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Sapling growth in response to light and nitrogen availability in a southern New England forest

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Abstract

In the northeastern US, the availability of light and nitrogen (N) limits the rate of woody plant growth in the forest understory and N limits forest productivity. Interspecific differences in the growth responses of saplings to the availability of these resources could affect the species composition of forest communities. While many studies have examined the relationship between shade-tolerance and forest dynamics, few studies have examined the relationship between natural variation in N availability and sapling growth. The objective of this study was to compare the relative importance of natural variation in light and N availability on sapling growth in a northwestern Connecticut forest.

We studied six species that differ in shade-tolerance and presumed N requirements. We randomly selected individuals growing in the understory and in single- and multiple tree-fall gaps representing a natural gradient in light and N availability. Light availability was measured using hemispherical photography. N availability was measured as the rate of N mineralization and nitrification in buried bag soil incubations during the mid-summer. For each species, we developed species-specific regression models of sapling growth as a function of light and N availability. Variation in light availability explained 21–79% of the variation in sapling growth. The six species differed in their growth rates under high light and under low light. Only red maple and sugar maple growth were significantly related to N availability and N availability explained <7% of the variation in the growth of these two species. Red maple growth increased with increasing N mineralization under high light. Sugar maple growth increased with increasing nitrification under low light. In the four remaining species there was no significant relationship between sapling growth and N availability. Despite the correlation between N availability and forest productivity regionally, our results imply that light availability is the dominant resource limiting sapling growth in this forest. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The probability that a tree of a given species reaches the forest canopy is often determined by its performance as a sapling (Horn, 1975; Canham, 1989; Clark

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and Clark, 1991; Kobe et al., 1995; Kobe, 1996). Light and nitrogen (N) commonly limit the rate of plant growth and N limits forest productivity (e.g., Sipe and Bazzaz, 1995; Reich et al., 1997; Walters and Reich, 1997; Fahey et al., 1998). Variation in the availability of resources coupled with interspecific differences in resource use by saplings should have an effect on the species composition of forests (Latham, 1992; Pacala et al., 1996). Yet the empirical basis for joint resource limitation by light and N in field grown saplings is poorly established and the community-level implications are uncertain.

Shade-tolerance has been the subject of much empirical and modeling research (e.g., Lorimer, 1983; Canham et al., 1994; Kobe et al., 1995; Hugh and Aarssen, 1997) and interspecific differences in shade tolerance clearly affect forest dynamics. For example, Kobe et al. (1995) found that under low light, small differences in juvenile tree growth led to differences in mortality that were greater than 2 orders of magnitude among species. Pacala et al. (1996) found that small changes in the growth–mortality relationships of juvenile trees altered species relative abundances during succession and slowed the rate at which late-successional species dominated a forest stand.

In contrast, sapling growth in response to natural variation in N availability has been infrequently studied (c.f. Walters and Reich, 1997) despite a large body of controlled-environment studies showing that N limits the growth rate of many tree species (e.g., Burke et al., 1991; Bazzaz et al., 1993; Knox et al., 1995; Canham et al., 1996; Wait et al., 1996). At least three explanations account for the small number of non-manipulative field studies. Firstly, N availability is heterogeneously distributed making the measurement error in N availability potentially large. Secondly, growth rates in even the most productive ecosystems are N limited (Reich et al., 1997) implying that the natural range of variation in N availability is smaller than the potential range of a species' growth response. Together measurement error and limited variation in N availability make it difficult to detect a relationship between growth and natural variation in N availability. Thirdly, variation in N availability is often regulated by a change in the species composition of forests across soil types (e.g., Pastor et al., 1984; Chapin et al., 1986a; Zak et al., 1989). Changes in soil type (e.g., texture, parent material composition)

change soil water holding capacity, phosphorus supply, cation availability, and N availability making it difficult to determine whether one or several resources regulate tree growth (Whitney, 1991).

N availability differs significantly and predictably beneath different canopy tree species on the same soil type in NW Connecticut (Finzi et al., 1998a). Rates of mid-summer N mineralization and nitrification are two-times greater beneath red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and white ash trees (*Fraxinus americana* L.) than beneath red oak (*Quercus rubra* L.), beech (*Fagus grandifolia* Ehrh.), and hemlock (*Tsuga canadensis* Carr.) trees. Interspecific differences in litter chemistry and production are responsible for the spatial variation in N mineralization and nitrification within stands beneath different tree species (Finzi and Canham, 1998; Finzi et al., 1998b). Given that N availability in New England forests limits plant growth (Aber et al., 1993), and the non-random mosaic of N availability at our study sites in NW Connecticut (Finzi et al., 1998a), we hypothesized that variation in light and N availability beneath different canopy tree species or in gaps created by different canopy tree species would affect sapling growth rates. The objective of this study was to compare the relative importance of natural variation in light and N availability on sapling growth in a northwestern Connecticut forest.

2. Methods

2.1. Tree species and study sites

Forests in this region include elements of both the conifer-hardwood forests of northern New England and the oak forests of southern New England. We studied six species that are dominant in mid- to late successional stands: beech, eastern hemlock, sugar maple, red maple, white ash, and northern red oak.

This research was conducted on land belonging to the Great Mountain Forest (GMF) and the Bridgeport Hydraulic Company (BHC). Both properties are located in northwestern Connecticut (approximately 42°N, 73°15'W) on the Canaan Mountain plateau at elevations of 350–550 m. Soils throughout the plateau are acidic, sandy loams derived from glacial till over mica-schist bedrock. The soils on the plateau are

classified as typical dystrochepts (Hill et al., 1980). Sites were located in areas where we could find several individuals of one or more species and we sampled up to 11 individuals per species per site. There were a total of 20 sites used in this study, ranging in size from 0.2 to 0.5 ha. Sites were only located in mesic, upland areas and not in poorly drained (e.g., red maple swamps), or excessively well drained (e.g., localized ridge-tops, outwash plains) areas.

2.2. Data collection

2.2.1. Growth rates

We harvested a total of 206 saplings ranging in radius from 0.5 to 4.0 cm (at 10 cm above the soil surface, Table 1). Sample sizes for each species ranged from $n = 26$ for red oak to $n = 39$ for sugar maple and beech. Saplings were tagged early in the growing season, and harvested in the autumn after leaf-fall. Once the saplings were harvested, we measured the current year's radial growth using a microscope placed over a sliding-stage micrometer attached to a personal computer. We used the program TREERING Version 3.0 (developed at IES by C.D. Canham) to measure the radial growth with 0.01 mm accuracy.

