Calcium and magnesium in wood of northern hardwood forest species: relations to site characteristics

M.A. Arthur, T.G. Siccama, and R.D. Yanai

Abstract: Improving estimates of the nutrient content of boles in forest ecosystems requires more information on how the chemistry of wood varies with characteristics of the tree and site. We examined Ca and Mg concentrations in wood at the Hubbard Brook Experimental Forest. Species examined were the dominant tree species of the northern hardwood forest and the spruce–fir forest. The concentrations of Ca and Mg, respectively, in lightwood of these species, mass weighted by elevation, were 661 and 145 μg/g for sugar maple (*Acer saccharum* Marsh.), 664 and 140 μg/g for American beech (*Fagus grandifolia* Ehrh.), 515 and 93 μg/g for yellow birch (*Betula alleghaniensis* Britt.), 525 and 70 μg/g for red spruce (*Picea rubens* Sarg.), 555 and 118 μg/g for balsam fir (*Abies balsamea* (L.) Mill.), and 393 and 101 μg/g for white birch (*Betula papyrifera* Marsh.). There were significant patterns in Ca and Mg concentrations with wood age. The size of the tree was not an important source of variation. Beech showed significantly greater concentrations of both Ca (30%) and Mg (33%) in trees growing in moist sites relative to drier sites; sugar maple and yellow birch were less sensitive to mesotopography. In addition to species differences in lightwood chemistry, Ca and Mg concentrations in wood decreased with increasing elevation, coinciding with a pattern of decreasing Ca and Mg in the forest floor. Differences in Ca and Mg concentration in lightwood accounted for by elevation ranged from 12 to 23% for Ca and 16 to 30% for Mg for the three northern hardwood species. At the ecosystem scale, the magnitude of the elevational effect on lightwood chemistry, weighted by species, amounts to 18% of lightwood Ca in the watershed and 24% of lightwood Mg but only 2% of aboveground biomass Ca and 7% of aboveground Mg.

Résumé : L'amélioration des estimés du contenu en nutriments des tiges dans les écosystèmes forestiers exige plus d'information sur les variations de la chimie du bois en fonction des caractéristiques de l'arbre et du site. Nous avons examiné les concentrations de Ca et Mg dans le bois à la forêt expérimentale de Hubbard Brook. Les espèces dominantes de la forêt de feuillus nordiques et d'épinette–sapin ont été examinées. Dans le bois clair de ces espèces, les concentrations de Ca et Mg pondérées par l'altitude étaient respectivement de 661 et 145 μg/g pour l'érable à sucre (*Acer saccharum* Marsh.), 664 et 140 μg/g pour le hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.), 515 et 93 μg/g pour le bouleau jaune (*Betula alleghaniensis* Britt.), 525 et 70 μg/g pour l'épinette rouge (*Picea rubens* Sarg.), 555 et 118 μg/g pour le sapin baumier (*Abies balsamea* (L.) Mill.) et 393 et 101 μg/g pour le bouleau blanc (*Betula papyrifera* Marsh.). Il y avait des patrons significatifs dans les concentrations de Ca et Mg selon l'âge du bois. La dimension de l'arbre n'était pas une source importante de variation. Le hêtre avait des concentrations de Ca (30%) et de Mg (33%) significativement plus élevées lorsque les arbres croissaient sur les sites humides relativement aux sites plus secs; l'érable à sucre et le bouleau jaune étaient moins sensibles à la mésotopographie. En plus des différences entre les espèces dans la chimie du bois clair, les concentrations de Ca et Mg dans le bois diminuaient avec l'altitude, ce qui coïncidait avec une diminution de Ca et Mg dans la couverture morte. Les différences dans les concentrations de Ca et Mg dans le bois clair reliées à l'altitude variaient de 12 à 23% pour Ca et de 16 à 30% pour Mg chez les trois espèces de feuillus nordiques. À l'échelle de l'écosystème, l'importance de l'effet de l'altitude sur la chimie du bois clair, pondéré par espèce, représente 18% du Ca du bois clair dans le bassin versant et 24% du Mg du bois clair, mais seulement 2% du Ca et 7% du Mg de la biomasse aérienne.

[Traduit par la rédaction]

Introduction

Nutrient budgets are used to describe the fluxes and pools of nutrients in ecosystems. Biomass accumulation can be an important ecosystem sink for nutrients, comparable in eastern deciduous forests with the flux of nutrients in leaching and streamwater (Knoepp and Swank 1994; Likens et al. 1996, 1998). Quantifying nutrient accumulation in biomass

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is, therefore, important to the development of accurate ecosystem budgets. Detecting change in nutrient storage over time requires even more precise accounting of biomass pools and nutrient concentrations. While tree mass may be frequently estimated from diameter inventories, concentrations are not often remeasured. At the Hubbard Brook Experimental Forest (HBEF), for example, concentrations of tissues have not been measured since 1965 (Likens and Bormann 1970), although nutrient contents, based on new mass estimates, are calculated every 5 years.

