hemlock stands are mediated both by availability of light and nitrogen, and by species' life-history strategies.

*Keywords:* birch regeneration, hemlock forests, positive feedback, resource interactions, seedling growth and demography

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## Introduction

Ever since Frederic Clements (1916) proposed his theory of plant succession, species' effects on their environment have been recognized as an important component of plant community dynamics. Whether species-mediated changes favour individuals of the same or different species often determines the subsequent structure and dynamics of the community (Horn 1975; Connell & Slatyer 1977; Bazzaz 1983). If the presence of a species at a

site changes environmental conditions to promote recruitment of conspecifics, this species may come to dominate and persist in a community until the next major disturbance event. This situation was originally known as a 'climax' (Clements 1916), but more recently has been termed a 'positive feedback switch' (Wilson & Agnew 1992). Despite the potential importance of these feedbacks in controlling plant community structure, mechanisms underlying such patterns have rarely been established experimentally (van Breemen & Finzi 1998; Petraitis & Latham 1999). In this paper, we examine mechanisms responsible for a positive feedback in temperate forests.

Northern hardwood forests in North America are often composed of distinct stands dominated by either eastern hemlock (*Tsuga canadensis* (L.) Carr.) or sugar maple (*Acer saccharum* Marsh.) (Pastor & Broschart 1990). Many of these stands have persisted for thousands of years with little change in composition (Davis *et al.* 1994, 1998), perhaps as a result of a positive feedback between current stand composition and future seedling regeneration (Frelich *et al.* 1993). Hemlock-dominated stands are similarly present in New England forests, although the surrounding matrix is composed of a number of broad-leaved deciduous tree species [including red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.)] rather than predominantly sugar maple.

Stands of hemlock and broad-leaved species present seedlings with quite different conditions for regeneration. Differences in understorey conditions between these contrasting stand types have long been acknowledged (Moore *et al.* 1924; Oosting & Hess 1956), and recently have been quantified: under hemlock, light availability is lower (Canham *et al.* 1994), and soils are more acidic, with lower nutrient availability, than under broad-leaved tree species (Finzi *et al.* 1998a, b). Such variation may influence the distribution and abundance of herb species (Beatty 1984; Turner & Franz 1986), as well as tree regeneration dynamics (Woods 1984; Collins 1990; Cornett *et al.* 1997).

The ultimate factors leading to patch development and persistence in northern hardwood forests remain unclear. It has been proposed that the low light and nitrogen conditions under hemlock trees favour regeneration of hemlock over other species, while the deep litter layer and low soil moisture content under sugar maple trees favour sugar maple (Frelich *et al.* 1993; Davis *et al.* 1994). However, SORTIE, a spatially explicit forest dynamics model, predicts that it is light availability patterns that predominantly drive development of stands dominated by either hemlock or sugar maple/beech (*Fagus grandifolia* Ehrh.) (Pacala *et al.* 1996). Furthermore, it has long been thought that the low soil pH in hemlock stands inhibits development of understorey vegetation and seedling regeneration (Daubenmire 1930). All of these hypotheses must now be tested directly.

In the present study, we considered how interactions between resource availability and seedling regeneration dynamics may contribute to positive feedbacks in hemlock stands. We hypothesized that low light levels, low nitrogen availability and low soil pH in such stands limit seedling regeneration but that, of the various species, the performance of hemlock seedlings will be least affected, due to their high tolerance of understorey conditions (Godman & Lancaster 1990; Kobe *et al.* 1995). We tested these hypotheses by examining patterns of emergence, sur-

vival and growth of seedlings that arose naturally from the seed bank in hemlock stands when soil samples were exposed to different experimental conditions (varying light, nitrogen and pH).

## Materials and methods

### SOIL COLLECTION

In December 1996, soil divots were collected from a hemlock-dominated stand at Harvard Forest (Petersham, Massachusetts, USA; 42°32' N, 72°11' W, elevation 340 m a.s.l.). The study area comprised principally eastern hemlock (*T. canadensis*; over 75% basal area), with scattered individuals of white pine (*Pinus strobus* L.), red oak (*Q. rubra*), red maple (*A. rubrum*), black birch (*Betula lenta* L.), yellow birch (*Betula alleghaniensis* Britt.), paper birch (*Betula papyrifera* Marsh.) and American beech (*F. grandifolia*), in approximately decreasing order of importance (Foster & Zebryk 1993). The surrounding broad-leaved matrix was dominated by red oak and red maple, with occasional birch trees.

Within the stand, four sampling points were established along each of three parallel 100 m transects, each separated by 50 m. At each sampling point, six intact soil divots were collected. Each divot measured 35 × 30 cm and included both O and A horizons (10–15 cm deep). Divots were placed over coarse silica sand in plastic containers (20 cm deep), and then transported to the experimental garden at Harvard University (Cambridge, MA). The sand provided suitable drainage but no additional nutrients. Divots were left in the garden over winter and subjected to experimental treatments in early spring.

In the forest, seed rain at each sampling point was measured throughout the following year (1997) using conical muslin litter traps (opening 0.2 m<sup>2</sup>) suspended 50 cm above the forest floor with a PVC frame (modified from Hughes *et al.* 1987). Seed traps were emptied once during the summer of 1997 (for red maple seeds) and then monthly from September to December. For most species (hemlock, maples), we were able to distinguish filled vs. empty seeds, and we only recorded filled seeds. For the birch species, we counted all seeds and then subsampled to look at the percentage of seeds filled (*c.* 80% for most samples).

### EXPERIMENTAL TREATMENTS AND ANALYSIS

Each set of six intact soil divots collected from each sampling point in the field was exposed to a factorial combination of two light and three soil treatments. Thus, each experimental combination was applied to four replicate soil divots within each

transect, and this pattern was then replicated across three transects.

To control light availability, the soil divots were placed in shade-houses (each  $2 \times 2 \times 2$  m), set up in a split-block design. One half of each shade-house was exposed to low light (1.5% full sun and a red:far red ratio of 0.28), mimicking conditions within a typical hemlock stand (Kozłowski *et al.* 1991; Canham *et al.* 1994), and the other half was exposed to high light (60% full sun and a red:far red ratio of 1.1), simulating conditions in a multiple tree-fall forest gap (Bazzaz & Wayne 1994). Light quantity was manipulated using different grades of neutral shade-cloth, while light quality was simultaneously altered with coloured filter plastic placed beneath the shade-cloth (Lee *et al.* 1997). We placed vertical slits in sections of the shade-cloth not receiving direct sunlight to ensure adequate ventilation within the shade-houses and prevent temperatures from climbing much above ambient air temperature. We constructed one shade-house for each sampling transect (three in total), and placed all soil divots from one transect in the same shade-house, dividing divots equally between light treatments.

The plastic covering over the shade-houses did not permit rain water to reach soil divots, and so all divots were watered thoroughly every 2–3 days. We measured moisture content once during the growing season (in August) and found no significant differences between shade-houses or between experimental treatments. At that time, average soil moisture across the soil divots was  $0.556 \text{ g g}^{-1}$  ( $\pm 0.008 \text{ g g}^{-1}$  standard error), which was well within the range of soil moisture values observed in hemlock stands in the field (S. Catovsky, unpublished data).