2.2.2. Light availability

We used the gap light index (GLI-% of full sun) developed by Canham (1988) to measure the amount of light available to individual saplings during the growing season. Above each study sapling, fish-eye photographs were taken at 1.5 m height on over-cast

days in the middle of the summer preceding harvest. The study saplings that were taller than 1.5 m were gently pulled to the side so that their foliage was not included in the photograph. Photographs were taken with an 8 mm true fish-eye (equiangular) lens.

2.2.3. Index of nitrogen availability

Nitrogen availability to each sapling was measured as a single, mid-summer in situ soil incubation using a modification of the buried bag procedure developed by Eno (1960). Buried bags were located ~50 cm from the base of each sapling. At each sample location we excavated an initial sample containing both forest floor and mineral soil to a depth of 15 cm. Immediately adjacent to the initial sample, we cored forest floor and mineral soil using an AMS soil bulk density sampler (5 cm × 15 cm) fitted with a polycarbonate liner. The liner was then removed from the corer, wrapped in a polyethylene bag on both ends, capped, and replaced into the original hole. This sample remained in the ground for 28 days, from mid-July to mid-August 1994.

We did not conduct buried bag estimates of net N mineralization throughout the year for each sapling. Therefore, we do not know unequivocally whether the variation in N availability we measured among sites is representative of annual among site differences. However, in an independent data set, we found that variation in mid-summer rates of net N mineralization among sites were consistent with annual among site differences in N availability (Finzi et al., 1998b) leading us to believe that our mid-summer index of

Table 1

Selected attributes of the harvested saplings used in growth analysis. 'Radius' refers to the radius of the sapling 10 cm above the soil surface. All cells indicate the ranges of the resources over which the saplings were growing.

Species	n	Radius (mm)	Gap light index (% full sun)	Mineralization ^a ($\mu\text{g} [\text{g soil}]^{-1}$ 28 per day)	Nitrification ^b ($\mu\text{g} [\text{g soil}]^{-1}$ 28 per day)
Red maple	35	9.5–33.0	0.7–46.9	0.0–58.7 ^c	2.0–27.4
Sugar maple	39	5.5–33.5	0.7–46.0	2.9–40.7	3.7–30.1
Beech	39	5.5–23.5	0.3–35.4	6.8–44.1	3.9–22.7
White ash	36	5.2–24.5	1.1–41.7	4.5–31.5	1.9–27.9
Red oak	24	5.0–25.5	2.9–42.9	2.6–32.7	0.0–14.2
Hemlock	31	7.5–40.0	0.3–42.9	1.1–42.7	2.1–13.8

^a Mineralization rates were increased by $8.26 \mu\text{g} [\text{g soil}]^{-1}$ 28 per day, the largest rate of immobilization during the mid-summer.

^b Nitrification rates were increased by $3.9 \mu\text{g} [\text{g soil}]^{-1}$ 28 per day, the largest rate of NO_3^- immobilization during the mid-summer.

^c Only two incubations had rates higher than $40 \mu\text{g} [\text{g soil}]^{-1}$ 28 per day.

N availability is an adequate surrogate for N availability throughout the growing season.

Both the initial samples and the core samples were treated identically in the laboratory. Following retrieval from the field, all samples were passed through an 8 mm mesh sieve to remove most large roots and stones. A 20.0 g subsample of the sieved soil was placed in a 250 ml extraction cup to which 200 ml of 2 M KCl was added. The extracted soil samples were shaken every 10 min for 1 h and allowed to settle over night. The following morning, the supernatant was analyzed colorimetrically for NH_4^+ and NO_3^- on an autoanalyzer (Alpkem Enviroflow Model 3590). The remainder of the sample was dried in a drying oven at 70°C for 5 days and used to determine gravimetric soil water content and bulk density.

2.3. Statistical analyses

We used nonlinear regression analysis to model the effects of resources on growth. We fit the models in a two-stage processes. For each species, we first modeled growth as a function of light availability. We focused on the relationship between light and growth first because increases in light from <2% in the understory to >50% in gaps are associated with increases in sapling growth that cannot be explained in the absence of light availability (Pacala et al., 1994, 1996). We then added the rate of N mineralization (or nitrification) as a second independent variable.

We used univariate and bivariate Michaelis–Menten functions to model the effects of light and N on growth. These functions are commonly used (e.g., Tilman, 1982; Rastetter et al., 1991; Rastetter and Shaver, 1992; Pacala et al., 1994; Bridgman et al., 1995), they are easily and biologically interpretable, and their behavior depends on a small number of parameters (P_1 , P_2 , and in the bivariate case, P_3). For example, in a univariate Michaelis–Menten function the parameter, P_1 , defines the rate of asymptotic growth and the parameter, P_2 , shapes the growth response under low resource availability. Large P_1 values indicate that saplings grow rapidly when resource availability is high (and conversely for small values of P_1). Large P_2 values indicate that when resources are scarce, a small increase in resource availability leads to a large increase in growth (and conversely for a small P_2).

We used the following univariate, Michaelis–Menten regression equation to model the effects of light on growth:

$$\Delta R = rf(L) + e \quad (1)$$

where,

$$f(L) = \frac{P_1 \times \text{Light}}{P_1/P_2 + \text{Light}} \quad (2)$$

and,

$$e \sim N(0, \sigma^2) \quad (3)$$

ΔR in Eq. (1) is the ring width increment of an individual of radius, r , growing under light level L . P_1 and P_2 in Eq. (2) are the asymptotic growth and growth at low light parameters, respectively. We tested for the normality of the residuals and found that they were normally distributed with homogeneous variance. We, therefore, modeled the residuals with a normal distribution centered around 0 with variance σ^2 .

We compared the light-dependent growth model to growth as a function of light and N mineralization (or nitrification). To test for joint limitation we fit the following bivariate Michaelis–Menten function:

$$\Delta R = rf(L, N) + e \quad (4)$$

where

$$f(L, N) = \frac{P_1 \times \text{Light} \times \text{Nitrogen}}{(P_1/P_2 + \text{Light}) \times (P_1/P_3 + \text{Nitrogen})} \quad (5)$$

ΔR , r , P_1 , P_2 , and e are as in Eqs. (2)–(4). However, P_1 is now modified by both light and nitrogen availability. P_3 is the slope at low nitrogen parameter. Because species could differ in their uptake of NO_3^- from soils, we regressed sapling growth on N mineralization or nitrification. Eq. (5) is negative for negative rates of N mineralization and nitrification but growth was always > 0. We, therefore, added the smallest (negative) rate of mineralization and nitrification to all mineralization and nitrification observations, respectively (Table 1). This does not change the variability among observations but simply shifts their center (Casella and Berger, 1990).

