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Sapling growth as a function of light and landscape-level variation in soil water and foliar nitrogen in northern Michigan

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Abstract Interspecific differences in sapling growth responses to soil resources could influence species distributions across soil resource gradients. I calibrated models of radial growth as a function of light intensity and landscape-level variation in soil water and foliar N for saplings of four canopy tree species, which differ in adult distributions across soil resource gradients. Model formulations, characterizing different resource effects and modes of influencing growth, were compared based on relative empirical support using Akaike's Information Criterion. Contrary to expectation, the radial growth of species associated with lower fertility (*Acer rubrum* and *Quercus rubra*) was more sensitive to variation in soil resources than the high fertility species *Acer saccharum*. Moreover, there was no species tradeoff between growth under high foliar N versus growth under low foliar N, which would be expected if growth responses to foliar N mediated distributions. In general, there was functional consistency among species in growth responses to light, foliar N, and soil water availability, respectively. Foliar N influenced primarily high-light growth in *F. grandifolia*, *A. rubrum*, and *Q. rubra* (but was not significant for *A. saccharum*). In *A. saccharum* and *A. rubrum*, for which soil water availability was a significant predictor, soil water and light availability simultaneously limited growth (i.e., either higher light or water increased growth). Simple resource-based models explained 0.74–0.90 of growth variance, indicating a high degree of determinism. Results suggest that nitrogen effects on forest dynamics would be strongest in high-light early successional communities but that water

availability influences growth in both early successional and understory environments.

Keywords Forest dynamics · Forest composition · Forest communities · Resource effects · Species distributions · Succession

Introduction

Consistent associations between tree species distributions and soil characteristics (e.g., Whitney 1991; Host and Pregitzer 1992; Schwarz et al. 2003) have prompted studies on how species-specific performance varies among community types in the landscape, with a focus on intraspecific variation in seedling/sapling survivorship and growth (Kobe 1996; Montague and Givnish 1996; Walters and Reich 1997; Schreeg et al. 2005). Presumably, among-site variation in species-specific performance reflects variation in resource availability (Finzi and Canham 2000; Bigelow and Canham 2002), although performance could also be influenced by disease (Castello et al. 1995), herbivory (Fine et al. 2004), and any other factor that varies across sites. Among-site variation in soil resource availability can arise from composition of soil parent material (van Breemen et al. 1997), geomorphology (Zak et al. 1989; Host et al. 1988), fine textured soil layers (McFadden et al. 1994), disturbance history, and other factors. Nitrogen (N) and soil water availability frequently co-vary with forest composition (Zak et al. 1989; Pastor et al. 1984), which could reflect effects of species' occupancy on N (Finzi et al. 1998). At the same time, however, seedling and sapling performance should respond to that variation in resource availability, and differential species responses in turn would shape forest composition.

If changes in tree species dominance across the landscape arise from differences in species responses to N and water, then there must be shifts in species performance rank across gradients in those resources. JABOWA and FORET and descendent forest simulation models often

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assume a species tradeoff of relatively rapid growth under low fertility (exhibited by species tolerant of those conditions) versus high fertility (exhibited by species intolerant of low fertility) (e.g., 'low N tolerance' in Aber et al. 1979; Bugmann and Cramer 1998). This tradeoff is based on the premise that carbon balance and growth mediate species distributions across soil resource gradients (e.g., Schumacher et al. 2004). However, greenhouse tests of rank reversals of species' relative growth rates (RGR) at low versus high soil resource conditions are equivocal (Latham 1992; Walters and Reich 1996; Lusk et al. 1997). Furthermore, if growth responses mediate species distributions, then the growth of species that are associated with high fertility would be expected to be more sensitive to low soil resources than species associated with lower fertility (Aber et al. 1979).

Whole plant growth responses to water and N ultimately are based on the physiological responses to those resources. Although instantaneous carbon gain is limited by either water deficits or light intensity, annual growth could be simultaneously limited by both resources because stomatal closure due to water deficits could occur sporadically at any light level (e.g., Sack and Grubb 2002). On the other hand, water demand may be higher and relatively more limiting at higher light levels, consistent with more pronounced impacts of drought on growth at higher light levels (Kolb et al. 1990; Canham et al. 1996, but see Sack and Grubb 2002 for a critique of these studies). Higher foliar N also could ameliorate the effects of water deficits through increasing water use efficiency (Ripullone et al. 2004).

Nitrogen plays a key role in determining photosynthetic potential as a constituent of chlorophyll for light capture and Rubisco for initial fixation of CO₂ (Evans 1989), leading to a positive correlation between maximum photosynthetic rates and foliar N concentrations across species and environments (Field and Mooney 1986; Reich et al. 1997). Assuming that growth follows light-saturated photosynthetic responses, foliar N may limit growth under high but not low light, as frequently observed (Grubb et al. 1996; Meziane and Shipley 1999; Canham et al. 1996; Catovsky and Bazzaz 2002). Photosynthetic capacity also carries a respiratory cost that could select against high foliar N levels under low light (Walters and Reich 1999), minimizing foliar N effects on low-light growth. On the other hand, foliar N could increase light absorption (Field and Mooney 1986) and low-light carbon gain (e.g., Walters and Reich 1997).

How resources influence growth could affect forest dynamics and species distributions across resource gradients. For example, if a soil resource influenced growth under only high light intensity, that soil resource would be unlikely to affect regeneration in the understory and later stages of forest succession. To test effects of resources on sapling growth, I sampled foliar N (as an index of plant-available N), light and soil water availability, and radial growth in saplings of four species, which show contrasting landscape distributions as adults, across a broad fertility gradient in glaciated

northwest lower Michigan. Several formulations of species-specific growth models encapsulated different effects of light intensity, soil water availability, and foliar N on sapling radial growth (Fig. 1). Models were compared based on relative strength of data support (Burnham and Anderson 2002) and were used to test the following hypotheses:

1. Species associated with mesic, high fertility sites show higher sensitivity of sapling growth to soil water availability and foliar N than species associated with drier and lower fertility sites.
2. There is a tradeoff among species of sapling growth at high soil resources versus low soil resources that is consistent with mature tree distributions across fertility gradients.
3. (a) Foliar N influences growth at high but not low light intensity, consistent with N determining photosynthetic potential. (b) Alternatively, foliar N and light intensity simultaneously limit radial growth, consistent with the role of N in light-capturing pigments
4. (a) Soil water availability influences growth at high but not low light intensity, consistent with increased water demands under high light. (b) Alternatively, soil water and light intensity simultaneously limit growth, consistent with stomatal closure due to water deficits at all light levels.

Methods

Sites and species

This study was conducted in the Manistee National Forest in Lake, Wexford, and Manistee Counties in the northwestern lower peninsula of Michigan (~44°12'N, ~85°45'W). Glacial landforms and associated forest community types here provide broad variation in soil fertility. Net N mineralization and nitrification rates, nitrate and ammonium pools (Zak et al. 1989), and exchangeable calcium and magnesium increase along the outwash to ice-contact to moraine fertility gradient; but potassium, phosphorus, and manganese show no trend (Kobe, unpubl. data). MNF thus provides a natural gradient in soil nitrogen and water availability without confounding effects of climate, elevation, and latitude (e.g., via daylength).

