Original article

Characterizing base-cation immobilization in the stem of six hardwoods of eastern Canada

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Abstract – Rates of base-cation immobilization in the stem of basswood, beech, red oak, red maple, sugar maple and white ash were compared to identify the relative potential for impoverishing soils. Two natural stands in southern Quebec were studied. Allometric equations predicting stem nutrient content from stem diameter were developed. Between 20 and 25 trees per species were sampled for age and stem diameter at breast height, and the area covered by the projection of the tree crown on the ground. Rates of K, Ca and Mg immobilization were assessed by dividing stem nutrient content by age and crown projection. Stem K and Ca content for similar stem diameter classes were highest in white ash and sugar maple, respectively, whereas red oak was lowest in stem Mg content. Overall rates of base-cation immobilization were highest in mid-successional white ash (1.9 g m^{-2} yr^{-1}) and red oak (1.4 g m^{-2} yr^{-1}).

allometric equation / base-cation / hardwood / immobilization / stem

Résumé – Caractérisation de l'immobilisation des cations basiques dans le tronc de six espèces forestières feuillues de l'Est du Canada. Les taux d'immobilisation des cations basiques dans les tiges de tilleul, de hêtre, de chêne rouge, d'érable rouge, d'érable à sucre et de frêne d'Amérique ont été comparés pour identifier les espèces avec un potentiel élevé d'appauvrissement du sol par l'immobilisation des cations basiques. L'étude a été réalisée dans deux peuplements naturels du sud du Québec. Des équations allométriques entre le contenu en cations et le diamètre des arbres ont été établies. Vingt à 25 arbres ont été mesurés pour le diamètre et l'âge à la hauteur de poitrine, et la projection de la couronne au sol. Les taux d'immobilisation de K, Ca et Mg ont été calculés en divisant le contenu en nutriments par l'âge et la projection de la couronne. Le contenu des tiges en K et Ca par classe de diamètre était le plus élevé pour le frêne d'Amérique et l'érable à sucre, respectivement, alors que le chêne rouge était le plus bas en Mg. Les taux d'immobilisation globaux étaient les plus élevés chez les espèces de mi-succession comme le frêne d'Amérique (1,9 g m^{-2} yr^{-1}) et le chêne rouge (1,4 g m^{-2} yr^{-1}).

cation basique / équation allométrique / feuillu / immobilisation / tige

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1. INTRODUCTION

It has long been established that any site which serves as the medium of growth for a tree will be altered as a consequence of the tree's presence. The influence of a tree in altering a forest site has predominantly been examined with respect to selected processes of nutrient cycling. Changes in the chemical, and to a lesser extent the physical environment in the immediate vicinity of the tree are commonly linked to processes of decomposition, mineralization, and crown leaching [1, 3, 10–12, 19]. Processes by which nutrients are stored in trees and not returned to the soil until death, have not been the focus of attention. Limited research suggests interspecific differences in base-cation uptake and immobilization and direct influence on soil nutrient availability and fertility [8, 24, 31, 34].

Immobilization of base-cations in woody tissues is a process that can lead to soil nutrient depletion if actively cycled cations are not replaced by weathering or supplied from outside the site [23]. The effects of tree growth on soil nutrients can, therefore, be partly assessed by comparing per-unit-area rates of nutrient immobilization with ecosystem inputs [15]. Evidence for effects of nutrient immobilization on soil fertility includes rapid soil acidification observed under fast-growing and nutrient-demanding hardwoods [2, 17, 24]. Results on interspecific differences in rates of soil acidification among hardwoods are few. In a recent study, soil pH decreases in a sequence starting with sugar maple (*Acer saccharum* Marsh.) > white ash (*Fraxinus americana* L.) > red maple (*Acer rubrum* L.) > beech (*Fagus grandifolia* Ehrh.) > red oak (*Quercus rubra* L.) [16]. Soil acidification depends on the average basal area increment of the trees [21]. Based on these observations, we hypothesized that mid-successional and fast-growing species would have the highest rates of base-cation immobilization. To test this hypothesis as well as to identify species with the highest potential to impoverish soil of base-cations through immobilization in stems, we assessed the rate of base-cation (K, Ca and Mg) immobilization of selected hardwoods of eastern Canada.

2. MATERIALS AND METHODS

2.1. Site description

The study site was in the Morgan Arboretum of McGill University on the island of Montreal in southern Quebec (45° 25' N, 73° 57' W, 30 m above sea level).

Most of the arboretum is composed of natural forest stands that range from pioneer to climax forest stands typical of the Great Lakes-St. Lawrence forest [35]. Two stands differing in tree species composition, soil types and other characteristics were selected (*table I*). The first stand was composed of dominant sugar maple, American basswood (*Tilia americana* L.), and white ash. The soils developed on a loamy till and are classified as Sombric Brunisol of the Saint-Bernard series [28]. The second stand was composed of American beech, red maple and red oak. The soils developed on a fluvial sand and are classified as Ferro-Humic Podzols [32].

2.2. Nutrient inputs

Fluxes of base-element nutrients in precipitation for the stations of Hemingford-Four Winds and Rémi, both located within 50 km of the Morgan Arboretum, were obtained from the precipitation monitoring program of Quebec [5]. Average annual fluxes (kg ha^{-1} yr^{-1}) at these stations were 0.35 (K), 1.50 (Ca), 0.25 (Mg) and 0.30 (Na).