We estimated coefficients (P_1 , P_2 , and P_3) with the method of maximum likelihood estimation (= log likelihood in Table 3) using the Metropolis Algorithm and simulated annealing (Szmura and Barton, 1986).

Ninety-five percent confidence intervals for the parameter estimates were obtained from the property that $-2 \times \log$ -likelihood is asymptotically χ^2 distributed (Casella and Berger, 1990). We calculated a partial- F statistic for Eq. (5) to assess whether or not the additional parameter associated with N availability was significant. Thus, we treated the step from a nonlinear regression analysis of light-only to a nonlinear regression analysis of light and N as a forward-selection, multiple regression problem (SAS Institute, 1987). As with most multiple regression models, we chose to use $\alpha = 0.15$ as the cut-off level of significance to keep a variable in the model (SAS, Cary, NC).

3. Results

3.1. Resource availability

The mean quantities of available light, soil moisture, N mineralization, and nitrification at each site are presented in Table 2. Light availability ranged from

0.3–46.7% of full sun. Soil moisture content ranged from 0.05–0.63 g (g soil)⁻¹. Nitrogen mineralization and nitrification rates ranged from –8.26 to 27.0 μg (g soil)⁻¹ 28 per day, and from –3.90 to 26.3 μg (g soil)⁻¹ 28 per day, respectively. Soil moisture and light availability were not correlated with one another (Fig. 1a). Soil moisture and N mineralization rates were not correlated with one another (Fig. 1d). Nitrogen mineralization and light availability were negatively correlated with one another whereas N mineralization and nitrification were positively correlated with one another (Fig. 1b and c, respectively).

3.2. Sapling growth responses

For all species, variation in sapling growth was significantly related to variation in light availability (Fig. 2). Light availability explained 21–79% of the variation in sapling growth (Table 3). Species differed in both their asymptotic growth rate (P_1) and their rate of growth under low light (P_2 , Table 3). Asymptotic growth was highest for hemlock ($P_1 = 0.3416$) and

Table 2

Selected site characteristics relating to resource availability. Each study site was given a unique number (1–21) and contained between 1 and 6 species. Each decimal value is the mean with the standard error of the mean in parentheses.

Site	No. of Saplings	Species ^a	Light (% full sun)	Soil moisture (g H ₂ O [g soil] ⁻¹)	Initial NH ₄ ⁺ (μg [g soil] ⁻¹)	Initial NO ₃ ⁻ (μg [g soil] ⁻¹)	Mineralization (μg [g soil] ⁻¹ 28 per day)	Nitrification (μg [g soil] ⁻¹ 28d ⁻¹)
1	15	RM,SM,B,A,O	5.71 (0.47)	0.21 (0.01)	3.58 (0.56)	1.31 (0.17)	5.83 (1.20)	5.26 (0.86)
2	10	A	7.64 (1.81)	0.16 (0.01)	3.74 (0.32)	1.47 (0.29)	4.37 (1.15)	3.83 (0.97)
3	5	RM,SM,O	7.60 (2.16)	0.28 (0.02)	10.36 (0.60)	0.89 (0.33)	23.99 (4.68)	16.01 (4.02)
4	16	RM,SM,A,O	9.89 (1.26)	0.27 (0.01)	11.25 (1.26)	0.16 (0.06)	8.69 (1.67)	9.10 (0.90)
5	16	RM,A,O	11.68 (4.20)	0.16 (0.01)	9.38 (1.22)	0.00 (0.00)	5.57 (1.96)	1.62 (0.62)
6	19	RM,SM,B,A	2.94 (0.64)	0.21 (0.01)	4.61 (0.37)	0.47 (0.11)	8.38 (1.30)	7.52 (1.23)
7	9	RM,O	3.61 (0.73)	0.26 (0.02)	8.76 (1.49)	0.06 (0.02)	6.62 (1.49)	0.38 (0.15)
9 ^b	5	A,O	39.01 (3.28)	0.30 (0.04)	7.64 (1.47)	0.26 (0.11)	4.98 (3.27)	2.47 (1.31)
10	9	B,H	2.86 (0.74)	0.50 (0.03)	10.71 (1.01)	0.22 (0.08)	11.58 (3.71)	4.16 (0.95)
11	3	SM,B,O	18.50 (9.19)	0.18 (0.01)	5.24 (0.57)	0.00 (0.00)	3.02 (1.37)	1.06 (0.29)
12	4	RM,SM	2.71 (0.57)	0.17 (0.01)	11.29 (2.27)	0.09 (0.03)	0.10 (1.40)	0.03 (0.09)
13	3	RM	46.39 (0.53)	0.30 (0.07)	4.31 (0.54)	0.83 (0.58)	4.64 (4.67)	4.98 (3.09)
14	17	ALL SPECIES	7.65 (1.04)	0.21 (0.02)	5.36 (0.48)	0.09 (0.35)	4.66 (1.06)	3.49 (0.90)
15	7	RM,SM,H	24.08 (5.85)	0.24 (0.03)	6.00 (1.66)	1.80 (0.87)	4.02 (3.07)	6.85 (2.37)
16	35	ALL SPECIES	24.67 (2.66)	0.24 (0.01)	7.12 (0.63)	0.33 (0.10)	3.01 (1.03)	2.53 (0.59)
17	13	B,H	0.59 (0.09)	0.36 (0.02)	9.64 (1.34)	0.49 (0.19)	5.14 (2.13)	1.71 (0.80)
18	6	RM,O,H	7.36 (1.41)	0.38 (0.08)	8.77 (1.06)	0.00 (0.00)	0.70 (1.16)	0.40 (0.40)
19	13	H	23.09 (2.87)	0.33 (0.02)	9.98 (1.59)	0.11 (0.04)	5.51 (2.01)	1.19 (0.49)
20	17	B,H	13.06 (2.96)	0.37 (0.02)	11.99 (1.56)	0.13 (0.07)	13.30 (3.29)	2.90 (1.20)
21	13	SM,A	11.13 (5.48)	0.35 (0.04)	10.14 (0.86)	0.28 (0.14)	7.73 (3.41)	1.93 (1.08)

^a Species acronyms for RM: red maple, SM: sugar maple, B: beech, A: white ash, O: red oak, H: hemlock.