The calculation of nutrient stores in biomass typically rests on the assumptions that wood chemistry for a single species does not vary significantly among sites within the ecosystem and that measures of tissue nutrient concentrations can be used to calculate budgets well after the date of measurement. These assumptions of constancy across sites and over time are useful because of the difficulties of obtaining more spatially and temporally detailed nutrient data. Spatially and temporally limited data, collected for the construction of whole watershed nutrient budgets (Henderson et al. 1978; Johnson et al. 1982; Johnson and Swank 1973; Likens and Bormann 1970; Whittaker et al. 1979) have been used repeatedly in subsequent studies (Knoepp and Swank 1994; Johnson and Todd 1990; Likens et al. 1994, 1998; Yanai 1992) without addressing the possibility that unmeasured intrawatershed variability could affect mean concentrations or the potential that tissue concentrations have changed over time. At the HBEF, the sampling schemes used to describe the nutrients stored in biomass were based on a few trees (usually six) of each species, with each tree sampled extensively, producing an excellent representation of the nutrient content of the important species (Whittaker et al. 1979). This approach was appropriate for the first descriptions of nutrient cycles in ecosystems and for comparing very different systems. More spatially intensive sampling will be required to detect patterns of tissue nutrient concentrations and content within these systems. Wood is the most massive single component of living biomass in the forest and is, therefore, an important term in estimates of biomass nutrient stores (Whittaker et al. 1979).

In this study we tested the assumption of constancy across elevational and topographic sites by examining the concentrations of Ca and Mg in lightwood of the major tree species in a first-order watershed at HBEF. "Lightwood" is used to refer to the color of the wood and to distinguish it from "darkwood" and does not necessarily connote physiological sapwood as opposed to heartwood (Whittaker et al. 1979). Using increment cores, we examined lightwood of the six most important species at the HBEF to determine the relationships between lightwood chemistry and tree size, wood age, elevation (which is also a gradient in climate), and convex versus concave mesotopography (perennially wet versus typically dry soils). Darkwood in some species is much higher in concentrations of Ca and Mg than is lightwood (Whittaker et al. 1979). We sampled the wood of saplings to determine whether the wood that later becomes darkwood is initially similar to lightwood or darkwood. Finally, we assessed the potential importance to cation budgets of revised estimates of Ca and Mg concentrations in biomass.

Methods

Study site

All trees sampled for this study were located adjacent to watershed 6, the "biogeochemical reference" watershed of the HBEF (43°56′N, 71°45′W), which ranges in elevation from 530 to 790 m. The climate is classified as humid continental (Trewartha 1954). The study site is forested by northern hardwoods, namely yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), and sugar maple (*Acer saccharam* Marsh.). Some of the upper portion of the site supports red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), and white birch (*Betula papyrifera* Marsh.). Most of the trees in our study area originated following a period of heavy cutting from about 1910 to 1917 (Bormann and Likens 1979). Detailed information about the HBEF has been summarized by Likens and Bormann (1995) and Likens (1985).

All references to the 1965 lightwood data are from Likens and Bormann (1970) and Whittaker et al. (1979). Lightwood chemistry was estimated from disks taken from a small number of trees of each species at each of three elevations.

Field sampling

We sampled lightwood using an increment borer because it is efficient and permits the sampling of many individual trees. While it is not the best way to obtain a representative sample of the bole for chemistry, we have used this approach in this study primarily to identify the effects of wood age, tree size, and site conditions on wood chemistry.

The lightwood of trees was sampled in 1992, 1993, and 1994 to address slightly different research objectives. Trees were sampled in 1992 to determine the relationship of wood age to chemistry in lightwood of dominant trees. Four or five dominant trees of yellow birch, American beech, and sugar maple were cored at each of three elevations: low (545 m), middle (680 m), and high (780 m). Dominant canopy trees in good condition were selected for sampling at each location. Trees with a wide range of diameters (5.5–102 cm) were sampled at the three elevations in the northern hardwood forest in 1993 to determine whether there were any diameter-related trends in lightwood chemistry. In 1994, we obtained cores from the three dominant species at the highest elevations in the study area: white birch, red spruce, and balsam fir. In total, 423 trees were sampled in the 3 years (Table 1).

Increment cores were obtained from living tree stems at breast height with 4 or 5 mm diameter increment borers. Tree diameter and species were recorded. Because it was not possible to maintain chemical cleanliness on cores used for ring counting, in 1992, two cores were taken from each tree, one 2 to 3 cm above the other. One core was used for chemical analysis; using the second core, the number of years in each 1-cm length was estimated and assigned an age. In 1993 and 1994 one core per tree was collected. Cores were placed in straws and returned to the laboratory, where they were refrigerated at 4° C until processing.

