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EVIDENCE THAT SOIL ALUMINUM ENFORCES SITE FIDELITY OF SOUTHERN NEW ENGLAND FOREST TREES

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ABSTRACT. Tree species composition of hardwood forests of the northeastern United States corresponds with soil chemistry, and differential performance along soil calcium (Ca) gradients has been proposed as a mechanism for enforcing this fidelity of species to site. We conducted studies in a southern New England forest to test if surface-soil Ca is more important than other factors in determining survival of seedlings of six common canopy tree species. Our hypothesis was that the calcicole species *Acer saccharum* and *Fraxinus americana* would show elevated survival rates at higher Ca levels, and that the calcifuge species *A. rubrum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis* would show lower survival at high Ca. Other factors examined were 1) exchangeable magnesium (Mg), potassium (K), and aluminum (Al); 2) understory light availability; and 3) identity of overstory tree species. In one study, seedlings were transplanted into plots fertilized with Ca or Mg sulfate and survival was measured over 2 years. In the other study, 1-year or 2-year survival of naturally established seedlings in stands dominated by mature trees of one of the six study species was followed. Fertilization with Ca or Mg did not affect survival of planted seedlings, but ambient exchangeable Al was strongly negatively correlated with survival of *F. americana*. Of the three species with sufficient naturally established seedlings, exchangeable Al plus a proxy for light (overstory tree identity) were the most important determinants of survival. Survival of *A. saccharum* declined and *A. rubrum* and *F. grandifolia* increased at higher levels of exchangeable Al. This pattern is consistent with the positions of these species along the soil gradient. We conclude that soil chemistry effects on seedling survival play a role in establishing the soil relationships characteristic of these species as adults, but that Al is more important than Ca in establishing these effects during the seedling stage.

Key Words: northern hardwood forest, calcicole, calcifuge, seedling survival, canopy tree, exchangeable calcium, exchangeable aluminum, site fidelity, plant-soil relationship

Tree communities in northern hardwood forests of the northeastern United States are characterized by affinities of tree species for soil characteristics. Calcicole species such as *Acer saccharum* and *Fraxinus americana* are most common on soils high in

exchangeable base-forming cations such as calcium (Ca) and magnesium (Mg), and the calcifuge species *A. rubrum*, *Quercus rubra*, *Tsuga canadensis*, and *Fagus grandifolia* are more prevalent in poorer soils that are acidic and high in exchangeable aluminum (Balter and Loeb 1983; Finzi et al. 1998; Pearson 1962; Schwarz et al. 2003; Smith and Vankat 1991; van Breemen et al. 1997). Differential species performance along soil gradients during the regeneration phase is often assumed to be a cause of this pattern (Grubb 1977).

Recent attention has centered on soil Ca regulation of forest composition and function in the northeastern United States and elsewhere (Bellemare et al. 2005; Decker and Boerner 1997; Kobe et al. 2002; McLaughlin and Wimmer 1999; Yanai et al. 2005). Augmentation of depleted soils with Ca enhanced seedling survival of *Acer saccharum* on granite-derived soils of central New Hampshire (Juice et al. 2006), but another study at the same location found a more direct role of aluminum (Al) in determining *A. saccharum* seedling survival (Kobe et al. 2002). Calcium and Al can interact closely to determine plant performance (Cronan and Grigal 1995); the calcium displacement hypothesis holds that a decreased ratio of Ca to Al (e.g., due to Ca-poor parent material) leads to increased Al saturation of root surface adsorption sites, causing decreased root survival and growth (Bengtsson 1992). Both Ca and Al may affect establishment of mycorrhizal associations which enhance plant nutrition (Coughlan et al. 2000; Kelly et al. 2005). Regardless of the mechanism of Ca effects on seedling survival, questions remain as to whether Ca promotes seedling survival of other calcicole species besides *A. saccharum*, such as *Fraxinus americana*, and whether Ca depresses survival of calcifuge species such as *Fagus grandifolia*.

We carried out two studies to evaluate the role of soil effects on seedling survival in establishing plant-soil relationships in a transitional oak–northern hardwood forest in northwestern Connecticut. Past studies at this site have documented a strong relationship between soil Ca and Mg and overstory tree species composition (Finzi et al. 1998; van Breemen et al. 1997), and this relationship appears to be already established by the sapling phase (Bigelow and Canham 2002). We carried out one experiment by planting seedlings into plots previously fertilized with Ca or Mg, and another by examining survival of naturally established seedlings on substrates that varied in soil chemistry due to differing

parent material and local tree species composition (Dijkstra 2003; Dijkstra et al. 2003). We predicted that survival of *Acer saccharum* and *Fraxinus americana* seedlings would be greatest on high-Ca and high-Mg soils, and that the reverse would be true for *A. rubrum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis* seedlings.

