

Canopy tree – soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions¹

Nico van Breemen, Adrien C. Finzi, and Charles D. Canham

Abstract: We compared the distribution of adult trees and relatively stable soil properties as part of a study of feedbacks between canopy tree species and soils. In southern New England, soils under *Fraxinus americana* L. (FRAM) and *Acer rubrum* L. (ACRU) had high contents of total CaO and MgO. Under *Quercus rubra* L. (QURU) and *Fagus grandifolia* Ehrh. (FAGR), contents of CaO and MgO were low. Sites with *Acer saccharum* Marsh. (ACSA) and *Tsuga canadensis* (L.) Carr. (TSCA) varied across a wide range of total CaO and MgO. However, below 0.8% CaO, ACSA was absent and FAGR, QURU, and TSCA were dominant. From 0.8 to 1.5% CaO, ACSA and FRAM increased with increasing CaO content, while the frequency of other species declined. Above 1.5% CaO, there was no relationship between CaO content and ACSA and FRAM abundance, but FAGR and QURU were largely absent. Canopy tree species also varied significantly with texture, which we attribute to the higher Ca and Mg contents of the more sandy soils, rather than to soil physical effects. Correlations between Ca availability and forest composition are well known for calcareous versus noncalcareous soils. Apparently, much subtler variations in supply of mineral nutrients also alter competitive interactions and impose patterning on the distribution of canopy trees within stands.

Résumé : La distribution d'arbres adultes et les propriétés relativement stables du sol ont été comparées au cours d'une étude des réactions réciproques entre les espèces d'arbres de la voûte et les sols. Dans le Sud de la Nouvelle-Angleterre, les sols sous *Fraxinus americana* L. (FRAM) et *Acer rubrum* L. (ACRU) contenaient un fort taux de CaO et de MgO total. Sous *Quercus rubra* L. (QURU) et *Fagus grandifolia* Ehrh. (FAGR), le contenu en CaO et en MgO était par contre bas. Les sites avec *Acer saccharum* Marsh. (ACSA) et *Tsuga canadensis* (L.) Carr. (TSCA) présentaient une grande variation du CaO et du MgO total. Cependant, au-dessous de 0,8% de CaO, ACSA était absent, alors que FAGR, QURU et TSCA étaient dominants. Entre 0,8 et 1,5% de CaO, la proportion d'ACSA et de FRAM augmentait avec la hausse du contenu en CaO, alors que la fréquence des autres espèces était à la baisse. Au-dessus de 1,5% de CaO, il n'y avait pas de relation entre le contenu en CaO et l'abondance d'ACSA et de FRAM; toutefois, le FAGR et le QURU étaient la plupart du temps absents. Les espèces d'arbres de la voûte variaient aussi, de façon significative, avec la texture du sol; moins à cause de ses effets physiques qu'à cause de la teneur plus élevée en Ca et Mg des sols plus sablonneux. Les corrélations entre la disponibilité du Ca et la composition de la forêt sont bien connues pour les sols calcaires versus les sols non calcaires. Apparemment, des variations beaucoup plus subtiles dans les réserves des nutriments minéraux modifient aussi les interactions entre les espèces et imposent des patrons de distribution des arbres de la voûte à l'intérieur des peuplements.

[Traduit par la Rédaction]

Introduction

It is axiomatic among vegetation scientists that differences in the physical environment play a central role in determining the

distribution of both canopy and understory species in forests (e.g., Whitney 1991; Host and Pregitzer 1992; McFadden et al. 1994). Variation in community composition among sites that vary in topography and parent material is often clearly related to differences in water and nutrient availability at these scales. For example, Whitney (1991) described a microclimate – soil moisture gradient determined by topography and landscape position in southern New England. Along this gradient, species such as white ash (*Fraxinus americana* L.) and sugar maple (*Acer saccharum* Marsh.) occupy the most productive soils, while pitch pine (*Pinus rigida* P. Mill.), trembling aspen (*Populus tremuloides* Michx.), and bear oak (*Quercus ilicifolia* Wangehn.) occupy the most infertile soils.

The relationships between species distribution and more subtle differences in soil properties within a given landscape unit have received much less attention (Hairston and Grigal 1991). Studies at these finer spatial scales are critical to our understanding of long-term forest dynamics because forest succession is essentially a tree-by-tree replacement process (Horn 1975). Subtle variation in soil properties may alter the

Received July 23, 1996. Accepted March 10, 1997.