^b Site 8 was logged during the growing season. No data are presented for this site.

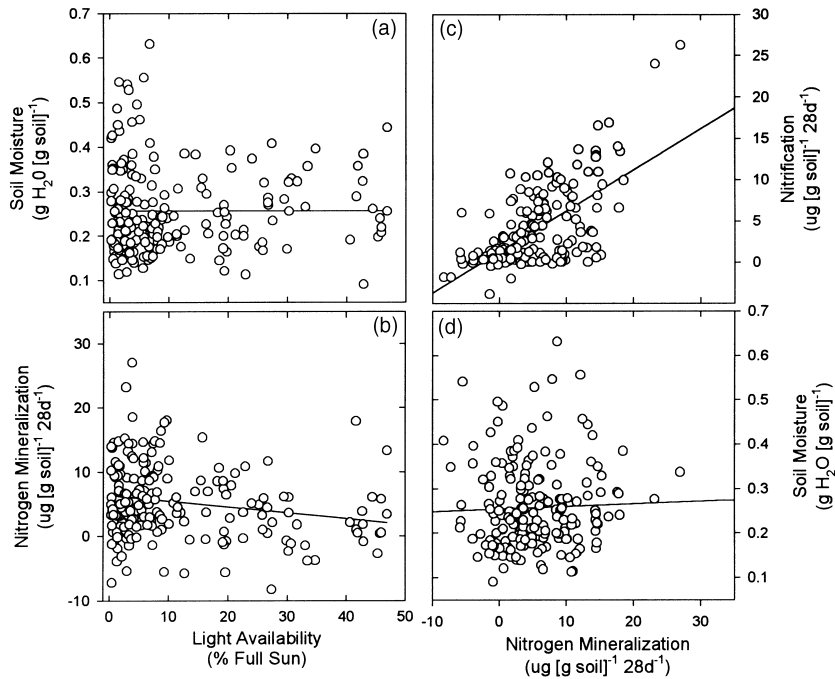


Fig. 1. A correlation analysis of the resources measured in this study. Each datum is associated with one of the 206 saplings sampled in this study. The Pearson product-moment correlation coefficient (and significance) for each plot is as follows (a) 0.01 ($p = 0.9744$); (b) -0.20 ($p = 0.0052$); (c) 0.63 ($p < 0.0001$); (d) 0.03 ($p = 0.6246$).

lowest for sugar maple ($P_1 = 0.0956$). The sensitivity of growth under low light was highest for beech ($P_2 = 0.0616$) and lowest for red maple ($P_2 = 0.0125$).

Red maple growth was significantly related to variation in light availability and the rate of N mineralization (Table 4). The asymptotic growth rate parameter (P_1) in red maple increased from 0.1082 in the light-only model to 0.1400 in the light and N mineralization model indicating higher growth with increasing light availability and N mineralization rates

(Fig. 3a). The growth under low N mineralization parameter (P_3) was significant but large ($P_3 = 0.1190$). The growth under low light parameter (P_2) was unchanged relative to the light-only model ($P_{2,L} = 0.0125$ versus $P_{2,L+N} = 0.0130$). As a result, red maple growth under low light was largely unaffected by variation in N mineralization rates (Fig. 3a).

Sugar maple growth was positively correlated with light availability and the rate of nitrification (Table 4). However, the functional form of the relationship between growth, light, and N availability differed

Table 3

Sapling growth in response to light availability. P_1 and P_2 refer to the asymptotic growth rate and slope at low light, respectively.

Species	P_1	P_2	Log likelihood	r^2	F	d.f.	$pr > F$
Red maple	0.1082 (0.0717, 0.1447)	0.0125 (0.0050, 0.0198)	-4.23	0.39	14.01	2,33	<0.001
Sugar maple	0.0956 (0.0624, 0.1289)	0.0258 (0.0079, 0.0436)	-4.67	0.21	4.96	2,37	<0.05
Beech	0.1776 (0.1396, 0.2155)	0.0616 (0.0251, 0.0982)	-3.43	0.32	8.72	2,37	<0.01
White ash	0.2246 (0.1299, 0.3191)	0.0159 (0.0078, 0.0240)	-2.72	0.55	20.51	2,34	<0.0001
Red oak	0.1983 (0.1244, 0.2722)	0.0172 (0.0052, 0.0292)	-3.81	0.41	8.28	2,24	<0.01
Hemlock	0.3416 (0.1949, 0.4881)	0.0197 (0.0086, 0.0307)	-1.90	0.79	56.54	2,30	<0.0001

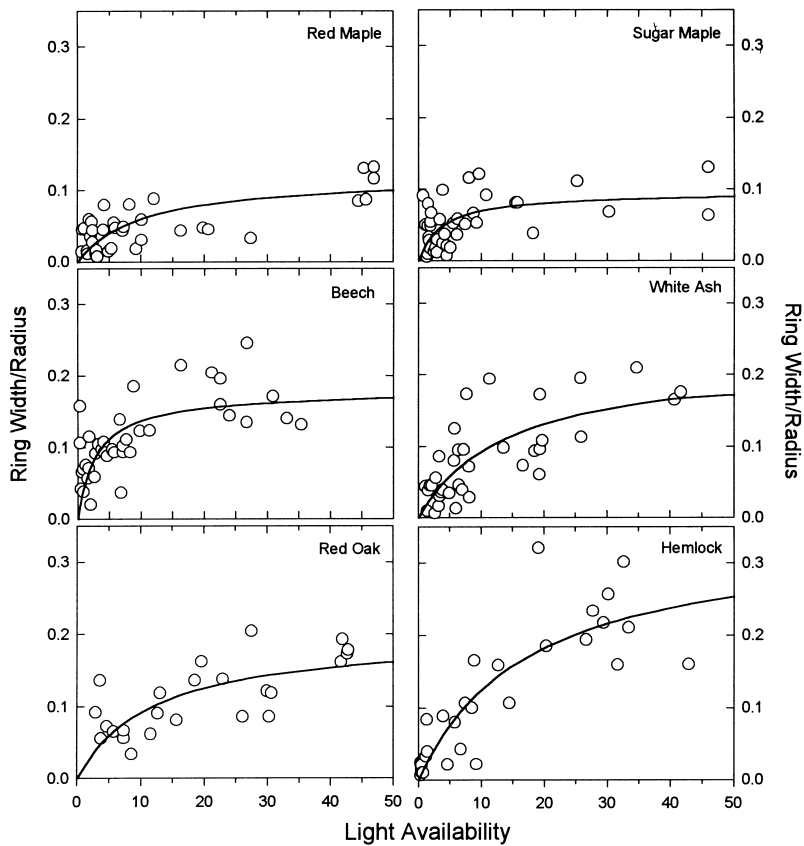


Fig. 2. Species-specific growth as a function of light availability.