For trees sampled in 1993 at the middle elevation (n = 48 beech, 48 yellow birch, and 49 sugar maple), we noted whether individual cored trees were in wet sites (located in swales or along ephemeral streams) or on drier sites (all other sites). This enabled us to assess the relationship between wood chemistry and mesotopographic position for this subset of data.

Darkwood was not analyzed on the tree cores described above because it falls apart in the increment corer. Between 1988 and 1992, the darkwood of large trees was sampled opportunistically from disks, when trees were felled for other research purposes. Darkwood concentrations reported in this paper are from a total of 34 trees distributed among the three dominant species: yellow birch, sugar maple, and American beech. During this same period,

Table 1. Number of trees sampled per species and elevation or site at Hubbard Brook Experimental Forest.

	Site			
Species	Low	Middle	High	Spruce–fir
Yellow birch	38 (39.9, 17.3–86.2)	53 (36.8, 12–101.7)	28 (36.8, 7.3–93)	10 (28.5, 17.6–54.9)
Sugar maple	48 (35.8, 6.5–91.5)	53 (31.6, 11–73.5)	36 (22.8, 9–49.1)	
American beech	41 (32.0, 11.2–67.5)	52 (24.8, 10.4–47.8)	32 (18.7, 5.5–37.8)	
White birch				11 (24.7, 16.4–30.8)
Red spruce				9 (29.8, 24.7–39)
Balsam fir				12 (28.1, 16.6–47.9)

Note: Mean diameter (cm) and diameter range are given in parentheses.

12 sugar maple, 10 yellow birch, and 11 beech saplings, 2–5 cm diameter at breast height (DBH), were cut for analysis of the chemistry of the bole centers. These samples were collected from saplings at the low elevation, growing on a regenerating clearcut under conditions thought to be very similar to those under which the mature Hubbard Brook forest developed and thus representing the best samples for comparison to heartwood chemistry.

To sample forest floor on watershed 6 in 1992, 80 of 208 plots (25 × 25 m) on the watershed were sampled. We used a stratified random sampling design to determine which plots to sample to ensure that a proportional number of samples were collected across the elevational range of the watershed. Within each plot, a point for sample collection was chosen at random. At each point, a 15 × 15 cm block of forest floor was collected to the depth of mineral soil (Federer 1984). Each block was divided into two horizons for analysis, the Oie and Oa.

Chemical analysis

The cores collected for chemical analysis were treated differently in 1992 than in 1993 and 1994 to accomodate slightly different goals. In 1992 there were two cores per tree, one for chemical analysis and the other for aging. On the chemical core, bark was removed and the wood sectioned into 1-cm lengths to the darkwood boundary. Lightwood was analyzed as described below. The cores collected in 1992 (27 total for three species) comprised the data set for analysis of wood chemistry with age.

In 1993 and 1994, the outer 2 cm of the core was removed for analysis of growth rate used in another study. The remainder of the lightwood was sectioned into 1-cm segments. For trees greater than 10 cm DBH, two 1-cm core segments were analyzed, and the values were combined to yield a mean value for the tree; for trees <10 cm DBH (15 trees total), a single 1-cm segment was analyzed. The remainder of the core segments were dried and have been preserved for future study in the long-term archive system of the Hubbard Brook Ecosystem Study (Veen et al. 1994).

Each 1-cm segment of lightwood to be used for chemical analyses was placed in a clean crucible and dried at 80°C to constant mass. The sample was weighed and returned to the crucible and ashed at 500°C. The ashed core segments remained as cohesive units, which were placed into preweighed 100-mL polyethylene bottles. Ten millilitres of 6 M HNO_3 were added to dissolve the ash. The volume was brought up to approximately 50 mL with distilled water, the bottle reweighed and the precise mass recorded.

Calcium and Mg were analyzed by inductively coupled plasma spectroscopy (ICP). Detection limits for solutions analyzed by ICP were 0.01 μg/g for Ca and Mg. The ICP was calibrated at the beginning of every sample run and checked against standard solutions every 10 samples. Drift of less than 5% was allowed; if drift was 5% the machine was recalibrated. Approximately 15% of all samples analyzed were replicates or blanks. Accuracy was tested through repeated analysis of U.S. Bureau of Standards tissue standards. Analyses of peach (*Prunus persica* L.) leaf standards yielded observed mean Ca concentration of 1.63 ± 0.05 mg/g (slightly higher than the certified value of 1.56 ± 0.02 mg/g); and mean Mg concentration of 0.45 ± 0.001 mg/g (certified value 0.43 ± 0.008).