Four species, which as adults differ in affinity with landforms and soil resources (Host et al. 1988; Burns and Honkala 1990), were included in this study. *Acer saccharum* (sugar maple) canopy trees occur primarily on moraines in Manistee National Forest (MNF) and are generally associated with fertile fine textured soils; *Fagus grandifolia* (American beech) occurs on moraines but also extends into sites of intermediate fertility at MNF (Kobe, pers. obs.) and elsewhere on coarse textured tills (Leak 1978; van Breemen et al. 1997; Schwarz et al. 2003). *Acer rubrum* (red maple) and *Quercus rubra* (red oak) reach their highest canopy dominance on sites that

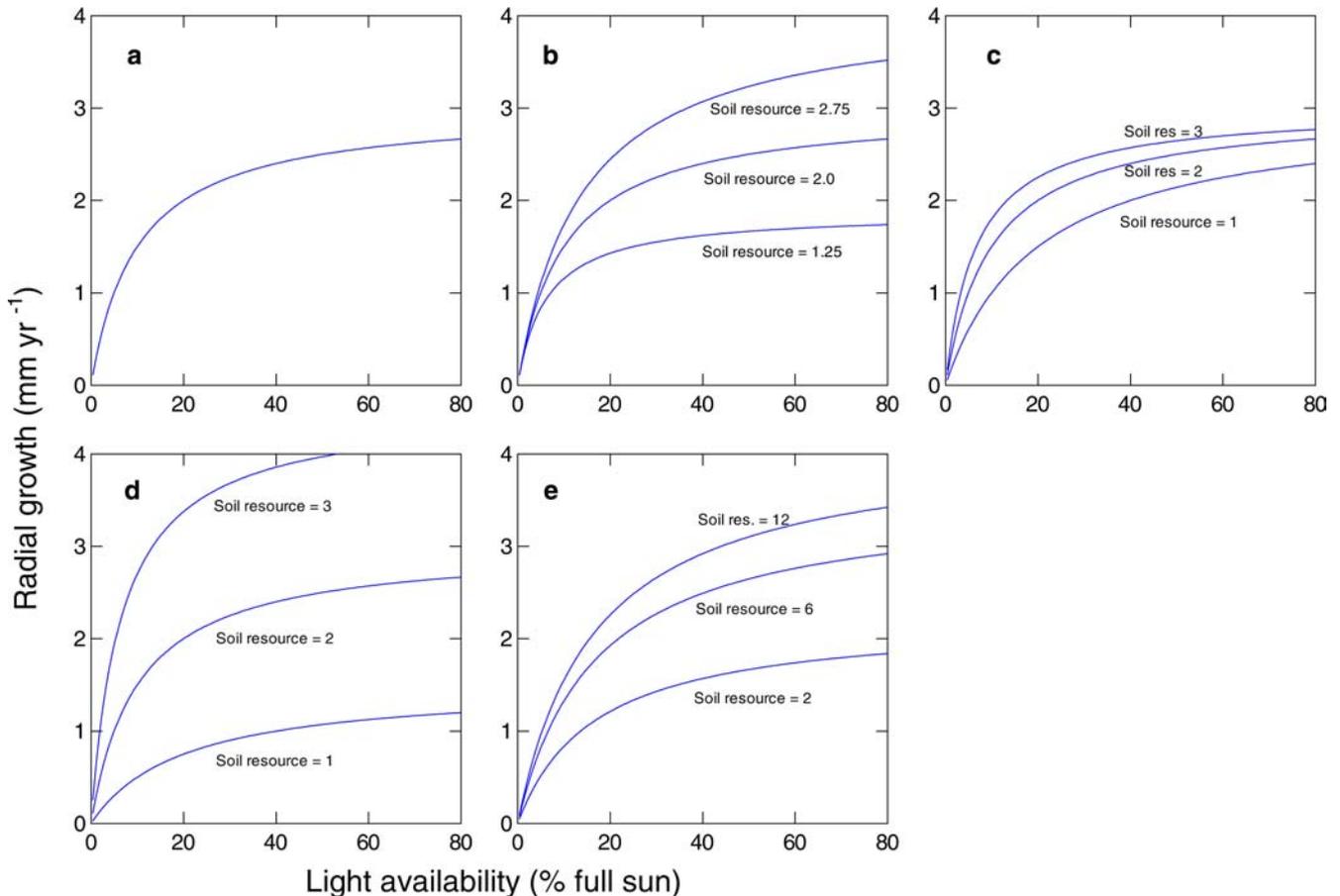


Fig. 1 Conceptual graphs of hypothesized growth models in Table 1. **a** Model 1, asymptotic relationship between growth and light ($A=0.3$, $S=0.03$); **b** Model 2, soil resource effects on high light or asymptotic growth ($A'=0.15$, $S=0.03$); **c** Model 3, soil resource effects on low-light growth ($A=0.3$, $S'=0.015$); **d** Model 4, soil resource effects on both low- and high-light growth that are proportionate (a special case of simultaneous resource limitation)

($A'=0.15$, $S'=0.015$). **e** Model 5, light and soil resource simultaneously limit growth, but soil resource effects at high and low light are not necessarily proportionate because growth asymptotes with respect to both light and the soil resource ($A=0.5$, $S_{\text{light}}=0.03$, $S_{\text{soil-resource}}=0.2$). Models 6–8 in Table 1 represent hybrids of the above cases

are intermediate in mineral nutrient availability (poor moraines) or that have relatively low soil water availability (kame terraces, other ice-contact features). Adults of these species generally follow these distributions at MNF, but it is possible to find saplings across a broader range of soil resources (Kobe, pers. obs.), which facilitated our sampling and which also suggested a recruitment bottleneck between sapling and canopy tree stages.

Field and lab sampling and measurements

My goal was to sample extant saplings from a broad range of soil resource and light conditions. Soil resources were stratified in the field by locating saplings across a wide range of forest ecosystem types, using an ecological classification system that is based on the presence of herbaceous indicator species (Cleland et al. 1990; Host and Pregitzer 1992). Different forest ecosystem types are associated with different soil textures (McFadden et al. 1994) and rates of net N mineralization (Zak et al. 1989).

For example, *Allium tricoccum* and *Osmorhiza claytoni* indicate relatively high fertility or soil water, *Trientalis borealis* intermediate fertility or soil water, and *Andropogon gerardii* and *Arctostaphylos uva-ursi* indicate low fertility or soil water. Although soil water and nutrient availability vary continuously, three coarse fertility classes (low, intermediate, and high) were established based on the presence of these and other indicator species, in order to initially stratify samples of saplings across presumed variation in soil resources; soil water availability and foliar N were later measured for each selected sapling. To ensure that saplings were being sampled at a broad range of light levels within each fertility class, I established three coarse groupings of light intensity (low, intermediate, and high). Low light levels were sampled from understory environments, intermediate light levels from natural tree fall gaps or thinning operations, and high light environments from multiple tree fall gaps or in the vicinity of recent harvests. Light intensity was later measured with hemispherical canopy photographs. From June to November 1997, extant

Table 1 Mean, standard deviation, median, and ranges of the variables used in this study

Species	Sample size		Diameter (mm)	Radial growth (mm year ⁻¹)	Light avail. (% full sun)	Foliar N (% mass)	Foliar N–high fertility (% mass)	Foliar N–low fertility	Vol. soil water (cm ³ cm ⁻³ soil)
AB	80	Mean (SD)	20.90 (7.45)	1.13 (0.74)	14.11 (14.72)	2.45 (0.33)	2.57(0.30)	2.23(0.26)	5.75 (3.13)
		Median	20.46	0.94	7.83	2.47	2.62	2.18	5.45
		Range	7.91–37.26	0.21–3.31	0.22–66.57	1.54–3.08	1.64–3.08	1.54–2.67	1.10–12.90
RM	73	Mean (SD)	17.01 (5.26)	0.67 (0.47)	15.82 (18.20)	1.76 (0.20)	1.88 (0.14)	1.69 (0.20)	6.17 (3.67)
		Median	17.05	0.53	6.99	1.77	1.85	1.71	4.50
		Range	7.84–29.53	0.096–2.46	1.29–72.58	1.20–2.20	1.61–2.20	1.20–2.18	1.70–14.90
RO	53 ¹	Mean (SD)	18.38 (5.58)	0.90 (0.77)	20.49 (22.82)	2.48 (0.35)	2.84(0.30)	2.34(0.26)	4.90 (2.56)
		Median	17.81	0.68	8.84	2.45	2.84	2.37	3.90
		Range	7.65–32.50	0.08–3.48	1.57–81.41	1.79–3.28	2.41–3.28	1.79–2.98	1.80–11.90
SM	70 ²	Mean (SD)	16.78 (5.43)	0.77 (0.52)	13.46 (16.98)	1.95 (0.31)	2.05 (0.39)	1.87 (0.22)	7.99 (2.90)
		Median	15.25	0.63	5.31	1.89	2.06	1.85	8.65
		Range	8.03–29.84	0.17–2.28	1.08–70.40	1.37–2.85	1.37–2.85	1.44–2.44	1.70–14.80

