NITROGEN-INDUCED CHANGES IN SEEDLING REGENERATION AND DYNAMICS OF MIXED CONIFER–BROAD-LEAVED FORESTS

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Abstract. Most research on forest dynamics has focused on species' light requirements as the major driver for successional change. However, soil resource availability may modify seedling responses to light and ultimately alter the course of succession. In the present study, we examined how seedlings in mixed conifer–broad-leaved forests in eastern North America differed in their growth and mortality responses to manipulated nitrogen availability. We then incorporated these responses into an individual-based model of forest dynamics (SORTIE) to assess potential longer-term consequences of seedling responses to nitrogen for temperate forest community dynamics. We grew seedlings of six study species, both individually and in mixed-species competitive stands, in a common garden for two years. The earlier successional broad-leaved species (yellow birch and red maple) consistently showed the greatest increases in biomass in response to nitrogen addition, while the most late successional of the broad-leaved species (sugar maple) and all the coniferous species did not grow significantly larger with increased nitrogen. We found a significant correlation between species' early growth rate and nitrogen growth enhancement. For those species that underwent significant nitrogen-induced shifts in growth and/or mortality, we adjusted their parameters in the seedling/sapling growth and mortality submodels of SOR-TIE (covering up to 10 cm dbh). Simulations revealed that nitrogen effects on both seedling growth in high light and seedling mortality in low light (data from parallel experiment) changed overall forest structure and dynamics. Increased nitrogen led to: (1) further dominance of young forests by earlier successional species (yellow birch in particular), through its impacts on seedling high-light growth, and (2) even greater persistence of later successional species (predominantly hemlock) in older forests, through its impacts on seedling low-light mortality. These findings were robust to an uncertainty analysis that incorporated experimentally derived error into the seedling/sapling submodels. In contrast, the identity of the species replaced by yellow birch and hemlock was more sensitive to uncertainty in parameter values. We conclude that seedling physiological and demographic responses to increased nitrogen availability have the potential to scale up and influence successional dynamics in mixed temperate forests, provided these effects persist throughout seedling and sapling life stages.

Key words: forest gap; forest succession; mixed conifer–broad-leaved forests; nitrogen availability; seedling growth; seedling regeneration; SORTIE model; temperate forest community dynamics.

INTRODUCTION

Forests are now recognized as dynamic communities, characterized by change and disturbance rather than stasis (Foster et al. 1996). As a result, there has been a growing realization that a mechanistic understanding of forest structure and composition requires the investigation of processes that regulate the population dynamics of individual component species (Shugart 1998). To date, most research has focused on tree species' effects on and responses to light availability as the major drivers of forest successional dynamics (Canham et al. 1994, Pacala et al. 1994, Kobe et al. 1995).

However, soil resource availability could modify seedling responses to light, and ultimately alter the course of forest succession (Kobe 1996, Finzi and Canham 2000, Caspersen and Kobe 2001). Understanding nitrogen effects in temperate forests is now especially critical because: (1) nitrogen is a particularly limiting soil resource in these forests (Vitousek and Howarth 1991), and (2) human activities are leading to increased nitrogen loading in such systems (Vitousek et al. 1997*a*).

To assess the potential effects of nitrogen availability on temperate forest community structure, we need to examine how nitrogen influences the different processes controlling successional trajectories in these forests. Species growth and mortality early in life have both been identified as particularly important drivers of forest dynamics (Pacala et al. 1996). However, we currently have relatively limited information on how

nitrogen availability affects regeneration patterns, and how these nitrogen effects might scale up to influence forest dynamics in the longer term, i.e., over the course of forest succession. Part of the difficulty arises because previous research has examined nitrogen effects on just one aspect of regeneration, e.g., growth in forest gaps vs. the understory (Canham et al. 1996, Walters and Reich 1997), and done so without direct manipulation of nitrogen in the field (reviewed in Grubb 1994). Thus, to provide a more comprehensive view of nitrogen effects on forest dynamics, we designed two parallel experiments to examine seedling responses to nitrogen addition at two critical stages in a tree's life cycle: (1) persistence in the understory seedling bank (low light) (Marks and Gardescu 1998) and (2) seedling growth after canopy gap formation (high light) (Canham 1989). Full results of the understory study are reported elsewhere (Catovsky and Bazzaz 2002a).

Mixed temperate forests may be particularly sensitive to variation in soil nitrogen availability because they contain two very different groups of tree species: evergreen coniferous and deciduous broad-leaved. These groups may respond differently to increasing nitrogen, given their differences in leaf longevity and life-history strategy (Bond 1989, Becker 2000). In the present study, we examined how seedlings of three coniferous and three broad-leaved species common to mixed temperate forests in eastern North America differed in their responses to nitrogen addition. We tested the prediction that coniferous and late-successional species would be less responsive to changes in nitrogen availability than would broad-leaved and early-successional species, as their evergreen habit and slow seedling growth rates often correlate with more conservative patterns of nutrient uptake and use (Reich et al. 1995, 1998b, Bazzaz 1996, Aerts and Chapin 2000). Because seedlings typically regenerate in dense stands within forest gaps (Peet and Christensen 1987), we considered responses of seedlings grown both individually and in mixed-species competitive stands. We then examined how the seedling growth and mortality responses to increased nitrogen availability influenced forest successional dynamics using SORTIE, a spatially explicit, individual-based model of forest dynamics (Pacala et al. 1996). Rather than precisely predicting successional trajectories under different nitrogen regimes, we used SORTIE as a tool to highlight the potential consequences of seedling responses to soil nitrogen for temperate forest dynamics.

MATERIALS AND METHODS

Soil and seed collection

Soil was collected from hemlock- and red oak-dominated forest stands at Harvard Forest (Petersham, Massachusetts, USA; 42°32′ N, 72°11′ W, elevation 340 m) in April 1998. The stands were located in the Tom Swamp tract and were chosen so that hemlock and red oak contributed >50% of the basal area in each of three stands. Details of the stands are described elsewhere (Catovsky and Bazzaz, in press). The soil was collected from one area in each stand as intact soil divots (40 × 50 cm, 15 cm depth to include all of O and some of A horizon), and was then transported back to an experimental garden at Harvard University (Cambridge, Massachusetts, USA). Using a trowel, divots were divided vertically into smaller soil squares, which were placed over coarse silica sand in plastic containers. Individuals were grown in 12-L tree pots (16 × 16 cm, 48 cm deep), with ~8 L of sand beneath a 16 × 16 × 15 cm soil square. For mixed-species plantings, we used wider but shallower containers (20 L; 30 × 35 cm, 20 cm deep), with a 5-cm layer of sand at the bottom. This potentially increased root as well as shoot competition, and led to an overall reduction in species allocation to roots when grown in stands vs. individually (36% vs. 53%). We initially planned to look at differences in species' responses between stand types as well, but subsequent analyses revealed that the soil did not differ significantly between hemlock and red oak stands ($F_{1,93}$ = 3.00 for ammonium, 0.35 for nitrate, $P > 0.05$ for both), and neither did species' responses ($F_{1,232}$ = 1.74 for individually grown seedlings, 0.04 for competitively grown seedlings, $P > 0.05$ for both). Thus, for the purposes of this experiment, species' responses were pooled across stand types. However, we kept a "site" term in our models, so that variation from our six different study locations could be taken into account.