We measured additional variables that might either contribute to the formation of plant-soil relationships, or influence survival and thus create experimental noise. The additional variables were soil pH and exchangeable Al and K, understory light availability, and identity of overstory species. The rationale for considering light is that shading by overstory plants can severely limit photosynthesis and, by extension, survival (Kobe et al. 1995; Messier et al. 1999). Potassium availability declines with increasing soil acidity at our study site, and potassium deficiency has been implicated in sugar maple decline (Fyles et al. 1994). Measurement of these additional variables, particularly exchangeable aluminum, turned out to be crucial in understanding patterns of seedling mortality at our study site.

MATERIALS AND METHODS

The study took place on the Canaan Mountain plateau in Litchfield County, Connecticut (41°58′N, 73°15′W); the mountain is part of the Berkshires range of the Appalachians, and the forest region is transitional between maple and beech-dominated forests to the north and the oak-dominated forests of the central Atlantic region (Nichols 1935). Most of the study took place within the privately owned Great Mountain Forest (GMF). The bedrock of the plateau is mica-schist, resulting in acid soils of low fertility, but there are areas of higher fertility within the forest which may have resulted from glacial deposition of dolomitic limestone scoured from surrounding valleys. Upland soils where the tree species we studied are most prevalent are loamy, well-drained Inceptisols (Dystrudepts and Typic Eutrudepts; Gonick et al. 1970), but *Acer rubrum* was most prevalent on aquic soils (Aeric Epiquepts, Humic Endoaquepts) that were high in organic matter.

Exchangeable calcium in surface soils at our study sites varies from >200 $mmol_c$ kg^{-1}—suitable for agriculture—to below detection limits, but most areas are low in calcium (Table 1: reanalysis of data in Bigelow and Canham 2002). Previous work at GMF has shown considerable variation in surface-soil cations at

Table 1. Variation in exchangeable nutrients and soil pH throughout the study area. Upper 0.15 m of soil. Sample size is 461 except for pH (N = 1070). Units are $mmol_c\ kg^{-1}$ except for pH. Data are from Bigelow and Canham (2002).

Soil Nutrients	Mean	SD	Max
Ca^{2+}	42.6	47.6	361
Al^{3+}	31.0	29.3	180
Mg^{2+}	12.0	13.4	96
K^{+}	3.0	2.4	26
pH	4.7	0.64	7.2

the scale of influence of individual trees (Dijkstra 2003; Dijkstra and Fitzhugh 2003; Dijkstra et al. 2001; Dijkstra et al. 2003; Finzi et al. 1998; van Breemen et al. 1997). The pH of surface soils is significantly correlated with concentrations of major cations: Al^{3+}, K^{+}, and NH_4^{+} are predominant on more acid soils (e.g., pH $<$ 4.5), and Ca^{2+} and Mg^{2+} are predominant at higher pH.

Fertilization study. This study was carried out by planting seedlings into fertilized plots that had previously been established for an experiment on growth limitation of saplings (Bigelow and Canham 2007). Two fertilizer treatments in addition to the control were used: 320 kg $ha^{-1}yr^{-1}$ of calcium as $CaSO_4$, and 49 kg $ha^{-1}yr^{-1}$ of magnesium as $MgSO_4$, continued for three years (1999–2001). Fertilizer was applied evenly to the soil surface in disks around individual saplings. Both treatments led to persistent elevated concentrations of the target cations (Figure 1). Sulfate (SO_4^{2-}) was selected as an accompanying anion for delivery of Ca^{2+} or Mg^{2+} to avoid altering availability of pH-sensitive, non-target chemical soil factors. Application of calcium sulfate fertilizer either does not affect soil pH (Pierce et al. 1999) or has a slight acidifying effect (Bakker et al. 1999). In our study there was an initial acidification which disappeared prior to planting the seedlings (Figure 1). There were 20 replicates each of $CaSO_4$ and $MgSO_4$ fertilization treatments and controls. Planting plots were chosen to include the eight areas within the forest where the fertilized saplings were clustered. Maximum distance between these areas was ~4 km; no two fertilization plots were closer than 10 m from one another.

Seeds of *Acer saccharum*, *Fraxinus americana*, *A. rubrum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis* were purchased from Sheffield's Seed Co. (Locke, NY), using provenances as close