Table 4

Partial- F and partial- r^2 statistics for growth as a function of light and N availability using the double Michaelis–Menten function in Eq. (4).

Species	Variable	Partial- r^2	Model- r^2	Partial- F	Probability > F
Red maple	light	0.39	0.39	9.06	<0.001
	mineralization	0.07	0.46	4.55	<0.05
Sugar maple	light	0.21	0.21	3.91	<0.05
	nitrification	0.04	0.25	1.65	<0.15
Beech	light	0.32	0.32	8.56	<0.01
	mineralization	0.00	0.32	0.01	NS ^a
White ash	light	0.55	0.55	12.59	<0.0001
	mineralization	0.00	0.55	0.01	NS ^a
Red oak	light	0.41	0.41	4.58	<0.05
	nitrification	0.00	0.41	0.01	NS ^a
Hemlock	light	0.79	0.79	22.20	<0.0001
	nitrification	0.00	0.79	0.01	NS ^a

^a NS is not significant at $p > 0.15$.

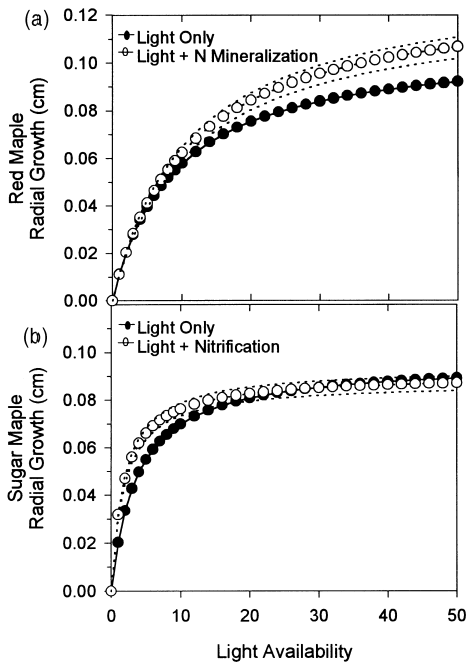


Fig. 3. Sapling growth in response to light availability and N availability in (a) red maple and (b) sugar maple. Each line is the predicted mean growth rate. The closed symbols are the light only growth model. The open symbols are growth predicted as a function of light availability at the mean measured N availability for each species (red maple = $15.5 \mu\text{g} [\text{g soil}]^{-1} 28$ per day, sugar maple = $10.4 \mu\text{g} [\text{g soil}]^{-1} 28$ per day). The dotted lines above and below the line with the open symbols are growth in the upper and lower quartile of N availability for each species.

from red maple. In sugar maple, the asymptotic growth rate parameter did not differ between the light-only model and the light and nitrification model ($P_{1,L} = 0.0956$ versus $P_{1,L+\text{NO}_3} = 0.1022$). The growth under low NO_3^- parameter was small and significant ($P_3 = 0.0389$). The rate of nitrification increased the growth under low light parameter estimate ($P_{2,L} = 0.0258$ versus $P_{2,L+\text{NO}_3} = 0.0555$). Consequently, sugar maple growth under low light increased with increasing nitrification but asymptotic growth was unchanged (Fig. 3b).

Beech, white ash, red oak, and hemlock growth rates were unaffected by variation in N mineralization or nitrification. The partial-F statistic associated with the additional N parameter in each model was not significant ($P > 0.15$) and there was no change in the amount of explained variation in sapling growth with

the additional parameter (Table 4). Residuals analysis corroborates these results. There was no correlation between residual variation in any of these species (Fig. 4).

4. Discussion

4.1. Resource availability

We thought that an increase in light availability (e.g., an increase in gap size) would increase soil moisture and temperature and stimulate the rate of N mineralization and nitrification (Matson and Vitousek, 1985; Denslow et al., 1998). However, light availability was uncorrelated with soil moisture, and soil moisture was uncorrelated with N mineralization (Fig. 1). The canopy gaps in this study were several years in age and there was a well established fern layer (pers. observ.). The fern cover may have reduced incident radiation on the soil surface, decreasing soil temperature and increasing the rate of evapotranspiration relative to soil under a more recent disturbance. This would offset any increase in soil moisture and temperature associated with canopy tree removal and result in little or no correlation between light and soil moisture, and soil moisture and N mineralization (Fig. 1a and d, respectively).

There was a statistically significant, negative correlation between light availability and N mineralization (Fig. 1b). Because the size and the activity of microbial biomass depends on labile C and N inputs to soils (Dalenberg and Jager, 1981), the negative correlation between light and N mineralization was likely due to a decrease in the input of labile organic matter associated with the absence of canopy trees. The correlation between light and N mineralization appeared to be statistically rather than biologically significant; due to a large sample size ($n = 206$) the correlation was statistically significant whereas the correlation coefficient was small ($\sigma = -0.20$) and the scatter large (Fig. 1b). The positive correlation between the rate of net nitrification and N mineralization (Fig. 1c) is consistent with our previous studies. Finzi et al. (1998a) found that nitrification was controlled by the rate of ammonium supply to oxidizing bacteria rather than other chemical properties of the soil (e.g., pH) or soil moisture.

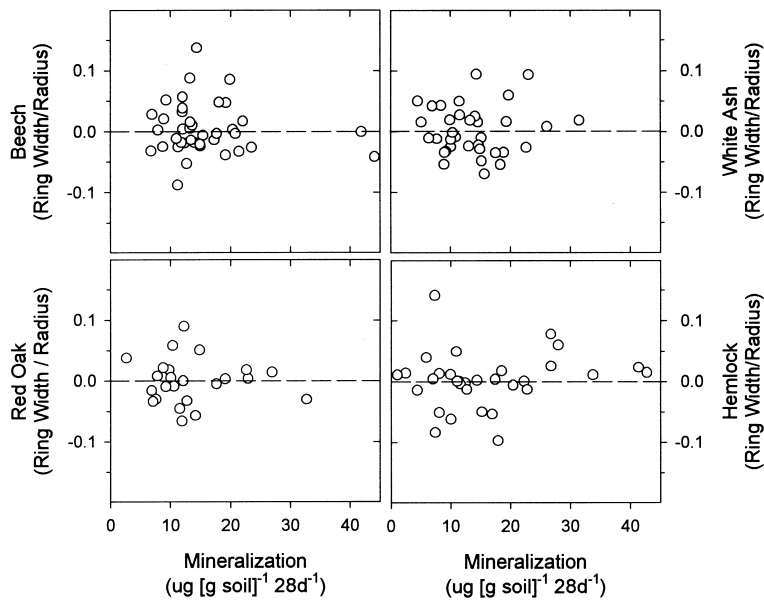


Fig. 4. Plots of the residual variation in growth as a function of N mineralization for four of the six study species.