We chose tree species that spanned a range of shade-tolerance classes (Table 1) from both gymnosperm and angiosperm groups, enabling us to distinguish differences in species' responses due to evolutionary history from life-history strategy. In addition, all species are currently important components of mixed temperate forests in New England (Foster et al. 1998). Seeds of all study species were collected from multiple trees at Harvard Forest in the autumn of 1996 (most species) and spring of 1997 (red maple). Seeds were air-dried and stored at 4°C until late autumn 1997, when they were placed in cloth bags and buried in trays of wet, coarse sand. These trays were placed outside through the winter to stratify the seeds and were collected the following spring. In 10 cm deep germination flats, seeds were spread out evenly over a peat-based potting mix with added perlite, and then covered with a thin layer of vermiculite. Flats were placed in the experimental garden in mid-April and seeds were left to germinate. The flats were monitored daily and watered when necessary. Seedlings began to germinate in early to mid-May, and were transplanted into containers in mid-June when most seedlings had two to three true leaves. We planted seedlings in both "noncompetition" and "competitive mixed-species" treatments. For the noncompetition treatment, one seedling was planted per individual pot. For the competition treatment, 42

TABLE 1. Details of experimental study species in hemlock- and red oak-dominated forest stands at Harvard Forest, Petersham, Massachusetts.

Species	Common name	Leaf habit	Successional position†
Tsuga canadensis (L.) Carr.	eastern hemlock	evergreen coniferous	5
Picea rubens Sarg.	red spruce	evergreen coniferous	4
Pinus strobus L.	white pine	evergreen coniferous	3
Acer saccharum Marsh.	sugar maple	deciduous broad-leaved	5
Acer rubrum L.	red maple	deciduous broad-leaved	4
Betula alleghaniensis Britt.	yellow birch	deciduous broad-leaved	3

† Based on Baker's Table and mortality–light relationships in Kobe et al (1995). Successional position/shade tolerance is on a scale of 1–5, where 1 is the least and 5 is the most shade tolerant.

seedlings were planted in each container, representing a seedling density of 390 individuals/m², approximating the mean density (300 individuals/m², range: 30–1200 individuals/m²) for seedlings established from the seed bank following a canopy disturbance in this region (Catovsky and Bazzaz 2000). In the mixed-species treatments, seedlings were planted in a hexagonal array, such that each "target" plant had six neighbors. Three individuals of each species were planted in the 18 central "target" locations, and four individuals of each species were planted in the 24 outer "edge" locations. Seedling positions were randomized within these target and edge locations, and the positions were established using a planting template with holes marked for each seedling.

Experimental treatments and growth conditions

We grew 54 individuals of each species and 54 mixed-species plantings for the experiment: 6 sites × 3 nitrogen levels × 3 replicates. All containers for individuals and mixed plantings were buried in the ground in the experimental garden underneath a large plastic greenhouse (30 m long, 6.5 m wide, 3.5 m tall), in which a continuous flow of air was maintained with the use of large embedded fans at one end. The plastic covering of the greenhouse resulted in 60% of possible photosynthetically active radiation and was chosen to simulate light levels in a multiple tree-fall gap in temperate forests (Bazzaz and Wayne 1994). These larger scale disturbances dominate the major successional changes that occur within New England forests (Oliver and Stephens 1977, Peterken 1996), producing a disturbance intensity of 1% annually (when averaged over time) (Canham and Loucks 1984). Within the greenhouse, the individuals and mixed-species plantings were arranged in three large blocks, with one replicate of each treatment combination placed in each block. Seedlings were given daily watering treatments from automatic sprinklers within the greenhouse. Water was applied generously so that it would not be a limiting factor in this experiment.

Each individually grown seedling or mixed planting received one of three nitrogen addition treatments (0,

2.5, or 7.5 g N·m⁻²·yr⁻¹). In both 1998 and 1999, seedlings were given nitrogen eight times per year at ~three-week intervals, beginning mid-April and ending mid-September. At each addition, nitrogen was applied as dissolved ammonium nitrate solution of varying concentration. Individual seedlings were given 10 mL of 0, 0.030, and 0.090 mol N/L, and mixed plantings were given 100 mL of 0, 0.012, and 0.036 mol N/L. The treatments were designed to provide a substantial perturbation to the natural nitrogen cycle, representing nitrogen treatments that added considerably to net nitrogen mineralization (4–8 g N·m⁻²·yr⁻¹) and nitrification rates (0.5–2 g N·m⁻²·yr⁻¹) (Catovsky and Bazzaz, *in press*), and current levels of nitrogen deposition (0.6 g N·m⁻²·yr⁻¹) (Munger et al. 1998) at Harvard Forest. Nitrogen was added as ammonium nitrate, because both ammonium and nitrate each compose close to half of the deposition in New England (Ollinger et al. 1993).

Seedling mortality censuses were taken at the end of the first growing season (1998), and at both the beginning and end of the second growing season (1999). Fallen litter of deciduous species was removed between the two growing seasons. In late September 1999, all seedlings were harvested (16 mo after start of experiment). Leaves, stems, and roots of all seedlings were separated. Isolated roots were obtained by carefully washing away the soil. For mixed-species stands, every individual's root system was carefully separated by hand. Plant material was dried at 70°C for 7 d and then weighed.

Multifactor analyses of variance were used to investigate influence of nitrogen addition on seedling growth and mortality (Sokal and Rohlf 1995). Linear models included nitrogen addition as a continuous factor, species as fixed discrete factors, and site (for the six different study locations) and block within greenhouse both as random factors. The mixed-species planting analysis also included a nested plot term representing each planting. Significant multifactor interactions involving nitrogen were investigated by examining the magnitude and significance of regression slopes (dependent variable vs. nitrogen addition). Bio-

mass data were natural logarithm transformed to ensure that the assumptions of analysis of variance were met (normality of residuals, homoscedascity).

Seedling biomass and nitrogen measurements

In August 1999, a leaf sample was taken from every surviving seedling growing individually. Samples were photocopied and leaf area subsequently calculated using NIH Image software version 1.6 (NIH, Bethesda, Maryland, USA). The leaf samples were weighed after drying in an oven for 48 h at 70°C, and specific leaf mass calculated (SLM, g/m^2). Dried leaf material was ground using a Mikro-Dismembrator (B. Braun Biotech International, Allentown, Pennsylvania, USA). A subsample (2–5 mg) of the ground leaf was used to determine foliar nitrogen concentrations, using a Fisons CHN Analyzer 1500 Series 2 (Beverly, Massachusetts, USA).

Season-long integrated nitrogen availability was determined using ion exchange resin bags placed in all mixed-species plantings and in a subset (one-sixth) of individually grown seedlings from June until September 1999 (Binkley and Vitousek 1989). The bags were constructed with 22 mL of mixed bed strong acid (cation) and strong base (anion) gel resins (Sybron Chemicals, Birmingham, New Jersey, USA) sealed in nylon mesh, and placed at a depth of 5 cm in the soil. After removal from the soil, 4 g of dried resin (70°C, overnight) was extracted with 100 mL of 2 mol/L potassium chloride solution (25°C, 24 h), and then frozen immediately following suction-filtration. Ammonium and nitrate in all soil and resin extracts were measured using a Lachat continuous flow ion analyzer using methods 12-107-06-1-A and 12-407-04-1-B (Lachat Instruments, Milwaukee, Wisconsin, USA). Blanks were created from resin bags that had been sealed in polyethylene bags for the length of the growing season. These resins were extracted in the same way as the resins placed in the soil and were used to determine the lower threshold of detection.

SORTIE parameterization

To explore changes in community dynamics mediated through seedling responses to nitrogen availability, we incorporated results of the nitrogen fertilization experiments into the forest dynamics model SORTIE. We used the model as a tool to explore how nitrogen-induced changes in seedling demography could potentially alter the dynamics of mixed temperate forests. The modeling exercise was not designed to generate specific predictions about effects of nitrogen availability on successional trajectories in these mixed forests, but rather to highlight the potential importance of seedling responses to soil nitrogen in driving these dynamics.