In the laboratory, darkwood and sapling tissue samples were removed from disks using a steel drill to obtain approximately 100–300 mg of wood. Samples were placed in a crucible, ashed, dissolved with 6 M HNO_3, and analyzed as described above for 1-cm core segments.

Forest floor samples were oven-dried at 80°C and ground (2 mm). Subsamples (500 mg) were digested in 6 M HNO_3, and the extracts analyzed by ICP as described above.

Statistical analysis

Differences in Ca and Mg concentration among species and elevations were analyzed using analysis of variance (ANOVA). This two-way ANOVA and the species by elevation interaction could only be applied to the three elevations of the hardwood zone; there were not enough trees sampled in the spruce–fir zone for sufficient degrees of freedom. Because of significant species, elevation, and interaction terms, single-factor ANOVA was used to determine the significance of differences in wood chemistry among the four sites and among the six species. Means between species and between elevations were compared using the Tukey–Kramer test. We also used ANOVA for each species separately to determine whether lightwood, darkwood, and the wood of sapling centers were similar. All effects were evaluated at $p = 0.05$.

Regression was used to analyze the radial variation (variation attributable to wood age) in wood chemistry of trees cored in 1992. Regression analysis was applied separately to each tree. Regression analysis cannot properly be applied to the entire data set because samples taken from the same tree are not independent. We used a t test to determine whether the slopes of the regressions of Ca and Mg concentrations on wood age were significantly different from zero. This analysis was applied to each species separately because of significant differences in lightwood chemistry among the three species. Regression analysis was also used to determine the effect of tree diameter on Ca and Mg concentration in lightwood applied to each species separately.

Correlation analysis was used to determine the relationship between elevation and forest floor Ca and Mg concentration and content using $n = 80$ forest floor samples and the elevation of each sample plot. Significance for regression and correlation analyses was evaluated at $p = 0.05$.

Mesotopographic position (convex or concave) was noted only for stems cored at the middle elevation. Analysis of variance was used to examine whether lightwood chemistry varied with mesotopography. Because of significant species, site, and species by site interaction terms, means between sites and within species were compared using t tests. All statistical analyses were conducted with JMP statistical software (SAS Institute Inc. 1995).

Table 2. Analysis of variance of Ca and Mg concentration in sapwood of yellow birch, sugar maple, and beech (n = 381 trees).

Source	df	F	$P > F$
Calcium			
Elevation	2	26.08	<0.0001
Species	2	43.25	<0.0001
Elevation × species	4	2.36	0.0551
Error	372	20.64	<0.0001
Magnesium			
Elevation	2	9.86	0.0001
Species	2	36.18	<0.0001
Elevation × species	4	2.35	0.0540
Error	372	13.98	<0.0001

Results

Effects of tree species, wood age, and tree diameter

Wood chemistry differed significantly among tree species (species effect in the ANOVA; Table 2). Mean concentrations of Ca and Mg were higher in sugar maple (661 µg/g Ca, 145 µg/g Mg) and beech (664 µg/g Ca, 140 µg/g Mg) than in yellow birch (515 µg/g Ca, 93 µg/g Mg; Table 3). The difference among species was larger for Mg (36%) than for Ca (22%). The effects of wood age and tree diameter on wood chemistry also differed among species; these effects were tested separately for each species, as follows.

To describe the effects of age of lightwood formation on wood chemistry for each species, we first regressed Ca and Mg concentrations against the age of the core segments analyzed from individual trees cored in 1992. Individual trees exhibited a range of slopes, both positive and negative. We analyzed these slopes by species, to determine whether the mean slope was equal to zero. In yellow birch, the mean slopes were signficantly positive; concentrations of Ca ($p < 0.01$) and Mg ($p < 0.001$) were higher in the older core segments than in younger. In sugar maple, the mean slope for Mg was significantly negative ($p < 0.05$); concentrations of Mg were higher in recent wood than in older segments. There was not a significant trend in slope for Ca or Mg in beech, nor for Ca concentrations in sugar maple.

In addition to the effect of age of lightwood formation on wood chemistry, there was a significant difference in the Ca and Mg concentration in lightwood and darkwood for sugar maple, yellow birch, and beech. This difference was greatest for sugar maple, for which darkwood is three to five times more concentrated than lightwood (Table 3).

We also compared the Ca and Mg concentrations of the centers of sapling trees with darkwood to determine whether the wood that later becomes darkwood is initially similar to lightwood or darkwood. We found that sugar maple darkwood is five times more enriched in Ca and Mg than sapling centers (Table 3). In yellow birch, Ca was two times greater in darkwood than in sapling centers, but there was no difference in Mg concentrations. Magnesium concentration was 1.4 times greater in darkwood than in saplings of beech, but there was no significant difference in Ca concentration. There were some significant differences between sapling centers and lightwood chemistry for Mg but not for Ca. Magnesium concentration was lower in lightwood than in sapling centers of sugar maple and higher in yellow birch lightwood than in sapling centers. Overall, the chemistry of sapling centers was more similar to that of lightwood than of darkwood.