N. van Breemen.² Department of Soil Science and Geology, Wageningen Agricultural University, P.O. Box 37, 6700 AA Wageningen, The Netherlands.

A.C. Finzi.³ Department of Ecology and Evolutionary Biology, University of Connecticut, Box U-42, Storrs, CT 06269-0129, U.S.A., and Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545, U.S.A.

C.D. Canham. Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545, U.S.A.

¹ Contribution to the program of the Institute of Ecosystem Studies.

² Author to whom all correspondence should be addressed.

³ Present address: Duke University Phytotron, P.O. Box 90340, Durham, NC 27708, U.S.A.

balance of competitive interactions among tree species. There are also clearly mechanisms by which dominant plants can alter the properties of soils beneath their crowns (Gersper and Holowaychuk 1970; Crozier and Boerner 1986; Boerner and Koslowsky 1989; Andersson 1991). This raises the potential for complex feedback loops between canopy tree occupancy and soil properties. This also makes the interpretation of correlations between soil nutrient availability and species distribution within stands particularly problematic. Do species occupy neighborhoods with soils that differ in nutrient availability or do species colonize soils that were initially similar and through their occupancy alter nutrient availability?

To disentangle the complex set of feedbacks between canopy tree distribution and soils, we examined a series of soil chemical and physical properties beneath the canopies of six dominant tree species in the transition oak – northern hardwood forests of southern New England. The soil properties were chosen to range from relatively stable characteristics independent of tree identity (including soil texture and total elemental composition) to relatively plastic characteristics more easily influenced by overstory tree distribution (including soil pH, exchangeable cations, and C and N contents). The primary objective of the portion of the study reported here was to identify relationships between relatively stable soil properties and the distribution of canopy tree species within stands. We focused on soil texture and total elemental composition because they (1) were unlikely to have been influenced by vegetation in these relatively young ($\leq 10^4$ years) soils, but (2) had the potential to influence water and nutrient availability to canopy trees. Both assumptions were supported by the results of the study. Two associated papers will deal with the effects of canopy trees on soil pH, exchangeable cations, and soil C and N dynamics.

Materials and methods

Study sites

Our research was conducted in two replicate stands of transition oak – northern hardwood forest located on Canaan Mountain at elevations of 300–500 m in northwestern Connecticut (42°N, 73°15'W). The species composition of these stands includes elements of the oak forests of southern New England and the northern hardwood forests of the northeastern United States and Canada. The six dominant canopy tree species at the two sites were (in descending order of shade tolerance) American beech (*Fagus grandifolia* Ehrh.) (FAGR), eastern hemlock (*Tsuga canadensis* (L.) Carr.) (TSCA), *Acer saccharum* (ACSA), red maple (*Acer rubrum* L.) (ACRU), *Fraxinus americana* (FRAM), and northern red oak (*Quercus rubra* L.) (QRU). In the text, we refer to each species using an acronym based on the first two letters of the genus and the specific-epithet (i.e., ACSA = *Acer saccharum*). One site was located on land belonging to the Bridgeport Hydraulic Company north of the Wangum Reservoir. The second stand was located in the Great Mountain Forest (GMF) east of Wampee Pond. The two sites are referred to in the text using the name of the adjacent water body. The ground surface under the Wampee stand is very uneven, with boulders emerging through the soil surface. The canopy is second growth, with canopy tree ages ranging from 80 to 150 years. The topography of the Wangum site is more uniform. Several large trees occur within the mapped stand, but the majority of trees is in the same age-class as those found at Wampee. Neither site appears to have been used for agriculture following European settlement. At both sites, the regolith consists of 0- to 1-m-thick

well-drained Wisconsinian glacial till over a mica schist bedrock. Soils at both sites are Typic Dystrachrepts.

Field methods

At each site, we randomly selected six replicate canopy trees of the six study species. Soil samples were collected away from the stem-flow zone of each tree (>2 m from tree bases, Boerner and Koslowsky 1989) but still within the vertically projected crown of each target tree. Beneath each canopy tree, we identified two sampling locations with a mineral soil depth of at least 15 cm by means of a <2 mm diameter galvanized iron probing rod. The sampling locations were normally 0.5–5 m apart from one another. We obtained three soil cores at each location using soil bulk density samplers (5 cm diameter \times 15 cm depth) with polycarbonate liners. The liners were pre-cut vertically to facilitate processing of soils in the laboratory. The first core was used to sample the forest floor by first removing coarse woody debris and fresh litter from the forest floor and then coring through the forest floor to the underlying mineral soil (forest floor depth was always <15 cm). The other two cores were obtained after removing most of the forest floor, to retrieve the first 15 cm of mineral soil, and were located immediately adjacent to the forest floor core. One of the mineral soil cores was used for chemical and physical analyses and the other was used for examination of soil morphology. The respective cores (forest floor or mineral soil) at the two replicate locations were pooled for analyses ($n = 6$ for each species at each site).