We summarize the important attributes of SORTIE here to provide a context for our nitrogen parameterizations, but see Pacala et al. (1996) for a detailed description and analysis of the model. SORTIE predicts long-term community changes in tree species density, spatial distributions, and age and size structure by repeated iterations of four submodels governing individual tree behavior: (1) seedling recruitment as function of distance to and size of parent trees, (2) light extinction through crown interception, (3) seedling/sapling growth as a function of light availability, and (4) seedling/sapling mortality as a function of recent growth. The four submodels of SORTIE were calibrated from field studies for nine major tree species in central/southern New England. SORTIE operates on a five-year time step and tracks every individual tree in continuous space.

A model run begins with user-specified numbers, sizes, and species of individual trees. Subsequent establishment of seedlings arises from the reproduction of trees on the simulated plot, governed by a species-specific seedling recruitment submodel (Ribbens et al. 1994). The submodel specifies the number of seedlings produced by an individual tree, which is scaled to tree diameter, and the spatial distribution of those seedlings. Each tree in SORTIE experiences a light environment as modified by neighbors (Canham et al. 1994). Incoming radiation, characterized by a spatial distribution of sky brightness, is attenuated as it intercepts crowns of individual trees. Tree crowns are represented in the model as cylinders, whose dimensions are determined by species-specific allometric equations. Besides crown volume, species also differ in leaf and branch density. Thus, the amount of light reaching a particular tree is calculated as the attenuation of light from the sky hemisphere, passing through reconstructed crowns with species-specific light extinction. Heterogeneity in light availability is caused by variation in the size, density, and composition of neighbors. Light availability in turn determines the species-specific growth rate of juvenile trees (≤750 cm in height) as a Michaelis-Menten function (Pacala et al. 1994):

$$\Delta \text{radius} = \text{radius} \times \frac{G_1 \times \text{light}}{\dfrac{G_1}{G_2} + \text{light}} \qquad (1)$$

where G_1 (the asymptote) and G_2 (slope of the growth function at zero light) are estimated from field data and govern high-light and low-light growth, respectively. Trees >750 cm height add a constant area increment for each time step of the model. Juvenile trees die with a probability that is a function of recent growth rates (Kobe et al. 1995). The relationship between probability of mortality in any given 2.5-yr period and the preceding five years of radial growth is characterized by an exponential function:

$$P(\text{mort})_{2.5 \text{ yr}} = M_1 \times e^{-M_2 \times g} \qquad (2)$$

where g is the average radial growth rate over the most recent five years and M_1 and M_2 are species-specific

parameters estimated from data with $0 < M_1 \leq 1$. M_1 represents mortality at zero growth (typically at very low light levels), and M_2 characterizes the sensitivity of mortality to changes in carbon balance or recent growth rates. Non-juvenile trees experience a constant probability of mortality (Pacala et al. 1996).

Here we focused on the potential effects of increased nitrogen availability on community dynamics as mediated by the seedling growth and mortality responses to nitrogen of the six study tree species. Although SORTIE has not been calibrated for Harvard Forest, our interest was not to simulate this site per se, but to assess if the magnitude of the observed seedling growth and mortality responses to increased nitrogen had the potential to alter species composition and successional trajectories of such mixed temperate forests. We ran three sets of SORTIE simulations: control (0 g N· m^{-2}·yr^{-1}), low nitrogen addition (2.5 g N·m^{-2}·yr^{-1}), and high nitrogen addition (7.5 g N·m^{-2}·yr^{-1}). For the SORTIE control simulations, we used model parameters as reported for Great Mountain Forest (GMF) in northwest Connecticut. GMF and Harvard Forest are similar in soils, species composition, and climate, and are broadly representative of central New England forests (Westveld 1956). With the exception of red spruce, all species in our nitrogen fertilization experiments were included in the GMF calibration of SORTIE. Red spruce shows similar growth, mortality, and foliage density as eastern hemlock (Burns and Honkala 1990), so we substituted hemlock parameter values for red spruce in these simulations.

For the increased nitrogen simulations, we adjusted the parameters of the seedling/sapling growth and mortality submodels of SORTIE relative to the control for species that underwent significant shifts in these parameters following nitrogen addition. These submodels cover seedling/sapling performance up to 10 cm diameter breast height (dbh), after which the adult response functions take over.

Growth.—Nitrogen additions only influenced growth under the high light conditions of a simulated gap (current experiment), but not in the low light of the understory (Catovsky and Bazzaz 2002a). Thus, to simulate nitrogen effects on growth of each species, we multiplied the high light growth parameter (G_1) in Eq. 1 by the ratio of average seedling growth in each nitrogen treatment to average seedling growth in the control (Growth$_N$/Growth$_C$) to obtain estimates of $G_{1,N}$ for both the low and high nitrogen amendments. If nitrogen additions did not result in a significant change in growth, the enhancement ratio was kept at unity. We only used growth responses from seedlings grown without competition, because those grown with competition experienced a variable light environment, depending on their position within the canopy. As SORTIE measures growth as changes in radius rather than biomass, we converted the relative biomass changes (Growth$_N$/Growth$_C$) to relative diameter growth changes using allometric growth equations of the form $M = aD^b$,

where M is biomass, D is stem diameter, and a and b are allometric constants (ter Mikaelian and Korzukhin 1997).

Mortality.—Nitrogen additions only had significant effects on seedling mortality under the low light conditions of the understory experiment (Catovsky and Bazzaz 2002a), but not in high light gap conditions (current experiment). To simulate these nitrogen effects, we modified mortality submodel parameters (M_1 and M_2, Eq. 2) according to nitrogen-induced changes in mortality relative to the controls (%Mortality$_N$/ %Mortality$_C$). Species' parameters were adjusted when nitrogen significantly altered mortality in at least one of the experimental treatments used in the understory experiment: planted seedlings, seed addition, or natural regeneration (Catovsky and Bazzaz 2002a). If nitrogen significantly affected more than one of these treatments, then the pooled average across these treatments was used. In SORTIE, average mortality for a species under a particular nitrogen condition can be calculated by integrating Eq. 2 for positive growth rates. This calculation indicates that average mortality can be summarized as M_1/M_2. Thus, nitrogen-induced changes in mortality for both the low and high nitrogen treatments are characterized by multiplying M_1 or dividing M_2 by %Mortality$_N$/%Mortality$_C$ to obtain $M_{1,N}$ or $M_{2,N}$ estimates for the low and high nitrogen treatments. For most species, we modified M_1, the probability of mortality at zero growth (or very low light) (Eq. 2), because it most closely represented the mortality data from the experiment (carried out under the very low light conditions of the understory). The only exception was red maple, whose M_1 estimate is 0.99 (Kobe et al. 1995). Because M_1 represents the probability of mortality at zero growth and because red maple showed increased mortality with nitrogen addition, it was biologically non-sensible to alter M_1 to a value greater than 1. Instead, we modified red maple's M_2 parameter to simulate the nitrogen-induced increase in mortality. Furthermore, in SORTIE, species-specific mortality depends on an individual's recent radial growth. To uncouple the independent effects of nitrogen additions on growth and mortality, mortality was corrected for nitrogen effects on growth by dividing M_2 (decay parameter determining how quickly mortality decreases with increases in growth) by the growth enhancement under a particular treatment.