Tree diameter explained little of the variation in lightwood chemistry, despite the significant effects of the age of wood formation on lightwood chemistry. For Ca concentration, the effect of tree diameter was not significant for any species. For Mg, two species showed significant effects but in opposite directions. For sugar maple, Mg concentrations were lowest in the smallest trees ($p < 0.0001$, $r^2 = 0.27$), while for beech, Mg concentrations were highest in the smallest trees ($p < 0.001$), although tree size explained little of the variation ($r^2 = 0.09$). There were no significant effects of tree diameter on wood chemistry in red spruce, balsam fir, or white birch, but sample sizes for these species were small (Table 1).

Effects of elevation and mesotopography

Overall, Ca and Mg concentrations in lightwood decreased significantly with elevation (Tables 2 and 3). Differences in Ca and Mg concentrations among species were greatest at the low elevation and smallest, though still significant, at the high elevation, resulting in a significant interaction term in the analysis of variance (Table 2). Sugar maple and beech showed a greater decrease in Ca concentration with elevation (about 30%) than did yellow birch (13%). For Mg, the decline in concentration with elevation was greater for sugar maple (40%) than for yellow birch and beech (20%). Lower mean Ca concentration was found in trees sampled in the spruce–fir forest than in the high-elevation northern hardwood forest (Table 3), although the elevation of these two forests was the same. The species that dominate the spruce–fir forest tended to have lower Ca concentrations than the northern hardwood species. Yellow birch, which was sampled in both forest types, also had significantly lower Ca concentrations in the spruce–fir forest than at the high-elevation northern hardwood site (429 µg/g compared with 480 µg/g; Table 3). The mean Mg concentration in trees in the spruce–fir forest was not different from the mean concentration in the high-elevation hardwood site. In fact, yellow birch had higher Mg concentration in the spruce–fir forest than in the high-elevation hardwood site (Table 3).

Forest floor Ca and Mg were also related to elevation. The Ca and Mg concentrations (µg/g) and contents (g/m^2) of the forest floor horizons decreased with elevation (Fig. 1). The significance and r^2 for each of these regressions varied considerably. For Ca concentration in the Oie horizon, r^2 was 0.37, whereas Ca content had an r^2 of 0.22. For Mg concentration in the Oie, r^2 was 0.27, compared with an r^2 of 0.08 for content. Nonetheless, a pattern of declining Ca and Mg concentration and content with elevation was significant for all regressions except for Mg content in the Oa horizon ($p = 0.06$; $r^2 = 0.04$) and paralleled the trend of declining wood Ca and Mg with elevation. Between the low (545 m) and high (780 m) elevations from which the trees were sampled for this study, the forest floor Ca content ranged from 13.8 to 5.7 g/m^2, a 59% difference across 235 m. For Mg, concentrations ranged from 1.45 to 0.93 g/m^2, a 36% difference. High variance in forest floor depth in the spruce–fir

Table 3. Concentrations of Ca and Mg in lightwood, darkwood, and sapling centers of six important tree species at Hubbard Brook Experimental Forest.

	Lightwood						Darkwood		Sapling centres at low elevation (This study)
Species	Low elevation	Middle elevation	High elevation	Spruce–fir	Mass weighted by elevation (This study)	1965	This study	1965	
Calcium (μg/g)									
Sugar maple	734*ax* (20)	632*ay* (19)	562*az* (23)		661	1000 (n = 6)	3948 (n = 9; 485)	3200 (n = 2)	816 (n = 12; 49)
American beech	736*ax* (21)	692*ax* (19)	569*ay* (24)		664	600 (n = 10)	842 (n = 12; 69)	800 (n = 9)	823 (n = 11; 68)
Yellow birch	544*bx* (22)	505*bx* (19)	480*abx* (26)	429*aby* (38)	515	600 (n = 6)	1108 (n = 16; 82)	900 (n = 3)	515 (n = 10; 24)
Red spruce				525*bc* (39)	525	600 (n = 4)			
Balsam fir				555*c* (34)	555				
White birch				393*a* (36)	393				
Magnesium (μg/g)									
Sugar maple	168*ax* (7)	133*ay* (7)	118*ay* (8)		145	200 (n = 6)	544 (n = 9; 66)	600 (n = 2)	109 (n = 12; 9)
American beech	147*ax* (8)	150*ax* (7)	123*ax* (9)		140	200 (n = 10)	234 (n = 12; 18)	200 (n = 9)	165 (n = 11, 14)
Yellow birch	100*bxy* (8)	92*bxy* (7)	84*bx* (9)	106*aby* (12)	93	100 (n = 6)	170 (n = 16; 13)	200 (n = 3)	140 (n = 10; 9)
Red spruce				70*a* (13)	70	100 (n = 4)			
Balsam fir				118*b* (11)	118				
White birch				101*ab* (12)	101				

