

Community organization of tree species along soil gradients in a north-eastern USA forest

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Summary

1 A study was carried out in oak-northern hardwood forest in NW Connecticut USA involving measurements of growth, light and soil environment of saplings of six canopy trees that are strongly associated with particular soil types as adults. The objectives were to determine patterns of growth response along soil factor gradients, and to discriminate among modes of community organization (fundamental niche differentiation, shifting competitive hierarchy or continuum concept).

2 Relationships were found between tree species distributions and all measured soil factors (pH and exchangeable calcium, magnesium, potassium, aluminium, ammonium and nitrate).

3 Growth and light data were fitted to a nested series of functions based on the Michaelis-Menten equation. For five of six species, likelihood-ratio tests indicated that functions that incorporated pH or other soil factors predicted growth better than functions based only on light availability.

4 Species differed in the direction and strength of response to soil factors. *Fraxinus americana* had decreased growth on high-magnesium soils, *Acer rubrum* had increased growth on high-aluminium soils, *Quercus rubra* and *Fagus grandifolia* had increased growth on high-calcium soils and *Tsuga canadensis* had increased growth on high-nitrate soils.

5 Growth responses were consistent with either fundamental niche differentiation and continuum concept (*Acer rubrum*), shifting competitive hierarchy and continuum concept (*Fagus grandifolia*, *Quercus rubra* and *Tsuga canadensis*) or were not consistent with any theory (*Acer saccharum* and *Fraxinus americana*).

6 Because saplings are associated with the same soil-types as mature trees, further studies in this system should focus on earlier stages of the plant life cycle: dispersal, germination and seedling establishment.

Key-words: continuum concept, fundamental niche differentiation, northern hardwood forest, shifting competitive hierarchy, soil calcium, soil-species relationship

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Introduction

Spatial separation of plant species according to soil factors is well known (e.g. Warming 1909; Ellenberg 1939; Yang & Lowe 1956; Whittaker & Niering 1965; Austin & Austin 1980; Goldberg 1982; Nagy & Proctor 1997). Where soil gradients are mild and extreme features such as hydric, serpentine or limestone patches are lacking the reasons for sorting may be unclear (Wilson & Nisbet 1997) but could be according to fundamental niche differentiation, shifting competitive hierarchy or the continuum concept.

Under fundamental niche differentiation (FND), species segregate because they have optimal performance (i.e. physiological optima) at different points along a gradient (Whittaker 1975), whereas with shifting competitive hierarchy (SCH) all have physiological optima at the upper end of a resource gradient, but species differ in competitive ability and poorer competitors are displaced to the resource-poor end (Keddy 1989). The continuum concept (CC) incorporates elements of both FND and SCH, with the balance depending on the nature of the gradient (Austin & Smith 1989). Thus plants segregate according to SCH along a gradient of consumable resources, but via FND if the gradient involves non-consumed factors such as temperature or pH. There is continuing debate as to which theory best describes plant community

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organization along environmental gradients (Latham 1992; Huston 1994; Shipley & Keddy 1994; Howard & Goldberg 2001).

FND predicts that species that are most abundant at low resource levels will show declining performance when individuals are grown with more resources, whereas SCH and CC suggest that performance should improve as resource levels increase. This apparently simple means of distinguishing among theories is confounded by the explanation under SCH for poor performance at higher resource levels, i.e. competition from other species. It is therefore necessary to distinguish between performance limitation due to poor physiological functioning at a given resource level rather than performance limitation due to resource depletion by neighbouring plants. Some workers feel that only direct experimentation, including removal of neighbours, can distinguish between these mechanisms (Keddy 1989; Turkington & Mehrhoff 1990), but such procedures are impractical in forests.

We suggest that an alternative approach, suitable for forest understories, is to assess performance of individual plants based on measurements of local availability of light and soil resources (Pacala *et al.* 1994). This approach ignores the source of variation in resources, although it is assumed that light availability relative to full sun is determined by neighbouring vegetation. Soil samples taken from the rooting zone provide an indication of nutrient availability that could be determined by either supply processes or depletion by neighbouring plants. The distinction between SCH and FND is framed in terms of physiological optima, and the determinants of availability are therefore immaterial.

In this approach, data are collected over a broad range of environmental variation and fitted to mathematical functions that express growth with respect to light and potentially limiting soil resources (Pacala *et al.* 1994). The response of each species to higher soil resource levels but constant light levels can be evaluated and community-wide response patterns can be built up. As well as testing the main theories of plant community organization, the parameters of the function obtained can be used in dynamic simulation models for additional tests of theory (Silander & Pacala 1990).

SPECIES–SOIL RELATIONSHIPS IN NORTHERN HARDWOOD FORESTS

Dominant canopy trees in northern hardwood forest are strongly segregated along soil gradients. In a transition oak-northern hardwoods forest in north-west Connecticut USA, *Acer saccharum* Marsh. (sugar maple) and *Fraxinus americana* L. (white ash) occurred on soils with high exchangeable calcium (Ca^{2+}), magnesium (Mg^{2+}) and potassium (K^+) and low exchangeable aluminium (Al^{3+}) and total nitrogen (N) (van Breemen *et al.* 1997; Finzi *et al.* 1998a,b). Where total content of exchangeable Ca^{2+} , Mg^{2+} and K^+ was low and Al^{3+} was high these species were, however,

replaced by *Quercus rubra* L. (northern red oak), *Tsuga canadensis* (L.) Carr. (eastern hemlock), *Fagus grandifolia* Ehrh. (American beech) and *Acer rubrum* L. (red maple). Such patterns may be due to the effects of soil on shade tolerance (Kobe *et al.* 1995). Intraspecific growth and/or mortality rates of *A. saccharum*, *Fraxinus* and *Tsuga* differed among calcareous and acidic soils, and when parameters reflecting these differences were used in a forest dynamics model (SORTIE; Pacala *et al.* 1993) the resulting simulations accurately predicted composition of the canopy at the landscape scale (Kobe 1996).

We extended the investigation between tree species and soil properties at Great Mountain Forest, the forest studied by Kobe *et al.* (1995), Kobe (1996), van Breemen *et al.* (1997) and Finzi *et al.* (1998a,b). Our objectives were to quantify how the growth of juvenile trees is related to soil factors and to interpret growth responses in the context of competing theories of plant community organization.

Materials and methods

The study was carried out in north-west Connecticut, USA, on the Canaan Mountain plateau at elevations from 300 to 500 m. Soils were distributed among Millsite, Hollis, Chatfield, Charlton, Canton and Bice complexes (Donald Parizek, unpublished data), which are excessively or well-drained loamy Inceptisols formed from glacial till. The bedrock lithology is metamorphic schist and gneiss (Gonick *et al.* 1970).