We modified species' parameter estimates for the SORTIE growth and mortality submodels as described above in order to assess potential consequences of two levels of increased nitrogen availability on forest community dynamics. All other parameters in these simulations were the same as in the control simulations, i.e., all parameters controlling seedling recruitment, tree allometric relationships, mature tree growth and mortality, and attenuation of light availability. We ran 40 replicate 9-ha simulations with different random number seeds for each of the control, low nitrogen, and high nitrogen treatments (referred to as ''baseline

runs''). We present mean relative basal areas for these runs and the range for the central 95% of runs, which represent stochastic variation in model predictions. Inherent stochasticity in the model arises from the two probabilistic submodels; one specifying seedling/sapling mortality probability and the other the probability of seedling establishment.

SORTIE uncertainty analysis

We also performed an uncertainty analysis to assess how error in species' mean responses to nitrogen additions translated into uncertainty in SORTIE community-level predictions. We calculated variance in radial growth enhancements ($Growth_N/Growth_C$) using the following estimator for variance of a ratio for independent samples (de Vries 1986):

$$\text{var}\left(\frac{\overline{\text{Growth}_N}}{\overline{\text{Growth}_C}}\right) = \left(\frac{\overline{\text{Growth}_N}}{\overline{\text{Growth}_C}}\right)^2 \times \frac{(\text{var Growth}_N)}{(\overline{\text{Growth}_{N_i}})^2}$$

$$\times \frac{(\text{var Growth}_C)}{(\overline{\text{Growth}_C})^2}. \qquad (3)$$

The ratio variance, normalized by the smaller sample size of the nitrogen or control treatments, provided an estimate of the standard error of the growth enhancement for each species under low or high nitrogen additions relative to controls. A sampling distribution for each species-treatment growth enhancement was developed as a normal distribution centered about the mean growth enhancement, with the standard error of the mean growth enhancement.

The sampling distribution represents the distribution of mean growth enhancements under a nitrogen treatment relative to the control. From the sampling distribution, we generated 40 possible mean growth enhancements for each species (6) and nitrogen treatments (2) using S-Plus 2000 (MathSoft Corporation, Seattle, Washington, USA). In a similar manner, we generated 40 possible mean mortality alterations for each species and nitrogen level. For each nitrogen treatment, 40 mean growth and mortality manifestations were compiled across species to result in 40 sets of species-specific growth and mortality changes, which were then used to alter SORTIE parameters as described above. For each nitrogen treatment, this resulted in 40 SORTIE parameter sets, encompassing the statistical uncertainty that we observed in species-specific mean seedling growth and mortality responses to nitrogen additions. The 40 SORTIE runs from these parameter sets (i.e., uncertainty analysis runs) yielded a distribution of potential model results given the observed error in growth and mortality responses to our nitrogen addition experiments. By propagating the statistical uncertainty associated with nitrogen effects on seedlings to SORTIE predictions of relative species basal area, we identified robust predictions of potential changes in composition in response to nitrogen availability. We took a conservative approach to assessing significant differences in species relative basal areas between control and nitrogen treatments. We evaluated significant differences with respect to the degree of overlap between the central 95% or 90% of control vs. nitrogen treatment in both the baseline and uncertainty analysis runs. These 95% and 90% criteria of nonoverlap correspond to rough approximations of probability levels of 0.05 and 0.10.

In addition, simple Pearson correlation coefficients were calculated between variation in each of the altered parameters in the model and species' relative abundance at different times. Each of the model's runs represented one sample point in each of the correlations, and 210 such correlations were calculated (7 parameters $\times$ 6 species $\times$ 5 time points). The squared correlation coefficients (r^2) were used to measure the proportion of the variance in the relative abundance of each species explained by each parameter (Turner et al. 1994).

RESULTS

Seedling gap experiment

Nitrogen additions led to a significant increase in availability of both ammonium and nitrate in the soil matrix ($F_{1,96} = 45.89$ for ammonium, 49.81 for nitrate, $P < 0.001$ for both). Ammonium increased from 0.027 to 0.080 mg/g resin, and nitrate from 0.088 to 0.490 mg/g resin (0 vs. 7.5 g $N \cdot m^{-2} \cdot yr^{-1}$ treatments). This effect was consistent across individually and competitively grown seedlings (no significant nitrogen $\times$ density interaction, $F_{1,96} = 2.20$ for ammonium, 0.66 for nitrate, $P > 0.05$ for both). Resin bags trapped more nitrate overall than ammonium, but in both cases, nitrogen increased the amount of ion extracted from the resin.

For both individually and competitively grown seedlings, increased soil nitrogen availability led to increased growth of only the two fastest growing species (Fig. 1; significant nitrogen $\times$ species interactions in both models, $F_{5,243} = 2.77$ and $P < 0.05$ for individuals, $F_{5,726} = 4.56$, and $P < 0.001$ for stands). Red maple showed significant nitrogen-induced growth enhancements both as an individual and in competition, while yellow birch only showed biomass enhancements when grown individually and not in mixed-species treatments. The other broad-leaved species, sugar maple, and all the conifer species showed no significant growth responses to nitrogen addition. For competitively grown seedlings, there was a significant positive correlation ($r = 0.92$, $P < 0.01$) between early seedling growth rates (as assessed by mean biomass in control treatments) and species' responsiveness to nitrogen (slope of the regression between biomass and nitrogen addition level). For individually grown seedlings, there was a marginally significant positive correlation ($r = 0.70$, $P = 0.12$). In contrast to growth, seedling mortality in high light was not influenced by nitrogen avail-
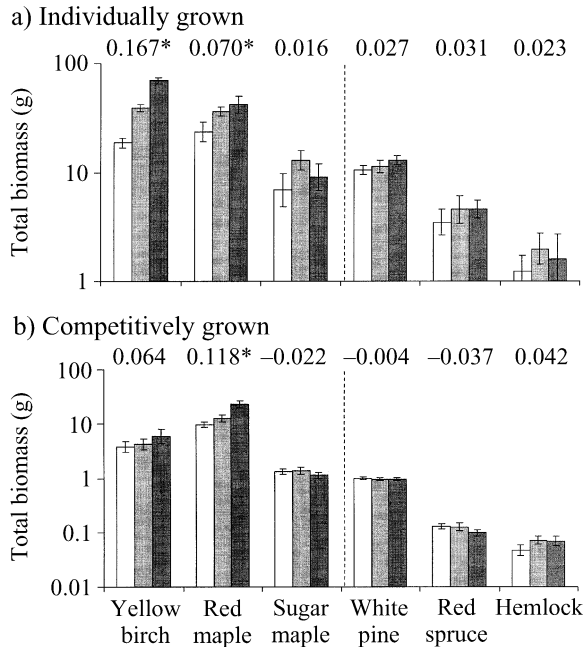
a) Individually grown

b) Competitively grown

FIG. 1. Effects of nitrogen addition (white = 0, light gray = 2.5, and dark gray = 7.5 g N·m^{-2}·yr^{-1}) on final biomass of seedlings after 16 mo of growth (mean ± 1 SE), grown either (a) as individuals or (b) in mixed-species stands. Means and standard errors were calculated from natural-logarithm transformed data and then back-transformed (but note log scale). Values above each species represent slope coefficients calculated using transformed data. Slopes significantly different from zero ($P < 0.05$) are denoted with an asterisk.

ability over the course of the two years (no significant nitrogen or nitrogen × species effects, $F_{1, 259} = 0.03$ and $F_{5, 259} = 0.51$, $P > 0.05$ in both cases).