Note: For lightwood chemistry by elevation, standard errors (in parentheses) use a pooled estimate of error variance from the ANOVA (Table 2). Values with different letters are significantly different among species within elevation (*a–c*) and among elevations within species (*x–z*). Mean lightwood concentrations are mass weighted by the concentration of Ca and Mg in lightwood in each species at each elevation. Balsam fir and white birch values are those measured in the spruce–fir sites only without mass weighting. Values for 1965 are from Likens and Bormann (1970). Balsam fir and white birch were not included in the 1965 sampling. For darkwood and sapling centres for this study, n and SE are given in parentheses.

Fig. 1. Content of Ca (*a*) and Mg (*b*) in the Oie forest floor horizon by elevation at the Hubbard Brook Experimental Forest in 1992. The regression lines are as follows: Ca (g/m^2) = (–0.0334 × elevation (m)) + 32.50 (r^2 = 0.22, p = 0.0001); Mg (g/m^2) = (–0.00222 × elevation (m)) + 2.66 (r^2 = 0.08, p = 0.01).

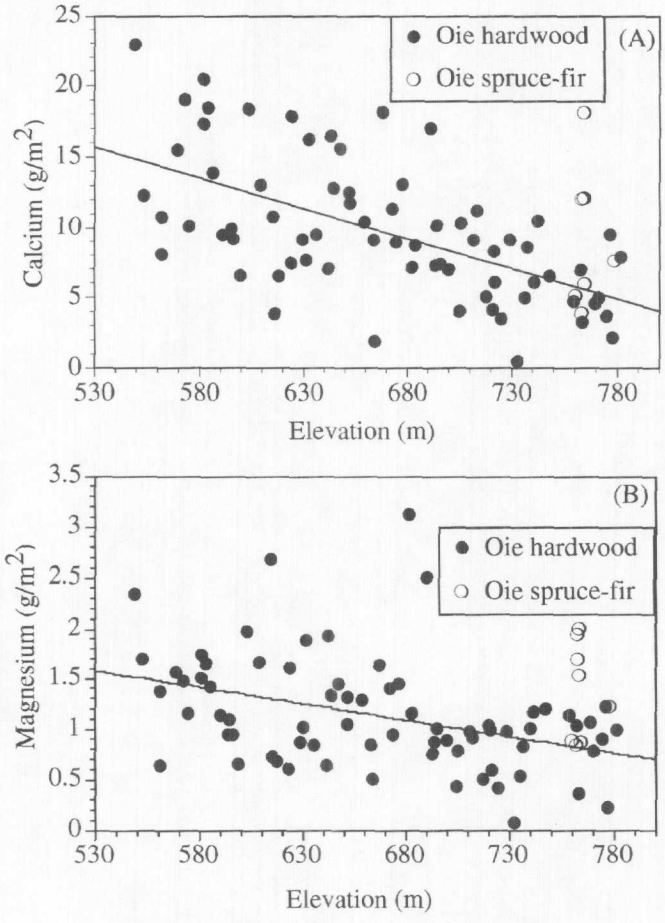
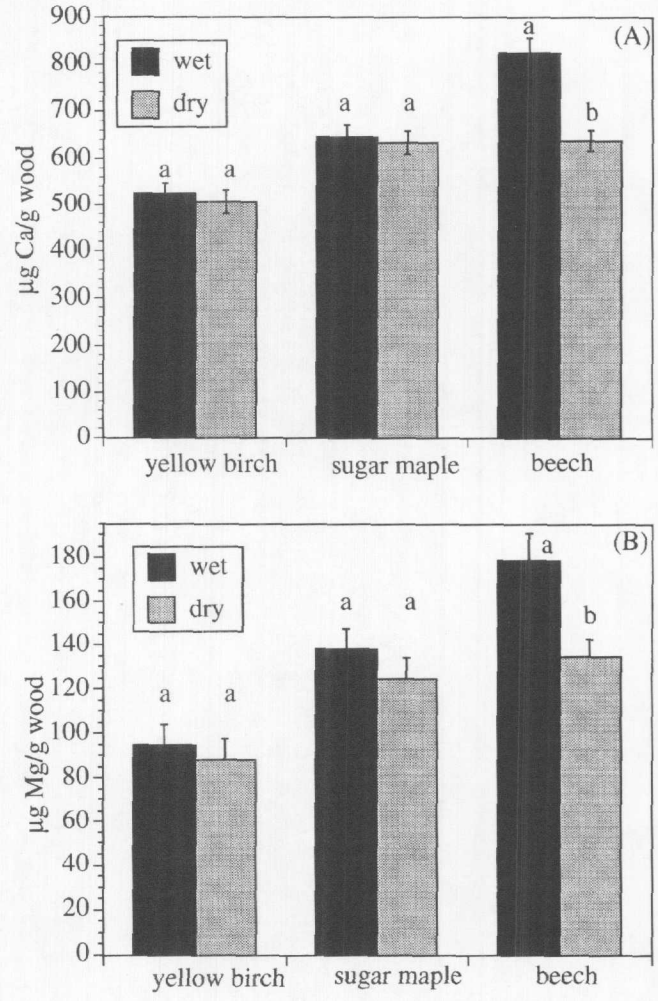