4.2. Sapling growth responses

The six species we studied differed in their growth in response to light availability (Fig. 2). Only sugar maple and red maple responded to variation in N availability (Fig. 3). In all cases, light accounted for nearly all of the explained variation in growth (Tables 3 and 4). These results are consistent with prior research suggesting that light availability is the dominant control over sapling growth on these soils in these forests (Pacala et al., 1994, 1996; Kobe et al., 1995).

The parameter estimates for sapling growth in response to light availability in this study (Table 3) differed slightly from those presented in Pacala et al. (1994) but often fell within their 95% confidence intervals. The biggest differences were in the growth of red oak and red maple. In Pacala et al. (1994), the asymptotic growth rate parameter (P_1) of red oak was the largest of all species whereas in this study red oak asymptotic growth was the 4th largest. Similarly, in Pacala et al. (1994) the slope of the low-light growth response (P_2) in red maple was the 3rd smallest of all species studied whereas in this study the slope at low light growth parameter was the smallest of all species studied. The difference in growth between species and studies could be due to inter-annual variation in

growth conditions but are more likely related to the saplings being harvested over a wider range of soil texture- and presumably nutrient availability -in Pacala et al. (1994) than in the current study. Their sites included very sandy soils on ridge-tops and on outwash plains. We restricted our sampling to a single soil type: a relatively mesic, fine sandy loam (Typic Dystrochrept, Hill et al., 1980) that is the dominant soil type on the Canaan Mountain Plateau.

Red maple and sugar maple differed in the functional form of their growth response to variation in N availability. Nitrogen availability had no effect on red maple growth under low light but increased growth under high light relative to the light-only model (Fig. 3a). Conversely, N availability increased sugar maple growth under low light but did not change growth under high light (Fig. 3c). The growth-response curve for red maple supports the idea that light in the understory is the sole limiting resource affecting sapling growth (c.f. LINKAGES model, Pastor and Post, 1986) but contrasts clearly with sugar maple. Sugar maple growth under high light may have been limited by a resource other than N. We fit regression models of growth as a function of light and the gravimetric content of soil water in the incubated soils. We found no correlation between

growth and soil moisture (data not shown, analyses performed for all species). This implies that other mineral resources (e.g., calcium or phosphorus) could be important to sugar maple growth under high light.

Red maple and sugar maple also differed in the form of N (e.g., NH_4^+ versus NO_3^-) with which growth was correlated. Red maple growth was significantly related to the rate of net N mineralization implying that both NH_4^+ and NO_3^- could be important to the growth of this species. Sugar maple growth was positively correlated with nitrification but not mineralization implying that NO_3^- availability is more important to the growth of sugar maple than is the availability of NH_4^+ .

Our results are consistent with Walters and Reich (1997) who found a positive correlation between sugar maple growth and nitrification rates in the shaded understory of Wisconsin forests. Our results and those of Walters and Reich (1997) are inconsistent with Rothstein et al. (1996) who found that excised sugar maple roots had 30 times higher NH_4^+ uptake capacity (V_{max}) than NO_3^- uptake capacity. There are three possible explanations for this apparent discrepancy among studies. Firstly, buried bag soil incubations stimulate nitrification rates. In the absence of uptake by trees, the build-up of NH_4^+ in a buried bag increases the amount of substrate available for oxidation to NO_3^- (Fig. 1c, Binkley and Hart, 1989). If this were the case in our study, the relationship between sugar maple growth and nitrification could be apparent rather than real. Secondly, the higher NH_4^+ uptake capacity measured in sugar maple could be due to an evolutionary constraint on higher ion-carrier affinity for non-mobile soil nutrients (e.g., NH_4^+) than mobile soil nutrients (e.g., NO_3^- , Chapin et al., 1986a). Higher affinity for NH_4^+ could confer a competitive advantage to sugar maple through the uptake of non-mobile soil N and the formation of an NH_4^+ depletion zone around sugar maple roots in sites where NH_4^+ is the dominant form of available N. While greater root affinity for NH_4^+ than NO_3^- is common among diverse species (Bloom and Chapin, 1981; Chapin et al., 1986a; Rothstein et al., 1996) it is not universal (Koch et al., 1991; Lajtha, 1991). Thirdly, sugar maple could preferentially consume NO_3^- to maintain charge balance in the acquisition of positively charged soil cations, notably calcium (Ca^{2+}) (Epstein, 1972; Havill et al., 1974; Wilmot et al., 1994; Kobe et al., 1995; Finzi et al., 1998b). In this case, sugar maple

preference for NO_3^- would be real but mediated by a large metabolic demand for calcium (see below). We cannot exclude one explanation in favor of another given our current data set, but we suggest that mechanistic studies on the N-nutrition of sugar maple are warranted.

At most, 25% of the variation in sugar maple growth was accounted for by variation in light availability and nitrification (Tables 3 and 4). In a previous study, we found that adult sugar maple trees increased the quantity of exchangeable calcium in the soils beneath their crowns independent of the underlying variation in the Ca-content of the parent material (Finzi et al., 1998b). Wilmot et al. (1994, 1996) found that base cation fertilization increased growth in sugar maple stands in Vermont. Kobe (1996) found that sugar maple mortality rates in NW Connecticut forests were lower on calcareous bedrock than on the acidic, mica-schist bedrock sites used in this study. Collectively, these studies suggest that the availability of Ca is very important to the growth of sugar maple in New England.

For the remaining species (beech, white ash, red oak, and hemlock) there was no significant effect of N mineralization or nitrification on sapling growth. Forest fertilization studies in the northeast demonstrate that N can limit NPP and that the growth rate of at least some species in a forest stand are N limited (Mitchell and Chandler, 1939; Chapin et al., 1986b; Fahey et al., 1998). The evidence for N limitation in forest fertilization studies is corroborated by manipulative experiments in the greenhouse (e.g., Knox et al., 1995; Canham et al., 1996) and in common-gardens (Wait et al., 1996). With a large body of experimental evidence in support of N limited growth, why didn't sapling growth increase in response to N availability for all species? Three factors could explain these results.