In addition to the soil cores, all trees within a 15 m radius (i.e., a “neighborhood”) of the “target” tree were identified and had their distance, diameter, and cardinal compass direction from the target tree recorded. For each neighborhood, we calculated the fraction of the total basal area accounted for by each of the six dominant species.

Laboratory methods

The mineral soil cores were cut with a sharp knife along the vertical division in the polycarbonate liner. We looked for evidence of agriculture, fire, and drainage class using the presence of plowed soil layers, charcoal, and mottling, respectively. Variation in soil color was described using a Munsell color chart. For analyses of texture and total elemental composition, we sampled upper mineral soil (0–7.5 cm depth, UMS) and lower mineral soil (10–15 cm depth, LMS) layers separately. The UMS was separated from the forest floor on the basis of soil morphology. Following the separation of these soil depths, samples were dried for 4 days at 105°C and then sieved through an 8-mm-mesh sieve to remove roots and stones (>1.0 cm diameter). For the analyses reported here, the duplicate samples (locations) beneath each canopy tree were mixed in a 1:1 mass ratio.

Elemental analysis

The elemental composition of the UMS and LMS samples was determined by X-ray fluorescence spectroscopy. Finely ground soil (0.6 g) was melted with 2.4 g of $\text{Li}_2\text{Br}_4\text{O}_7$ at 1100°C by means of induction. The resulting glass beads were analysed with a Philips PW 1404 XRF spectrometer using geostandard reference samples prepared similarly (Buurman et al. 1996). Analytical results are expressed as mass fractions of the oxide component (e.g., SiO_2 , Al_2O_3 , CaO) to the ignited soil.

Soil texture analysis

Soil texture (contents of sand, silt, and clay) was determined only in the LMS using the hydrometer method (Sheldrick and Wang 1993). First, soil organic matter was removed by adding 10.0 mL of 30% H_2O_2 to a 50.0-g soil sample in a 250-mL beaker. Samples were stirred and cooled in an ice bath when a violent reaction occurred. Additional H_2O_2 (2–5 mL) was added as reactions subsided. Following the last H_2O_2 addition, samples were heated at 90°C for 45 min to remove excess H_2O_2 . Following pretreatment, samples were transferred to a mixer cup to which 5 mL of 1 M sodium hexametaphosphate ($(\text{Na}_6(\text{PO}_3)_6$, HMP) was added. Deionized water (500 mL) was added to the mixer cup and samples were mixed in an electric mixer

for 5 min. This suspension was then poured into a Bouyoucos cylinder and brought to volume (1130 mL) to include water displacement by the hydrometer. The hydrometer was removed and the soil resuspended with an impeller for 1 min. The hydrometer was then placed in the cylinder and a reading was made after 40 s. Samples were once again resuspended for a replicate measurement after 40 s. The average of these two readings served as the basis for the sand fraction calculation. Following the second reading, the hydrometer remained in the suspension for 120 min for a final reading to determine the clay content. The silt fraction was calculated as $100\% - \% \text{sand} - \% \text{clay}$. Temperature corrections for all measurements were made by recording the suspension temperature at the same time the hydrometer was read. Blank hydrometer readings were measured at the beginning of each session and were calibrated to include 1 N HMP.