Each soil divot was exposed to one of three soil manipulations: unamended (control), increased nitrogen availability, and increased soil pH. Nitrogen was added as a solution of ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ) over 10 applications through the growing season, equivalent to  $5 \text{ g m}^{-2} \text{ year}^{-1}$ . This rate was chosen to match background net nitrogen mineralization rates in conifer stands in this region (Aber *et al.* 1989), and thus approximately to double nitrogen availability. Soil pH was increased by surface application of coarse powdered lime (96% calcium carbonate,  $\text{CaCO}_3$ ) at the beginning of the experiment. Such pH-manipulated soil divots received the equivalent of  $1 \text{ kg lime m}^{-2}$ , based on the lime requirement of the soil (Carter 1993), which had been determined in an earlier analysis (University of Massachusetts Soil and Plant Tissue Testing Lab, Amherst, MA).

In addition to direct manipulation of light and soil resources for each soil divot, we examined the effects of experimental treatments on the actual conditions produced under each resource combination. Light availability in each half of the shade-houses

was assessed at hourly intervals through the course of 1 day in mid-July using a Li-Cor LI-190SA quantum sensor attached to LI-1000 data-logger (Lincoln, NB). Effects of soil treatments were determined by taking 2-cm diameter soil cores from each divot at the end of the experiment. The soil was then sifted and homogenized through a 3.5-gauge sieve (mesh size 5.6 mm). Two grams of air-dried soil from each sample was mixed with 20 ml of distilled water, and its pH determined (Orion 250 A pH meter, Boston, MA). Ten grams of sifted soil was mixed with 100 ml of 2 N potassium chloride (KCl) solution, and incubated at  $25^\circ\text{C}$  for 48 h. The mixture was then filtered and frozen. Extracts were analysed for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  ion concentrations on a Technicon TRAACS 800 analyser (Braun and Luebbe, Buffalo Grove, IL).  $\text{NH}_4^+$  was measured using the Berthelot Reaction chemistry (method number 780-86T), and  $\text{NO}_3^-$  was measured using hydrazine sulphate reduction (method number 782-86C). The detection limit for both these methods was  $0.2 \text{ mg l}^{-1}$ . The water content of each soil sample was determined by weighing 2–3 g of soil before and after drying in an oven at  $105^\circ\text{C}$  for 48 h, so that nutrient availability could be expressed per g dry soil.

#### SEEDLING MEASUREMENTS

At approximately 2-weekly intervals from 5 May until 25 September 1997, we monitored seedling emergence from the soil seed bank and subsequent survival. On emergence, plants were tagged and identified to species when possible. Many *Betula* individuals died before they had developed true leaves, particularly under low light conditions, and thus could not be distinguished from one another. Therefore, we present *Betula* emergence and survival only on a genus level. Our inability to identify beyond genus prevented observation of individual *Betula* species' responses to experimental treatment combinations, because any species-specific responses could have been swamped by those of the other species within the genus. In high light treatments, however, where survival and growth were higher, all species but *B. alleghaniensis* and *B. lenta* could be identified and distinguished.

To record individual seedling growth through the season, surviving plants were harvested after the last census. Individual root systems were obtained by washing away the soil and separating individual root systems by hand. Plant material was dried at  $70^\circ\text{C}$  for 7 days and then weighed.

#### DATA ANALYSIS

Only species that emerged in more than 10 soil divots were included in the analyses (i.e. birch spe-

cies, hemlock and white pine). Other species were excluded because of low statistical replication. Seedling emergence, growth and survival were examined using multi-factor analyses of variance, with light, soil and species effects included as main fixed factors in the models. A random block term was included to incorporate variation due to both transect and shade-house, while a plot-level term, grouping soil units taken from the same sampling point, was included as a random factor nested within block. The mean squares of most terms were tested over the residual error mean square. Light effects were tested over the light  $\times$  block interaction, following the split-block design (Sokal & Rohlf 1995), while block effects were tested over plot mean square from nesting. Community composition was examined with multivariate analysis of variance on plot scores from the first two axes of detrended correspondence analysis. In addition, we used Fisher's exact test to examine community-wide seedling survival in low light.

Treatment effects on experimental conditions were examined in a similar way, but with some modifications. Light effects were examined with diurnal photon flux density (PFD) measurements taken on the level of a shade-house. Thus, individual divots were not included in the analysis, while time was added as another fixed factor. Soil analyses were examined with the basic design described above, but with no species term. In addition, as nitrogen analyses were performed for both  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , both components were incorporated into a mixed-model multivariate analysis of variance.

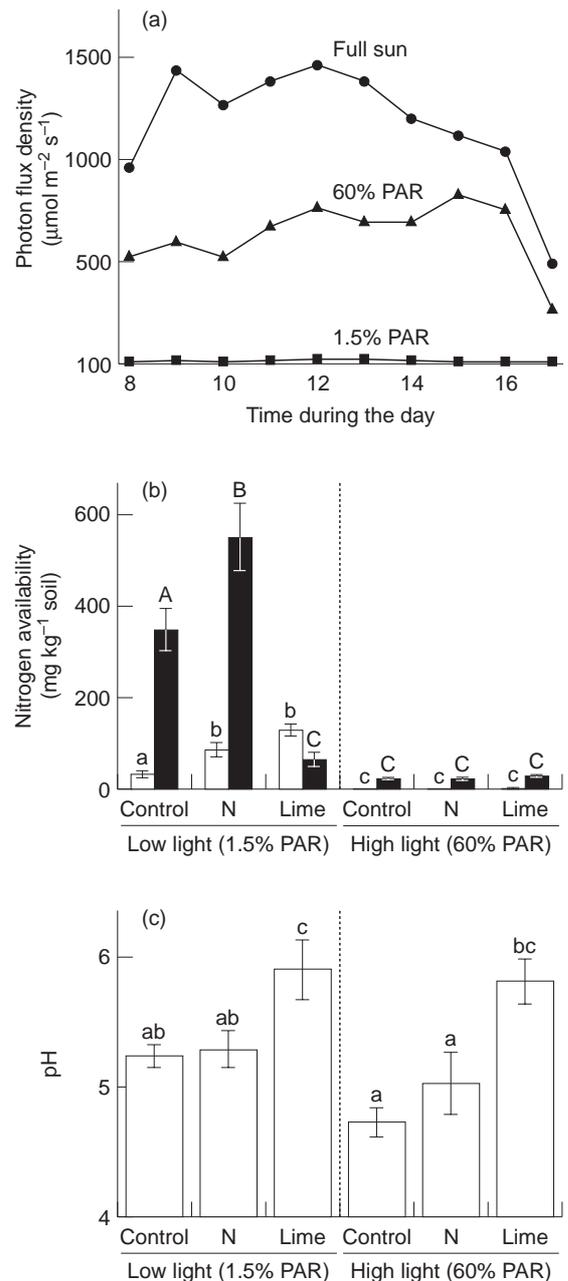
When necessary, the data were transformed to ensure that the assumptions of ANOVA were met (normality of residuals, homoscedasticity). For each significant main effect with more than two levels and for each significant interaction, we examined the significance of individual treatment mean comparisons using Scheffé *post hoc* tests (Day & Quinn 1989).