Nitrogen additions increased species' foliar nitrogen concentrations, expressed on either an area or mass basis (significant nitrogen effects in ANOVA, $F_{1, 241} = 55.42$ and 33.38, respectively, $P < 0.001$ for both), and these responses were consistent across all species (no significant nitrogen × species interactions, $F_{5, 241} =$

1.44 for area and 1.73 for mass, $P > 0.05$ for both). Overall, nitrogen addition increased foliar nitrogen from 16.0 mg/g in control seedlings to 20.5 mg/g in high nitrogen seedlings (25% increase). These changes only led to significant increases in total foliar nitrogen content ($F_{1,50} > 17.0$, $P < 0.001$) for the two broad-leaved species that grew larger with added nitrogen (yellow birch and red maple; 4.5 and 2.6 times greater from control to high nitrogen, respectively) and for the one conifer species that showed a tendency towards increased growth (white pine, 1.9 times greater).

Modeled effects on composition

In all SORTIE control runs (original parameters used, no nitrogen effects), conifers consistently dominated the forest community (Fig. 2), with white pine making the largest contribution to community composition at 200 yr (29% of total basal area), with further dominance by the late-successional conifers, hemlock and red spruce, developing over the next 300 yr (each end close to 36%). Yellow birch remained a consistent component of the forest community (10–13% throughout), while both maple species showed steady declines in relative abundance after an initial peak around 50 yr (14% for red maple, 9% for sugar maple).

To examine potential effects of nitrogen availability on forest dynamics mediated through seedling regeneration, SORTIE parameters were adjusted based on the results of both of our seedling experiments (Table 2). As described above, in high-light simulated gap conditions, nitrogen only influenced seedling growth and not mortality, and it was only the fast-growing broad-leaved species that showed a significant response to increased nitrogen at early growth stages. Therefore, in the nitrogen SORTIE simulations, the high-light growth parameter (G_1) was adjusted for both yellow birch and red maple (Table 2). In contrast, in the low light conditions of the forest understory, nitrogen addition only influenced seedling mortality and not growth. All study species except sugar maple were significantly affected by increased nitrogen to some de-

FIG. 2. Changes in mean adult relative basal area (*y*-axis) through time generated from SORTIE simulations with original control parameters (from Pacala et al. 1996) for the six study species.
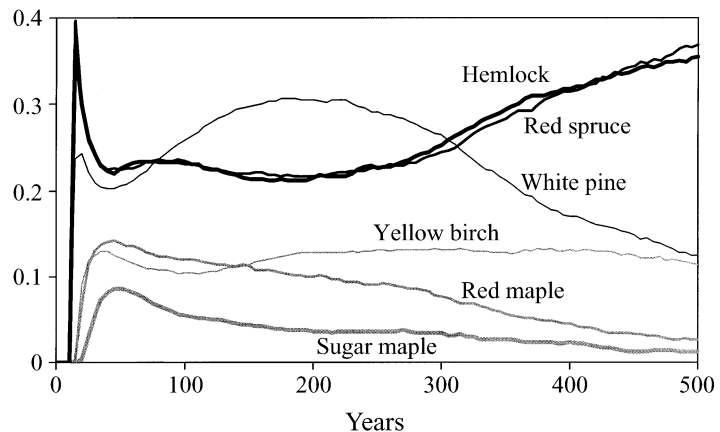
TABLE 2. Nitrogen-induced changes in SORTIE growth and mortality parameters. Effects are shown as change in the nitrogen treatment relative to control (Growth$_N$/Growth$_C$ or %Mortality$_N$/%Mortality$_C$), with only changes that were statistically significant ($P < 0.05$) included.

	High-light growth parameter (G_1)		Low-light mortality parameter (M_1)	
Species	Low N	High N	Low N	High N
Yellow birch	1.36	1.72	1.44	1.54
Red maple	1.16	1.27	1.90	2.56
Sugar maple	...	...	...	...
White pine	...	...	2.00	2.35
Red spruce	...	...	1.09	1.10
Hemlock	...	...	0.93	0.03

Notes: Low N corresponds to 2.5 g N·m^{-2}·yr^{-1}, and high N corresponds to 7.5 g N·m^{-2}·yr^{-1}. Values greater than 1 correspond to a nitrogen-induced increase in the parameter, while values less than 1 correspond to a nitrogen-induced decrease in the parameter. For red maple, the M_2 parameter (mortality sensitivity to carbon balance) was altered instead (see *Materials and methods: SORTIE parametrization: Mortality* for details).

gree (Catovsky and Bazzaz 2002*a*). Nitrogen addition increased mortality of white pine and red maple by more than two-fold, while the nitrogen-induced increases in mortality of yellow birch and red spruce were considerably smaller (Table 2). Hemlock was the only species whose mortality was significantly decreased by increased nitrogen availability.

Increasing nitrogen availability altered these basic successional dynamics by favoring particular species at different times in the course of succession. We first focused on effects of nitrogen addition on predicted adult relative basal areas, taking into account only the bounds of the stochastic variation in SORTIE (baseline runs) (Fig. 3). Increased nitrogen availability led to increased community contribution from yellow birch throughout all but the very late stages of succession (500 yr). Very early on (25 yr), yellow birch relative basal area increased from 12% in the control to 18% in low nitrogen and 24% in high nitrogen, and this increase persisted throughout the first 250 yr of succession (Fig. 3a–d). At later stages of succession (250 and 500 yr), nitrogen availability enhanced community dominance by the most late-successional species in the system, hemlock (from 29% to 34% and 42%) (Fig. 3d, e). In contrast to these increases, three mid-successional species (red maple, white pine, red spruce) all showed declines in their representation within the mixed forest community. Nitrogen-induced declines in red maple began relatively early in succession (at 50 yr, 14% control vs. 12% low nitrogen and 10% high nitrogen) and, like yellow birch, persisted throughout all but the very late stages (up to 250 yr) (Fig. 3a–d). Nitrogen led to decreased abundance of white pine between 100 and 500 yr (on average, 22% control vs. 18% low nitrogen and 14% high nitrogen), while declines for red spruce only occurred at the beginning
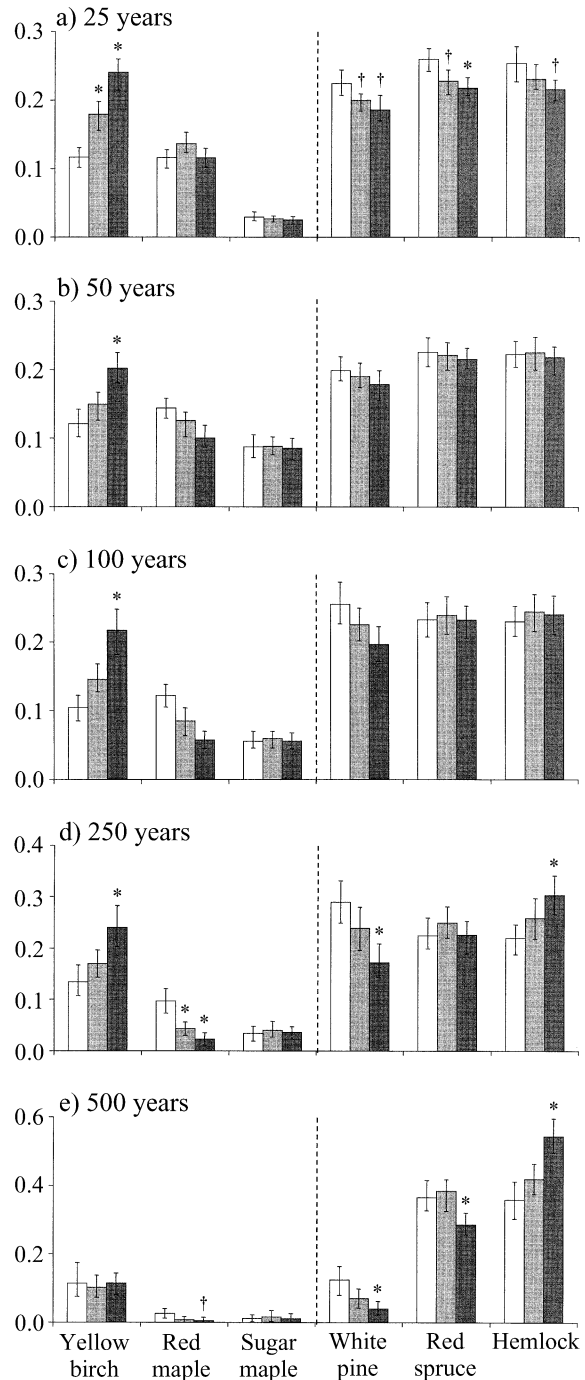