Foliar N statistics are by site fertility class, with 'high fertility' denoting moraines and 'low fertility' ice contact features (e.g., kames, eskers) and outwash plains for all species but sugar maple. For sugar maple, high fertility includes rich moraines and low fertility includes poor moraines and ice contact features

AB American beech, RM red maple, RO red oak, and SM sugar maple

¹ Because of missing data, sample size for red oak volumetric soil water was 52

² Because of missing data, sample size for sugar maple foliar N was 63

saplings (diameters at the end of 1997 ranged 7.6–37.3 mm, Table 1) were located in the nine combinations of fertility by light intensity groupings, aided by field knowledge of US Forest Service personnel. The sampling goal was to attain at least five individuals of each species in each of the nine combinations and a total sample size of 80 for each species. Final species sample sizes ranged 53–80 (Table 1) and achieved broad coverage across variation in light intensity, foliar N, and soil moisture (e.g., Fig. 2). Nevertheless, sugar maple saplings could not be found and sampled under very low soil resource conditions (e.g., outwash sites).

I estimated whole-growing-season light intensity for each sapling by taking a color hemispherical canopy photo (Canham 1988) with Minolta camera fitted with 180° fish-eye lens. Photos were taken between July and September 1998. Images were taken above the leader of

each sapling, gently bending the sapling out of the way for taller individuals. Developed color slides were scanned with a Polaroid QuickScan slide-scanner and resulting images were analyzed with GLA software (Frazer et al. 1999) to estimate seasonally integrated % total transmittance.

I measured individual tree soil water availability to 30 cm depth with time domain reflectometry (Moisture Point, Environmental Sensors, Inc., Vancouver, BC) on three separate occasions: 15 July, 10–11 August, and 19–20 August 1998. For each sampling, 1–3 TDR measurements within 50 cm of the target sapling were taken. Multiple measurements for a sapling on a particular date were highly repeatable, with a maximum relative variation of < 10%. Although water values varied temporally, measurements among all dates were correlated ($P < 0.05$). Due to equipment problems and time constraints, some saplings were not measured on 15 July. Thus, the mean of the 10–11 August and 19–20 August sampling dates, a period which experienced negligible precipitation, was used as a relative index of soil water availability.

In August 1997 and July 1998, three fully expanded leaves from the outer crown of each sapling were removed and composited. The leaves were placed into polyethylene bags in an ice chest and within 12 h of sampling were transferred to paper coin envelopes and dried in an oven at 70°C for at least 72 h. Dried leaf samples were ground with a ball-canister pulverizer (Kinetic Laboratory Equipment Co., Visalia, CA, USA) and stored in airtight glass vials until analysis. Nitrogen concentrations (as % of leaf mass) were measured with CHN Analyzer (Carlo Erba, Italy). For each sapling, I averaged foliar N concentration from 1997 to 1998 to use as an index of plant available N. Note that saplings in higher fertility sites (based on indicator species) had higher foliar N concentrations (Table 1); foliar N in sugar maple seedlings also is correlated with nitrification rate at similar sites in Wisconsin (Walters and Reich 1997).

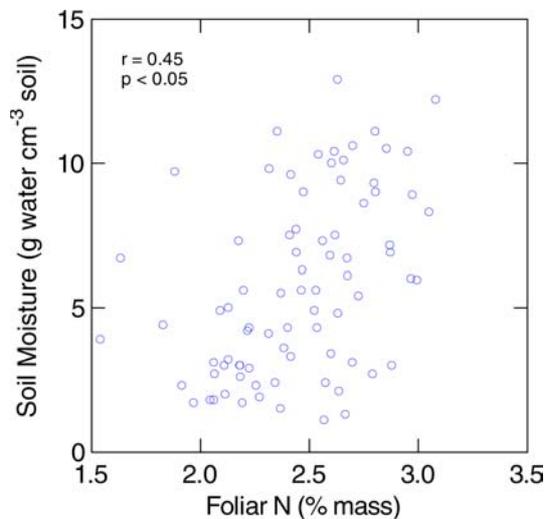


Fig. 2 Covariance between soil water availability and foliar N in American beech

To get baseline size data, I measured diameter with calipers at 10 cm above ground level after radial growth had ceased during autumn 1997 and 1998 (marking the location to minimize subsequent measurement error). Between September and November 2000, saplings were harvested, measured for total height and extension growth for 2000 and a stem cross section at the 10 cm height mark was removed for lab measurement of radial growth. Stem cross sections were air-dried and scanned with an Epson Expression 836XL high resolution flatbed scanner. Images were analyzed with WinDendro software (Regent Instruments, Blain, Quebec) to estimate annual ring widths. Field and lab measurements of diameter were strongly related; air drying resulted in ~7% shrinkage across all species and stem sizes (lab diameter₁₉₉₈ = 0.93 × field diameter₁₉₉₈, $r^2 = 0.99$, $P < 0.0001$). Annual ring widths were averaged among four radii, selected to correspond with the smallest and widest diameters intersecting the pith. For modeling, I used the average annual radial growth from 1997 to 1999 instead of a single year to (1) encompass greater temporal variation in climate; (2) compensate for non-circular wavy rings exhibited by some stems, which were counterbalanced over multiple years; and (3) account for lagged growth responses to resource availability. The 1997–1999 interval was selected because resource measurements were concentrated in 1998.

Statistical analysis

I used the nonlinear routine of Systat (ver. 10, SPSS Corp., Chicago, IL, USA) to fit models of radial growth as a function of light, soil water availability, and foliar N. The Systat loss function was specified as the negative natural log likelihood of a normal probability density function. Model functional forms were compared with Akaike's Information Criteria corrected for small sample sizes (AIC_c). Models with minimum AIC_c have the greatest empirical support; models within 2 AIC_c units have similar levels of empirical support (Burnham and Anderson 2002). I also tested relative growth rate (RGR, $(\ln(\text{diam}_{\text{fall}199}) - \ln(\text{diam}_{\text{fall}196}))/3$) as the response variable, which consistently resulted in poorer model fits and increased bias versus absolute growth (AGR). Here I report results for AGR only, as MacFarlane and Kobe (2001) compare RGR and AGR. The significance of predictive factors was assessed through parameter 95% support limits. The coefficient of determination (r^2) was calculated as the square of the correlation coefficient between actual and predicted growth.

Pacala et al. (1994) modeled sapling radial growth as a Michaelis-Menten function:

$$\Delta\text{radius} = \text{radius} \frac{A \times \text{Light}}{A/S + \text{Light}}, \quad (1)$$

where A and S are parameters estimated from the data, respectively, correspond with the asymptotic (or high light) growth rate and the slope of the growth function

at zero light (summarizing low-light growth). Equation 1 was extended by Finzi and Canham (2000) to include effects of soil N availability as a bivariate Michaelis-Menten function:

$$\Delta\text{radius} = \text{radius} \frac{A \times \text{Light} \times \text{Nitrogen}}{(A/S_{\text{light}} + \text{Light}) \times (A/S_{\text{Nitrogen}} + \text{Nitrogen})}, \quad (2)$$

where the parameters S_{Light} and S_{Nitrogen} are estimated from the data and respectively correspond with the slope of the growth function at zero light and zero N. Equation 2 encapsulates simultaneous limitation. That is, at less than asymptotic growth rates, an increase in N or light would result in increased radial growth. Bigelow and Canham (2002) modified Eq. 1 by specifying A or S as linear functions of soil resources (e.g., substituting ' m [foliar N] + b ' for A). Thus, soil resource effects could be partitioned to low light if soil resources modified S or high light if soil resources modified A .