## Results

### TREATMENT EFFECTS

PFD in the two light treatments differed significantly from one another ( $F_{1,2} = 8640$ ,  $P < 0.0001$ ; Fig. 1a), with the high light treatment averaging 54.4% of PFD in the open, and low light averaging 1.2%. Light environment did vary across blocks ( $F_{2,36} = 4.22$ ,  $P < 0.05$ ), but there was no significant light  $\times$  block interaction ( $F_{2,36} = 1.29$ ,  $P > 0.05$ ).

Both light and soil treatments significantly affected overall soil nitrogen availability (MANOVA light  $\times$  soil interaction,  $\lambda_{\text{Wilks}} = 0.416$ ,  $P < 0.0001$ ; Fig. 1b) as well as the individual nitrogen forms (light  $\times$  soil,  $F_{2,48} = 25.28$  for  $\text{NH}_4^+$  and 4.00 for  $\text{NO}_3^-$ ,  $P < 0.0001$  and 0.05, respectively). Soil cores



**Fig. 1** Effects of treatments on experimental conditions (means  $\pm$  1 SEM): (a) PFD levels across shade-houses ( $n = 3$ ) for both low (1.5% PAR,  $\blacksquare$ ) and high (60% PAR,  $\blacktriangle$ ) light treatments, along with open sky PFD ( $\bullet$ ); (b) availability of  $\text{NO}_3^-$  ( $\square$ ) and  $\text{NH}_4^+$  ( $\blacksquare$ ) in soil divots; (c) pH of soil blocks. For soil treatments, columns without any shared letters (lower case for  $\text{NO}_3^-$  and pH, upper case for  $\text{NH}_4^+$ ) are significantly different from one another (Scheffé *post hoc* comparisons,  $P < 0.05$ ).

were taken 1 week after the final fertilization event, by which time much of the added nitrogen had been taken up in the high light treatments by the dense seedling growth that had developed through the course of the experiment (see below). As a result,

**Table 1** Identity and average density of species that emerged from the soil seed bank

Species	Common name	Growth habit	Density (m <sup>-2</sup> )
<i>Betula</i> spp.*	Birch	Canopy tree	320
<i>Tsuga canadensis</i> (L.) Carr.	Hemlock	Canopy tree	12
<i>Pinus strobus</i> L.	White pine	Canopy tree	4
<i>Rubus flagellaris</i> Willd.	Blackberry	Understorey herb	1.5
<i>Gaultheria procumbens</i> L.	Wintergreen	Understorey herb	1
<i>Vaccinium</i> spp.†	Blueberry	Understorey shrub	1
<i>Acer rubrum</i> L.	Red maple	Canopy tree	0.3
<i>Prunus serotina</i> Ehrh.	Black cherry	Canopy tree	0.3
<i>Populus tremuloides</i> Michx.	Quaking aspen	Canopy tree	0.1
<i>Prunus pensylvanica</i> L.f.	Pin cherry	Canopy tree	0.1

\*Includes *Betula lenta* L. (black birch), *Betula alleghaniensis* Britt. (yellow birch), *Betula papyrifera* Marsh. (paper birch), and *Betula populifolia* Marsh. (grey birch).

† Includes *Vaccinium corymbosum* Ait. (highbush blueberry) and *Vaccinium angustifolium* L. (lowbush blueberry).

nitrogen availability was consistently low in all high light treatments (25 mg N kg<sup>-1</sup> soil in high light vs. 400 mg N kg<sup>-1</sup> in low light). In low light, soil treatment effects were clear (Fig. 1b). Nitrogen additions caused significant increases in both the availability of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> (*post hoc*s,  $P < 0.01$  and  $0.05$ , respectively), enlarging the NH<sub>4</sub><sup>+</sup> pool by 58% and the NO<sub>3</sub><sup>-</sup> pool by 170%. In low light, liming altered the composition of nitrogen species present in the soil by increasing the proportion of NO<sub>3</sub><sup>-</sup> from 8% to 67%. This change in composition meant that NO<sub>3</sub><sup>-</sup> availability did not differ between nitrogen and lime treatments (*post hoc*s,  $P > 0.05$ ) but that NH<sub>4</sub><sup>+</sup> was significantly lower in the lime treatment than in either of the other two treatments ( $P < 0.0001$ ). Liming probably increased the activity/abundance of nitrifying bacteria, which are commonly inhibited in acid soils (Paul & Clark 1996).

Both soil and light treatments influenced final soil pH. Liming significantly increased soil pH by 0.8 pH units, on average ( $F_{2,48} = 14.6$ ,  $P < 0.0001$ ; Fig. 1c). In addition, soils from high light treatments had significantly lower pH values than those from low light ( $F_{1,2} = 98.7$ ,  $P < 0.01$ ). This light effect may again have been caused by the presence of high seedling density in high light soil divots.

#### SEEDLING DEMOGRAPHY

Most of the seedlings emerging from the soil seed bank were birch (94%; Table 1), with smaller amounts of hemlock (4%) and white pine (1%). There were scattered individuals of other herb, shrub and tree species, each represented by less than five individuals across all soil divots.

There was substantial heterogeneity in seedling emergence between transects/shade-houses (significant block effect; Table 2). In addition, seedling emergence differed significantly between species (Tables 1 and 2), with higher birch emergence than

that of all other species (*post hoc*s,  $P < 0.0001$ ) and higher hemlock emergence than all species except birch ( $P < 0.05$ ). Soil treatments had no effects on seedling emergence, while light treatments differentially influenced emergence depending on species (significant light  $\times$  species interaction; Table 2). Birch was the only species whose emergence was affected by light, decreasing by 43% from high to low light (Fig. 2).

Similarly, light effects on seedling survival were species-dependent (significant light  $\times$  species interaction), while soil conditions did not affect survival (Table 2). Birch seedling survival increased most

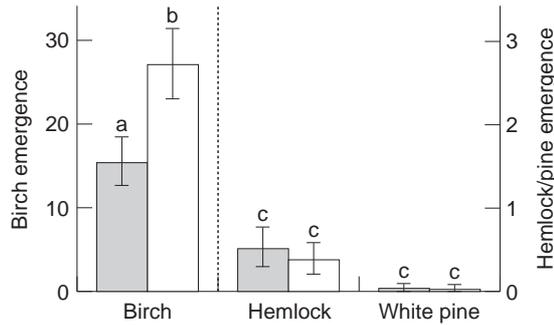
**Table 2** ANOVA  $F$  ratios for seedling demographic parameters: emergence (per soil divot) and percentage seedling survival through the growing season. Significance shown as follows: NS,  $P > 0.05$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ 

Factor†	d.f.	Emergence‡	% Survival§
Block	2	13.92 **	0.49 NS
Plot	9	1.24 NS	2.95 **
Light	1	74.39 *	7.12 NS
Light $\times$ block	2	0.06 NS	10.82 ***
Soil	2	0.18 NS	0.88 NS
Light $\times$ soil	2	0.42 NS	1.65 NS
Species	3	273.29 ***	2.77 NS
Light $\times$ species	3	6.69 **	26.02 ***
Soil $\times$ species	6	0.44 NS	0.77 NS
Light $\times$ soil $\times$ species	6	0.09 NS	0.35 NS

†Mean squares of most factors were tested over error mean square (d.f. 185 for emergence, 95 for survival). Plot was nested within block, and its mean square was used to test for a block effect, while light effects were tested over the light  $\times$  block mean square.