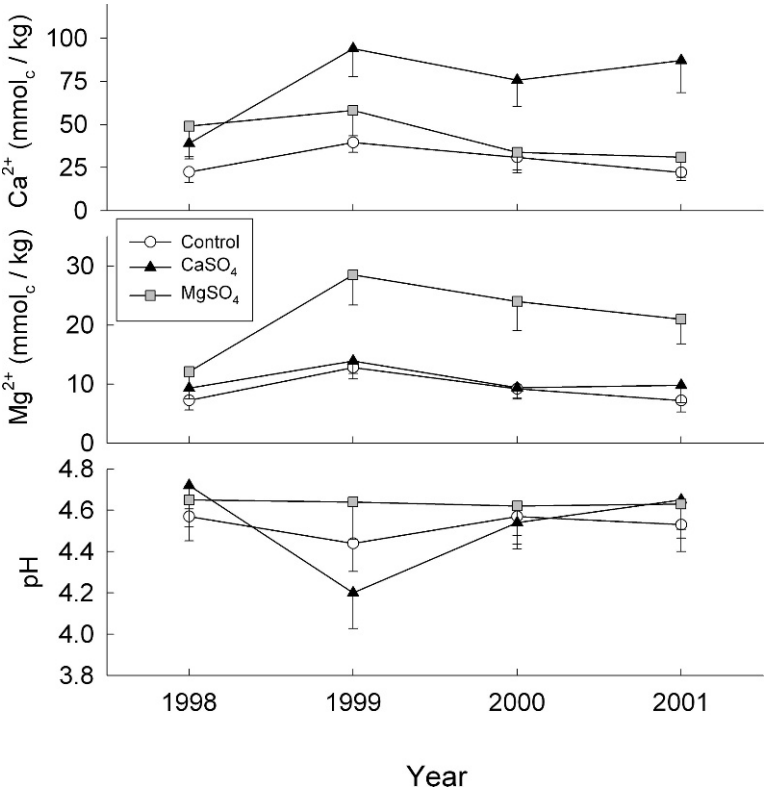

Figure 1. Time trend for exchangeable cations and pH (upper 0.15 m of soil) demonstrating efficacy of fertilization with $CaSO_4$ or $MgSO_4$. Seedlings were planted in 2001. Upper panel, Ca^{2+}, middle panel, Mg^{2+}, lower panel, pH.

as possible to the study area. Seeds were germinated in a low-nutrient medium (100% calcined clay: Turface Pro-League Sports Field Conditioner, Profile Products, Buffalo Grove, IL) and grown for two months in a greenhouse; watering was done regularly but no nutrients were added. Sixty groups (20 per treatment) of seedlings were set out in spring 2001. Each group comprised 18 seedlings (6 species $\times$ 3 seedlings per species, with 0.10 m triangular spacing creating a hexagon). Seedling groups were planted with the hexagon center $\sim$0.50 m from the stems of saplings that were being fertilized.

Chemistry of surface soil was measured at all sites prior to fertilization, and at a subset of sites in the fall of each subsequent

year, to assess effectiveness of fertilization. Five subsamples were collected from 0 to 0.15 m depth (encompassing organic and mineral horizons) at each sampling location with a probe of 17.5 mm internal diameter, then they were combined. Soil was air-dried and sieved to pass an 8 mm mesh, then sieved to pass a 2 mm mesh, then the 2–8 mm fraction and the <2 mm fractions were recombined; this was done to break up soil aggregates while preserving some of the larger pieces of organic debris. One hundred ml of 0.1 M $BaCl_2$ were added to 10 g of soil, then the resulting slurry was shaken by hand and placed on a rotary table at 125 revolutions/minute for 1–2 hr., allowed to settle overnight, filtered through Whatman 41 ashless filter paper, preserved with 0.04 ml chloroform, and stored at 4°C. Cation analyses were done by inductively coupled plasma emission spectrometry (Perkin-Elmer P400, Norwalk, CT). These measurements showed that treatments increased concentrations of the desired nutrients without altering soil pH or other factors (Figure 1; Bigelow and Canham 2007). Light availability to groups of seedlings was assessed with hemispherical image analysis: photos of the canopy were taken at 1.3 m height then analyzed with the program GLA 2.0 (details in Bigelow and Canham 2002). Light was expressed as global transmission (direct plus diffuse light in understory as a percent of above-canopy light).

Seedlings were visited several times during the 2001 and 2002 growing season to assess mortality from factors other than soil chemistry (e.g., predation, litterfall). Seedlings dying of such disturbances (>2/3 of the 180 planted seedlings of *Quercus rubra* and *Acer rubrum*) were excluded from analysis. Data from the final census in August 2002 were used in the survival calculations.

Data were analyzed by logistic regression using the logistic procedure in SAS (SAS Institute 1999). Data were analyzed for each species individually. Survival was analyzed as a function of treatment (Ca^{2+} or Mg^{2+} fertilization or control), soil chemistry prior to fertilization, and light environment. To limit the number of factors analyzed, pre-treatment soil chemistry data (exchangeable Ca^{2+}, Mg^{2+}, K^{+}, and Al^{3+}) were reduced by principal components analysis (Proc Princomp; SAS Institute 1999). Two principal component axes encompassed 85% of the variation in the soil chemistry data; the first axis was strongly associated with Ca^{2+} and Mg^{2+}, and the second axis was strongly associated with Al^{3+} and K^{+}. Statistical analysis was therefore done on the sum of

exchangeable Ca^{2+} and Mg^{2+} (expressed in units of millimoles of positive charge per kg dry soil; $mmol_c\ kg^{-1}$) and the sum of Al^{3+} and K^+.