FIG. 3. SORTIE simulations showing effects of nitrogen addition (white = 0, light gray = 2.5, and dark gray = 7.5 g N·m^{-2}·yr^{-1}) on species' adult relative basal area at different time points in succession (25, 50, 100, 250, and 500 yr). Bar heights correspond with the species' mean relative basal area from 40 replicate runs of SORTIE. Error bars correspond with predicted relative basal areas from the central 95% of the simulations and represent inherent stochasticity in the model originating from probabilistic submodels in SORTIE. Nitrogen treatments that led to a significant change in relative basal area for a given species–time combination are shown with symbols above the bars: †, no overlap in central 90% of model prediction; *, no overlap in central 95% of model prediction.

(25 yr) and end (500 yr) of the successional sequence (Fig. 3a, e).

Our uncertainty analysis revealed which of these community level predictions were robust to observed error in seedling growth and mortality responses to nitrogen (Fig. 4). Here we again assessed significant nitrogen effects on community composition by examining overlap in the central 95% (and 90%) of predictions, which in this case incorporated both stochastic variation in the model and error in seedling growth and mortality responses. Most of the changes in relative basal area under low nitrogen addition (2.5 g $N \cdot m^{-2} \cdot yr^{-1}$) did not remain significant in the uncertainty analysis, but a number of the high nitrogen changes (7.5 g $N \cdot m^{-2} \cdot yr^{-1}$) did. Most notable was the robustness of the nitrogen-induced increase in yellow birch relative basal area early in succession, although the wider error bounds of the uncertainty analysis meant that the increase only extended to 100 yr (Fig. 4a–c), rather than 250 yr (compare Figs. 3d and 4d). The significant increase in hemlock relative basal area later in succession was also robust to experimental error, but only at the very late stages of succession (500 yr, Fig. 4e) and not earlier (e.g., 250 yr, Fig. 4d). For the other species (red maple, white pine, red spruce), the nitrogen-induced declines in relative basal area that occurred in the baseline runs were less robust in the uncertainty analysis. Examining overlap in the central 90% of SORTIE predictions, we found significant declines in white pine and red maple relative basal area at mid-successional time points, e.g., 100 and 250 yr (Fig. 4c, d), and red spruce very early in succession (25 yr, Fig. 4a). However, most changes that were significant for these species in the baseline runs were no longer significant in the uncertainty analysis.

As well as evaluating the robustness of our model results, the uncertainty analysis was used to partition variance in species' relative abundance due to the separate growth and mortality parameters (Fig. 5). Sugar maple was the only species whose parameters were not altered in the high nitrogen model runs, and, as a result, changes in model parameters explained relatively little (<30%) of the variance in its relative abundance through time (Fig. 5c). For the earlier successional species (Fig. 5a, b, and d), variation in their individual growth/mortality parameters explained much of the variance in their relative abundance (82% for yellow birch, 77% for red maple, 53% for white pine; expressed relative to total variance explained in each case). For both yellow birch and red maple very early in succession, positive growth effects contributed a greater proportion of the variance in relative abundance than did negative mortality effects (e.g., 22% vs. 7% for yellow birch, 23% vs. 11% for red maple). However, this effect was quickly reversed, particular for red maple, whose growth contributions did not persist beyond the first 25 yr (Fig. 5b). By the end of the successional sequence, nitrogen-induced changes in mortality ex-
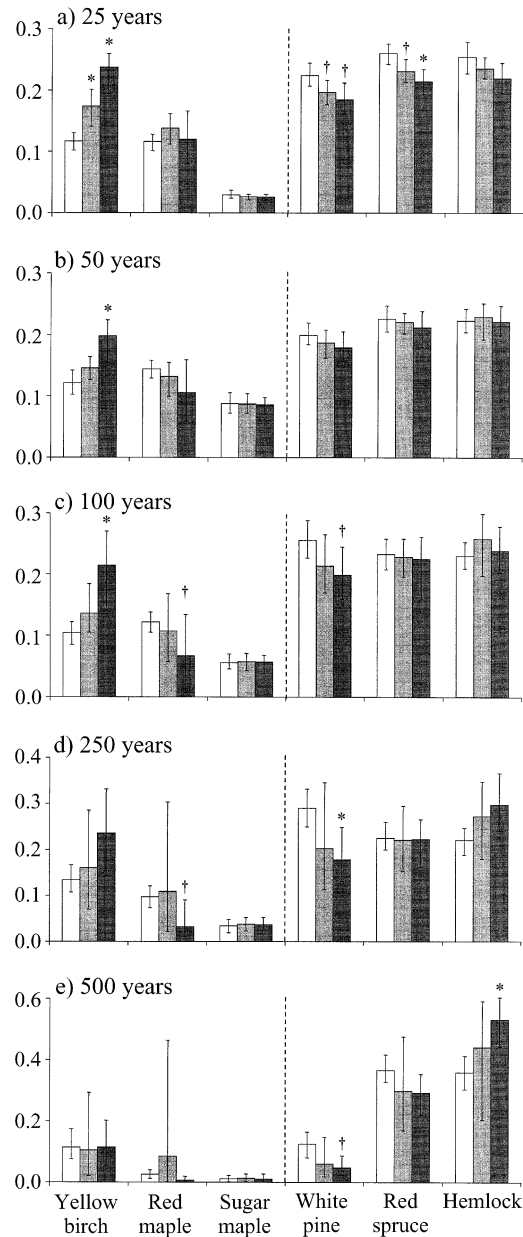