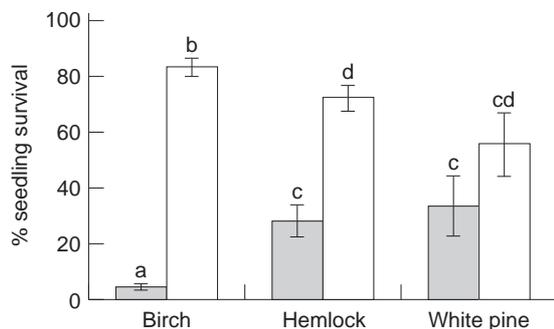
‡Mean squares for emergence  $F$  ratios: error = 1.71, plot = 2.13, light  $\times$  block = 0.11.

§Mean squares for percentage survival  $F$  ratios: error = 1.27, plot = 3.73, light  $\times$  block = 13.68.



**Fig. 2** Mean number of seedlings emerging (per soil divot) under low (1.5% PAR, ■) and high (60% PAR, □) light treatments. Means and standard errors were calculated from square root-transformed data (pooled across soil treatments and blocks; each mean  $n = 36$ ) and then back-transformed. Note the difference in scales for birch vs. other species. Columns without any shared letters are significantly different from one another (Scheffé *post hoc* comparisons,  $P < 0.05$ ).

with increasing light availability (an almost 20-fold increase), compared with a 2.5-fold increase for hemlock and no significant increase for white pine (Fig. 3; *post hocs*,  $P < 0.001$  for birch and hemlock,  $P > 0.05$  for pine). Relationships between survival of different species changed with light treatment. In low light, birch had significantly lower survival than either hemlock or white pine (*post hocs*,  $P < 0.01$ ), while in high light, hemlock had lower survival than birch ( $P < 0.05$ ). Lack of an overall light effect on survival was primarily the result of a strong light  $\times$  block effect (mean square = 13.68), which was likely to have been caused by substantial heterogeneity in white pine emergence.



**Fig. 3** Mean percentage of seedlings surviving through the growing season ( $\pm 1$  SEM) under low (1.5% PAR, ■) and high (60% PAR, □) light treatments. Means and standard errors were calculated from logit-transformed data (pooled across soil treatments and blocks; each mean  $n = 6-36$ ) and then back-transformed. Columns without any shared letters are significantly different from one another (Scheffé *post hoc* comparisons,  $P < 0.05$ ).

Examination of survival data at the level of individual soil divots provided evidence for interactions between light and soil treatments. In low light, nitrogen significantly increased the proportion of soil divots that had at least one surviving birch seedling compared with control soils, while liming caused a marginally significant decrease in the number of divots with surviving hemlock (Table 3).

#### SEEDLING GROWTH

Average seedling growth of different species responded in different ways to changing light availability (Table 4; significant light  $\times$  species interaction), but not to altered soil conditions. All tree seedlings increased growth with higher light levels, but the magnitude of change was species-specific (Fig. 4). Birch seedlings showed the greatest increases in growth with increasing light (300 times larger), while hemlock and white pine showed more modest, but significant, increases (5 and 15 times larger, respectively). There were no differences in growth between any species at low light (*post hocs*,  $P > 0.05$ ). In contrast, at high light, birch seedlings grew the most, followed by white pine, and then hemlock (*post hocs*,  $P < 0.0001$ ). Birch seedlings also showed the greatest variation in individual seedling size parameters, especially at high light (Table 5). High seedling density and asynchrony in emergence date created a strong size hierarchy within high light stands by the end of the experiment.

Experimental treatments influenced individual seedling biomass, along with patterns of emergence and survival, and thus affected each species' contributions to final seedling community biomass. Light and soil both differentially influenced species' total biomass responses, although light effects were not

**Table 3** Number of soil divots in low light treatment (1.5% PAR) that contained no survivors or at least one surviving seedling of a particular species at the end of the growing season

Species	Treatment	Number of divots		Fisher's $p^*$
		None	$\geq 1$	
Birch	Control	11	1	0.054
	Nitrogen	6	6	
	Lime	10	2	
Hemlock	Control	3	5	0.138
	Nitrogen	5	1	
	Lime	6	1	
White pine	Control	2	1	0.857
	Nitrogen	3	1	
	Lime	1	0	

\*Probability of observing differences between treatment frequencies (nitrogen, lime) and control frequencies by chance (based on two-tailed Fisher's exact test).

**Table 4** ANOVA *F* ratios for seedling growth parameters: individual seedling biomass and total seedling biomass per soil divot (individual biomass × number of seedlings). Significance shown as follows: NS,  $P > 0.05$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

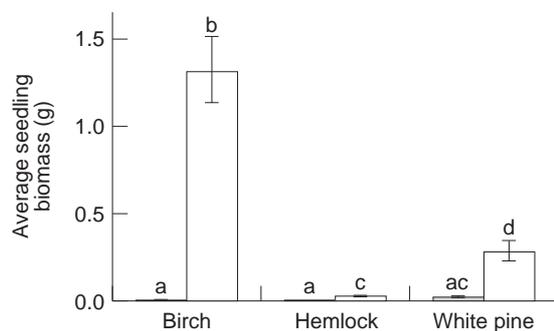
Factor†	d.f.	Individual biomass‡	Total biomass§
Block	2	2.47	NS
Plot	9	1.82	NS
Light	1	55.75	*
Light × block	2	2.68	NS
Soil	2	0.35	NS
Light × soil	2	0.25	NS
Species	3	44.52	***
Light × species	3	46.71	***
Soil × species	6	0.99	NS
Light × soil × species	6	0.28	NS

†Mean squares of most factors were tested over error mean square (d.f. 47 for individual biomass, 185 for total biomass). Plot was nested within block, and its mean square was used to test for a block effect, while light effects were tested over the light × block mean square.

‡Mean squares for individual biomass *F* ratios: error = 0.34, plot = 0.61, light × block = 0.90.