The logistic procedure provided a test of the null hypothesis that no independent variables affected survival. If this null hypothesis was rejected, the Type 3 analysis of effects was used to identify the treatment or covariate that had most influence on seedling survival (SAS Institute 1999). Goodness of fit was assessed using a generalization of the coefficient of determination for discrete data (Maddala 1983):

$$R^2 = 1 - \left(\frac{L(0)}{L(B)}\right)^{\frac{2}{n}}$$

Here, $L(0)$ is the likelihood (not log-transformed) of a null model, $L(B)$ is the likelihood of the scientific model under consideration, and n is the number of observations (i.e., number of groups of seedlings).

Natural gradient study. We censused naturally regenerating seedlings in 36 plots dominated by one of the six study species. The plots, which were selected during an earlier experiment (Dijkstra 2003), were 25-meter-diameter circles in which ≥50% of basal area (40% for *Fraxinus americana*) was made up by one species. Four 2 m^2 quadrats were randomly placed in each plot for a total of 144 quadrats (6 species × 6 plots per species × 4 quadrats per plot). Censuses of seedlings that had germinated in the spring of the year were conducted at the beginning and the end of the 2001 and 2002 growing seasons; 2001 and 2002 cohorts were tallied and analyzed separately.

Surface soil chemistry was measured in each quadrat. Through an oversight, hemispherical photographs were not taken at each quadrat, so as a proxy for light we used the ranking of overstory trees in transmittance of light through their crowns. The order of ranking, from lowest to highest, was *Tsuga canadensis* < *Fagus grandifolia* < *Acer saccharum* < *A. rubrum* < *Quercus rubra* < *Fraxinus americana* (Canham et al. 1994).

Effects of soil chemistry (pH and exchangeable Ca^{2+}, Mg^{2+}, K^+, and Al^{3+}) and transmittance ranking on survival of each species were assessed by fitting data to a series of models and using Akaike's Information Criterion, corrected for small sample size (AIC_c) to select the most informative model. The first model was a

univariate logistic model:

$$p = \frac{e^{a+bx}}{1+e^{a+bx}} \quad (1)$$

where p is probability of survival, x is an independent variable, and a and b are model parameters that are estimated. The second was a bivariate model:

$$s = \frac{e^{a+bx+cy}}{1+e^{a+bx+cy}} \quad (2)$$

which accommodates an additional variable (y) and accompanying multiplicative parameter (c). Each soil factor was tested with model 1, but only soil factors that showed signs of fitting the data well were tested in model 2. The modeling approach requires ~20 observations per parameter (Burnham and Anderson 2002) and the simplest model had 2 parameters (i.e., a and b in Equation 1), so we analyzed only cohorts with individuals in ≥40 quadrats.

Optimization was done with simulated annealing (Goffe et al. 1994) in the R statistical language (R Development Core Team 2008) as implemented in the Anneal function in the Likelihood package (Lora Murphy, unpubl. *R package*). Akaike's Information Criterion, corrected for small sample size (AIC_c), was used to select among models. Because the response variable, survival, had only two possible values, we used the binomial distribution. The model with lowest AIC_c (i.e., AIC_{min}) was considered to have the strongest support from the data, but models with AIC_c within 2 units of AIC_{min} are considered to also have substantial support.

RESULTS

Planted seedlings. Only *Fraxinus americana* experienced a significant effect of any treatment or covariate on survival (Table 2; Figure 2); for the remaining species, either the global null hypothesis was not rejected (*Acer saccharum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis*) or the logistic model did not converge (*A. rubrum*). Two species, *Q. rubra* and *A. rubrum*, suffered high mortality from predation, and the resulting small sample sizes may have limited the power to detect treatment effects. Fewer *F. americana* seedlings survived in the fertilization treatments ($p = 0.02$; Figure 3). The sum of pre-treatment Al^{3+} and K^+ was

Table 2. Results of logistic regression on two-season survival of planted northern hardwood seedlings. N_0 is number of seedlings initially planted (180) minus deaths from predation or litterfall, N_1 is number of seedlings surviving to last census, and $p(b = 0)$ is probability of the null hypothesis that survival is unaffected by fertilization or soil chemistry. DNC indicates that model did not converge.