I integrated these modeling approaches to test whether the effects of foliar N or soil water availability were manifested as: (1) simultaneous limitation with light intensity (i.e., best fit to Eq. 2); (2) high-light growth effects (A specified as a function of soil resources); (3) low-light growth effects (S specified as a function of soil resources); (4) proportionate high- and low-light growth effects (both A and S specified as a function of soil resources); (5) simultaneous limitation of light and one soil resource with the other soil resource modifying A (asymptotic growth), S_{light} (low-light growth), or $S_{\text{soil resource1}}$ (growth at low soil resource 1). Thus, for each species, I fit and compared several growth models to test for effects of light, N, and water and to test for how effects of those resources were manifested (Table 2, Fig. 1).

To test for disproportionate effects of tree size on growth, I also estimated an exponent on initial tree radius for all models (Table 2). For example, Eq. 1 was modified as:

$$\Delta\text{radius} = \text{radius}^{\theta} \frac{A \times \text{Light}}{A/S + \text{Light}}, \quad (3)$$

and all models in Table 2 were modified similarly. If $\theta < 0$, then larger saplings produce less growth per unit of initial size than smaller saplings. Conversely, $\theta > 0$ would indicate that larger saplings produce greater growth per unit of initial size than smaller saplings.

To confirm model results of foliar N and soil water effects at different levels of light intensity, I tested correlations of residuals from the growth-light model (Eq. 1) versus foliar N and soil water at low (< 5% full sun) and high (> 5 and > 10% or 20%) light.

Results

Resource covariance

Although I attempted to independently stratify resources through the selection of saplings in the field, soil

Table 2 Functional forms and biological interpretations of tested models

Model	Parameters	Biological interpretation
1. $\frac{A \times \text{Light}}{A/s + \text{Light}}$	A: asymptotic growth (here at high light) S: growth at low light	Non-linear positive effect of light on growth, with effect approaching saturation at higher light levels.
2. $\frac{(A/r \times \text{Soil-resource})\text{Light}}{((A/r \times \text{Soil-resource})/s) + \text{Light}}$	A': coefficient of soil resource; product is asymptotic growth at high light S: as in model 1.	Soil resource (N or water) modifies asymptotic (high-light) growth.
3. $\frac{A \times \text{Light}}{(A/(s' \times \text{Soil-resource})) + \text{Light}}$	A: as in model 1. S': coefficient of soil resource; product is growth at low light	Soil resource (N or water) modifies low-light growth.
4. ^a $\frac{(A/r \times \text{Soil-resource})\text{Light}}{((A/r \times \text{Soil-resource})/(s' \times \text{Soil-resource})) + \text{Light}}$	A': as in model 2. S': as in model 3.	Soil resource (N or water) proportionately modifies low- and high-light growth.
5. $\frac{A \times \text{Light} \times \text{Soil-resource}}{(A/s + \text{Light})(A/S_{\text{soil-resource}} + \text{Soil-resource})}$	A: asymptotic growth (here: at high light and high soil resource) S: as in model 1. S _{soil-resource} : growth at zero soil resource	Simultaneous limitation of light and a soil resource (N or water).
6. $\frac{(A/r \times \text{Soil-resource}2)\text{Light} \times \text{Soil-resource}1}{(((A/r \times \text{Soil-resource}2)/s) + \text{Light})((A/r \times \text{Soil-resource}2)/S_{\text{soil-resource}}) + \text{Soil-resource}1}$	A': as in model 2. S: as in model 1. S _{soil-resource} : as in model 5.	Same as model 5 and soil resource that is not simultaneously limiting increases asymptotic growth.
7. $\frac{A \times \text{Light} \times \text{Soil-resource}1}{(((A/S_{\text{soil-resource}}) + \text{Light})((A'/S_{\text{soil-resource}}) + \text{Soil-resource}1)}$	A: as in model 5. S': as in model 3. S _{soil-resource} : as in model 5. A, S: as in model 5. S': as in model 3.	Same as model 5 and soil resource that is not simultaneously limiting increases low-light growth.
8. $\frac{A \times \text{Light} \times \text{Soil-resource}1}{(((A/s) + \text{Light})((A/S_{\text{soil-resource}} \times \text{Soil-resource}2) + \text{Soil-resource}1)}$	S _{soil-resource} : coefficient of soil resource; product is growth at low soil resource 1	Same as model 5 and soil resource that is not simultaneously limiting increases growth at low levels of the simultaneously limiting soil resource.

See Fig. 1 for plotted functions

^aEq. 4 simplifies to: $\frac{(A/r \times \text{Soil-resource})\text{Light}}{(A'/s) + \text{Light}}$

water and foliar N were positively correlated ($P < 0.05$) in beech ($r = 0.45$), red maple ($r = 0.42$), and red oak ($r = 0.47$). The weak correlations between foliar N and water availability (Fig. 2) were unlikely to cause unstable or biased parameter estimates arising from multicollinearity. The stability of parameter estimates is evidenced by tight 95% support limits (Table 4). For red oak and beech, foliar N and soil water effects were tested separately in growth models and in no case did the effects of one resource become significant in the absence of the other. For red maple, the weak covariance between N and soil water availability did not preclude detecting significant independent effects of N and soil water.

There was also a negative correlation between foliar N and light intensity in sugar maple ($r = -0.42$), likely due to an accumulation of high N under low light levels (or conversely, the dilution of foliar N with carbon under high light). However, foliar N levels still varied between 1.37 and 2.06% above growth-saturating light levels ($> 20\%$ full sun) and the models that were fit allowed for characterizing independent effects of foliar N at high versus low light. Furthermore, growth residuals at high light ($> 5, 10, \text{ and } 20\%$ full sun) were not correlated with foliar N. Foliar N accumulation at lower light could also influence growth through increased light capture, but foliar N and radial growth were not significantly correlated over restricted ranges of 0–5% and 0–10% full sun (Table 3).

Size effects on growth

For all species except red oak, large saplings produced relatively less radial growth per unit radius than small saplings, as indicated by θ estimates less than one. However, effects were weak, with the upper 95% support limit of θ approaching one in all cases (Table 4). Furthermore, there were no significant correlations between growth residuals and sapling diameter for any species in the models that did not incorporate θ . Complexity introduced into models with the addition of θ also increased uncertainty in estimates of other parameters. For these reasons, growth models without θ are emphasized hereafter.

Resource effects on growth

In all species, light was highly significant in predicting radial growth (Likelihood ratio test, $P < 0.0001$). Among the species-specific models with the greatest empirical

ability, respectively. For the three species (American beech, red oak, and red maple) for which foliar N was a significant predictor of growth, foliar N tended to influence high-light growth rates, entering into the species-specific models as a multiplier of A (asymptotic growth parameter) (Table 5). As a confirmation of modeling results, foliar N was correlated with residuals from growth-light models at higher but not lower light levels for these three species (Table 3). At lower light levels, plotted growth functions of minimum and maximum observed foliar N levels share a common slope; these functions begin to diverge at the light level at which the lower foliar N line reaches asymptotic growth (Fig. 3). For American beech, this light level was $\sim 10\%$ full sun and for red oak 20% full sun. In contrast to N effects under low light, under the highest measured light levels of $\sim 75\%$ full sun, radial growth was twice as fast under the highest versus lowest foliar N levels for both American beech and red oak (Fig. 3). Thus, foliar N generally influences growth at high but not low light intensity, supporting hypothesis 3A.

For the two species (sugar and red maple) for which soil water availability was a significant predictor of growth, soil water and light availability simultaneously limited radial growth, as supported by best model fits to model 5 (Tables 2 and 5). Confirming modeling results, soil water was correlated with residuals from growth-light models at both low and high light levels for red and sugar maple, although the correlation was marginally significant for sugar maple at both light levels and for red maple at lower light (Table 3). Effects of soil water on sugar maple radial growth were weak (Fig. 3), explaining an additional 3% of growth variance in comparison to inclusion of only light intensity as a predictor resource (r^2 of 0.78 vs 0.75) (Table 4). The slope of the sugar maple growth function at low water availability (S_{water}) was negligibly greater than zero (Table 4). Across the range of measured soil water, 95% support of the functional relationships between radial growth and water availability overlap (through mapping uncertainty in parameter estimates) (Fig. 3). Reduced parameter uncertainty led to tighter 95% support intervals in sugar maple radial growth as a function of light intensity alone (Fig. 4). Although soil water is a statistically significant predictor of sugar maple growth, its biological significance as measured here is weak. Nevertheless, water and light intensity simultaneously limited annual radial growth, supporting hypothesis 4B.