The forest is in the transition zone between oak-dominated forest of the central Appalachians and the northern hardwoods of New England. It comprises > 4000 Ha of contiguous forest that was heavily exploited for charcoal in the 18th and 19th centuries, but was only lightly harvested in the 20th century. A small portion of the forest consists of conifer plantations, mainly *Pinus strobus* L. (eastern white pine).

The six tree species sampled were those studied by Finzi *et al.* (1998a,b; see above). In June and July 1998, c. 180 saplings of each species were selected by searching near logging-access roads. Saplings were defined as pre-reproductive trees between 0.5 and 4 m in height. Light availability was estimated from colour hemispherical-lens photographs taken prior to leaf fall in August and September 1998. A photograph of the canopy was taken using a levelled, orientated camera mounted on a tripod placed directly over the stem of the sapling. The stem was displaced to one side when necessary. Photos were processed using GLI/C software (Canham 1988b), which provides an estimate of the combined incident diffuse and direct-beam radiation over a growing season expressed as a percentage of the light available to a sapling growing in full sun.

Extension growth of the uppermost stem or branch (distance from previous year's bud scar to the base of the current bud) was measured at the end of the growing season (October and November 1998); this

measure is a reasonable surrogate for annual whole-plant growth (Canham 1988a; Walters & Reich 1997).

SOILS ANALYSIS

Soil sampling was done from August to October 1998. Leaf litter was brushed away from the soil surface, then soil was sampled with a probe of 17.5 mm internal diameter. Soil was taken from 0 to 0.1 m depth because saplings are likely to have the majority of their roots in this upper soil layer, and because the rocky soils make it difficult to consistently insert the probe more deeply. Five samples were taken in an arc that was 0.25 m from the base of each sapling, then these were combined into a single composite sample per sapling.

A Fisher Accumet pH meter (Model 610 A) was used to measure pH. Highly organic soils were suspended in a 10 : 1 slurry of deionized water and 2.0 g of sample; mineral soils were suspended in a 2 : 1 slurry of deionized water and 10 g of sample (Hendershot *et al.* 1993).

Half of the soil samples from each species were randomly selected for determination of NH_4^+ and NO_3^- . These samples were processed the day following collection; each was sifted through an 8-mm sieve, then rocks and debris of > 8 mm diameter were discarded. The sample was then sifted through a 2-mm sieve to break up aggregates, and the < 2 mm soil fraction was recombined with the 2–8 mm fraction to preserve larger, organic debris from the forest floor. To obtain soil moisture content for moisture correction, 10 g of sieved soil was weighed, oven-dried at 70 °C for 2 days, then weighed again. If the sample for analysis appeared high in organic matter, 100 mL of 2 M KCl was added to 10 g of soil (Mulvaney 1996); if not, then only 60 mL of KCl was added because the smaller volume helped to bring NO_3^- within detection limits. The flasks were agitated at 125 revolution min^{-1} for 1 h then allowed to settle overnight. The slurry was filtered through Whatman 41 filter paper into 20-mL scintillation vials. One drop (0.03–0.05 mL) of chloroform was added to each vial for preservation, then the vials were stored at 4 °C.

Analyses of NH_4^+ and NO_3^- were performed with an automated colourimetric system (Technicon II; Scientific Instruments, Tarrytown, New York, USA). Ammonium was analysed with a salicylate reaction, and NO_3^- was reduced to NO_2^- with a copper-cadmium column then analysed with a sulfanilamide reaction (Mulvaney 1996). Both methods had lower detection limits of 0.01 mg/L.

Soils for cation analyses were extracted with barium chloride (BaCl_2), because high-molarity KCl extractions can cause inaccurate estimates of exchangeable cations in acidic, high-mica soils (Hendershot & Duquette 1986). One hundred millilitres of 0.1 M BaCl_2 were added to 10 g of air-dried sieved soil, then soil slurries were filtered through ashless paper and preserved as described above. After several months' storage, many extracts had developed clear, jelly-like growths that clogged analytical instruments, and these extracts had lower Ca^{2+} than fresh extracts of the same

soils. Stored extracts were therefore discarded and c. 45% of the archived soil samples, stratified by species and pH, were re-extracted and analysed. Cation analyses were done using inductively coupled plasma atomic emission spectrometry (Perkins-Elmer P400, Norwalk, Connecticut, USA; Soltanpour *et al.* 1996). Blanks and National Institute of Standards-certified materials were used to ensure accurate analyses; lower detection limit was 0.1 mg/L.

STATISTICAL ANALYSIS

Relationships among soil factors were explored by regressions of element concentrations against pH. Factor analysis was performed on the correlation matrix, and only factors with eigenvalues > 1 were retained (Systat 1998). Comparisons of species distributions along soil gradients were made by analysis of variance in Systat (1998). Normality of distributions were tested using the Shapiro-Wilk statistic in the Univariate procedure of SAS (1988). Because distributions of all soil factors were strongly left-skewed, data were transformed ($\log_{10}(x + 1)$; Sokal & Rohlf 1995) prior to analysis.

Effects of soil factors on growth were examined by fitting a nested series of functions to the data (Hilborn & Mangel 1997). The core equation was the Michaelis-Menten (1913) function, $G = aI/(aI + I)$ (equation 1), where G represents branch extension growth, a corresponds to the asymptotic maximum growth, s corresponds to the slope of the graph at zero light, and I is light availability. The function is commonly used to model sapling growth (Pacala *et al.* 1993; Kobe *et al.* 1995; Kobe 1996; Wright *et al.* 1998; Finzi & Canham 2000).

The effects of soil factors were brought into the function by substituting the linear term $b + cF$ for a (b and c are fitted parameters and F represents any soil factor), producing the equation $G = (b + cF)I/((b + cF)s + I)$ (equation 2). A different modification was made by substituting the linear term $d + fF$ for s (d and f are fitted parameters), resulting in the equation $G = aI/((aI/(d + fF)) + I)$ (equation 3). Finally, substitutions were made for both a and s resulting in $G = ((b + cF)I)/((b + cF)/(d + fF) + I)$ (equation 4). Thus, a system of four nested equations was created in which the basic equation incorporated only the effect of light on growth, more-complex equations added the effect of soil factors at either high or low light, and the most complex equation added the effect of soil factors at high and low light.