Statistical analyses

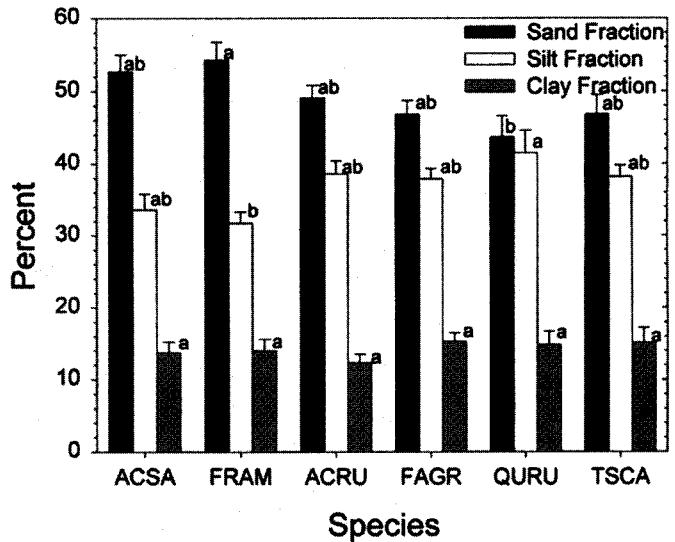
All statistical analyses were performed using proc GAM in SAS (SAS Institute, Inc. 1987). Independent variables included site (as a random effect blocking factor), species (as a fixed effect with six levels: ACRU, ACSA, FAGR, FRAM, QURU, and TSCA), and horizon (also a fixed effect with two levels: UMS (0–7.5 cm) and LMS (10–15 cm)). For dependent variables measured in only one horizon, our experiment is a simple, randomized blocked design (with site as the blocking factor). For analyses including measurements from both horizons, our analysis assumes a blocked, split-plot design with species as the main-plot factor and horizon as the within-plot factor. Assumptions of normality and homogeneity of variance were met for all analyses reported here. We used Tukey's test to protect the experimentwise alpha at 0.05 for post hoc mean comparisons of site, species, and soil horizon.

Results

Soil morphology

All cores had a forest floor that ranged from 0.25 to 9.75 cm in thickness with an abrupt transition to the mineral soil (transition zone <3 mm). At both sites, the mineral soil was typically a loam or loamy sand with a profile consisting of a 2- to 15-cm-thick black (10YR2/1) to dark brown (10YR3/3) A horizon grading within 5 cm to a dark yellowish brown (10YR3/4 to 10YR4/6) B horizon. The great majority of the soil profiles appeared to be well drained, without morphological signs of wetness. However, the B horizon of two profiles at Wangum and 13 profiles at Wampee showed very faint grayish brown mottles, sometimes with brown (7.5YR4/4) iron oxide mottles, indicating infrequent water saturation. The slightly wetter soil conditions were observed under all canopy trees: ACSA (three times), FRAM (once), ACRU (twice), FAGR (four times), QURU (twice), and TSCA (three times). Two profiles at Wangum and eight profiles at Wampee showed signs of very slight podzolization in the form of bleached sand grains underlain by an incipient Bh horizon: 1- to 5-cm-thick dark reddish brown (5YR3/2 to 7.5YR4/4) material often grading to dark to strong brown in the next 4–10 cm. Signs of wetness and incipient podzolization did not show up together within a single soil profile. We observed incipient podzolization under FRAM (twice), ACRU (twice), FAGR (three times), and QURU (three times). Only at Wangum did we find soil morphological indications of former human activity in the form of charcoal accumulation in four profiles. One profile at Wangum had an abrupt boundary between the A and B horizons, which is often considered an indication of former plowing. However, the absence of similar boundaries in all other

Fig. 1. Comparison of the sand, silt, and clay fractions of the lower 10–15 cm of mineral soil beneath the six canopy tree species. Bars with different lowercase letters represent significant differences among species in sand and silt content ($p < 0.05$). There were no significant differences in the clay content beneath any of the six focal species.



profiles at the site (including profiles located within 10–20 m) leads us to conclude that the site was never plowed.

Soil texture

Sand content varied widely (30–73%) among individual cores and was slightly but significantly higher at Wampee ($\bar{x} = 50.7\%$) than at Wangum ($\bar{x} = 46.8\%$) ($df = 1,58$, $F = 4.73$, $p < 0.05$). Silt contents ranged from 15 to 57% among cores but were not significantly different between the two sites (Wampee $\bar{x} = 36.0$, Wangum $\bar{x} = 38.1$, $df = 1,58$, $F = 2.18$, $p < 0.15$). Clay contents varied from 3 to 24% among individual cores, without significant differences between sites (Wampee $\bar{x} = 13.2\%$, Wangum $\bar{x} = 15.1$, $df = 1,58$, $F = 2.04$, $p < 0.20$).

Sand contents varied significantly among tree species ($df = 5,58$, $F = 3.07$, $p < 0.05$), gradually decreasing in the order FRAM, ACSA, ACRU, TSCA, FAGR, QURU (pairwise differences significant only between FRAM ($\bar{x} = 54.4\%$) and QURU ($\bar{x} = 43.8\%$)), while the reverse was true in the silt fraction ($df = 5,58$, $F = 3.22$, $p < 0.05$) (Fig. 1). There was no significant variation in clay contents under the different canopy tree species ($df = 5,58$, $F = 0.48$, $p < 0.80$) (Fig. 1).