Red maple was the only species for which all the three measured resources were significant in predicting radial growth, with the best supported model:

$$\Delta \text{radius} = \text{radius} \frac{(A(\text{Foliar N}))\text{Light}(\text{Soil water})}{((A \times \text{Foliar N})/S_{\text{light}} + \text{Light})(A(\text{Foliar N})/S_{\text{Soil water}} + (\text{Soil water}))}. \quad (4)$$

support, there was functional consistency among species in growth responses to foliar N and soil water avail-

Across the range of measured light intensities and foliar N levels, red maple growth varied by a factor of

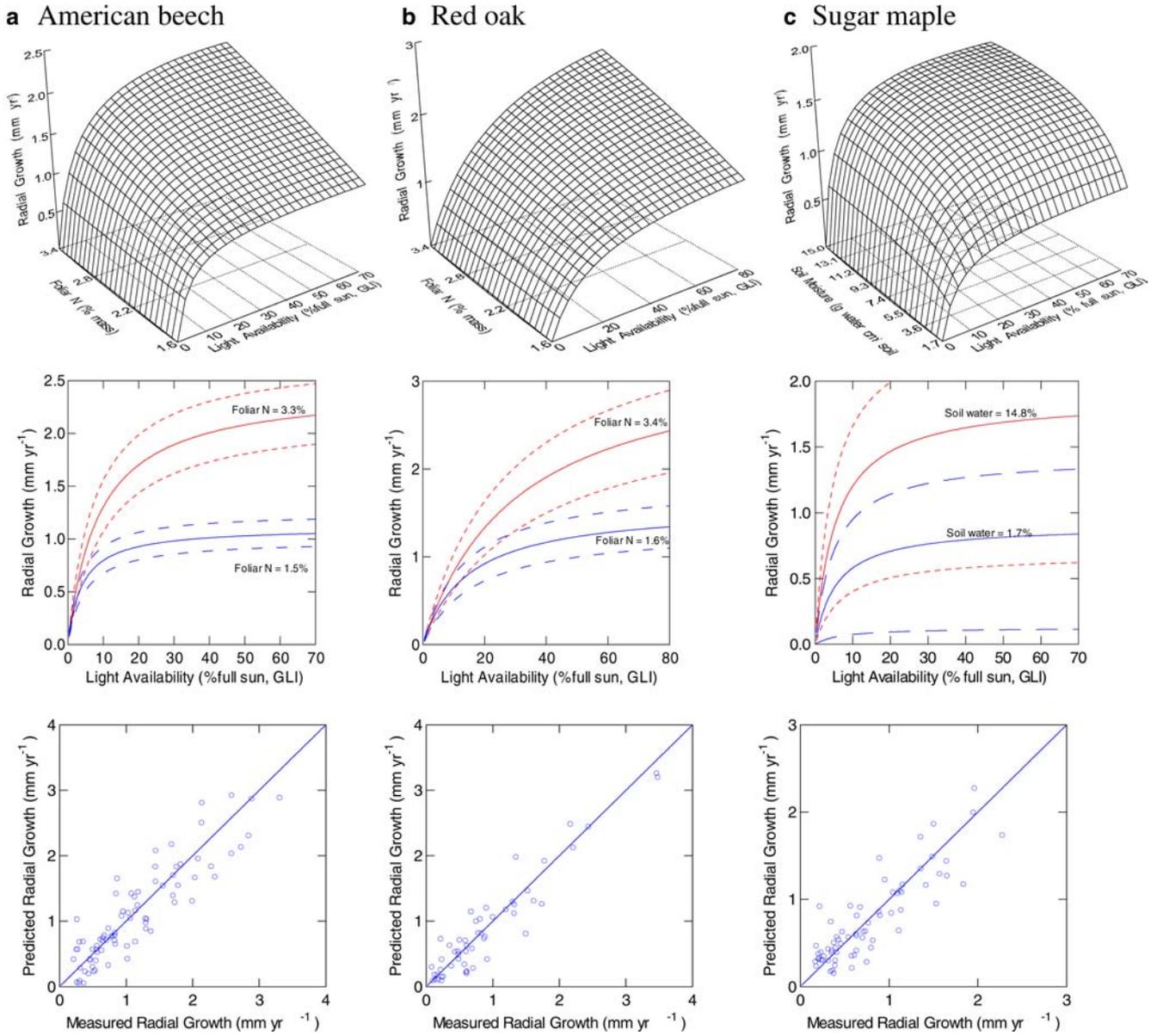


Fig. 3 Sapling radial growth as a function of light and soil resource indices for American beech and red oak and light and soil water for sugar maple. *Row 1* growth responses to light and foliar N for American beech and red oak and light and soil water for sugar maple. *Row 2* Slices through the 3D surfaces at indicated resource levels with 95% support limits (dashed lines). *Row 3* Model fits

Table 3 Pearson correlations between residuals from the growth-light model (Eq. 1) versus soil water and foliar N at low and high light levels

Species	Light intensity (% full sun)	Sample size	Correlation w/soil water	Correlation w/foliar N
AB	≤ 5	31		
	> 5	49	$r=0.31, P=0.029$	$r=0.32, P=0.025$
RM	≤ 5	27	$r=0.36, P=0.064$	
	> 5	46	$r=0.49, P=0.001$	$r=0.42, P=0.004$
RO	≤ 5	17		
	> 5	36 ¹		$r=0.35, P=0.037$
SM	≤ 5	34 ²	$r=0.28, P=0.118$	
	> 5	36 ³	$r=0.28, P=0.093$	

Blank cells indicate non-significant correlations ($P > 0.1$)

AB American beech, RM red maple, RO red oak, and SM sugar maple

¹N=35 for residual-TDR correlation

²N=31 for residual-foliar N correlation

³N=32 for residual-foliar N correlation

Table 4 Upper table: maximum likelihood estimates and 95% support (in parentheses) for all models with $\Delta AIC_c < 2$ (from Table 5). The most parsimonious models with the greatest empirical support are in bold (see Results) and are generally emphasized and shown in figures. Lower table: best models from upper table with θ estimates (encapsulating disproportionate size effects on growth)

Sample size	Model	A	A' (mod by res.)	S _{light}	S'(mod by res.)	S _{soil-resource}	S' water(mod by N.)	r ²
AB 80	2, soil res = fol N		0.074 (0.066, 0.083)	0.028 (0.021, 0.036)				0.80
AB 80	4, soil res = fol N		0.076 (0.067, 0.085)		0.010 (0.008, 0.013)			0.81
SM 70	5, soil res = water	0.218 (0.161, 0.276)		0.039 (0.023, 0.055)		0.091 (0.008, 0.174)		0.78
SM 63	8	0.213 (0.156, 0.271)		0.034 (0.022, 0.046)		0.062 (-0.004, 0.129)		0.77
SM 70	1	0.172 (0.151, 0.194)		0.028 (0.020, 0.035)				0.75
RO 53	2, soil res = fol N		0.099 (0.083, 0.115)	0.011 (0.008, 0.014)				0.90
RO 52	6, soil res1 = fol N, soil res2 = water		0.145 (0.070, 0.220)	0.032 (0.014, 0.049)		0.154 (0.106, 0.202)		0.90
RM 73	6, soil res1 = water soil res2 = fol N		0.134 (0.101, 0.166)	0.026 (0.017, 0.035)		0.088 (0.048, 0.128)		0.74
RM 73	8	0.257 (0.195, 0.318)		0.027 (0.018, 0.037)		0.045 (0.027, 0.063)		0.74