	Seedling Survival			
Species	N_0	N_1	$p(b = 0)$	R^2
Acer saccharum	164	73	0.53	0.068
Fraxinus americana	159	64	**<0.0001**	0.457
Acer rubrum	59	5	DNC	DNC
Fagus grandifolia	169	74	0.49	0.072
Quercus rubra	45	16	0.55	0.133
Tsuga canadensis	145	4	0.12	0.140

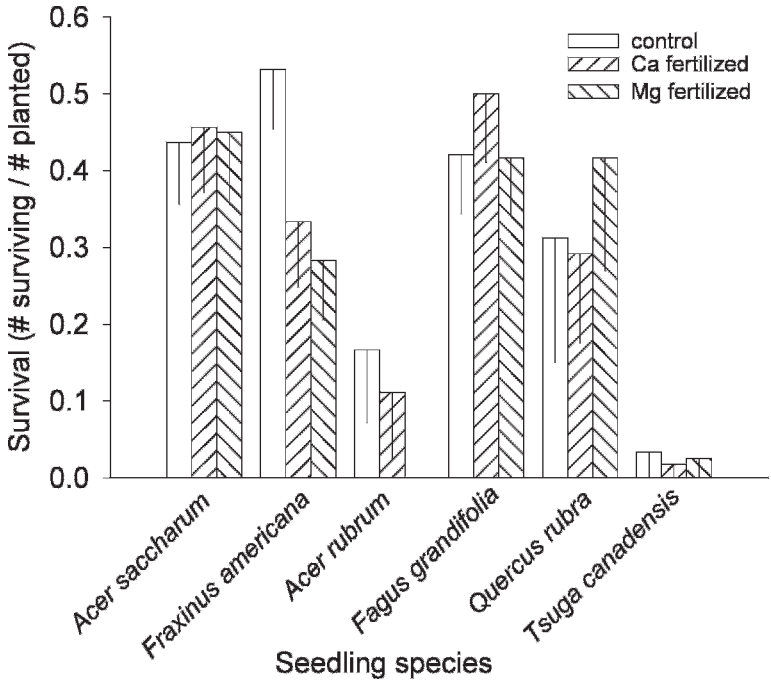

Figure 2. Two-year survival rates of planted seedlings fertilized with $CaSO_4$ or $MgSO_4$ compared to controls. Means with standard errors.

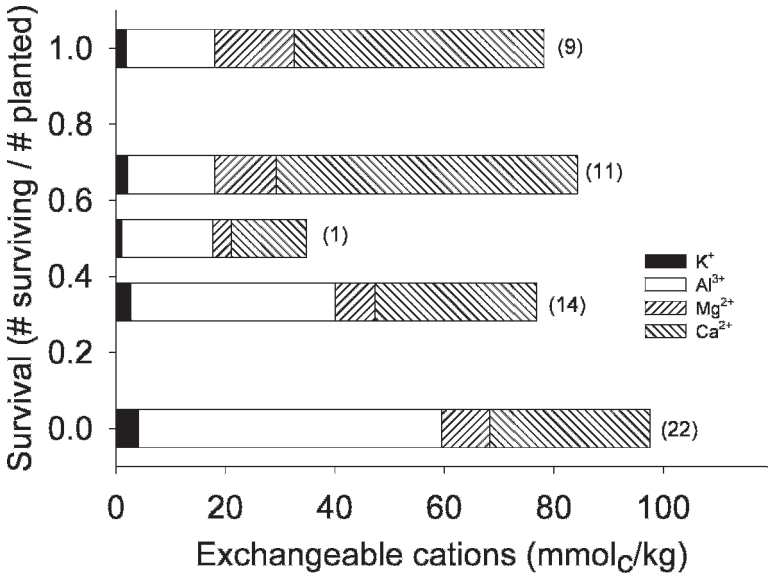

Figure 3. Survival of seedlings of *Fraxinus americana* plotted against soil chemistry measured in 1998 prior to fertilization. Survival is proportion surviving from groups of two or three seedlings (N = 57) planted in the same fertilized plot. Seedlings were planted in spring 2001; censused in Aug. 2002. Number of observations represented by each bar is in parentheses.

highly significant in predicting seedling survival ($p < 0.0001$); the graph of survival against exchangeable cations shows that Al^{3+} was much higher where *F. americana* seedlings died (Figure 3). The sum of Ca^{2+} and Mg^{2+} was not significant ($p = 0.56$) nor was light availability ($p = 0.40$).

Naturally established seedlings. There were not enough individuals in the 2001 or 2002 cohort of *Fraxinus americana*, *Quercus rubra*, or *Tsuga canadensis* for analysis of seedling survival (Table 3). The best models (i.e., those with minimum AIC_c) for survival of *Acer saccharum*, *A. rubrum*, and *Fagus grandifolia* seedlings all incorporated Al^{3+} (Tables 3, 4). The bivariate logistic equation incorporating Al^{3+} and transmittance ranking was the best model for both *A. saccharum* and *A. rubrum*. The relationship between exchangeable Al^{3+} and survival was opposite for the two species: survival was lower at high Al^{3+} (Table 5: $b < 0$) for *A. saccharum*, and higher at high Al^{3+} for *A. rubrum* ($b > 0$). The

Table 3. Mean survival rates of naturally established seedlings. N is number of quadrats with ≥1 seedling. Standard deviations are in parentheses.