Soil elemental composition and tree species distribution

All soils were non-calcareous and acidic with pH (H_2O) values between 3.35 and 5.40 (Finzi 1996). While the soils of the two sites did not differ in content of SiO_2 and Al_2O_3 , Wangum soils did contain distinctly more CaO, MgO, and K_2O and less Na_2O , MnO, and P_2O_5 than Wampee soils (Table 1).

Canopy trees were significantly associated with the content of CaO and MgO in the soil (Fig. 2). FRAM and ACRU were associated with the highest concentrations of CaO and MgO, while QURU and FAGR were found on sites with the lowest concentrations. Average contents of CaO and MgO beneath ACSA and TSCA were intermediate (Fig. 2). ACSA, FRAM,

Fig. 2. Element contents (mass fraction of oxide components in ignited material) of soils beneath each of the six target tree species. Significant pairwise differences are indicated by different lowercase letters above the bars. Error bars are +1 SE of the mean.

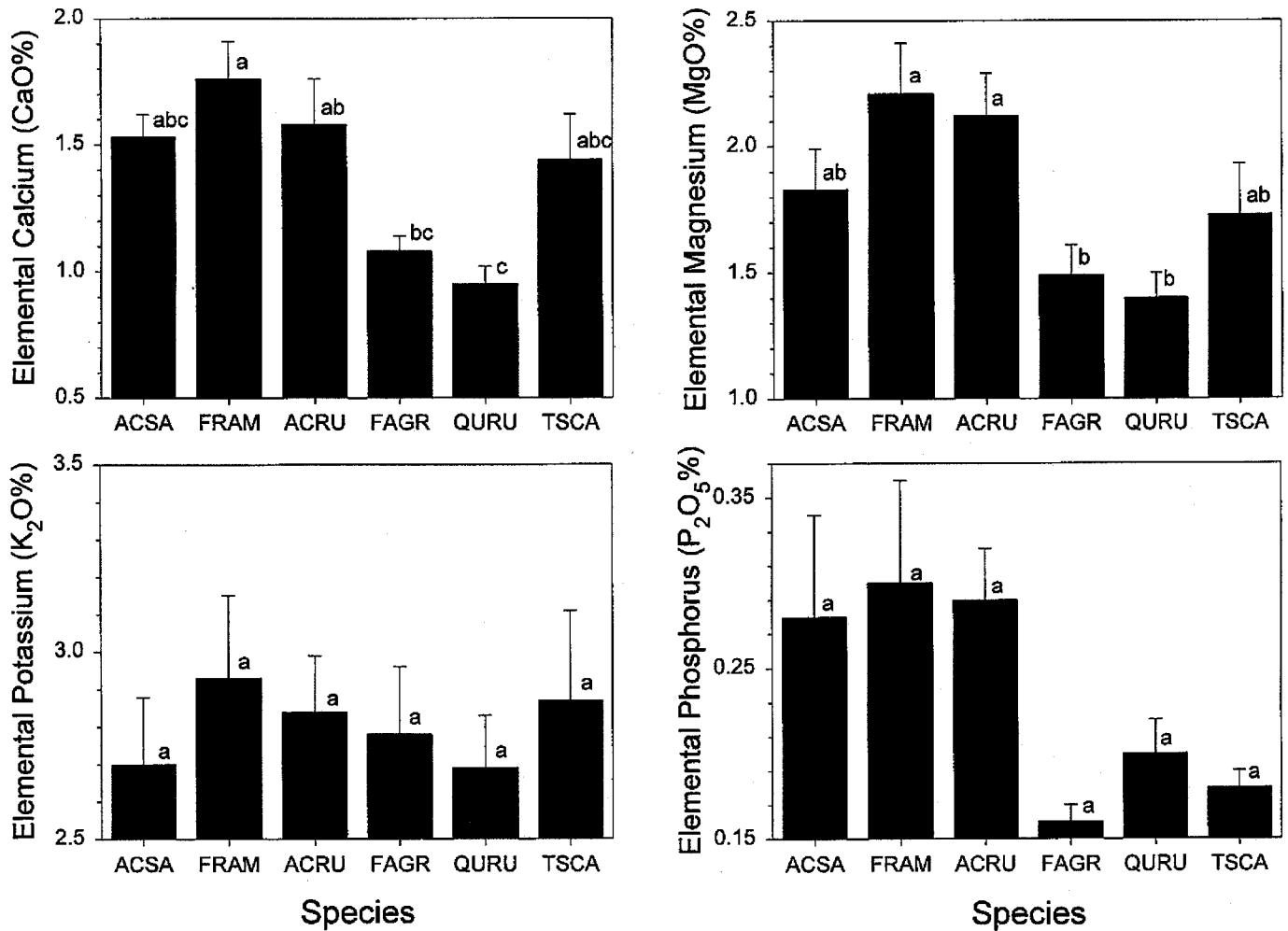


Table 1. Means and ranges of selected element oxide components (mass fraction (%)) in ignited soil) for Wampee and Wangum.

Mineral element	Wampee	Wangum
SiO ₂	68.1 (53.71–75.71)	68.5 (60.51–76.59)
Al ₂ O ₃	16.1 (12.56–23.22)	15.4 (11.41–17.78)
CaO*	0.97 (0.63–2.87)	1.70 (0.54–3.61)
MgO*	1.25 (0.54–3.07)	2.43 (0.85–3.82)
Na ₂ O*	1.69 (0.96–2.34)	1.34 (0.91–1.72)
K ₂ O*	2.11 (1.29–2.40)	3.60 (2.61–5.38)
MnO*	0.17 (0.06–2.62)	0.07 (0.03–0.18)
P ₂ O ₅ *	0.22 (0.11–1.21)	0.14 (0.09–0.28)

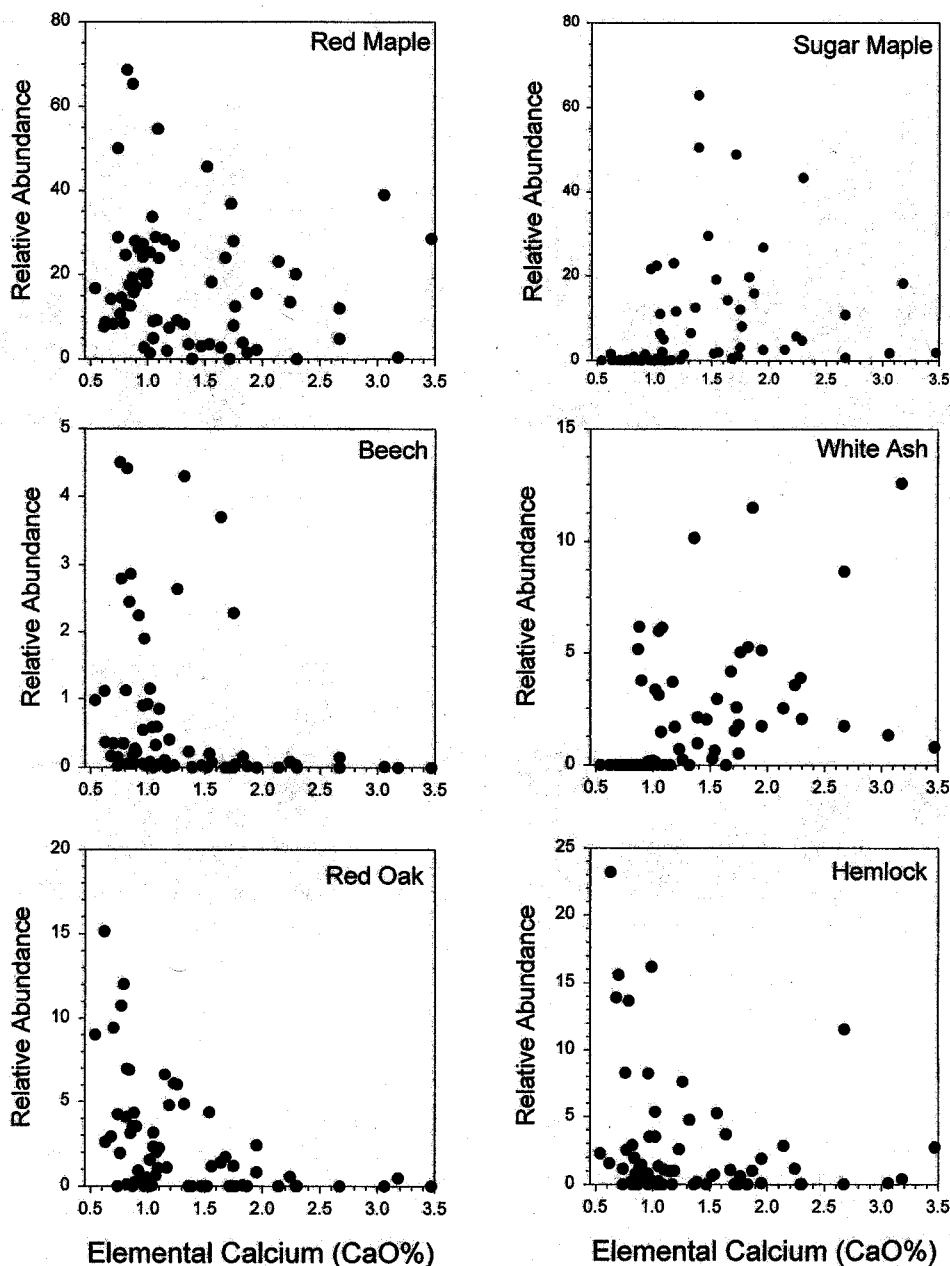
*Differences between sites significant at $p < 0.001$.