§Mean squares for total biomass *F* ratios: error = 7.52, plot = 11.97, light × block = 11.18.

contingent on soil conditions and vice versa (Table 4; significant light × species and soil × species interactions, but non-significant three-way interaction). High emergence, survival and growth of birch under high light conditions meant that birch dominated high light seedling communities, often by two orders of magnitude (Fig. 5a). In low light, in contrast, all species made similar contributions to seedling community biomass (no significant species differences; *post hoc*s,  $P > 0.05$ ). The large variability in white pine emergence from the soil seed bank meant that its contribution to final seedling composition did not differ between light treatments



**Fig. 4** Average biomass of seedlings per soil divot surviving through the growing season (mean per treatment ± 1 SEM) under low (1.5% PAR, ▨) and high (60% PAR, □) light treatments. Means and standard errors were calculated from natural logarithm-transformed data (pooled across soil treatments and blocks; each mean  $n = 3-36$ ) and then back-transformed. Columns without any shared letters are significantly different from one another within each light level (Scheffé *post hoc* comparisons,  $P < 0.05$ ).

( $P > 0.05$ ). Soil treatments did not have dramatic effects on species' total biomass within each soil divot, except that hemlock seedlings had significantly lower biomass in treated soils (nitrogen, lime) than in control soils (Fig. 5b; *post hoc*s,  $P < 0.05$ ).

In high light treatments, we were able to identify birch seedlings to species. We performed a second analysis on growth of individual birch species and their contribution to final seedling community biomass for all high light treatments. There were no significant interactions between soil and species effects for either analysis ( $F_{4,63} = 0.64$  and  $F_{4,88} = 0.29$ ,  $P > 0.05$  for both individual and total biomass), although there was a trend (non-significant) for increasing paper birch total seedling biomass and decreasing black/yellow birch total biomass in soils with nitrogen added. Individual black/yellow birch seedlings were significantly smaller than either paper birch or grey birch (1.32 g vs. 2.40 g and 3.65 g; *post hoc*s,  $P < 0.001$ ), while black/yellow birch and paper birch made significantly greater contributions to final seedling community biomass than did grey birch in general (11.71 and 15.11 vs. 1.80; *post hoc*s,  $P < 0.0001$ ).

#### SEEDLING COMMUNITY COMPOSITION

Final seedling composition of each soil divot was investigated using plot scores from detrended correspondence analysis (DCA) on both species abundance and species biomass data. In both cases, there was a significant light × soil interaction on final seedling community composition (Fig. 6;  $\lambda_{Wilks} = 0.651$ ,  $P < 0.01$  for abundance;  $\lambda_{Wilks} = 0.617$ ,  $P < 0.01$  for biomass), and these interactions were evident on both DCA axes in each case (Table 6). In

**Table 5** Range of individual seedling size parameters, separated by light treatment but pooled across soil treatments and blocks

Light	1.5% PAR			60% PAR		
	Birch	Pine	Hemlock	Birch	Pine	Hemlock
Dry weight	3–7 $\mu\text{g}$	15–40 $\mu\text{g}$	3–8 $\mu\text{g}$	2 $\mu\text{g}$ –18 g	0.1–0.5 g	8–100 $\mu\text{g}$
Height (cm)	< 1	< 3	< 1	1–50	4–8	1–4
Number of true leaves	1–2	5–8	3–6	2–60	10–40	3–25

both analyses, low light unamended soils had a significantly different final seedling composition (hemlock dominated) from any of the high light treatments, as well as the low light nitrogen-amended soils, which, like the high light treatments, were birch dominated. This difference was evident on both axes for abundance data, but only on axis 1 for biomass data.

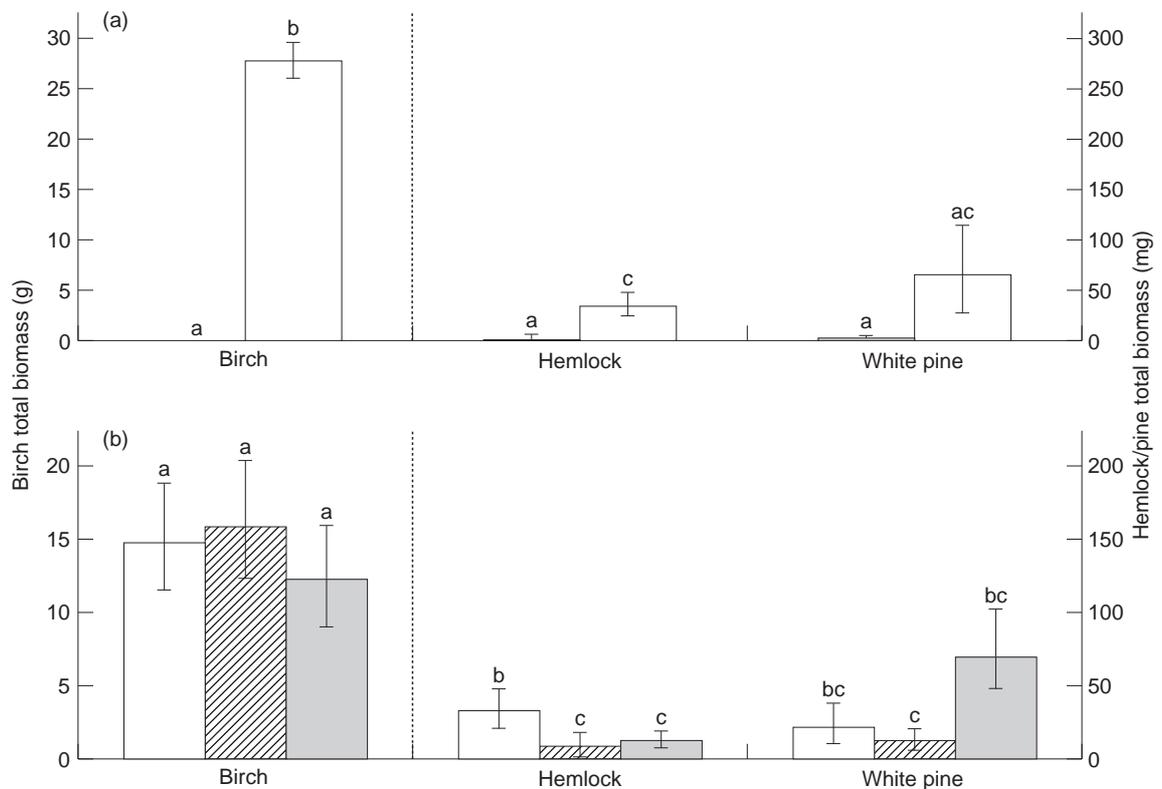
#### SEED RAIN

Patterns of seed rain across the experimental transects differed between species (significant species  $\times$  -

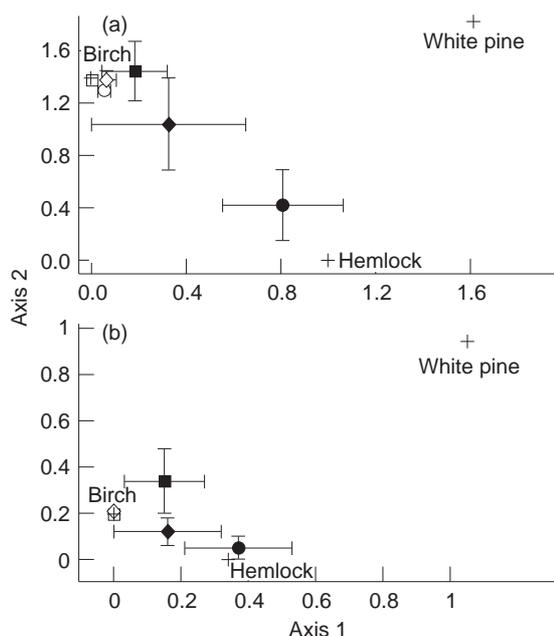
transect interaction,  $F_{8,36} = 5.04$ ,  $P < 0.01$ ; Fig. 7). Larger seeded species (red maple and sugar maple) had heterogeneous seed rain distributions across the transects (*post hoc*s,  $P < 0.05$ ), while smaller seeded species (birch, hemlock) had more even distributions ( $P > 0.05$ ).