Firstly, limited variation in the rate of N mineralization may have limited the range of sapling growth in response to N. Net N mineralization on ridge-tops and outwash plains are significantly lower than in mesic, fine-textured soils (Pastor et al., 1984; Zak et al., 1989; Graumlich, 1993; Kolb and McCormick, 1993; Knox et al., 1995). However, changes in soil type are often correlated with changes in soil texture, soil moisture-holding capacity, phosphorus availability, cation availability, and N availability. Alone or

collectively these differences could affect growth making it difficult to isolate N as the soil resource regulating sapling growth. To isolate the effects of N supply on growth we held soil type constant but this may have occurred at the expense of a larger gradient in N supply.

Secondly, belowground competition may have reduced the quantity of available N to saplings growing in the forest understory and in canopy gaps. The availability of N to a sapling in the forest understory is the difference between the rate of N supply and N uptake by competitors (microbes and canopy trees). Buried bag incubations estimate the rate of N supply in the absence of uptake by trees and could overestimate the amount of N available for sapling growth under low light. An overestimation of available N would affect the relationship between growth and N availability under low light. In contrast, under high light where canopy trees are absent and live root biomass often lower (Denslow et al., 1998), nitrogen-uptake by canopy trees is lower and buried bags should be an accurate predictor of available N. Sapling growth rates were higher in high light where canopy trees were absent (Table 2). With the exception of red maple, however, growth under high light was not stimulated when N mineralization rates were high (Table 4). The implication of these results is that belowground competition, even in multiple tree-fall gaps, can decrease the amount of available N for growth.

Thirdly, the dependence of growth on N from internal redistribution weakens the relationship between growth and soil N availability. Nutrient retranslocation from green leaves prior to senescence is an important mechanism of nutrient conservation at the scale of the individual plant and the whole ecosystem (Switzer and Nelson, 1972; Aerts, 1996; Killingbeck, 1996). In deciduous trees, nutrient retranslocation from leaves prior to senescence decreases tissue N concentrations by ~50% (Aerts, 1996). In closed-canopy forests, 33–39% of the N used in net primary production comes from internal recycling (Switzer and Nelson, 1972; Bormann and Likens, 1979; Gholz et al., 1985) implying that at least some species depend on N retranslocation from over-wintering tissues as a major source of nutrition in subsequent years. If a significant fraction of the N used in sapling growth is from storage rather than the uptake of mineralized N, then the correlation between

N mineralization and growth would be weaker than if saplings depended solely on N from the decomposition of organic matter. This may be especially important in conifer saplings (e.g., hemlock) with overlapping generations of foliage where nutrients are used over several growing seasons, translocated among needle cohorts prior to senescence (Zhang and Allen, 1996), and more efficiently resorbed than deciduous species (Killingbeck, 1996).

5. Conclusions

Variation in light availability was clearly related to variation in sapling growth and simulation experiments with the model SORTIE (Pacala et al., 1996) indicate that light plays a critical role in regulating the species composition of the forests in northwest Connecticut. Variation in N availability played little or no role in sapling growth for the six species we studied in this forest. This result is surprising given the clear role N plays in maintaining forest productivity regionally. Limited variation in N availability on this soil type, belowground competition, and nutrient retranslocation - individually or more likely, in combination - could influence the ability of saplings to respond to variation in N availability. We believe that careful manipulations of soil resource availability, belowground competition, and a characterization of internal N recycling are essential in identifying a general relationship between N availability, sapling growth, and forest dynamics.

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References

- Aber, J.D., Magill, A., Boone, R., Melillo, J.M., Steudler, P., Bowden, R., 1993. Plant and soil responses to chronic nitrogen additions at the Harvard Forest, Massachusetts. *Ecol. Applications* 3, 156–166.
- Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.* 84 (4), 597–608.
- Bazzaz, F.A., Miao, S.L., Wayne, P.M., 1993. CO₂-induced growth enhancements of co-occurring tree species decline at different rates. *Oecologia* 96 (4), 478–482.
- Binkley, D., Hart, S.C., 1989. The components of nitrogen availability in forest soils. *Advances Soil Sci.* 10, 57–112.
- Bloom, A.J., Chapin, F.S., 1981. Differences in steady-state net ammonium and nitrate influx by cold- and warm-adapted barley varieties. *Plant Physiol.* 68, 1064–1067.
- Bormann, F.H., Likens, G.E., 1979. *Pattern and Process in a Forested Ecosystem*. Springer, New York, 253 pp.
- Bridgman, S.D., Pastor, J., McLaugherty, C.A., Richardson, C.J., 1995. Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. *Am. Naturalist* 145 (1), 1–21.
- Burke, M.K., Raynal, D.J., Mitchell, M.J., 1991. Soil nitrogen availability influences carbon allocation in sugar maple (*Acer saccharum*). *Can. J. For. Res.* 22, 447–456.
- Canham, C.D., 1988. An index for understory light levels in and around canopy gaps. *Ecology* 69, 1634–1638.
- Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70 (3), 548–550.
- Canham, C.D., Finzi, A.C., Burbank, D.H., Pacala, S.W., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24, 337–349.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., Schnurr, J., 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Can. J. For. Res.* 26 (9), 1521–1530.
- Casella, G., R.L. Berger, 1990. *Statistical Inference*. Wadsworth and Brooks/Cole, Statistics/Probability Series. Pacific Grove, California.
- Chapin, F.S., Van Cleve, K., Tryon, P.R., 1986a. Relationship of ion absorption to growth rate in taiga trees. *Oecologia* 69, 238–242.
- Chapin, F.S., Vitousek, F.P.M., Van Cleve, K., 1986b. The nature of nutrient limitation in plant communities. *Am. Naturalist* 127 (1), 48–58.
- Clark, D.A., Clark, D.B., 1991. The impact of physical damage on canopy tree regeneration in tropical rain forests. *J. Ecol.* 79, 447–457.
- Dalenberg, J.W., Jager, G., 1981. Priming effect of small glucose additions to ¹⁴C-labelled soil. *Soil Biol. Biochem.* 13, 219–223.
- Denslow, J.S., Ellison, A.M., Sanford, R.E., 1998. Treefall gap size effects on above- and belowground processes in a tropical wet forest. *J. Ecol.* 86, 597–609.
- Eno, C.F., 1960. Nitrate production in the field by incubating soil in polyethylene bags. *Soil Sci. Soc. Am. Proc.* 24, 277–299.
- Epstein, E., 1972. *Mineral Nutrition of Plants: Principles and Perspectives*. Wiley, New York.
- Fahey, T.J., Battles, J.J., Wilson, G.F., 1998. Responses of early successional hardwood forests to changes in nutrient availability. *Ecol. Monogr.* 68 (2), 183–212.
- Finzi, A.C., Canham, C.D., 1998. Non-additive effects of litter mixtures on net N mineralization in a southern New England forest. *Forest Ecol. Manage.* 105, 129–136.
- Finzi, A.C., van Breemen, N., Canham, C.D., 1998a. Canopy tree – soil interactions within mixed species forests: species effects on carbon and nitrogen. *Ecol. Appl.* 8 (2), 440–446.
- Finzi, A.C., van Breemen, N., Canham, C.D., 1998b. Canopy tree – soil interactions within mixed species forests: species effects on pH and cations. *Ecol. Appl.* 8 (2), 447–454.
- Gholz, H.L., Fisher, R.F., Pritchett, W.L., 1985. Nutrient dynamics in slash pine plantation ecosystems. *Ecology* 66 (3), 647–659.
- Graumlich, L.J., 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper great lakes region. *Can. J. For. Res.* 23, 133–143.
- Havill, D.C., Lee, J.A., Stewart, G.R., 1974. Nitrate utilization by species from acidic and calcareous soils. *New Phytol.* 73, 1221–1231.
- Hill, D.E., Sautter, E.H., Gunick, W.N., 1980. *Soils of Connecticut*. Connecticut Agricultural Experiment Station. Bull. No. 787.
- Horn, H.S., 1975. Markovian properties of forest succession. In: Cody, M.L., Diamond, J.M., *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA, USA, pp. 196–211.
- Hugh, A.L., Aarssen, L.W., 1997. On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos* 80 (3), 575–582.
- Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77 (6), 1716–1727.
- Knox, R.G., Harcombe, P.A., Elsik, I.S., 1995. Contrasting patterns of resource limitation in tree seedlings across a gradient in soil texture. *Can. J. For. Res.* 25, 1583–1594.
- Kobe, R.K., 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecol. Monogr.* 66 (2), 181–201.
- Kobe, R.K., Pacala, S.W., Silander Jr., J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5 (2), 517–532.
- Koch, G.W., Bloom, A.J., Chapin, F.S., 1991. Ammonium and nitrate as nitrogen sources in two *Eriophorum* species. *Oecologia* 88, 570–573.