Species	2001 Cohort		2002 Cohort	
	N	Survival Mean (SD)	N	Survival Mean (SD)
Acer saccharum	69	0.35 (0.33)	14	0.69 (0.44)
Fraxinus americana	11	0.30 (0.40)	0	0
Acer rubrum	2	0.25 (0.35)	100	0.36 (0.35)
Fagus grandifolia	42	0.15 (0.21)	0	0
Quercus rubra	12	0.69 (0.46)	4	0.75 (0.50)
Tsuga canadensis	26	0.05 (0.10)	6	0.67 (0.52)

relationship between transmittance ranking of overstory species and seedling survival was similar for the two species; both had increased survival along the continuum from species casting dense shade to species casting light shade. The amount of variance explained was modest; 34% for *A. saccharum* and 28% for *A. rubrum*.

For *Acer rubrum*, the bivariate logistic function involving Al^{3+} and transmittance ranking was clearly superior to the next best model ($\Delta_i = 5.7$), but support for a role of Al^{3+} in determining *A. saccharum* survival was weakened by the small AIC_c difference between the best model and the second-best model ($\Delta_i = 1.5$), which

Table 4. Akaike's information criterion (AIC_c) and R^2 for models of survival of naturally occurring seedlings with respect to soil chemistry and overstory light transmission (compare AIC_c within columns; lowest AIC_c is most informative model). Only three species had cohorts with sufficient seedlings for parameter estimation. Null model is denoted by 0, logistic by 1, and bivariate logistic by 2. Crown light transmission ranking is indicated by τ.

Model	Variable	*Acer saccharum*		*Acer rubrum*		*Fagus grandifolia*	
		AIC_c	R^2	AIC_c	R^2	AIC_c	R^2
0	–	411.1	–	914.0	–	125.1	–
1	Ca^{2+}	412.7	0.062	909.0	0.085	126.8	0.010
1	Mg^{2+}	412.6	0.009	912.1	0.039	126.7	0.014
1	K^{+}	410.0	0.046	911.6	0.044	123.7	0.082
1	Al^{3+}	406.8	0.090	902.7	0.125	**117.9**	**0.200**
1	$\ln(Ca^{2+}/Al^{3+})$	401.7	0.024	904.4	0.108	124.5	0.063
1	pH	413.1	0.002	905.2	0.103	126.7	0.013
1	τ	388.0	0.305	907.2	0.085	123.4	0.090
2	Al^{3+}, τ	**386.5**	**0.343**	**885.4**	**0.280**	118.1	0.241
2	Al^{3+}, Ca^{2+}	408.6	0.094	901.1	0.157	120.2	0.201

Table 5. Parameter estimates and support intervals for best models of survival of naturally established seedlings. Sign of estimate shows the relationship between independent and dependent variables (positive or negative).

Species	Model	Parameter	Estimate	Support
Acer saccharum	2	*a*	-1.0	-1.1–-0.9
		b	-0.0092	-0.014–-0.0050
		c	0.19	0.16–0.22
Acer rubrum	3	*a*	-1.9	-2.0–-1.8
		b	0.0094	0.0073–0.012
		c	0.017	0.134–0.202
Fagus grandifolia	1	*a*	-2.1	-2.3–-1.8
		b	0.015	0.011–0.019

expressed survival as a function of transmittance ranking alone (Table 4). Nevertheless, among models expressing *A. saccharum* survival as a function of individual soil factors, Al^{3+} provided the best fit.

The univariate logistic model received the most support from the data for *Fagus grandifolia* (Table 4). R^2 was small (20%). Like *Acer rubrum*, *F. grandifolia* had higher survival at high levels of Al^{3+} (Table 4: $b > 0$; Figure 4). The model that incorporated transmittance ranking along with Al^{3+} was nearly as informative as the Al^{3+}-alone model ($\Delta_i = 0.2$), but the transmittance-ranking-alone model was much less informative ($\Delta_i = 5.5$).

DISCUSSION

Given the initial focus of the study on soil calcium it was surprising to find no influence of Ca augmentation on seedling survival. Instead, natural gradients of aluminum had a pervasive influence on survival, and thus plant-soil relationships, of the northern hardwood seedling community at our study site. Aluminum had a distinct negative effect on survival of the calcicole species *Fraxinus americana* and *Acer saccharum*, which is consistent with the fidelity of these species to rich mesic soils. *Acer rubrum* and *Fagus grandifolia* survived better on high Al^{3+} soils, which is also consistent with their frequent occurrence at the more acid, infertile end of the soils gradient. There was no soils-related survival trend detected for *Quercus rubra* (small sample size limited the strength of inference for this species) or *Tsuga canadensis*, despite the tendency