Effects of soil pH on growth were tested separately from effects of exchangeable ions because more data were available and measurements are little affected by variation in soil bulk density. Further, pH variation is a non-consumed gradient (i.e. a regulator gradient; Huston 1994), whereas nutrient elements form resource gradients. The effect of soil pH on growth was tested by fitting the series of four equations to growth and light data using soil pH as the soil factor F . Equations were fitted using the Gauss-Newton method in the non-linear

procedure of Systat (1998). Negative log-likelihoods were calculated with the loss statement of the non-linear procedure under the assumption that residuals were normally distributed. The likelihood of observing the data given a particular equation was assessed by likelihood ratio test (Hilborn & Mangel 1997). The likelihood ratio (i.e. twice the difference between the negative log-likelihood of two functions) was evaluated using the chi-square distribution, in which degrees of freedom were equal to the difference in the number of parameters of the two functions. This procedure allowed selection of the function that fitted the data best with fewest parameters. A conservative level of significance, $\alpha = 0.0174$, was used for individual species to keep the whole-experiment probability of making a type I error at < 0.1 (Dunn-Šidák procedure; Sokal & Rohlf 1995). Parameter estimates and support were generated with the Systat non-linear procedure.

To test for effects of soil factors other than pH on growth, the four nested equations were fitted to the growth data for each soil factor, then the soil factor that accounted for the most variance in the growth of a species was identified based on the mean-corrected r^2 (Wilkinson *et al.* 1996). The mean-corrected r^2 was used at this step because a full set of nutrient analyses was not available for every individual and thus

likelihoods could not be applied. After the soil factor accounting for the most variance was identified, negative log-likelihoods were calculated and selection of most-likely equation and calculation of equation parameters were done in the same way as for pH.

Results

SOIL FACTOR INTERRELATIONSHIPS

On soils of higher pH there was more exchangeable Ca^{2+} and Mg^{2+} , and less Al^{3+} , K^+ and NH_4^+ (Fig. 1, Table 1). The positive correlation between pH and Ca^{2+} and Mg^{2+} at our study site was expected because soil pH is determined in large part by the quantity of these base-forming cations (Bohn *et al.* 1985). Although K^+ is also a base-forming cation it showed decreasing availability at high pH, probably because K^+ is susceptible to fixation at high pH in high-mica soils (Bohn *et al.* 1985). Ammonium is susceptible to the same fixation reaction, but lower NH_4^+ at higher pH in our study may also have been due to enhanced activity of nitrifying micro-organisms. Nevertheless, availability of NO_3^- was only weakly related to pH.

Analysis of the correlation matrix yielded two components with eigenvalues > 1 that together explained

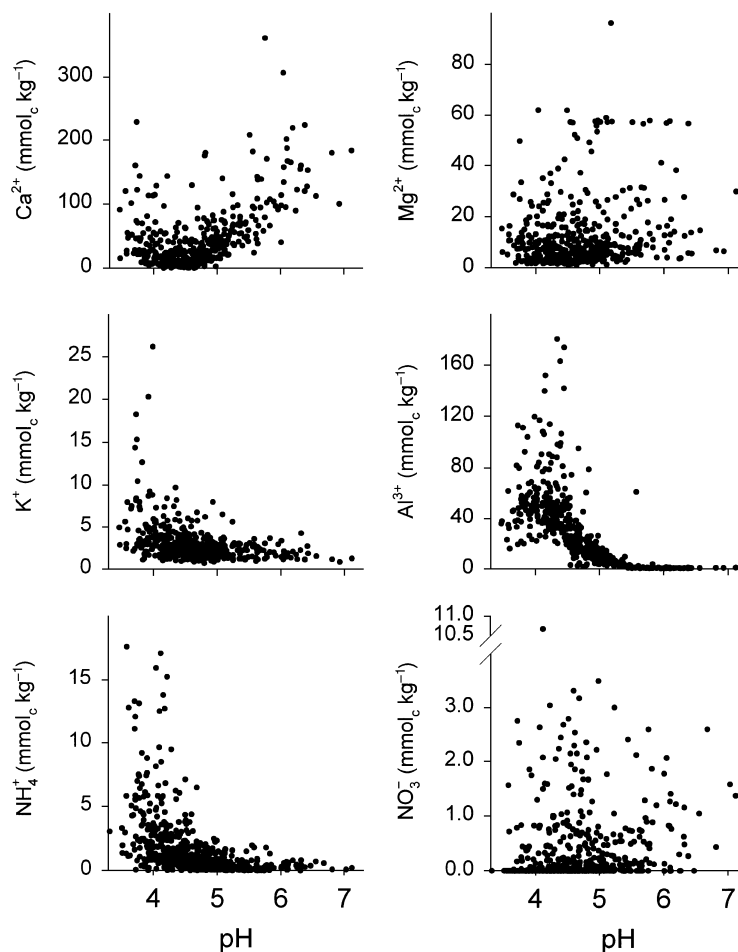
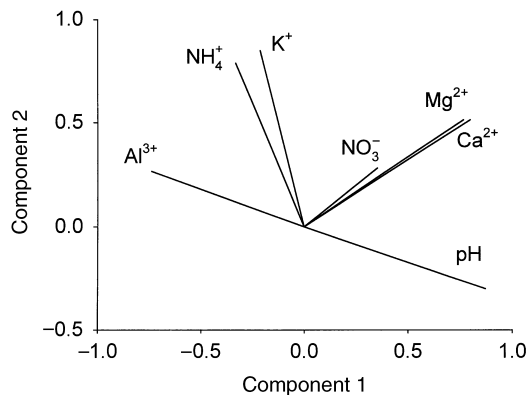


Fig. 1 Relationship between exchangeable ion concentration and soil pH in surface (0–0.1 m) soil samples taken at bases of saplings in an oak-northern hardwood forest.

Table 1 Regressions of exchangeable ions against soil pH

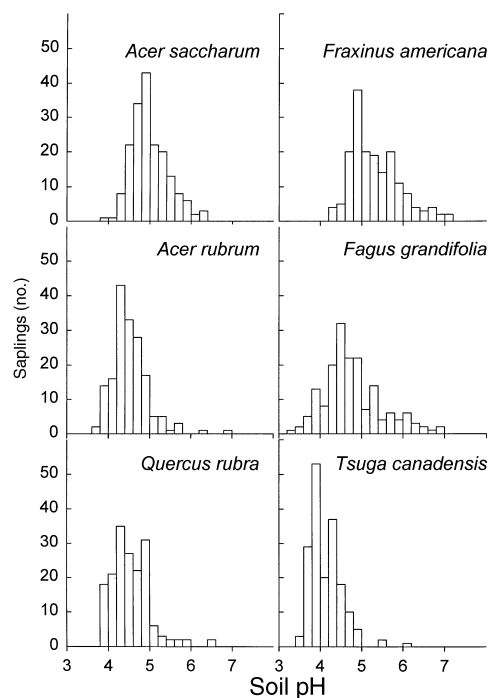
	N	P	r ² *	Regression
Ca ²⁺	455	< 0.001	0.278	39.4x - 142
Mg ²⁺	459	< 0.001	0.268	10.9x - 38.8
K ⁺	459	< 0.001	0.141	-1.44x + 9.73
Al ³⁺	459	< 0.001	0.398	-29.2x + 167
NH ₄ ⁺	578	< 0.001	0.205	-1.77x + 9.94
NO ₃ ⁻	578	0.003	0.013	0.147x - 0.334

*Adjusted multiple r².**Fig. 2** Component loadings plot of soil factor data.