FIG. 4. Uncertainty analysis of SORTIE simulations showing effects of nitrogen addition (white = 0, light gray = 2.5, and dark gray = 7.5 g $N \cdot m^{-2} \cdot yr^{-1}$) on species' adult relative basal area at different time points in succession (25, 50, 100, 250, and 500 yr). Bar heights correspond with the species' mean relative basal area from 40 runs of SORTIE, with parameters generated from a distribution based on the error in the experimental effects of nitrogen addition. Error bars correspond with predicted relative basal areas from the central 95% of these simulations, representing uncertainty in model predictions arising from observed error in nitrogen treatments. Nitrogen treatments that led to a significant change in relative basal area for a given species–time combination are shown with symbols above the bars: †, no overlap in central 90% of model prediction; *, no overlap in central 95% of model prediction.
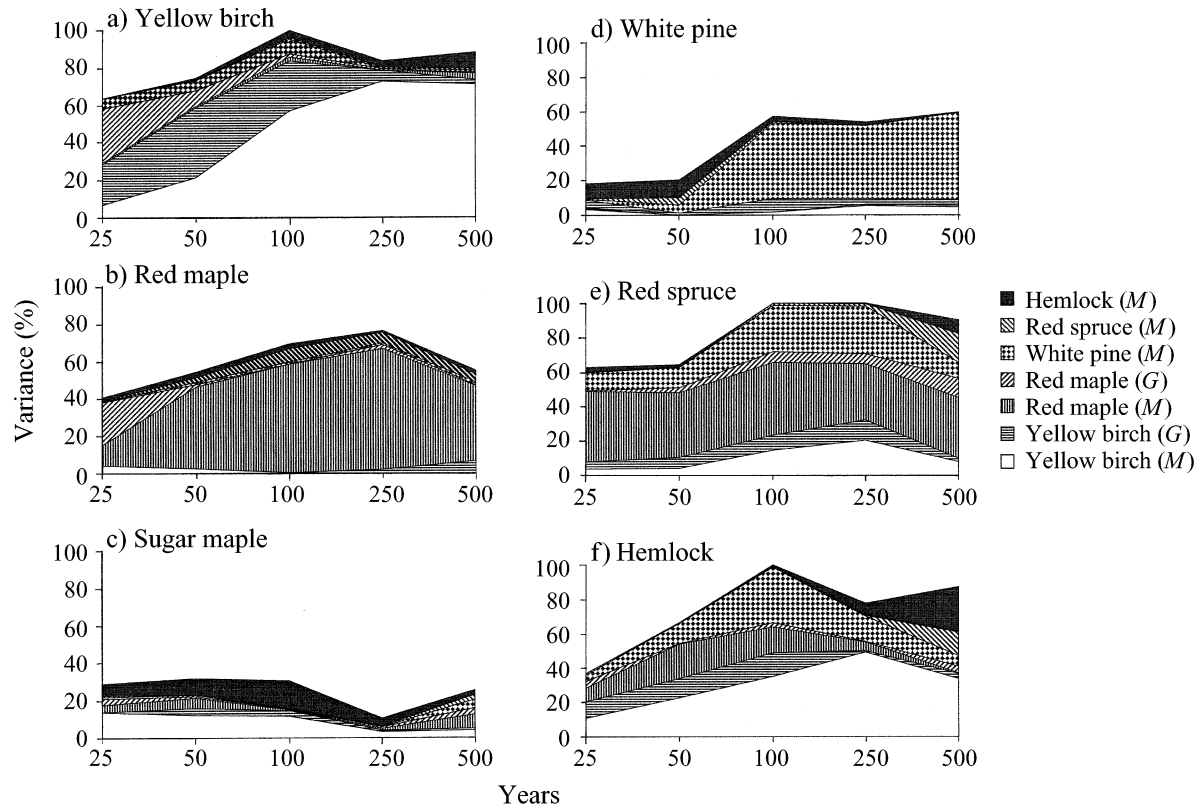
FIG. 5. Percentage of variance in relative abundance of the study species at different time points (25, 50, 100, 250, and 500 yr) explained by changes in model parameters (G = species growth function altered, M = species mortality function altered). Variance values were obtained from the squared Pearson correlation coefficients (r^2), and are only shown for the high nitrogen SORTIE runs (7.5 g $N \cdot m^{-2} \cdot yr^{-1}$).

plained 65–70% of the variance in relative abundance for both these species. Similarly, for white pine, mortality only explained a substantial proportion of variance in relative abundance after 100 yr, paralleling the onset of significant negative impacts of nitrogen on white pine relative abundance.

In contrast to this direct link between nitrogen-induced changes in species' model parameters and their relative abundance, the dynamics of the later successional species (red spruce and hemlock) were strongly determined by changes in the growth and mortality of other species throughout much of succession (Fig. 5e, f). Up until 250 yr, nitrogen-induced increases in red spruce mortality explained <1% of the variance in its relative abundance, while decreases in hemlock mortality explained <10% of the variance in its relative abundance. However, by 500 yr, when hemlock first showed a robust increase in relative abundance (Fig. 4e), nitrogen-induced decreases in hemlock seedling mortality explained >30% of the total variance in hemlock relative abundance (Fig. 5f). Similarly, for red spruce, nitrogen effects on mortality also contributed more to variance in relative abundance by 500 yr, but their contribution

was still restricted to <20%, and consequently did not lead to robust declines in red spruce relative abundance later in succession (Fig. 4e).

DISCUSSION

Species' responsiveness to increased nitrogen availability

Early seedling growth rate was a good predictor of species' responsiveness to increased nitrogen availability. When grown both individually and in competition, earlier successional broad-leaved species (yellow birch and red maple) consistently showed the greatest increases in biomass in response to nitrogen addition, while the most late-successional broad-leaved species (sugar maple) and all the coniferous species examined did not grow significantly larger in treatments with higher nitrogen availability. We found a significant correlation between a species' growth rate during the first two years of its life and its growth enhancement following nitrogen addition, suggesting that growth rate, more than leaf habit or even successional position, may be a species' trait closely tied to nitrogen responsiveness. Of course, all of these traits

(leaf habit, successional position, growth rate) are intimately related (Reich et al. 1998*a*), and thus all contribute in some way to determining the degree of nitrogen growth enhancement for a species. Preference for ammonium vs. nitrate could not be assessed in this experiment, but may be an important driver of seedling regeneration and community dynamics (Crabtree and Bazzaz 1993, McKane et al. 2002). Temperate forest soils are ammonium dominated, but often show peaks of nitrification (and nitrate concentrations) following disturbance (Mladenoff 1987, Bradley 2001).

The emergence of species growth rate as a good predictor of nitrogen responsiveness supports basic ecological theory that fast-growing species are more responsive to increases in resource availability (Grime 1979, Bazzaz 1996). Species' with high inherent growth rates typically have a suite of traits that give them the capacity to take up nutrients rapidly from the soil (Lajtha 1994, Aerts and Chapin 2000) and utilize these nutrients effectively to increase carbon uptake and plant growth (Grime et al. 1997, Reich et al. 1998*b*), while slow-growing species place greater emphasis on high nutrient retention and high nutrient use efficiency, at the expense of a greater potential for resource capture (Chapin 1980, Aerts and Chapin 2000). This relationship was particularly strong for seedlings grown in a competition treatment where nitrogen-induced fast early growth allowed certain seedlings to grow ahead of their competitors and thus experience reduced competition for light (Berntson and Wayne 2000). Yellow birch showed lower responsiveness to increased nitrogen availability under competition than as individuals, as its small initial seedling size often placed it subordinate to red maple in mixed-species stands. Plant competition often changes predictions about species' responses to global environmental change (Catovsky and Bazzaz 2002*b*).

What are the mechanisms underlying these species-specific responses? All species had greater foliar nitrogen concentrations with increasing nitrogen availability (except for red spruce), but the more responsive species were able to take up more nitrogen from the soil on a whole-plant basis. Species whose growth was not significantly affected by nitrogen amendment (conifers particularly) apparently were not able to utilize the additional nitrogen in their leaves for photosynthesis. The photosynthetic capacity of evergreen coniferous species has been shown to be much less responsive to foliar nitrogen concentrations than that of deciduous broad-leaved species (Reich et al. 1995, Shinano et al. 2001), although the physiological mechanisms for these differences are still equivocal (Becker 2000). Conifers might be less responsive to increases in foliar nitrogen than broad-leaved species, if they were to allocate a greater proportion of the additional nitrogen to structural rather than photosynthetic proteins (Bazzaz 1997). Alternatively, leaf structure might impose a greater stomatal limitation on photosynthesis

in conifers than in broad-leaved species (Sharkey 1985), so that conifers have a lower capacity to utilize additional nitrogen for photosynthesis. More detailed leaf-level physiological studies are needed to ascertain what determines a species' capacity to make use of higher foliar nitrogen concentrations.