and ACRU were associated with higher values of MnO and P₂O₅, but soils beneath these species were not significantly different in the content of these mineral components than soils beneath FAGR, QURU, and TSCA canopies. Species did not differ in their association with K₂O (Fig. 2).

Although the mean CaO content beneath ACSA canopies

did not differ significantly from that beneath other tree species, very few ACSA occurred in soils that were low in total CaO. We plotted CaO content in the UMS against the relative basal area of each of the six species in a 15-m radius around each target canopy tree (Fig. 3). Three ranges in CaO content can be discerned. At CaO contents below 0.8%, ACSA and FRAM were essentially absent, and sites were dominated by FAGR, TSCA, QURU, and ACRU. At CaO contents from 0.8 to 1.4% the abundance of both ACSA and FRAM increased with increasing CaO content, while the abundance of the other four species declined. Finally, at CaO contents above 1.4%, ACSA and FRAM were consistently present, but their abundance was independent of CaO content, and FAGR and QURU were essentially absent. In spite of the significant difference in mean CaO content between Wangum and Wampee, these three CaO ranges can be identified in both sites, and the six species behaved similarly in the two sites. Essentially the same patterns appeared in a plot of the CaO content in the LMS, and to a lesser extent for MgO (figures not shown). Species abundances in the neighborhoods surrounding the target trees were not significantly correlated with any element other than Ca.

Fig. 3. Relative abundances (fraction of tree basal area) for the six tree species within a 15-m radius of each sample location, as a function of total soil Ca content (expressed as % mass fraction of the oxide component in ignited soil).



Discussion

Causes of spatial variation in soil texture and elemental composition

Part of the differences in elemental composition between sites or species could have been caused by species-induced differences in rates of chemical weathering. Weathering would tend to decrease contents of Ca, Mg, Na, and K and increase contents of highly immobile elements such as Ti and Zr. Because weathering usually proceeds from the soil surface downwards, the extent of past weathering can be evaluated by comparing elemental contents of the soil layers at 0–7.5 and 10–15 cm depth. To test for weathering effects on elemental composition,

we examined a soil weathering index based on the molar ratio of mobile to immobile metal oxides $(K_2O + Na_2O + CaO + MgO)/(Al_2O_3 + Fe_2O_3 + TiO_2)$. The index was not significantly different between UMS (0.5997) and LMS (0.6001) ($df = 1,140$, $F = 0.00$, $p > 0.95$). Profiles with incipient podzolization had marginally significantly higher Al_2O_3 in the LMS than in the UMS, consistent with the effects of podzolization, but also showed no evidence for depletion of CaO, MgO, Na_2O , or K_2O from the upper mineral horizons. So mineral weathering had no significant effect on the total elemental composition of the surface horizons of these relatively young soils. This implies that the observed variations in soil elemental composition and texture have not been caused by the vegetation (confirming the

assumption made at the outset of the study) and must be attributed to variation in the composition of the glacial till.