70% of the variance (Fig. 2) in soil factors. Components 1 and 2, respectively, had eigenvalues of 2.804 and 2.131 and explained 40% and 30% of variance. Soil factors formed three clusters: a Ca²⁺-Mg²⁺-NO₃⁻ group, a K⁺-NH₄⁺ group, and a third axis showing the inverse relationship between pH and Al³⁺.

SPECIES DISTRIBUTIONS ALONG SOIL GRADIENTS

Relationships were found between species distributions and all soil properties (Table 2). *A. saccharum* and

**Fig. 3** Frequency distributions of saplings with respect to pH of upper 0.1 m of soil. Approximately 180 saplings of each species were sampled. The relationship between species and soil pH is statistically significant (ANOVA, d.f. = 1064, $F = 131.492$, $P < 0.001$).

Fraxinus were at the upper end of the pH gradient, and *Tsuga*, *Quercus*, *A. rubrum* and *Fagus* were at the lower end (Fig. 3). A similar trend occurred along the Ca²⁺ gradient, with *A. saccharum* and *Fraxinus* occurring on the highest-Ca²⁺ soils (Fig. 4). Despite the positive overall correlation between exchangeable Ca²⁺ and Mg²⁺ (Fig. 2), relationships between species and Mg²⁺ were not identical to those between species and Ca²⁺. *Fraxinus* and *Tsuga* occurred on soils with highest Mg²⁺, and *A. saccharum* occurred on soils of somewhat lower Mg²⁺. High Mg²⁺ under *Tsuga* may be an artefact

Table 2 Analysis of variance of effect of tree species on pH and exchangeable ions of upper 0.1 m of soil. Values of all soil factors were log(x + 1)-transformed prior to analysis to improve normality

Soil factor	Source	Sum of squares	Degrees of freedom	Mean squares	F	P
pH	Species	71.086	5	1.440	131.492	< 0.001
	Error	483.019	1064	0.011		
Ca ²⁺	Species	23.323	5	14.217	13.304	< 0.001
	Error	261.408	452	1.069		
Mg ²⁺	Species	14.003	5	4.665	8.119	< 0.001
	Error	67.375	455	0.575		
K ⁺	Species	227.932	5	2.801	18.913	< 0.001
	Error	451.757	455	0.148		
Al ³⁺	Species	50.103	5	45.586	45.914	< 0.001
	Error	179.561	455	0.993		
NH ₄ ⁺	Species	4.550	5	10.021	33.037	< 0.001
	Error	70.022	592	0.303		
NO ₃ ⁻	Species	7.202	5	0.910	7.693	< 0.001
	Error	11.655	592	0.118		

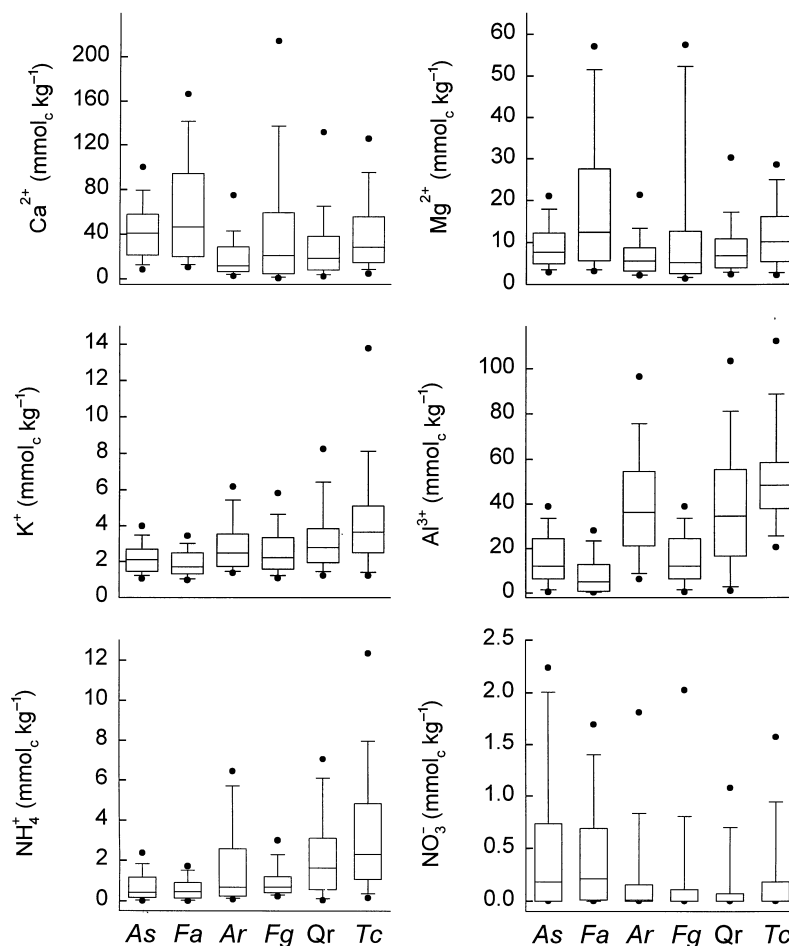


Fig. 4 Distribution of exchangeable ion content in soil according to species. Horizontal lines of boxes show 25th and 75th percentiles and median, error bars show 10th and 90th percentiles, and dots show 5th and 95th percentiles. Species are identified at page bottom by first initials of their Latin binomials.