Characterizing disproportionate effects of size on growth with θ	A	A' (mod by res.)	S _{light}	S' (mod by res.)	S _{soil-resource}	θ
AB 80	2, soil res = fol N	0.148 (0.06, 0.237)	0.049 (0.023, 0.075)			0.748 (0.533, 0.964)
SM 70	5, soil res = water		0.077 (0.022, 0.132)		0.144 (0.020, 0.269)	0.727 (0.484, 0.969)
RO 53	2, soil res = fol N	0.108 (0.039, 0.177)	0.011 (0.004, 0.019)		0.183 (0.035, 0.331)	0.969 (0.722, 1.217)
RM 73	6, soil res1 = water soil res2 = fol N	0.261 (0.094, 0.429)	0.046 (0.018, 0.075)			0.715 (0.455, 0.975)

AB American beech, RM red maple, RO red oak, and SM sugar maple

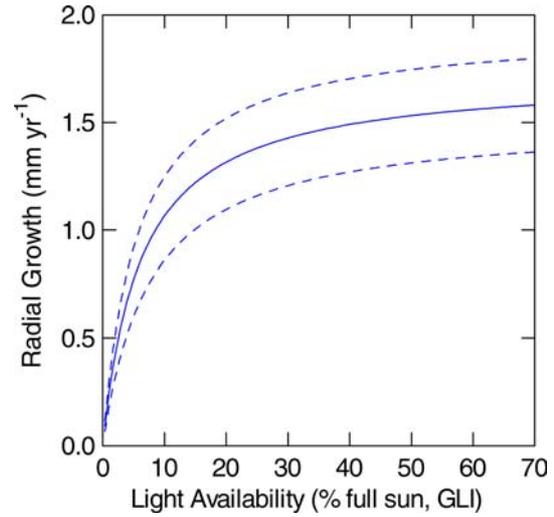


Fig. 4 Sugar maple radial growth as a function of light intensity. 95% confidence intervals shown with dashed lines

two at extremes of measured soil water. The highest versus lowest measured foliar N (at high light and all water levels) is associated with $\sim 50\%$ higher radial growth (Fig. 5). Consistent with responses in beech and red oak, foliar N influenced red maple growth at high but not low light levels; the slope of the growth function at low light did not diverge among different levels of foliar N regardless of soil water availability (Fig. 5). In contrast, soil water together with light availability simultaneously limited growth, as evidenced by the best fit to model 5 (Table 2). Thus, under most conditions, either higher light or soil water availability increased growth. There is clear divergence of growth in low versus high water availability at moderate and high foliar N, as indicated by non-overlapping 95% support limits (Fig. 5).

Although foliar N generally influenced high-light growth and soil water co-limited growth across light levels, there were alternative models that also had empirical support (within 2 AIC_c units of the best fit model, Burnham and Anderson 2002), which are briefly reviewed here. For beech, the hypothesis that foliar N acted as a multiplier on both high- and low-light growth (model 4) had substantial but weaker support than model 2 (Table 5). Models 2 and 4 each had two parameters, but model 4 was more complex because foliar N scales both A and S . By virtue of model simplicity and AIC_c support, model 2 is emphasized. In red oak, there was similar AIC_c support for model 2 (foliar N affects high-light growth) and model 6 (foliar N and light intensity co-limit radial growth and soil water acts on high-light growth) (Table 5). However, given variation in foliar N (1.79–3.28%), its effects on growth were very subtle at low light levels as characterized by model 6. For example, at 1% full sun and moderate water availability (6.8%), radial growth was predicted to vary from 0.16 to 0.2 mm across the full range of foliar N levels. Subtle effects encapsulated by more complex

Table 5 AIC_c differences (Δ AIC_c) for models in Table 2

Model	Resources	Parameters	AB	SM	RO	RM
Light limitation only						
1	Light	A, S _{light}	11.74	3.62	13.86	32.27
Soil resource modifying high-light growth						
2	Light, N	A' foliarN, S _{light}	0	8.47	0.19	23.65
2	Light, water	A' water, S _{light}	84.00	15.40	37.37	28.39
Soil resource modifying low-light growth						
3	Light, water	A, S' water	6.75	7.02	8.02	28.67
3	Light, N	A, S' foliarN	22.71	2.37	39.40	6.51
Soil resource proportionately effects high and low-light growth (special case of simultaneous limitation)						
4	Light, N	A' foliarN, S' foliarN	1.67	18.00	5.96	21.03
4	Light, water	A' water, S' water	105.29	32.36	69.92	62.09
Simultaneous limitation of light and soil resource						
5	Light, N	A, S _{light} , S _{foliarN}	2.89	9.58	5.36	^a
5	Light, water	A, S _{light} , S _{water}	12.79	0	21.94	5.17
Simultaneous limitation of light and soil resource 1, soil resource 2 modifying high-light growth						
6	Light, N, water	A' water, S _{light} , S _{foliarN}	14.43	5.08	0	4.59
6	Light, water, N	A' foliarN, S _{light} , S _{water}	10.10	4.76	14.58	0
Simultaneous limitation of light and water, foliar N modifying low-light growth						
7 ^b	Light, N, water	A, S' water, S _{foliarN}	13.24	6.37	22.89	2.32
Simultaneous limitation of light and water, foliar N modifying low water growth						
8 ^c			5.93	0.86	15.46	1.19

Δ AIC_c is calculated as (AIC_c for model i)–(AIC_{c, minimum}). Because the model with the greatest empirical support has the minimum AIC_c value, Δ AIC_c = 0 for the model with the strongest empirical support. Within each column, bold font denotes models within 2 AIC_c units of the best supported model

AB American beech, RM red maple, RO red oak, and SM sugar maple

^aParameter estimates did not converge for this species-model

^bParameter estimates did not converge for any species for a model characterizing simultaneous limitation of light and foliar N, with soil water modifying low-light growth

^cParameter estimates did not converge for any species for a model characterizing simultaneous limitation of light and foliar N, with soil water modifying low N growth

model 6 explained negligibly more variation than model 2 (r^2 0.898 vs 0.895). Because model 2 is simpler and had similar support to model 6, model 2 is emphasized. For both maple species, there was empirical support for the hypothesis that light and water co-limited growth and that foliar N modified growth under low soil water (Table 2, model 8), which would be consistent with increased water use efficiency under higher foliar N. For sugar maple, there was considerable uncertainty in foliar N effects on low water growth and 95% support for S' water (as modified by N) encompassed zero (Table 4).

There was a high degree of determinism in the functional relationships between radial growth, initial radius, and resources, as indicated by explained growth variance (r^2), which ranged from 0.74 for red maple to 0.90 for red oak (Table 4). For all species, residuals were balanced (Figs. 2 and 4) and showed no significant correlations with respect to initial radius, light intensity, foliar N, and soil water availability ($P > 0.05$, results not shown).

Species growth tradeoffs and distributions

Contrary to expectations (hypothesis 1), sapling radial growth in sugar maple, which is most strongly associated with high fertility sites as adults, was not sensitive to

measured variation in foliar N and showed weak responses to soil water availability. In contrast, red maple, which is associated with intermediate and low fertility conditions, showed strong growth responses to both soil water and foliar N. Similarly, red oak, also associated with intermediate sites as adults, showed strong growth responses to foliar N.

To test for species tradeoffs of growth under low versus high fertility (e.g., Aber et al. 1979; Bugmann and Cramer 1998), I calculated radial growth for 20 mm radius saplings under species-specific lowest and highest measured foliar N levels using the best fit models for each species. For all species, foliar N levels were higher under high fertility than low fertility sites (Table 1). Growth was calculated at 80% full sun because foliar N influenced growth most strongly at high light. To allow for the full manifestation of foliar N effects, growth also was calculated under the highest measured soil water levels for red maple and sugar maple, the species that showed significant effects of water.