Fig. 2. Calcium (*a*) and Mg (*b*) in lightwood of three species, yellow birch (n = 23 dry, 25 wet), sugar maple (n = 26 dry, 23 wet) and American beech (n = 33 dry, 15 wet), on wet and dry sites at the Hubbard Brook Experimental Forest. Error bars are 1SE; within species, bars with different letters are significantly different.



site explains the broad range of forest floor Ca and Mg contents (Fig. 1).

We examined Ca and Mg concentrations in lightwood of yellow birch, sugar maple, and beech in different mesotopographic positions. Mean cation concentrations were higher in trees growing in wet swales than on dry mounds across all species (p < 0.05). However, differences within species between wet and dry sites were significant only for beech (p = 0.05; Fig. 2). Calcium was 30% and Mg 33% higher in beech grown on wet swales than on dry mounds.

Discussion

Differences in wood chemistry among species is well documented (Kimmins et al. 1985), and was an expected outcome of this study. In addition, the responses of Ca and Mg in sapwood to Ca and Mg availability in soil vary in degree among species (Cutter and Guyette 1993, DeWalle et al. 1991), which may result in some species being better indicators of environmental change than others. Therefore, differences in wood chemistry due to environmental factors should be more pronounced in some species than others.

Sugar maple may be especially responsive to changes in soil chemistry. A relationship between sugar maple vigor and Ca and Mg availability has been demonstrated by Long et al. (1997). Liming forest plots on the Allegheny Plateau increased exchangeable Ca and Mg in the upper 15 cm of soil and resulted in increased diameter growth and crown vigor of sugar maple but not American beech. We have observed higher sugar maple mortality at higher elevations, corresponding to lower Ca concentration in the forest floor, but we cannot attribute cause and effect.

Higher concentrations of Ca and Mg in older wood, such as we found for yellow birch, have been documented previously (DeWalle et al. 1991). Differences in wood chemistry with the age of wood formation could be due to redistribution or translocation of Ca and Mg after the wood is formed (McClenahan et al. 1989), changes in soil chemistry (Bondietti et al. 1989), or reallocation of nutrients from labile pools to perennial tissues during stand development (Arp and Manasc 1988).

In this study, diameter was not significantly correlated to wood chemistry (in the case of Ca), or explained very little of the variation (in the case of Mg). The lack of relationship between our results on age of wood formation and diameter are not surprising, given our sampling approach. For the tree diameter data set, 1-cm increments were taken from two positions in the core, one of which was 2 cm in from the bark, the other of which was located at an unspecified distance from the darkwood–lightwood boundary. The age of each core segment was not recorded, precluding simultaneous analysis of tree diameter and age of wood formation. In addition, the correlation of the age of wood formation on tree diameter was evidently not strong enough to give important patterns with tree diameter.

Differences in lightwood chemistry associated with elevation were large. Differences in lightwood Ca with elevation were greater for sugar maple and beech (23%) than for yellow birch (12%); differences in Mg were greater for sugar maple (30%) than for beech and yellow birch (16%). The decline in forest floor cation concentrations with elevation could be either a cause or an effect of the decline in wood chemistry with elevation.

As a cause, forest floor chemistry may influence the chemistry of vegetation. The forest floor is an important rooting substrate at this site, hosting 43% of fine roots in the northern hardwood zone (Fahey and Hughes 1994). The smaller difference in wood chemistry between species at the higher elevations (Table 3) could be due to limited cation uptake from the more impoverished forest floor. Between 1982 and 1997, biomass of sugar maple declined by 60% in the highest elevation of watershed 6 and increased 7% at the lowest elevations (unpublished data). This finding suggests that sugar maple may be sensitive to Ca or Mg availability in the rooting zone, as found by Long et al. (1997).