Table 3 Negative log-likelihoods for models of extension growth. Equation 1 incorporates only light availability, and equations 2–4 also incorporate one soil factor, indicated in parentheses (a = pH; b = other factors). Bold font denotes most likely model for each species, chosen by likelihood ratio test ($\alpha = 0.0174$; Dunn-Šidák-adjusted to provide experimentwise $\alpha = 0.1$ for six species)

Equation	Parameters	<i>Acer saccharum</i>	<i>Fraxinus americana</i>	<i>Acer rubrum</i>	<i>Fagus grandifolia</i>	<i>Quercus rubra</i>	<i>Tsuga canadensis</i>
(a)		(pH)	(pH)	(pH)	(pH)	(pH)	(pH)
1	<i>as</i>	695.563	718.696	723.004	668.424	665.248	648.972
2	<i>bcs</i>	695.533	715.100	700.526	667.683	656.563	648.494
3	<i>adf</i>	695.532	718.360	703.244	666.651	656.168	648.130
4	<i>bcdf</i>	695.532	713.000	700.508	666.575	656.022	644.937
(b)		(Mg ²⁺)	(Mg ²⁺)	(Al ³⁺)	(Ca ²⁺)	(Ca ²⁺)	(NO ₃ ⁻)
1	<i>as</i>	298.393	325.205	308.456	286.410	314.436	360.831
2	<i>bcs</i>	297.743	321.708	300.727	286.068	312.460	357.553
3	<i>adf</i>	296.967	323.880	302.075	285.500	311.144	358.011
4	<i>bcdf</i>	296.941	319.802	300.611	281.404	310.666	357.227

of the sampling method; *Tsuga* tended to occur on soils that are high in organic matter and low in bulk density, so expressing the data on a weight basis may have led to high estimates of exchangeable elements for this species.

Exchangeable K⁺ and Al³⁺ showed trends with respect to species that were opposite to those of Ca²⁺

and pH; *A. saccharum* and *Fraxinus* were on soils with lowest K⁺ (Fig. 4). Species were separated into two groups with respect to Al³⁺, with *A. rubrum*, *Quercus* and *Tsuga* occurring on the soils with highest Al³⁺.

Ammonium values were highest under *Tsuga* and *Quercus* (Fig. 4). In contrast, only *A. saccharum* and

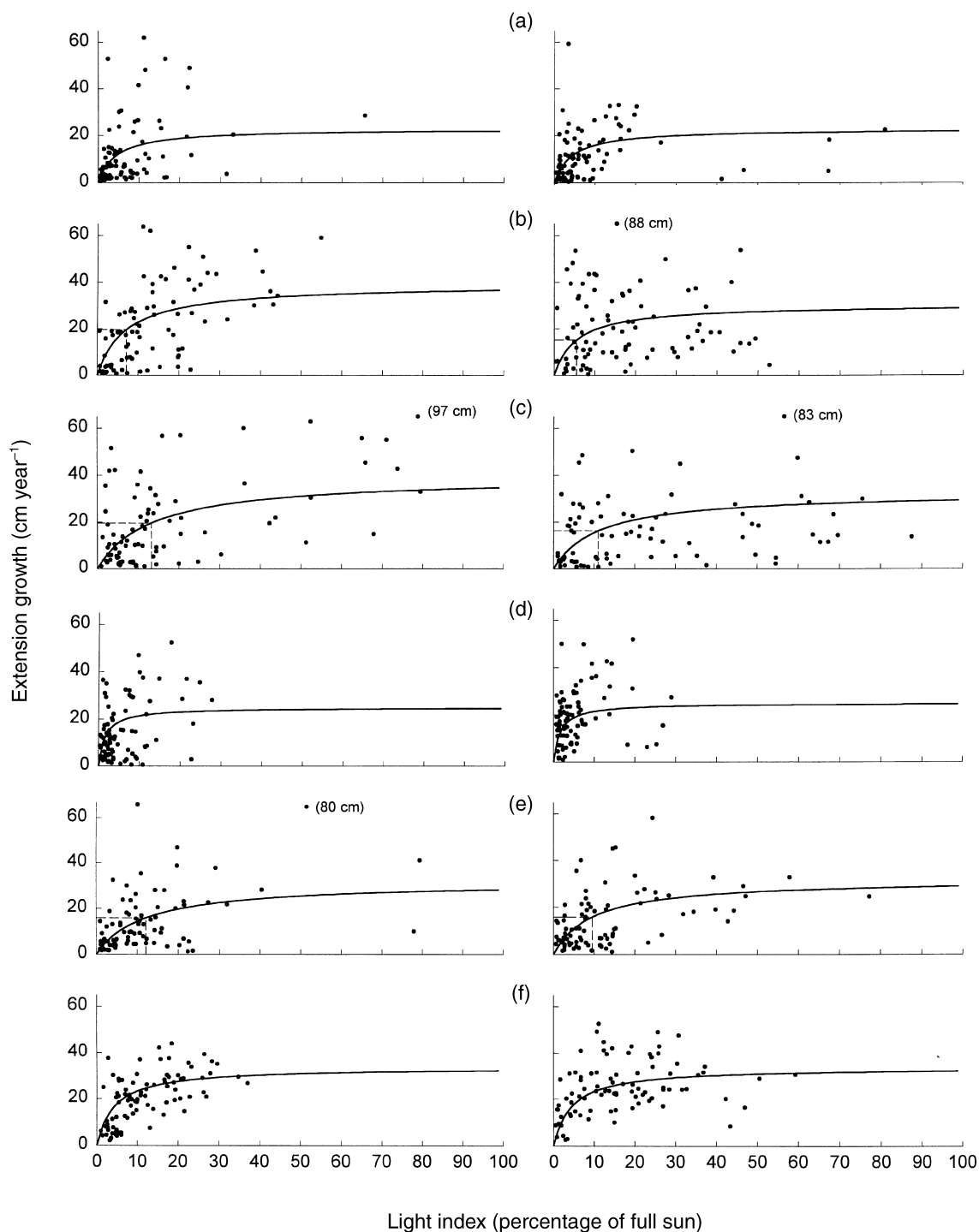


Fig. 5 Branch extension growth (measured and modelled) over one season with respect to light availability and soil pH for saplings of six species. Adjacent graphs show growth below (left, 25th percentile) and above (right, 75th percentile) median pH. For species with significant effects of pH on growth, boxes indicate light level at which modelled extension growth is half of maximum. (a) *Acer saccharum*; (b) *Fraxinus americana*; (c) *Acer rubrum*; (d) *Fagus grandifolia*; (e) *Quercus rubra*; (f) *Tsuga canadensis*.

Fraxinus saplings grew in soils with appreciable levels of NO_3^- .