#### Discussion

Our results demonstrate that low resource conditions in hemlock stands do set up a positive feedback at early stages of regeneration by favouring hemlock over other species. Hemlock dominated the



**Fig. 5** Total biomass of seedlings per soil divot surviving through the growing season (mean per treatment  $\pm$  1 SEM) under (a) light and (b) soil experimental treatments (light treatments: 1.5% PAR,  $\blacksquare$ ; 60% PAR,  $\square$ ; soil treatments: control,  $\square$ ; nitrogen, hatched bar; lime,  $\blacksquare$ ). Means and standard errors were calculated from natural logarithm-transformed data (pooled across blocks and across soil (a) and light (b) treatments; each mean  $n = 24$ –36) and then back-transformed. Note the difference in scale for birch vs. other species. Columns without any shared letters are significantly different from one another (Scheffé *post hoc* comparisons,  $P < 0.05$ ).



**Fig. 6** Scores of the first two axes from DCA on final community composition of soil divots, based on (a) species abundance and (b) species biomass data. Axes explained 56% and 33% of variation (for a) and 63% and 25% of variation (for b). Means ( $\pm$  SEM) of plot scores for each treatment are shown: high light, unamended, ○; high light, nitrogen, ◇; high light, lime, ◊; low light, unamended, ●; low light, nitrogen, ■; low light, lime, ◆. Species scores are shown with crosses (+). Means and standard errors were calculated from square root-transformed data (pooled across blocks; each mean  $n = 2-12$ ) and then back-transformed.

seedling community under conditions naturally found in hemlock stands (low light nitrogen), while resource supplementation by increasing either light

or nitrogen availability led to dominance by birch species (Fig. 6). Light had a particularly large effect on early regeneration dynamics following seedling emergence from the soil seed bank, and played an important part in the positive feedback effect. The two most common genera to emerge from the soil seed bank (birch and hemlock) exhibited contrasting responses to light treatments. Birch seedlings were particularly responsive to increased light availability (with survival and growth increasing more than emergence; Figs 3–5), leading to a large increase in birch contribution to total seedling community biomass in high vs. low light (99.5% vs. 20.1%). In contrast, hemlock seedlings exhibited much smaller changes in survival and growth in response to light availability, and so their relative contribution to final seedling community composition declined in high light treatments.

Species-specific responses to light availability have been observed in many previous studies (e.g., Pacala *et al.* 1996; Kobe 1999). The behaviour of birch and hemlock seedlings in different light environments might have been predicted to some extent from their respective successional positions (Bazzaz 1979, 1983). The birch species that emerged from the soil seed bank ranged from quite early successional (grey birch, paper birch) to mid-successional (yellow birch and black birch) (Burns & Honkala 1990). In contrast, hemlock is a quintessential late successional species, characterized by slow growth rates (Hibbs 1982; Kelty 1986) and extreme shade tolerance (Godman & Lancaster 1990; Kobe *et al.* 1995). In keeping with this dichotomy of successional position, previous studies have found that birch species respond favourably to increases in resource availability, especially high light and nitrogen (Crabtree & Bazzaz 1993; Wayne & Bazzaz 1993; Carlton &

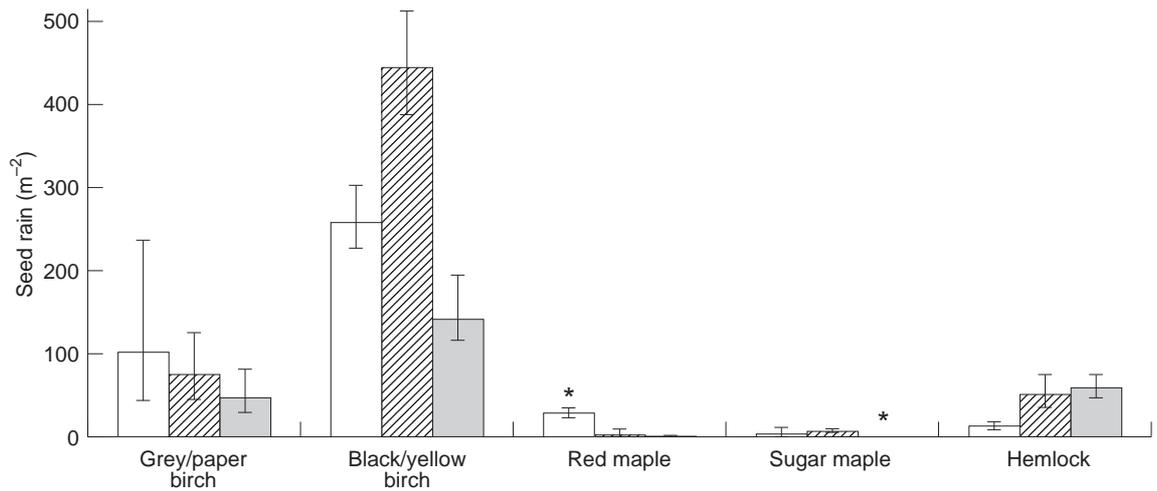
**Table 6** *F* ratios from separate ANOVAs (within MANOVA) on plot scores from detrended correspondence analysis using species abundance and species community biomass at the end of the growing season. Significance shown as follows: NS,  $P > 0.05$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

Factor†	d.f.	Species abundance‡				Species biomass§			
		Axis 1		Axis 2		Axis 1		Axis 2	
Block	2	3.12	NS	0.91	NS	3.79	NS	2.46	NS
Plot	9	2.88	*	1.04	NS	2.10	NS	1.63	NS
Light	1	7.59	NS	6.75	NS	2.26	NS	1.17	NS
Light $\times$ block	2	0.94	NS	1.42	NS	4.56	*	3.26	NS
Soil	2	6.53	**	7.45	**	2.84	NS	3.55	*
Light $\times$ soil	2	3.54	*	5.50	**	3.41	*	3.83	*

†Mean squares of most factors were tested over error mean square (d.f. 35). Plot was nested within block, and its mean square was used to test for a block effect, while light effects were tested over light  $\times$  block mean square.