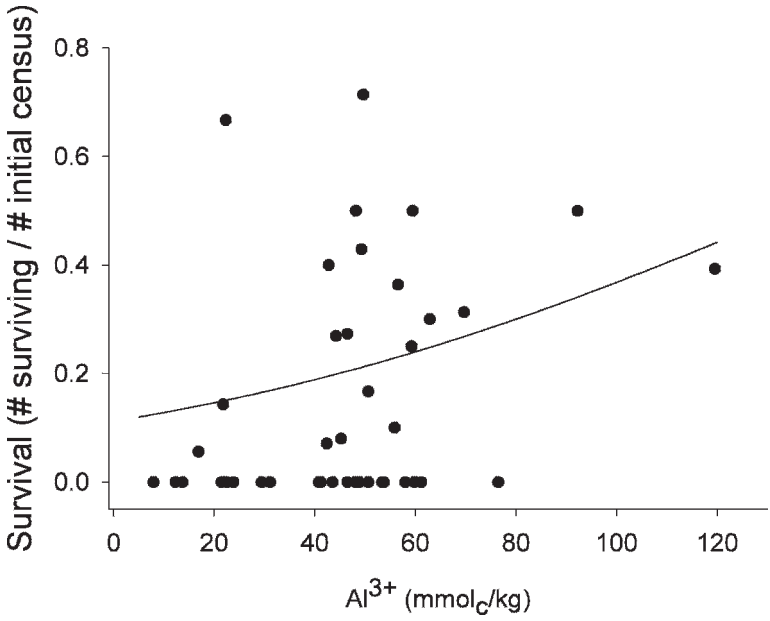

Figure 4. Survival of naturally established *Fagus grandifolia* seedlings plotted against exchangeable soil aluminum. Fitted line is univariate logistic curve (Eq. 1), $R^2 = 0.20$.

of adult individuals of these species to occur on more acid soils (Finzi et al. 1998).

Although Al^{3+} was the cation most closely associated with performance of the largest number of tree species, we cannot rule out the possibility that an unmeasured soil factor that co-varies with Al^{3+} was responsible for variation in performance of some species. For example, in acid soils the upper limits of availability of inorganic, non-occluded phosphorus (P) are set by direct precipitation with Al and iron (Fe) oxides. This threshold drops as pH decreases, thus a P limitation may masquerade as Al toxicity (Bohn et al. 1985). Nevertheless, in the young post-Holocene soils of the formerly glaciated northeastern United States, a large fraction of the demand for P for vegetation growth is obtained from organic forms of P (Walker and Syers 1976; Yanai 1992); availability of such P is controlled by exudation of phosphatases from roots and mycorrhizae rather than soil acidity (e.g., Fox and Comerford 1992). It seems more likely, then, that the variation in seedling

performance we observed was not a result of P limitation but rather is directly attributable to aluminum.

Lack of calcium effects on seedling survival in this study may appear at odds with the paradigm of Al and Ca as an interactive pair (Bengtsson 1992; Cronan and Grigal 1995); if Al toxicity limited survival, why didn't Ca application ameliorate it? One reason may be that the soils at our study site are at or above the threshold for ecosystem stress; even on the poorer areas, molar Ca:Al ratios are ≥ 1 (Dijkstra et al. 2001). More importantly, recent work on agronomic plants has cast doubt on the Ca displacement hypothesis itself, focusing instead on Al-mediated disruption of the cellular signaling role of Ca (Rengel and Zhang 2003; Schofield et al. 1998; Vitorello et al. 2005; Watanabe and Okada 2005). To be sure, Ca is still involved, but Ca concentrations in the symplasm where signaling occurs are 3–4 orders of magnitude lower than in the apoplasm, and are therefore unlikely to be strongly affected by low Ca concentrations in the external soil solution (Rengel and Zhang 2003). Mechanisms of Al toxicity other than Ca displacement from cell walls may help to explain our finding that despite the usual tendency to consider Al and Ca as an interactive pair, variation in soil Al^{3+} alone was the principal factor determining survival.

Aluminum effects on seedling survival can be mediated by mycorrhizal symbioses as well as roots, because mycorrhizae can differ greatly in their resistance to Al toxicity (Kelly et al. 2005). The northern hardwood tree species we studied are colonized by a diverse group of arbuscular mycorrhizae (e.g., Furlan et al. 1983; Klironomos 1995) and ectomycorrhizae (Booth 2004). Increases in soil pH can promote mycorrhizal colonization (Coughlan et al. 2000), and such colonization can enhance tree nutrient status (Dickie et al. 2002; Ouimet et al. 1996). St. Clair and Lynch (2005) found that liming increased photosynthesis rates of *Acer saccharum* but not *A. rubrum*, and that 50% of the increase was explained by enhanced mycorrhizal colonization. It is probable that the individuals we studied varied in mycorrhizal colonization along gradients of soil properties, and that these symbioses helped to determine the outcome of the study.