Alternatively, differences in forest floor chemistry with elevation could be an effect of differences in the nutrient status of vegetation. Like the forest floor and wood, summer foliage contained less Ca and Mg at higher elevations, especially for Ca in sugar maple (0.382% at high elevation compared with 0.592% at middle and low elevations; Likens et al. 1998). Any factors that cause tree leaves to have lower cation contents will be reflected in litter input to the forest floor.

Although we found significant differences in wood chemistry by species, the pattern differed from that of leaf chemistry by species. Whereas yellow birch had the lowest wood concentrations of Ca and Mg of the three northern hardwood dominants, it had the highest foliar concentrations (Likens et al. 1998). This contrast suggests that the allocation of Ca and Mg within tree biomass (leaves vs. wood) may be as important in explaining variation among species in tissue concentrations as the total amount of nutrient uptake.

Magnesium concentrations in lightwood across elevation varied more than Ca concentrations. One possible explanation is that Ca, which serves a structural role in wood formation, may be less responsive to changes in Ca and Mg in the forest floor. In addition, the variation in forest floor Mg with elevation was much less than for Ca, suggesting that differences in lightwood chemistry with elevation are not driven by the forest floor pattern as measured by total Ca and Mg concentrations.

The higher Ca concentration in beech lightwood in perennially wet sites suggests that Ca uptake by beech may be limited by soil moisture, which influences both mass flow and diffusion of nutrients to roots. In a given environment, species will differ in the degree to which nutrient uptake is limited by different factors, depending on the uptake kinetics and morphology of their roots (Williams and Yanai 1996). The other species were not as sensitive to mesotopographic position, although in all cases, cation concentrations in wood were higher in trees growing on wet than on dry mesosites. Eastern red cedar (*Juniperus virginiana*, L.) growing in the Missouri Ozarks exhibited a similar pattern, with higher Ca concentrations in lightwood from a seep than in trees grown in drier soils (Guyette and Cutter 1995).

A previous estimate of wood chemistry exists for this site, based on concentrations measured on samples taken from log cross sections (disks) in 1965 (Likens and Bormann 1970). The difference between the 1994 and 1965 values cannot be interpreted as change over time because the sampling methods differed. Furthermore, the number of trees sampled in 1965 was small, because whole trees were dissected for analysis. Cores from boles are less representative of each tree sampled but permit a much larger number of trees to be studied, covering a greater range of environmental conditions. For clarity, we show both estimates of Ca and Mg in lightwood and darkwood at Hubbard Brook (Table 3).

The results of this study can be used to indicate which sources of variation in wood chemistry might be most important to include when monitoring ecosystem nutrient cycling. Species differences are obviously important, and these have long been recognized and included in sampling designs. Differences between lightwood and darkwood are important as well, the importance varying among species. Including this source of variation requires estimating the proportion of darkwood and its chemistry. The elevational differences in Ca and Mg concentration in lightwood from the bottom to the top of the watershed varied among species by 12–23% for Ca and 16–30% for Mg (Table 3). Differences between wet and dry mesosites can affect beech lightwood by 30% for Ca and by 33% for Mg. Quantifying the areal extent of topographic lows could be important to understanding uptake of Ca and Mg on a watershed scale, especially where beech dominate such sites.

To illustrate the magnitude of the effect of site differences on lightwood chemistry, we estimated the effect of the elevational differences in lightwood concentrations on ecosystem Ca and Mg budgets. We calculated the amount of Ca and Mg in aboveground lightwood biomass using the species-specific low-elevation concentrations applied across the entire watershed and compared this to the amount estimated using the species-specific high-elevation concentrations. Our calculations apply only to the three northern hardwood species, yellow birch, sugar maple, and American beech, for which we have estimates of lightwood concentrations for three elevations. These three species account for approximately 92% of the aboveground lightwood biomass. The elevational differences in lightwood Ca and Mg concentrations applied to lightwood biomass result in an 18% difference in total lightwood Ca on the watershed and a 24% difference in lightwood Mg. Ecosystem storage is only slightly affected by the different calculations of bolewood

chemistry because lightwood, although massive (57% of the total aboveground biomass at this site), is relatively low in concentration compared with other tissues, especially leaves and fine roots. The effect of using high- versus low-elevation lightwood concentrations is to reduce total aboveground biomass Ca by 2% and Mg by 7%. The difference would be larger if similar changes were applied to wood in branches and coarse roots, but the allometric analysis of wood at HBEF does not include the separation of branch or root lightwood from branch or root bark. The effect of site wetness on lightwood chemistry in beech was greater than the effect of elevation, but including this factor in estimates of bolewood and whole watershed storage of Ca and Mg results in a smaller watershed effect because site wetness affects only beech over the small area of perennially wet sites. Including site differences in estimates of wood chemistry will be most important to calculations in which wood plays a large role, such as biomass removal in logging and accumulation of nutrients in aggrading forests.

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