‡Mean squares for species abundance *F* ratios. Axis 1: error = 8.78, plot = 25.33, light  $\times$  block = 8.27. Axis 2: error = 16.71, plot = 17.46, light  $\times$  block = 23.70.

§Mean squares for species biomass *F* ratios. Axis 1: error = 5.98, plot = 12.57, light  $\times$  block = 27.30. Axis 2: error = 4.39, plot = 7.16, light  $\times$  block = 14.29.



**Fig. 7** Seed rain across experimental transects (1, □; 2, hatched; 3, ▒), with only filled seeds reported. Bars represent means ( $\pm$  SEM) of four plots in each transect, calculated from natural logarithm-transformed data and then back-transformed. Asterisks (\*) mark transects that are significantly different from other transects within that species (Scheffé *post hoc* comparisons,  $P < 0.05$ ).

Bazzaz 1998b), while hemlock seedlings show more moderate responses to such increases (Pacala *et al.* 1994).

Although light availability was the predominant factor underlying the positive feedback acting at early stages of seedling regeneration, there were some significant interactions between light and soil treatments, especially nitrogen addition. Beatty (1984) similarly showed that soil properties in hemlock stands can exert a strong influence on the understorey community. In our study, the composition of low-light nitrogen-amended seedling communities converged during the growing season towards that of high light communities (i.e., birch dominance). In low light, high seedling mortality created communities of very low density (*c.* 10 seedlings  $m^{-2}$ ), so that small differences in seedling dynamics between treatments led to some large changes in eventual seedling community composition. Our original analysis of variance did not detect these small differences between relatively high mortality values. However, by using a community-wide analysis, we found that, in low light, nitrogen addition significantly increased the proportion of seedling communities with at least one surviving birch (from 8% to 50%), while tending to decrease the proportion with at least one surviving hemlock (from 63% to 17%, but not significant). These changes following nitrogen addition led to a shift from hemlock to birch dominance of the seedling community. Mechanisms for these changes, however, still require further investigation. Nitrogen addition could improve seedling growth and survival in low light by allowing seedlings to increase their photosynthetic capacity, perhaps due to a shift in allocation from root

growth to leaf area production (Peace & Grubb 1982), and/or due to increased foliar chlorophyll concentrations leading to increased quantum efficiency (Evans 1989).

Contrary to our expectations, liming had only marginal effects on seedling performance or overall seedling community composition. Soil pH has been shown to influence substantially light growth functions of two of the primary species that emerged from the soil seed bank in the present experiment (hemlock and white pine) (Kobe 1996). In addition, many investigators have suggested that the highly acidic soils within hemlock stands inhibit performance of understorey vegetation and seedling regeneration (Daubenmire 1930). In the present experiment, the only detectable pH effect was the marginally reduced survival of hemlock seedlings on limed soils in low light, which shifted the final composition of limed seedling communities away from hemlock dominance. This change, however, was not statistically robust because of the small number of soil divots with any surviving seedlings following liming.

Seedling regeneration dynamics in hemlock stands are not only a function of species-specific responses to resource availability, but are also dependent on patterns of seed rain into stands. We found, in particular, that very large numbers of birch seeds reached almost all of our experimental plots, and that these translated into high birch seedling emergence in most divots (average  $320 m^{-2}$ ). Seed rain and seedling emergence of birch exceeded that of hemlock (the most abundant canopy species and the second highest seed-producing species) by 8-fold and 50-fold, respectively. Although mature birch trees were

not particularly abundant in the hemlock stand sampled, the high numbers of seeds produced and their extensive dispersal distances (Houle 1994; Ribbens *et al.* 1994; Clark *et al.* 1998) ensured that many birch seeds fell in each plot within the stand. In contrast, a number of the larger-seeded tree species (e.g. red maple, red oak, and sugar maple; Hewitt 1998) made a much smaller contribution to seed rain and the seedling community.

As seed production in temperate forests can be quite variable from year to year (Houle 1994; Koenig & Knops 1998), it is important to examine to what extent the results of our experiment are contingent on seed rain conditions in the particular year of our study. The considerable similarity between the quantity and identity of seedlings emerging from the seed bank in our experiment and seed rain into the plots in the subsequent year suggest that dominance of seed availability by birch, followed by hemlock, with little contribution from larger-seeded hardwood species, is likely to be a relatively robust pattern. More recent measurements in other hemlock stands at Harvard Forest confirm that birch and hemlock consistently dominate seed rain (S. Catovsky & F. A. Bazzaz, unpublished data), while seeds of other common canopy species (maple, oak, pine) have more heterogeneous distributions in space and time (Carlton & Bazzaz 1998a). Seedling regeneration dynamics in these hemlock stands also match closely with those found in the present experiment: high birch and hemlock emergence, followed by low birch survival, and therefore dominance of the seedling bank by hemlock. In addition, dense regeneration of black birch following hemlock tree mortality in stands infested with an exotic insect pathogen (*Adelges tsugae*, the hemlock woolly adelgid; Orwig & Foster 1998) further confirms that the considerable potential for recruitment of birch within hemlock stands is likely to be a common feature in the New England landscape.

Results from the present experiment illustrate the importance of both resource availability and species' life-history strategies in determining patterns of regeneration in hemlock stands. As we only examined seedling dynamics for one season, we should be cautious about extrapolating our results much beyond these early stages of seedling regeneration. Nevertheless, within the first year of seedling growth we observed occurrence of a clear positive feedback in hemlock stands through preferential regeneration of hemlock over other species. Birch species had abundant seed dispersal into hemlock stands (while many species did not), but they could not establish under the low resource conditions (light and nitrogen) characteristic of hemlock stands, primarily due to low survival. Birch seedling survival was reduced by 95% from high to low light, causing the disappearance of the brief pulse of high birch seedling

density observed early in the season, even in low light. Birch seedling growth was also severely affected by low light availability, but these effects did not appear to drive changes in seedling community composition (Fig. 6; see also Kobe *et al.* 1995). Hemlock regeneration in such stands was favoured both through abundant seed rain from canopy dominants and through seedling tolerance of low resource availability. The present experiment highlights the different kinds of recruitment patterns that may be responsible for the development of positive feedbacks in plant communities.