Soil aluminum and northern hardwood trees. The relative sensitivities to Al^{3+} of the species in this study are generally consistent with the literature. The two trees that showed negative effects of Al^{3+} on survival are both calcicoles. *Acer saccharum* has

moderate Al^{3+} tolerance (Kobe et al. 2002; Schier and McQuattie 2002). Adverse growth effects begin at fairly high solution levels of Al^{3+} (e.g., 600 μM) though Ca^{2+} concentrations in tissues begin to diminish at 100 μM of Al^{3+} (Thornton et al. 1986). For comparison, soil solution concentrations of inorganic Al at our study site range from ~1–40 μM (Dijkstra and Fitzhugh 2003). Dendrochemical approaches have showed that growth of *A. saccharum* is sensitive both to high Al^{3+} and low Ca^{2+} (Watmough 2004). There is little work on Al^{3+} toxicity in *Fraxinus americana* although *F. excelsior*, a congener which is also a calcicole, is susceptible (Weber-Blaschke et al. 2002).

Both of the species that were positively influenced by increased Al^{3+} are reported to be highly tolerant of Al^{3+}. *Acer rubrum* is one of the few species to thrive near industrial aluminum smelters (Braen and Weinstein 1985; Watmough and Hutchinson 1997) and positive correlation of soil Al^{3+} with sapling growth has been reported previously (Bigelow and Canham 2002). Other species that reach high abundance on acidic, Al-affected soils include *Betula nigra* (McClelland and Ungar 1970). *Fagus grandifolia* seedlings tolerated solution Al^{3+} up to 3 mM without adverse effects on growth (Thornton et al. 1989).

Of the two tree species that were not influenced by soil Al, the widespread *Quercus rubra* has been reported to tolerate high (3 mM) levels of Al^{3+} in solution (Thornton et al. 1989), but has shown root growth reduction at concentrations as low as 115 μM (DeWald et al. 1990). Other workers have noted moderate sensitivity to soil Al (Demchik and Sharpe 2000; Joslin and Wolfe 1989). *Tsuga canadensis* is unlikely to be susceptible to Al toxicity because it acidifies its soil environment and thus has high exchangeable Al^{3+} in the forest floor and upper soil horizons (Dijkstra and Fitzhugh 2003). Seedlings of *T. canadensis* have shown increased survival on acidic substrates, a behavior which is consistent with high Al^{3+} tolerance (Catovsky and Bazzaz 2002; Marx 2005).

Soil aluminum and northern hardwood community organization. The correlation of exchangeable Al^{3+} levels and seedling survival reported herein is consistent with the observed segregation of northern hardwood species along gradients of Ca^{2+} and other nutrients at the scale of stand (Finzi et al. 1998; van Breemen et al. 1997) and landscape (Balter and Loeb 1983; Pearson 1962; Smith and Vankat 1991). Exchangeable Al^{3+} is usually inversely correlated

with pH and exchangeable Ca^{2+} (e.g., Bigelow and Canham 2002), thus most of the patterns that have been ascribed to Ca^{2+} availability gradients could equally be ascribed to Al^{3+} gradients. The presence of divergent responses to elevated soil Al^{3+} (i.e., decreased or increased survival according to species) makes Al^{3+} potentially more effective than Ca^{2+} as a factor inducing segregation of trees along soil gradients.

The present paper deals only with seedlings, yet it is at this phase or younger (i.e., germination) that plant-soil relationships are most readily established, because of abundant individuals and high mortality rates compared to later phases in the life cycle. Further, the correlation of species distribution and soil type at our study site cannot be explained by effects of adult trees on soils, because spatial variability in soil elemental composition at the study site is a parent material effect that cannot be explained by tree-induced processes (van Breemen et al. 1997). These points, along with the observation that plant-soil relationships are already well established by the sapling phase (Bigelow and Canham 2002), highlight the importance of the seedling establishment phase in setting up plant-soil relationships at our study site and, by extension, other areas of northern hardwood forest.

Light is consistently found to be an important factor driving patterns of tree regeneration in northern hardwood forests (Catovsky and Bazzaz 2000; Pacala et al. 1996). Most species increase in survival as light increases (Walters and Reich 2000), so it was surprising to find little effect of light on survival of the planted species in the present study. In the study of naturally established seedlings, the finding of an effect of transmittance ranking (admittedly a proxy for direct light measurement) on survival of *Acer saccharum* and *A. rubrum* was driven by low survival under *Tsuga canadensis*, which is ranked as having the lowest canopy transmittance but which also tends to occur in soils that are extremely acidic (Dijkstra and Fitzhugh 2003). Unraveling the relative importance of light and soil effects in determining effects of hemlock stands on regeneration is challenging, but the two factors can combine to produce a strong positive feedback (Catovsky and Bazzaz 2002).

Ultimately, the relative abundance of tree species in a stand or landscape is the outcome of many factors acting throughout the plant life cycle, among them predation, fire, harvesting, and availability of many chemical elements. Variation in soil Al is one

among many factors determining species composition in the northern United States, yet the present study suggests it has a disproportionately large role. Although Ca and Al are ineluctably combined at the cellular level, soil Al appears to be more important than Ca as a proximate agent for organizing trees species along soil nutrient gradients at our study site in southern New England.

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