EFFECT OF SOIL FACTORS ON GROWTH

For three of six species, equations that incorporated soil pH in addition to light fitted the growth data

better than the Michaelis-Menten equation (Table 3a). Although *A. saccharum* and *Fraxinus* are both calcicolous dwellers on high-pH soils, neither had a positive growth response on high-pH soils. *A. saccharum* showed no response to pH (Fig. 5a), while *Fraxinus* showed diminished high-light growth at high pH (Fig. 5b), confirmed by $c < 0$ in the best model (Table 4a). Neither

Table 4 Parameters and 95% support intervals for most-likely models of species' growth responses to light and soil pH (a) and other soil factors (b). Models are in parentheses after specific epithets

Unit	<i>A. saccharum</i> (equation 1)	<i>Fraxinus</i> (equation 2)	<i>A. rubrum</i> (equation 2)	<i>Fagus</i> (equation 1)	<i>Quercus</i> (equation 3)	<i>Tsuga</i> (equation 1)
(a)						
<i>a</i> cm	22.9 (16.8–29.0)			24.8 (16.8–29.0)	31.7 (23.0–40.5)	33.6 (29.4–37.8)
<i>s</i> cm/%	5.24 (2.65–7.83)	5.49 (2.63–8.34)	2.96 (1.58–4.34)	15.7 (7.4–23.9)		7.55 (4.88–10.22)
<i>b</i> cm		90.3 (43.4–137.2)	99.3 (54.8–143.8)			
<i>c</i> cm/pH unit		–10.6 (–18.6––2.6)	–14.3 (–22.9––5.62)			
<i>d</i> cm/%					–2.26 (–11.2–6.7)	
<i>f</i> cm/ (% · pH unit)					1.17 (–0.95–3.3)	
(b)						
	(equation 1)	(equation 2: Mg ²⁺)	(equation 2: Al ³⁺)	(equation 4: Ca ²⁺)	(equation 3: Ca ²⁺)	(equation 2: NO ₃ ⁻)
<i>a</i> cm	24.8 (15.0–34.6)				32.5 (22.2–42.8)	
<i>s</i> cm/%	4.62 (1.32–7.93)	8.27 (1.23–15.30)	1.73 (0.66–2.80)			7.62 (3.69–11.55)
<i>b</i> cm		45.3 (30.3–60.3)	7.01 (–12.09–26.10)	31.5 (21.7–41.3)		30.3 (24.7–36.1)
<i>c</i> cm · kg/mmol _c		–0.506 (–0.891––0.120)	1.17 (0.12–2.22)	–0.071 (–0.125––0.018)		8.47 (1.24–15.7)
<i>d</i> cm/%				4.59 (0.41–8.77)	0.670 (–0.830–2.170)	
<i>f</i> cm · kg/ % · mmol _c				0.456 (–0.118–1.030)	0.153 (–0.020–0.325)	

Table 5 Mean-corrected r^2 for model of extension growth with respect to light (equation 1), and for models that also incorporate soil factors (equations 2–4). Bold font denotes highest r^2 for species

Equation	Soil factor	<i>Acer saccharum</i>	<i>Fraxinus americana</i>	<i>Acer rubrum</i>	<i>Fagus grandifolia</i>	<i>Quercus rubra</i>	<i>Tsuga canadensis</i>
1		0.178	0.137	0.125	0.097	0.207	0.303
2	Ca ²⁺	0.239	0.143	0.197	0.130	0.250	0.277
2	Mg ²⁺	0.240	0.187	0.182	0.097	0.217	0.278
2	K ⁺	0.236	0.120	0.170	0.093	0.258	*
2	Al ³⁺	0.231	0.109	0.323	0.086	0.238	0.277
2	NH ₄ ⁺	0.164	0.126	0.092	0.083	0.226	0.302
2	NO ₃ ⁻	0.147	0.120	0.075	0.075	0.191	0.329
3	Ca ²⁺	0.252	0.115	0.128	0.143	0.275	0.276
3	Mg ²⁺	0.255	0.105	0.117	0.088	0.212	0.278
3	K ⁺	0.252	0.112	0.162	0.121	0.263	*
3	Al ³⁺	0.238	0.121	0.297	0.098	*	*
3	NH ₄ ⁺	0.125	0.123	0.103	0.071	0.223	0.298
3	NO ₃ ⁻	0.131	0.129	0.075	0.079	0.185	0.323
4	Ca ²⁺	0.253	0.170	0.219	0.232	0.283	0.283
4	Mg ²⁺	0.255	0.227	0.175	0.167	0.217	0.301
4	K ⁺	0.251	0.146	0.105	0.137	0.262	0.130
4	Al ³⁺	0.238	0.157	0.232	0.128	*	*
4	NH ₄ ⁺	0.174	0.127	0.110	0.084	*	*
4	NO ₃ ⁻	0.152	0.138	0.076	0.086	0.238	0.334

*Did not converge.

Fagus and *Tsuga*, despite dwelling on low-pH soils, showed a growth response to pH (Table 3a), but *A. rubrum*, also a calcifuge, showed a negative high-light response to high pH (Table 4a, Fig. 5c). However, *Quercus*, another calcifuge, had a positive growth response to high-pH soils (Table 3a, $f > 0$ in Table 4a), albeit manifest at low rather than high light (Fig. 5e).

Incorporation of soil factors other than pH into the series of growth equations resulted in higher r^2 values than when growth was modelled using only light

availability (Table 5). For four of six species, base cations produced the best fit; Mg²⁺ for *A. saccharum* and *Fraxinus*, and Ca²⁺ for *Fagus* and *Quercus*. Aluminium produced the highest r^2 for *A. rubrum*, and NO₃⁻ yielded the highest r^2 for *Tsuga*.

Species' growth in relation to exchangeable ions (Fig. 6, Tables 3b and 4b) was largely consistent with the species' growth in relation to pH (Tables 3a and 4a) given the correlations among availability of soil factors (Table 1, Figs 1 and 2). *A. saccharum* growth was an