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### References

- Aber, J.D., Nadelhoffer, K.J., Steudler, P. & Melillo, J.M. (1989) Nitrogen saturation in northern forest ecosystems. *Bioscience*, **39**, 378–386.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.
- Bazzaz, F.A. (1983) Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. *Disturbance and Ecosystems* (eds H.A. Mooney & M. Godron), pp. 259–275. Springer-Verlag, Berlin, Germany.
- Bazzaz, F.A. & Wayne, P.M. (1994) Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap–understorey continuum. *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground* (eds M.M. Caldwell & R.W. Pearcy), pp. 349–390. Academic Press, San Diego, CA.
- Beatty, S.W. (1984) Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology*, **65**, 1406–1419.
- van Breemen, N. & Finzi, A.C. (1998) Plant–soil interactions: ecological aspects and evolutionary implications. *Biogeochemistry*, **42**, 1–19.
- Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America*. Vol. 2. Hardwoods. United States Department of Agriculture, Washington, DC.
- Canham, C.D., Finzi, A.C., Pacala, S.W. & Burbank, D.H. (1994) Causes and consequences of resource het-

- erogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*, **24**, 337–349.
- Carlton, G.C. & Bazzaz, F.A. (1998a) Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecological Monographs*, **68**, 99–120.
- Carlton, G.C. & Bazzaz, F.A. (1998b) Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology*, **79**, 1305–1319.
- Carter, M.R. (1993) *Soil Sampling and Methods of Analysis*. Lewis, Boca Raton, FL.
- Clark, J.S., Macklin, E. & Wood, L. (1998) Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs*, **68**, 213–235.
- Clements, F.E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington, Washington, DC.
- Collins, S.L. (1990) Habitat relationships and survivorship of tree seedlings in hemlock–hardwood forest. *Canadian Journal of Botany*, **68**, 790–797.
- Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.
- Cornett, M.W., Reich, P.B. & Puettmann, K.J. (1997) Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer–deciduous forests. *Écoscience*, **4**, 353–364.
- Crabtree, R.C. & Bazzaz, F.A. (1993) Seedling response of four birch species to simulated nitrogen deposition: ammonium vs. nitrate. *Ecological Applications*, **3**, 315–321.
- Daubenmire, R.F. (1930) The relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. *Butler University Botanical Studies*, **1**, 61–76.
- Davis, M.B., Calcote, R.R., Sugita, S. & Takahara, H. (1998) Patchy invasion and the origin of a hemlock–hardwood forest mosaic. *Ecology*, **79**, 2641–2659.
- Davis, M.B., Sugita, S., Calcote, R.R., Ferrari, J.B. & Frelich, L.E. (1994) Historical development of alternate communities in a hemlock–hardwood forest in northern Michigan, USA. *Large-Scale Ecology and Conservation Biology* (eds P.J. Edwards, R.M. May & N.R. Webb), pp. 19–39. Blackwell Science, Oxford, UK.
- Day, R.W. & Quinn, G.P. (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59**, 433–463.
- Evans, J.R. (1989) Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia*, **78**, 9–19.
- Finzi, A.C., van Breemen, N. & Canham, C.D. (1998a) Canopy tree–soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications*, **8**, 440–446.
- Finzi, A.C., Canham, C.D. & van Breemen, N. (1998b) Canopy tree–soil interactions within temperate forests: species effects on pH and cations. *Ecological Applications*, **8**, 447–454.
- Foster, D.R. & Zebryk, T.M. (1993) Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology*, **74**, 982–998.
- Frelich, L.E., Calcote, R.R., Davis, M.B. & Pastor, J. (1993) Patch formation and maintenance in an old-growth hemlock–hardwood forest. *Ecology*, **74**, 513–527.
- Godman, R.M. & Lancaster, K. (1990) *Tsuga canadensis* (L.) Carr. *Silvics of North America*. Vol. I. Conifers (eds R.M. Burns & B.H. Honkala), pp. 604–612. United States Forest Service, Washington, DC.
- Hewitt, N. (1998) Seed size and shade-tolerance: a comparative analysis of North American temperate trees. *Oecologia*, **114**, 432–440.
- Hibbs, D.E. (1982) Gap dynamics in a hemlock–hardwood forest. *Canadian Journal of Forest Research*, **12**, 522–527.
- Horn, H.S. (1975) Forest succession. *Scientific American*, **232**, 90–98.
- Houle, G. (1994) Spatiotemporal patterns in the components of regeneration of four sympatric tree species – *Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. *Journal of Ecology*, **82**, 39–53.
- Hughes, J.W., Fahey, T.J. & Browne, B. (1987) A better seed and litter trap. *Canadian Journal of Forest Research*, **17**, 1623–1624.
- Kelty, M.J. (1986) Development patterns in two hemlock–hardwood stands in southern New England. *Canadian Journal of Forest Research*, **16**, 885–891.
- Kobe, R.K. (1996) Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs*, **66**, 181–201.
- Kobe, R.K. (1999) Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, **80**, 187–201.
- Kobe, R.K., Pacala, S.W., Silander, J.A. Jr & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Koenig, W.D. & Knops, J.M.H. (1998) Scale of mast-seeding and tree-ring growth. *Nature*, **396**, 225–226.
- Kozlowski, T.T., Kramer, P.J. & Pallardy, S.G. (1991) *The Physiological Ecology of Woody Plants*. Academic Press, San Diego, CA.
- Lee, D.W., Oberbauer, S.F., Krishnapilay, B., Mansor, M., Mohamad, H. & Yap, S.K. (1997) Effects of irradiance and spectral quality on seedling development of two Southeast Asian *Hopea* species. *Oecologia*, **110**, 1–9.
- Moore, B., Richards, H.M., Gleason, H.A. & Stout, A.B. (1924) Hemlock and its environment. I. Field records. *Bulletin of the New York Botanical Garden*, **12**, 325–350.
- Oosting, H.J. & Hess, D.W. (1956) Microclimate and a relic stand of *Tsuga canadensis* in the lower Piedmont in North Carolina. *Ecology*, **37**, 28–39.
- Orwig, D.A. & Foster, D.R. (1998) Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Club*, **125**, 60–73.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A. Jr, Kobe, R.K. & Ribbens, E. (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, **66**, 1–43.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr & Kobe, R.K. (1994) Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research*, **24**, 2174–2183.
- Pastor, J. & Broschart, M. (1990) The spatial pattern of a northern conifer–hardwood landscape. *Landscape Ecology*, **4**, 55–68.
- Paul, E.A. & Clark, F.E. (1996) *Soil Microbiology and Biochemistry*, 2nd edn. Academic Press, San Diego, CA.
- Peace, W.J.H. & Grubb, P.J. (1982) Interaction of light and mineral nutrient supply in the growth of *Impatiens parviflora*. *New Phytologist*, **90**, 127–150.

- Petraitis, P.S. & Latham, R.E. (1999) The importance of scale in testing the origins of alternative community states. *Ecology*, **80**, 429–442.
- Ribbens, E., Silander, J.A. Jr & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. W. H. Freeman, New York, NY.
- Turner, D.P. & Franz, E.H. (1986) The influence of canopy dominants on understorey vegetation patterns in an old-growth cedar–hemlock forest. *American Midland Naturalist*, **116**, 387–393.
- Wayne, P.M. & Bazzaz, F.A. (1993) Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. *Ecology*, **74**, 1500–1515.
- Wilson, J.B. & Agnew, A.D.Q. (1992) Positive-feedback switches in plant communities. *Advances in Ecological Research*, **23**, 263–336.
- Woods, K.D. (1984) Patterns of tree replacement: canopy effects on understorey pattern in hemlock–northern hardwood forests. *Vegetatio*, **56**, 87–107.

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