Scaling up seedling responses to nitrogen

Our understanding of controls on forest dynamics is constrained by the short-term and small-scale nature of most ecological experiments (individual seedlings grown in pots for up to three growing seasons) relative to the appropriate scale of interest (whole-ecosystem dynamics over many generations) (Bazzaz et al. 1996). As a result, we need to utilize different ways to extrapolate from the scale of our experimental studies to higher levels of organization (Ehleringer and Field 1993). In the current paper, we integrated the results of two field-based experimental manipulations into an empirically based forest dynamics model (SORTIE) to examine how the influence of nitrogen availability on seedling growth and mortality might affect our understanding of structure and dynamics of temperate forests in eastern North America. Current forest models are primarily driven by effects on and responses to light availability (Pacala et al. 1996). We now need to determine how such models can be applied to a range of forests within the same region, especially as soil fertility changes.

Our experimental work showed that, in the high light conditions of a simulated forest gap, increased nitrogen favored growth of fast-growing broad-leaved species (yellow birch and red maple), while in the low light conditions of forest understory, nitrogen promoted survival of the most shade-tolerant conifer species (hemlock), and increased mortality of a number of less tolerant species (red maple and white pine, in particular) (Table 2). Incorporating these changes into SORTIE revealed that seedling responses to nitrogen availability could act as an important driver of community dynamics in these mixed forests, potentially altering successional rates of change.

Nitrogen-induced changes at the community level arose from the combined effects of nitrogen on two distinct components of seedling regeneration: growth in high light and mortality in low light (Table 2 and Fig. 5). In some cases, the results of nitrogen on one component of seedling regeneration could be directly related to the SORTIE outcomes. For example, the decrease in white pine from 100 yr onwards could be attributed primarily to nitrogen-induced increases in seedling mortality in the understory for this species. In other cases, the resultant dynamics were a more complex combination of nitrogen effects on both growth and mortality. For both yellow birch and red maple, their changes in relative abundance through succession resulted from a trade-off between the positive effects of nitrogen on high-light growth and the negative ef-

fects of nitrogen on low-light survival. Yellow birch benefited from increased nitrogen availability on the whole, because the positive effects predominated early in succession and persisted for the first 100 yr, while the negative effects did not come into play until later in succession when other species exhibited even stronger negative effects of nitrogen on survival. By contrast, nitrogen reduced red maple abundance on the whole, because the negative effects of nitrogen on low-light survival outweighed the positive effects on high-light growth at all but the very earliest stages of succession. A third class of scaling between seedling regeneration and community dynamics was found for the late-successional conifer species, whose dynamics were dependent on nitrogen effects not only on the regeneration of their own seedlings, but also the seedlings of other species. For example, the increased relative abundance of hemlock later in succession arose both from increased low-light survival of its own seedlings, but also from decreased survival of seedlings of white pine, red maple, and particularly yellow birch.

Through its effects on seedling regeneration, higher nitrogen availability led to exaggerated successional dynamics in mixed temperate forests. The nitrogen-enhanced growth of faster growing species (yellow birch) led to their increased dominance earlier in succession, while the nitrogen-enhanced survivorship of later successional species (particularly hemlock) enabled them to maintain a more persistent seedling bank in the model, and enabled hemlock to increase its dominance in late-successional forests. This main finding was robust to an uncertainty analysis that incorporated experimentally derived error into the seedling/sapling growth and mortality submodels. In contrast, the identity of the species replaced by yellow birch and hemlock was less certain and more sensitive to uncertainty in our parameter values. Red maple and white pine are the most likely candidates to decline in abundance with higher nitrogen availability, but this outcome is likely to be site dependent.

The SORTIE model provided a useful way to examine the potential for seedling nitrogen responses to scale up and influence forest successional dynamics. However, the results should not be seen as definitive predictions of overall forest responses to enhanced nitrogen availability, because soil nitrogen will affect other components of forest dynamics beyond the seedling/sapling stage, e.g., growth, survivorship, and reproduction of mature trees (Mitchell and Chandler 1939, Magill et al. 1997). Even as a tool for examining the larger scale significance of nitrogen effects on seedling regeneration, this modeling approach makes certain assumptions: (1) that the changes observed for seedlings in the first two years are carried throughout the seedling/sapling stage, i.e., until reaching 10 cm dbh when the adult growth function takes over, and (2) that nitrogen-induced changes will apply equally to seedlings at all points in succession, i.e., whether 25 or 250 yr after a major disturbance. To establish whether these are reasonable assumptions or not, we need to determine the degree to which seedlings acclimate to novel environmental conditions (e.g., Bazzaz et al. 1993), and the extent to which nitrogen availability changes through succession (e.g., Vitousek and Reiners 1975).

Implications for future forest dynamics

Increasing human impacts on natural ecosystems has heightened the need to understand controls on ecosystem structure and function (Vitousek et al. 1997*b*). A multiple resource perspective is useful in this regard, as many novel perturbations involve changes in seedlings' resource environment (Field et al. 1992, Bazzaz and Catovsky 2002). If we can understand how species behave along a suite of resource axes, we should be able to predict patterns of forest dynamics under a range of future scenarios. For example, nitrogen deposition in temperate regions has emerged as one of the most dramatic human-induced changes since industrialization (Vitousek et al. 1997*a*). Natural ecosystems in all these temperate regions are commonly nitrogen limited (Vitousek and Howarth 1991), and nitrogen deposition might exert profound effects on their structure and function (Magill et al. 1997, Aber et al. 1998). Our SORTIE results have some bearing on predicting impacts of nitrogen deposition on mixed temperate forests, because using the model we were able to assess potential consequences of nitrogen-induced changes in seedling regeneration for long-term forest dynamics. Our findings suggest that, through effects on seedling growth and survival, increased nitrogen loading in the future will further favor growth of earlier successional species following natural disturbance events, while later successional species (particularly hemlock) will be able to maintain a more persistent seedling bank, and thus remain a dominant component of late-successional forests.

Increased nitrogen loading in the future will most likely change temperate forest community structure and dynamics, but the exact nature of any change will be determined by: (1) long-term ecosystem consequences of nitrogen deposition, and (2) interactions with other human impacts on forests. Our relatively simple modeling analysis does not account for a suite of other nitrogen-induced ecosystem-level changes that will all affect long-term forest responses to nitrogen deposition, e.g., degree of nitrogen retention within forests (see nitrogen saturation hypotheses; Aber et al. 1998, Emmett et al. 1998), sequestration of nitrogen within soil organic matter (Gundersen et al. 1998), timing and extent of vegetation uptake of nitrogen from the soil (Boxman et al. 1998), and leaching of base cations (Ca, Mg, and K) (Likens et al. 1996). In addition, human activities will exert a range of other perturbations on temperate forests that will interact with these nitrogen effects (Aber et al. 2001), such as (1) direct manage-

ment of forests and utilization of wood products (Irland et al. 2001), (2) introduction of invasive species, such as the hemlock woolly adelgid (*Adelges tsugae* Annand) (McManus et al. 2000), and (3) altered atmospheric composition, such as elevated CO_2 (Bolker et al. 1995). Incorporating modified seedling parameters into the SORTIE model provided a useful first indication of how nitrogen availability could potentially influence long-term forest dynamics through its impacts on seedling regeneration. Future attempts to predict the impacts of environmental change on forest structure and function should consider both these longer term ecosystem-level impacts, as well the effects on individual tree performance beyond its first few years as a seedling (e.g., Bazzaz et al. 1993).

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