Contrary to hypothesis 2, species radial growth at low versus high foliar N was not negatively correlated or consistent with species distributions across soil resource gradients (Fig. 6). Relative to other species, sugar maple had higher asymptotic growth under low N and lower asymptotic growth under high N, a pattern expected for

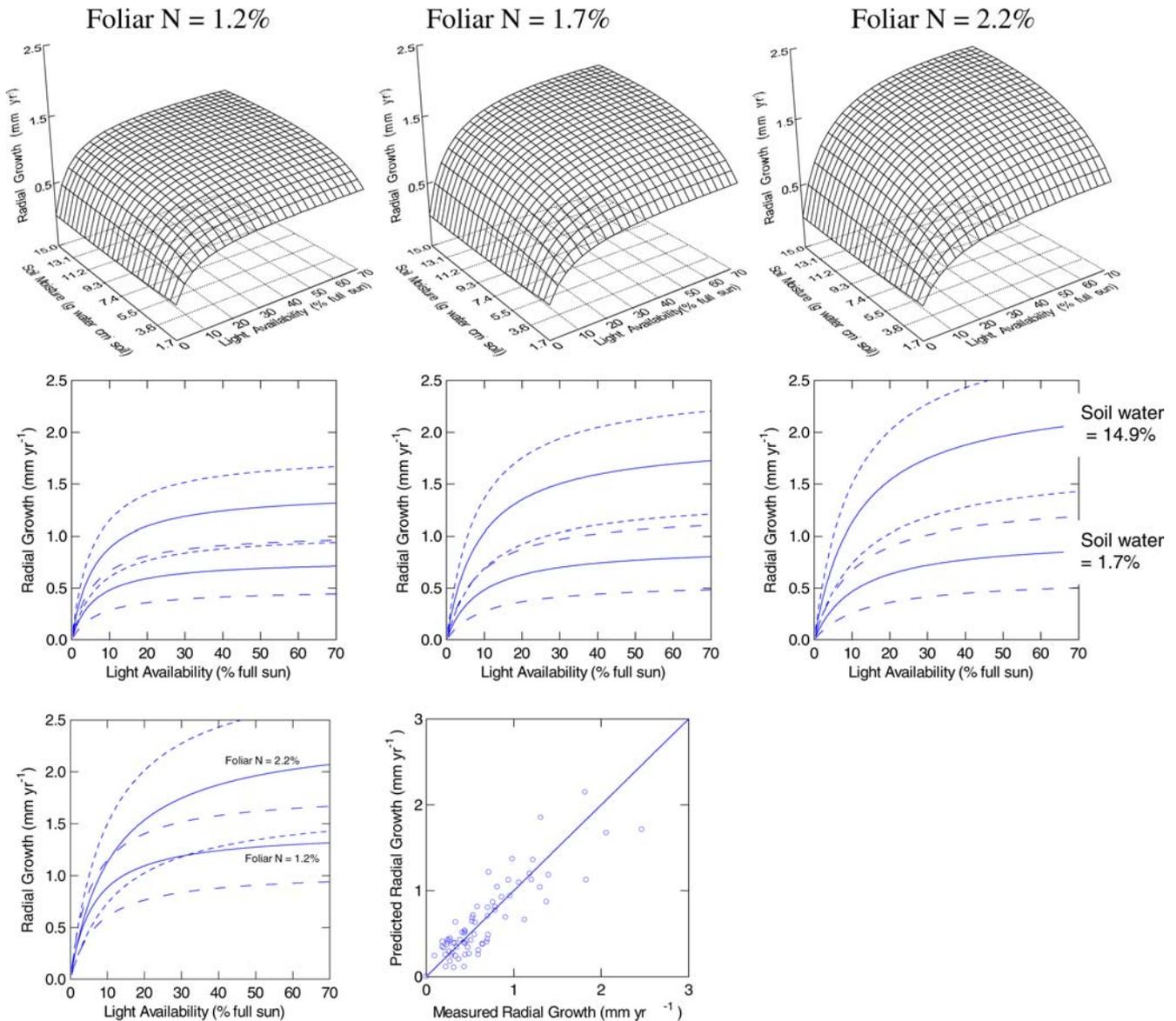


Fig. 5 Red maple sapling radial growth as a function of light and soil water availability at 1.2, 1.7, and 2.2% foliar N from left to right columns in first row. *Middle row* slices through the 3D surfaces, with *solid lines* showing the plotted function evaluated at the extremes of measured water availability (1.7 and 14.9%

volumetric) at the three foliar N levels; *dashed lines* show the propagation of parameter 95% support. *Long dashes* correspond with 1.7% and *short dashes* with 14.9% volumetric water. *Bottom row* slices through 3D response surface of growth versus light and foliar N (at 14.9% soil water). Measured versus predicted growth

a species adapted to low fertility (which sugar maple is not) under a growth-based tradeoff. In contrast, beech, red maple, and red oak had lower asymptotic growth under low foliar N and higher asymptotic growth under higher N, which would be expected for species adapted to high fertility.

Discussion

Growth responses and species distributions

Sugar maple adults are associated with high soil resource environments (Host et al. 1988; Leak 1978), but sugar

maple saplings showed the weakest responses to soil resources here. Sugar maple sapling growth was largely explained by variation in light intensity ($r^2=0.75$) with soil water and possibly foliar N having weak effects. I cannot exclude the possibility that sugar maple saplings were sampled over a narrower range of soil resources than red maple and red oak, especially over unmeasured resource gradients such as calcium that could be important in sugar maple growth (Kobe et al. 2002). However, ranges of sugar maple foliar N and soil water were similar to that of other species (Table 1). Furthermore, it is unlikely that effects of foliar N on sugar maple growth went undetected because foliar N had been diluted by faster growth at higher light intensity.

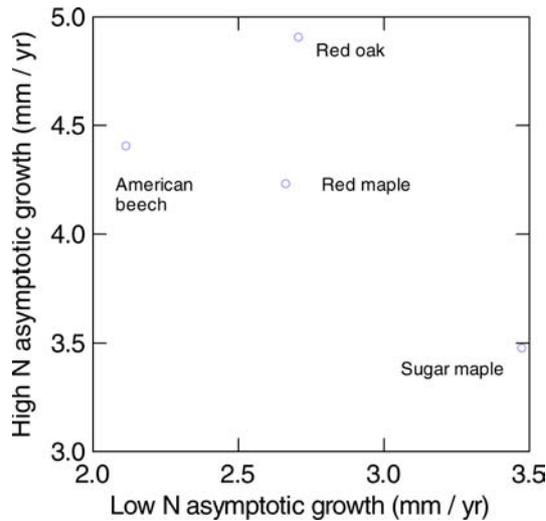


Fig. 6 Radial growth at high versus low foliar N levels for the four species examined in this study. Growth calculations for sugar maple and red maple assume high soil water

Analyses under separate low and high light ranges (where light and N did not covary) were consistent with model results that N did not affect growth. In contrast to sugar maple, red maple, red oak, and beech are associated with drier and lower fertility sites (Host et al. 1988; Leak 1978) and responded to foliar N; red maple also responded to soil water. Red maple and red oak adults reach their highest basal area on low-intermediate fertility sandy ice contact hills and well-drained moraines at MNF (Host and Pregitzer 1992). American beech adults have a distribution intermediate to that of sugar maple and red oak, occurring on well-drained sites of moderate to high fertility (Leak 1978, Kobe pers. obs.). In summary, in direct contradiction with expectations under hypothesis 1, sugar maple, associated with mesic and high fertility sites as canopy trees, had the weakest growth responses to soil resources; red maple, occurring on the driest and lowest fertility sites as adults among these species, had the strongest sapling growth responses to soil resource (consistent with Canham et al. 1996).