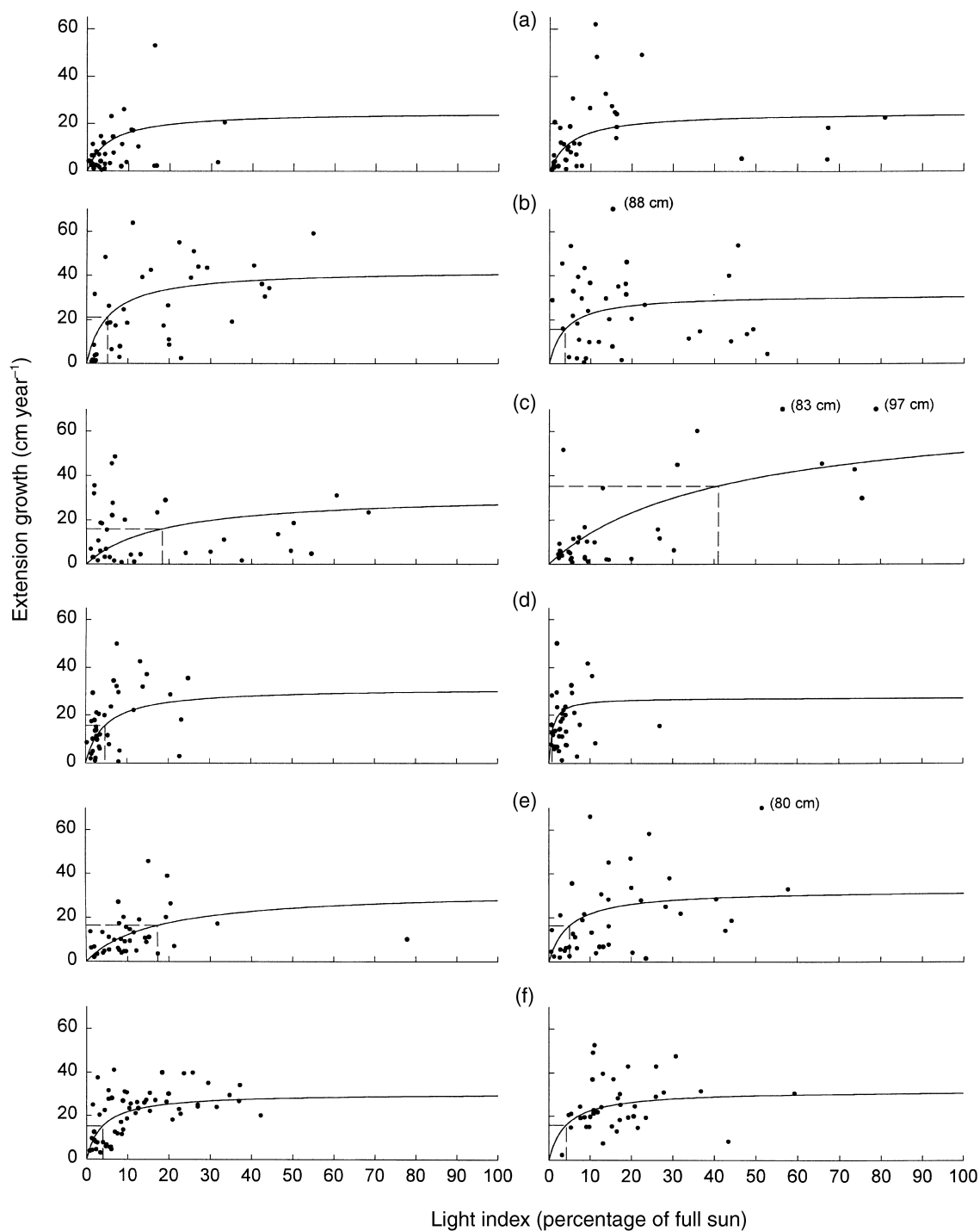


Fig. 6 Measured and modelled seasonal branch extension with respect to light availability and soil factors. Adjacent graphs present saplings growing below (left, 25th percentile) and above (right, 75th percentile) median value of a soil factor. For species with significant effects of a soil factor on growth, boxes indicate light level at which modelled extension growth is half of maximum. (a) *Acer saccharum*, Mg^{2+} ; (b) *Fraxinus americana*, Mg^{2+} ; (c) *Acer rubrum*, Al^{3+} ; (d) *Fagus grandifolia*, Ca^{2+} ; (e) *Quercus rubra*, Ca^{2+} ; (f) *Tsuga canadensis*, NO_3 .

exception because it was not significantly related to Mg^{2+} (Table 3b) despite high r^2 values of models incorporating this cation (Table 5). *Fraxinus* had decreased high-light growth on high- Mg^{2+} soils (Table 4b, $c < 0$). *A. rubrum* showed markedly better high-light growth on high- Al^{3+} soils (Tables 3b and 4b), even though Al^{3+} is not a plant nutrient and is potentially toxic. *Quercus*

had higher low-light growth on high- Ca^{2+} soils (Table 4b, $f > 0$), and *Fagus* had a mixed pattern of growth with respect to high- Ca^{2+} soils; lower high-light growth but improved low-light growth (Tables 4b, $c < 0$, $f > 0$). *Tsuga* was the sole species for which any form of N produced the best fit to growth; better high-light growth occurred at high levels of NO_3 (Table 4b, $c > 0$).

Discussion

SAPLING DISTRIBUTIONS AND SOIL PROPERTIES

The observed correlations between species and soil properties are unlikely to have been generated by effects of the saplings themselves upon the soil, because the leaf and root turnover from these small plants is unlikely to have been enough to measurably affect soil properties. Nevertheless, mature trees do influence soils (Finzi *et al.* 1998a,b), and it is possible that correlations between species and soil properties resulted from alteration of soil properties by adult trees, in combination with limited dispersal of offspring. Ribbens *et al.* (1994) documented mean dispersal distances at our study site ranging from < 6 m (*Fagus* and *Tsuga*) to > 15 m (*Fraxinus*). These distances are likely to exceed the potential range of influence of individual trees upon the soil, and given the high degree of local heterogeneity in tree species composition (Schnurr 2000) it is likely that many seeds are dispersed beyond local soil units. It is likely therefore that the observed pattern of saplings and soil properties was at least partially generated by differential growth and survival along soil gradients.

SAPLING PERFORMANCE AND SOIL CHEMISTRY

Our findings were generally consistent with those of Kobe (1996), who compared sapling growth and mortality of saplings growing on calcareous valley-bottom soils with saplings growing on the acidic upland soils where our study was carried out. There were no effects of site (calcareous compared with acidic) on *A. saccharum* growth in Kobe's work, and neither did we find any effect of soil chemistry on *A. saccharum* growth. Kobe found marginally slower growth of *Fraxinus* on calcareous soil, and this species grew more slowly on high-Mg²⁺ soils in our study. *Fagus* saplings in low light showed a (non-significant) trend towards faster growth at the calcareous site than at the acidic site in Kobe's study, and *Fagus* saplings in low light in our study grew faster on high-Ca²⁺ than low-Ca²⁺ soils. Kobe found a decrease in *Tsuga* growth on calcareous soils, and though saplings of this species in our study showed a trend of decreased high-light growth at higher soil pH, it was not accepted as significant ($P = 0.0176 > \alpha = 0.0174$).