Causes of correlations between soil texture or elemental chemical composition and tree species distribution

Given that the spatial variability in soil texture and elemental composition is a parent material effect and cannot be explained by tree-induced processes, its significant correlation with tree species distribution must be attributed to effects of those soil properties on the tree species. There are several mechanisms by which variation in both soil texture and elemental composition could influence tree species distributions within stands. In the loamy and sandy loam soils encountered here, variation in sand and silt content might affect water availability. However, four lines of evidence argue against differences in soil water availability as a factor influencing tree species distributions in our study sites. First, while the differences in soil texture were statistically significant, the magnitude of the differences was relatively small. Second, we calculated available water in the organic-free soil based on the empirical relationships between soil texture and water-holding capacity given by Krahmer et al. (1995) and found no significant differences between values calculated for different canopy trees. Third, we found that canopy trees of all six species occurred on soils showing signs of temporary water stagnation, although most individuals of each species were found on well-drained soils. Finally, Pacala et al. (1995) found no relationship between growth and water availability for saplings of these six species in these sites.

In the absence of a physical effect of soil parent material on species distribution, the textural differences between soils under different canopy trees are probably nutritionally related, through mineralogical differences in the sand and silt fractions. Although contributions of silt and sand fractions to cation exchange capacity in forest soils cannot be excluded (Turpault et al. 1996), we expect that the textural differences reflect differences in availability of CaO and MgO from minerals. Strong evidence is presented in Figs. 2 and 3 for an effect of subtle variation in soil elemental composition on canopy tree distribution within these stands. FRAM is most abundant in neighborhoods with soils high in CaO, while FAGR and QURU were largely restricted to neighborhoods with soils low in this component. ACSA, ACRU, and TSCA occurred on soils that varied broadly in their CaO content. However, ACSA is most abundant at higher values along the Ca gradient, while TSCA and ACRU are most abundant in neighborhoods with lower CaO contents. We found that ACSA and FRAM basal area increased with increasing MgO, but the pattern was not as striking as that of CaO. We interpret these findings as evidence for a significant effect of differences in supply of Ca and Mg by mineral weathering, depending on mineralogy and quantity of Ca- and Mg-bearing minerals in the soil, on the relative abundance of all six of the species studied in these sites. That differences in supply of Ca and Mg by weathering would exist while soil elemental contents have not been affected by chemical weathering may seem inconsistent. It is not. Exchangeable Ca and Mg are strongly correlated with total Ca and Mg in our soils, yet make up at most a few percent of total Ca and Mg (Finzi 1996), so they could have been supplied by weathering of an undetectably small amount of total soil Ca and Mg.

Kobe et al. (1995) and Kobe (1996) found that under deep shade (less than 5% of full sun), mortality of saplings of both ACSA and FRAM was much higher in non-calcareous than in calcareous soils, suggesting an important role for Ca nutrition in the dynamics of these species. Simulations with SORTIE, a spatially explicit model of forest dynamics calibrated at our sites (Pacala et al. 1993, 1996), indicate that the lower relative abundance of FAGR and TSCA on calcareous soils in this region can be explained by the greater competitive ability (i.e., greater shade tolerance) of ACSA relative to FAGR and TSCA, rather than because of poorer intrinsic performance of FAGR and TSCA on calcareous soils (Kobe 1996). Our results suggest that spatial variation in Ca supply from soil parent material plays a role in the dynamics of these species at considerably lower levels of available Ca than found in calcareous soils, where concentrations of dissolved Ca^{2+} are likely to be an order of magnitude higher than at our sites (van Breemen et al. 1988).

Our results imply that depletion of pools of Ca^{2+} in forest soils of the northeastern United States because of a combination of acid deposition and declines in atmospheric deposition of Ca^{2+} (Likens et al. 1996) could have profound, long-term effects on compositional dynamics in these forests.

Large differences in mineral substrate have been shown to lead to significant variation in the species composition of different landscape units (e.g., Host and Pregitzer 1992). We have shown here that within a given landscape unit, also much subtler differences in soil elemental chemistry can lead to clear spatial patterning in the distribution of canopy trees, presumably through effects of variation in the availability of mineral nutrients such as Ca on the growth and survival of tree species (Kobe et al. 1995; Kobe 1996). SORTIE (Pacala et al. 1993, 1996) emphasizes the importance of processes such as seed dispersal (Ribbens et al. 1994) and competition for light (Canham et al. 1994) in determining the spatial distribution of species within stands. The effects of variation in soil elemental chemistry on species distribution described here add a level of determinism to the much more stochastic processes described in these related studies.

Acknowledgements

The XRF analyses were performed by Ing A.J. Kuijper at the Department of Soil Science and Geology, Wageningen Agricultural University. This research was supported by grants from the National Science Foundation (DEB-9220620) and the National Aeronautics and Space Administration (NAGY-3703).

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