The lack of a sugar maple growth response to foliar N in this study is generally consistent with this species' negligible responses as saplings to nitrification rates ($P < 0.15$, Finzi and Canham 2000), pools of NH_4 and NO_3 (Bigelow and Canham 2002), and as seedlings, N fertilization under low and high light (Canham et al. 1996; Catovsky and Bazzaz 2002). In contrast, sugar maple relative stem length growth was correlated with both soil water and N availability across landscape-level variation in northern Wisconsin under $< 5\%$ canopy openness (Walters and Reich 1997) and relative growth rates of sugar maple seedlings under high light were greater on moraine than outwash during a drought year on similar MNF sites (Schreeg et al. 2005). There are at least three explanations for these inconsistent results. First, seedlings may respond more strongly than saplings to soil resources because seedlings may have lower water

use efficiency (Cavender-Bares and Bazzaz 2000) and their shallower and less extensive root systems could limit access to soil resources. Second, Schreeg et al. (2005) studied sugar maple under drought conditions, with a mean volumetric soil water content of 1.53% on outwash, which is lower than the minimum value measured here for any sapling of all species except beech. Finally, there was some empirical support that light and water co-limited sugar maple growth and that foliar N increased growth under low soil water. Interactions between foliar N and low soil water, and their influence on water use efficiency (Ripullone et al. 2004), should be more pronounced in small individuals with shallow rooting, especially under drought (as in Schreeg et al. 2005).

Species differences in growth responses to soil resources could arise from differences in root morphological traits. Greater rooting depth enables greater access to soil water (Nicotra et al. 2002) and red oak and beech both are tap-rooting as saplings (Burns and Honkala 1990) and showed no growth sensitivity to soil water (to 30 cm depth) here. The primary roots of red maple seedlings develop to 2–5 cm depth and then grow horizontally (Burns and Honkala 1990), which could explain red maple's sensitivity to soil water availability, assuming that horizontal rooting is maintained in saplings. Although not possessing a coarse tap root, 1-year-old sugar maple and red oak seedlings showed similar mean rooting depths (21–25 cm) at comparable MNF sites (Schreeg et al. 2005). Extrapolating to the saplings here, rooting depths of oak and sugar maple saplings would have exceeded the 30 cm depth to which soil water was measured. In comparison to the coarse tap roots of red oak, sugar maple's rooting depth is achieved through smaller roots with potentially less conductive tissue (Schreeg et al. 2005).

Increased contact between roots and soil could convey greater access to N and thereby reduce growth sensitivity to N, as shown by sugar maple. Although speculative because of the paucity of root data for these species, this proposition is supported by higher root mass fraction (g root mass/g plant mass) and specific root area (cm^2 root/g root) of sugar maple than red oak at MNF (Schreeg et al. 2005). In contrast, Comas et al. (2002) report higher specific root length (cm root/g root) in red oak than sugar maple within first and second order classes of roots (very fine and fine), but do not report absolute amounts of mass or length. Mycorrhizal symbionts could also increase access to both water and mineral nutrients, but were not assessed here.

Contrary to hypothesis 2, there was not a species tradeoff of sapling growth at high versus low foliar N that explains mature tree distributions. If growth and carbon balance were the main determinants of species distributions, then sugar maple would be expected to have relatively high growth under high foliar N and relatively low growth under low foliar N (occupying the upper left hand corner of Fig. 6). Conversely, red maple and red oak would be expected to have relatively high

growth at low foliar N and relatively low growth at high foliar N (lower right hand corner of Fig. 6). This growth-based trade-off is a common assumption in JABOWA and FORET forest models (Aber et al. 1979; Bugmann and Cramer 1998), but has no empirical support to date (Latham 1992; Walters and Reich 1996; Lusk et al. 1997).

Single versus simultaneous resource limitation

In general, foliar N influenced high-light growth, supporting hypothesis 3A and consistent with results for woody shrubs (Grubb et al. 1996), herbs (Meziane and Shipley 1999), and tree seedlings (Canham et al. 1996; Catovsky et al. 2002; Catovsky and Bazzaz 2002), suggesting that N most strongly influences carbon gain when photosynthesis is operating near maximum levels (Field and Mooney 1986; Reich et al. 1997). For sugar maple and red maple, there was some empirical support for the hypothesis that N increased growth at low soil water (regardless of light intensity). Thus, N and water could be simultaneously limiting under low water conditions (i.e., an increase in either water or N would increase growth), perhaps due to the foliar N effects on water use efficiency (Ripullone et al. 2004).

Soil water and light availability simultaneously limited annual growth in red maple and sugar maple here, consistent with proportionate drought-induced reductions of relative growth rate across irradiance levels for shade tolerant woody seedlings (Sack and Grubb 2002) and supporting hypothesis 4B. It is important to note that ‘simultaneous’ limitation here applies to annual and not instantaneous growth. Annual growth may be simultaneously limited by light and water because periods of drought during the growing season close stomata and preclude photosynthetic responses to irradiance in the understory; when drought is alleviated, light could become limiting. Thus, instantaneous growth likely is limited by either light or water (e.g., an increase in light intensity will not influence carbon balance when stomata are closed).

Implications for forest community dynamics

Given the different ways by which foliar N and soil water influence sapling growth, these resources would be expected to have different implications for forest community dynamics and succession. N availability may accelerate the rate of successional dynamics, influencing sapling growth in early succession when light levels are high. But patterns of species replacement are more strongly influenced by survival and growth in the low light of the forest understory (Kobe et al. 1995; Pacala et al. 1996), where N availability would exert less influence. Thus, variation in N availability is unlikely to qualitatively influence successional dynamics. Similarly, based on SORTIE simulations, elevated N enhances the dominance of fast-growing species early in succession,

speeds up the transition to shade tolerant species, and enhances the dominance of shade tolerant species at later seral stages, but does not fundamentally alter successional pathways (Catovsky et al. 2002).

In contrast to N availability, soil water influences growth proportionately across light levels and thus would be expected to influence dynamics under high light environments in early successional environments and in the low light of the forest understory. Both maple species, especially red maple, showed growth responses to soil water and would be expected to have a growth advantage under higher soil water in comparison to beech and red oak.

The high growth variance explained with these simple biologically-based models ($r^2=0.74$ for r. maple to 0.90 for r. oak) suggests a high degree of determinism in these forest systems (cf., Clark et al. 2003). These r^2 values are conservative because models were formulated to be biologically realistic and were chosen based on parsimony rather than to maximize fits. If growth-based tradeoffs existed among these species, the high degree of determinism exhibited by this dataset should have enabled their detection.

Conclusion

In the glaciated landscape of northern Michigan, tree species composition and the availability of soil water and N (and foliar N) vary across landforms (Zak et al. 1989). If sapling growth and carbon balance mediate effects of soil resources on species composition of mature trees, then we would expect that: (1) the growth of species associated with high resource sites (e.g. sugar maple) is more sensitive to soil resources than species associated with lower fertility (e.g. red maple and red oak) (hypothesis 1) and (2) growth ranks shift among species in low versus high fertility such that high fertility species grow relatively rapid under high fertility but relatively slow under low fertility (hypothesis 2). This study’s results do not support either expectation. In fact, both red maple and red oak responded more strongly to soil resources than sugar maple and there was no evidence for a species tradeoff of growth at low versus high fertility. Rather than a growth-based tradeoff, the landscape-level distributions of these species more likely arise from a species tradeoff between survivability on poor sites versus growth on rich sites (Schreeg et al. 2005).

The modeling approach enabled testing for both significant effects of resources and the manner in which resources influenced growth. In general, foliar N affected growth at high but not low light levels (supporting hypothesis 3A) while water availability influenced growth at all light levels (supporting hypothesis 4B). These different modes of influence of N and water on sapling growth could lead to differences in effects of those resources on forest dynamics. Nitrogen would be expected to influence growth rates under higher light

conditions, which might exist after larger-scale disturbances (e.g. clear cuts or multiple-tree fall gaps). However, N would exert little influence on growth in understory conditions or in small to moderate forest gaps and thus would not be expected to influence forest dynamics through advance regeneration. In contrast, water availability would affect growth at all light levels and thus would be expected to exert a stronger control on forest dynamics through influencing the growth of advance regeneration in the understory and sapling growth in the high light of early successional environments.

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