The present study highlights the role of base-cation availability in determining performance of saplings at the scale of the forest stand. In the study by Kobe (1996), landscape-scale comparisons made in the absence of soil chemistry measurements mean that growth effects due to N availability could not be ruled out. In our study only *Tsuga* growth showed a significant relationship with soil NO₃⁻ and this effect was small (Fig. 6f). Finzi & Canham (2000) found that N availability affected growth of *A. rubrum* and *A. saccharum* in

the same forest as the present study, but N availability accounted for < 7% of variation in growth. Base-cation availability may yet prove important to establishment of forest trees in other zones of the North American cold-temperate forest, where N availability is currently considered paramount (Walters & Reich 1997).

The finding of an increase in low-light growth on higher-fertility soils in *Fagus* supports the idea that soil fertility can affect shade tolerance (Coomes & Grubb 2000). Although the low-light growth parameter s was also significantly related to soil chemistry for *Quercus*, it is likely that the individuals that had the most effect on the results were not growing in extremely low light (e.g. < 4% of full sun; Walters & Reich 1996) but rather were growing in 5–20% of full sun (Fig. 5e). Most *Fagus* saplings, however, were growing in deep shade, where their growth was positively correlated with Ca²⁺ availability although several caveats apply. First, root sprouting is the dominant form of regeneration of *Fagus* in the north-eastern USA, and most saplings in this study possessed sturdy root connections to neighbouring trees. Although the degree of provisioning of saplings through such root connections is not known, positive effects of Ca²⁺ availability on shade tolerance may result from increased allocation of photosynthate from nearby adult trees. Secondly, there was no significant effect of pH on *Fagus* low-light growth despite the generally strong correlation between soil pH and exchangeable Ca²⁺. Thirdly, the 95% support for effects of Ca²⁺ on f is relatively broad and encompasses negative numbers (Table 4b). At best, then, this study presents only qualified support for a positive, direct effect of soil fertility on shade tolerance.

IMPLICATIONS FOR UNDERSTANDING OF NICHE STRUCTURE

Because *A. saccharum* and *Fraxinus* occurred at the upper end of the Ca²⁺ ± Mg²⁺ resource gradient we did not expect to be able to use their responses to distinguish among competing theories of community organization. It was surprising, nevertheless, to find that growth of these species was either unrelated to soil chemistry (*A. saccharum*) or was poorest on soils with higher Ca²⁺ and Mg²⁺ (*Fraxinus*). Poor performance of the latter species on rich soils could be due to low iron availability (Finzi *et al.* 1998b), which can interfere with synthesis of chlorophyll (Kozlowski *et al.* 1991). It is likely that soil fertility enhancement of survival, as opposed to growth, is responsible for the abundance of these species at the upper end of the fertility gradient (Kobe *et al.* 1995; Kobe 1996).

Of the four species that occur at the low end of the soil resource gradient, one showed a growth response that was strongly consistent with fundamental niche differentiation (FND) and continuum concept (CC), and the other three showed responses that were consistent in varying degrees with shifting competitive hierarchy (SCH) and CC. A regulator or non-resource

gradient (pH-Al³⁺) best explained the growth rate of *A. rubrum*. Because this species is most abundant at the low end of this gradient (i.e. on soils with low pH and high Al³⁺) and has decreased growth in individuals occurring further up the gradient, it behaves consistently with FND and CC. High soil Al³⁺ normally inhibits plant growth by inhibiting root elongation and interfering with uptake of other polyvalent cations such as Mg²⁺ and Ca²⁺ (Marschner 1995), so the *A. rubrum* growth response probably reflects tolerance of Al³⁺ rather than an affinity for it. The work by Finzi & Canham (2000) suggests that *A. rubrum* could have responded to increased NH₄⁺ availability at low pH, but the low correlation between exchangeable NH₄⁺ and growth in our study (Table 5) argues against this. Most likely, *A. rubrum*'s growth response reflects a direct response to soil pH that is not mediated by plant macronutrients.

Abrams (1998) has documented that *A. rubrum* has moved in recent decades beyond its typical habitat of wetlands and rocky outcrops to become a dominant species in upland forests throughout its range. This range expansion was ascribed both to fire suppression, because *A. rubrum* is not fire-tolerant, and to increased human-induced landscape heterogeneity, because *A. rubrum* can act both as an early and late successional species. Our data suggest an additional, complementary hypothesis: *A. rubrum* regeneration benefits from acid-rain-related soil acidification and base-cation depletion that is occurring region-wide (Likens *et al.* 1996).

In contrast to *A. rubrum*, *Quercus* and *Fagus* performed better on richer soils, apparently responding to higher Ca²⁺ despite being calcifugous species. Such improved performance at the upper end of a resource gradient, in combination with highest abundance at the low end of the resource gradient, is consistent with SCH and CC and is contrary to FND. Latham (1992) worked with *Fagus* and *Quercus* and other species in a greenhouse study and also found better performance at the highest levels of applied fertilizer; he highlighted the relevance of these results to SCH. Given the consistency of these findings, and the absence of an effect of soil chemistry on survival of these species (Kobe 1996), the preference of *Quercus* and *Fagus* for low-Ca²⁺ soils must be ascribed either to weak competitive ability or to effects of soil chemistry on germination and establishment.

Tsuga's response to soil NO₃⁻ is characteristic of species conforming to SCH and CC: it is most abundant on poorer, acidic soils even though its growth is enhanced at the upper end of the soil NO₃⁻ gradient. In contrast, Kobe's (1996) observation of diminished *Tsuga* growth on calcareous soils is more consistent with FND.

Conclusions

Because of the success of SCH in describing this community it must continue to be treated as a powerful means of explaining community organization. The

continuum concept was even more successful than SCH, correctly predicting the growth responses of four of six species because it allows for different responses according to gradient type. Nevertheless, it is unclear whether CC is intended to accommodate responses to different gradients within a plant community. Organization of plant species along different soil gradients within a community is probably common, yet measurement of large numbers of soil factors need not result in unmanageable complexity as in our study where a suite of soil variables resolved into three major axes of variation. Because species showed growth responses to different groups of soil factors, measurement of the suite of variables was essential to an adequate understanding of community dynamics.

Given that even small saplings were already segregated along soil nutrient gradients, further studies on soil effects on germination and establishment in these forests are necessary to understand species patterns along edaphic gradients. Edaphic restriction due to differential survival along soil resource gradients, at the sapling stage (Kobe 1996) or earlier in the life cycle, remains the best explanation for the generation of species-soil relationships. We expect that additional work in this community of trees in north-eastern USA will continue to yield insights into the functioning of ecological communities, and are in agreement with Harper (1981) that it is from repeated, detailed studies of particular communities that ecological generalizations are most likely to emerge.

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