- Kolb, T.E., McCormick, L.H., 1993. Etiology of sugar maple decline in four Pennsylvania forests. *Can. J. For. Res.* 23, 2395–2402.
- Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* 73, 2129–2144.
- Lajtha, K., 1991. Nutrient uptake in eastern deciduous tree seedlings. *Plant Soil* 160, 193–199.
- Lorimer, C.G., 1983. A test of the accuracy of shade-tolerance classifications based on physiognomic and reproductive traits. *Can. J. Botany* 61 (6), 1595–1598.
- Matson, P.A., Vitousek, P.M., 1985. Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest. *Indiana For. Sci.* 27 (4), 781–791.
- Mitchell, H.L., Chandler, R.F., 1939. The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. *Black Rock For. Bull.* 11.
- Pacala, S.W., Canham, C.D., Silander Jr., J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. For. Res.* 24, 2172–2183.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements II. Estimation, error analysis, and dynamics. *Ecol. Monogr.* 66 (1), 1–44.
- Pastor, J., Aber, J.D., McLaugherty, C.A., Melillo, J.M., 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65 (1), 256–268.
- Pastor, J., Post, W.M., 1986. Influences of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3–27.
- Rastetter, E.B., Shaver, G.R., 1992. A model of multiple-element limitation for acclimating vegetation. *Ecology* 73 (4), 1157–1174.
- Rastetter, E.B., Ryn, M.G., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Hobbie, J.E., Aber, J.D., 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂ climate, and N deposition. *Tree Physiol.* 9, 101–126.
- Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78, 335–347.
- Rothstein, D.E., Zak, D.R., Pregitzer, K.S., 1996. Nitrate deposition in northern hardwood forests and the nitrogen metabolism of *Acer saccharum* Marsh. *Oecologia* 108 (2), 338–344.
- SAS Institute, 1987. SAS/STAT Guide for Personal Computers, Version 6 edn., Cary, NC, USA.
- Sipe, T.W., Bazzaz, F.A., 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology* 76 (5), 1587–1602.
- Switzer, G.L., Nelson, L.E., 1972. Nutrient accumulation and cycling in loblolly pine plantation ecosystems the 1st 20 years. *Soil Sci. Soc. Am. Proc.* 36 (1), 143–147.
- Szmura, J.M., Barton, N.H., 1986. Genetic analysis of a hybrid zone between the fire-belied toads near Cracow in southern Poland. *Evolution* 40, 1141–1159.
- Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ, USA.
- Wait, D.A., Jones, C.G., Schaedle, M., 1996. Controlling growth and chemical composition of saplings by iteratively matching nutrient supply to demand: a bootstrap fertilization technique. *Tree Physiol.* 16 (3), 359–366.
- Walters, M.B., Reich, P.B., 1997. Growth of *Acer Saccharum* seedlings in deeply shaded understories of northern Wisconsin: effects of nitrogen and water. *Can. J. For. Res.* 27, 237–247.
- Whitney, G.G., 1991. Relation of plant species to substrate, landscape position, and aspect in north central Massachusetts. *Can. J. For. Res.* 21, 1245–1252.
- Wilmot, T.R., Ellsworth, D.S., Tyree, M.T., 1994. Relationships among crown condition, growth and stand nutrition in seven Vermont sugarbushes. *Can. J. For. Res.* 25, 386–397.
- Wilmot, T.R., Ellsworth, D.S., Tyree, M.T., 1996. Base cation fertilization and liming effects on nutrition and growth of Vermont sugar maple stands. *For. Ecol. Manage.* 84 (1-3), 123–134.
- Zak, D.R., Host, G.E., Pregitzer, K.S., 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern lower Michigan. *Can. J. For. Res.* 19, 1521–1526.
- Zhang, S., Allen, H.L., 1996. Foliar nutrient dynamics of 11-year-old loblolly pine (*Pinus taeda*) following nitrogen fertilization. *Can. J. For. Res.* 26 (8), 1426–1439.