Mineral weathering was estimated using the steady-state model PROFILE [39]. Ranges of soil properties used for estimating weathering rates in Saint-Bernard and Sainte-Sophie soils are presented in *table I*. Specific surface area was calculated from the measured particle-size distribution and soil bulk density with an algorithm as described by Jönsson et al. [25]. Soil CO_2 partial pressure was derived from the work of Castelle and Galloway [7] for acidic forest soils in Shenandoah National Park, Virginia. Weathering rates were estimated for the first 40 cm of mineral soil. Weathering rates of specific base-cations were estimated by partitioning the global weathering rates calculated with PROFILE according to the proportions of K, Ca and Mg weathering rates reported by Likens et al. [29].

2.3. Allometric equations

Trees selected for developing allometric equations were 20 to 50 cm in DBH (diameter at breast height; 1.3 m aboveground), dominants or co-dominants, and had a single, relatively straight stem and a live-crown ratio between 30 and 40%. Three trees were selected per species to represent the full range of DBH classes found on the site for each species. Trees were cut close to the ground in winter and five- to ten-cm-thick discs were cut from the base of the stem and from subsequent 3-m

Table I. Site characteristics.

	Sugar maple/basswood		Beech/red maple	
Slope	lower, flat		upper, flat	
Drainage	good		slow	
Stand age (yrs)	white ash	0–60	beech	0–80
	sugar maple	0–110	red oak	0–80
	basswood	0–100	red maple	0–100
Height of dominants (m)	32		26	
Soil[1] type	Sombric Brunisol		Ferro-humic Podzol	
texture (sand,silt,clay %)[2]	52,26,22		88,6,6	
coarse fragments (%)	15		0	
bulk density (kg m^{-3})	1400		1300	
moisture (%)	40		30	
pH	5.5		4.1	
K (cmol kg^{-1})	0.4		0.02	
Ca (cmol kg^{-1})	7.5		0.13	
Mg (cmol kg^{-1})	3.8		0.05	
CEC (cmol kg^{-1})	14.5		0.6	
Base saturation (%)	80		35	
Mean soil temperature[3]		7.5 ºC		
Mean air annual temperature		6.2 ºC		
Mean annual precipitation		930 mm		

[1] Soil characteristics are for the first 40 cm of mineral soil; soil moisture by continuous monitoring with TDR probes; soil pH and cations extracted with 0.1 M BaCl$_2$ [20].
[2] Soil texture and coarse fragment [27].
[3] Mean soil and air temperature, and mean annual precipitation [26].

intervals up to a stem diameter of 9 cm. Thus, the number of discs obtained for each tree was determined by the height of the tree. Four stem components were identified and measured for the purpose of this study: heartwood was defined as the central core of discolored wood with no separation of true heartwood or discoloration brought on by injury; sapwood was defined as the first five outside annual rings; a transition zone was defined as the area between the heartwood and the sapwood; and bark, where no differentiation was made between the outer bark (cork) and the inner bark (phloem and cambium).

Tissue samples for chemical analysis were obtained by drilling holes in each of the different components. Holes were distributed regularly over the entire area of each tissue component. In between sampling, the drill bit was cleaned with distilled water to prevent cross contamination. The material produced by drilling was oven dried for 48 h. A subsample was weighed, digested in a mixture of H_2O_2 and H_2SO_4 following the procedure of Thomas et al. [37] and analyzed for K, Ca and Mg by atomic absorption spectrometry. Wood density was determined by weighing a subsample of the discs encompassing all radial zones. These subsamples were dried at 65 ºC until constant weight before determining their volume by water displacement. Bark density was determined by weighing a dried cubical sample of measured dimensions.

Stem volume was estimated by summing up the volume of all truncated cones centered upon each disc. Volume estimations were made by stem components. Total

stem nutrient content was obtained by multiplying each truncated cone volume estimate by its nutrient concentration and wood density.

2.4. Nutrient immobilization

Trees sampled to estimate rates of nutrient immobilization did not include trees used to establish the allometric equations but were from the same stands and had characteristics similar to these trees i.e. dominants or co-dominants with a single, relatively straight stem, and a live-crown-ratio between 30 and 40%. Between 20 and 25 trees per species were sampled in winter 1998. Sugar maple, white ash and basswood were from the sugar maple/basswood stand, and beech, red oak and red maple were from the red maple/beech stand. Trees were cored at 1.3 m aboveground to their center to estimate their age after the seedling stage. Total ages would have underestimated the rates of nutrient immobilization of shade tolerant trees that can survive with minimal growth until released. Cores were stored in plastic straws in the field and transferred to the freezer at the laboratory. Cores were prepared for analysis by slicing the upper third of a freshly-thawed core with a razor-knife. Tree-ring chronologies were determined with the MacDendro system version 5.1 (Régent Instruments Inc., Québec, Canada). The tree crown area was estimated by measuring its projection to the ground based on the polygons formed by the three or four longest branches.

2.5. Statistics

Differences among allometric equations predicting hardwood biomass developed for a site in eastern Canada are not significant and a single general model for all species is suggested [8]. Because of this recommendation and the small number of trees harvested per species in our study, a modified, general-model approach was used. Species-specific models were developed only if a majority of trees of a particular species did not fit within a predetermined confidence interval of the general model. More specifically, the approach was iterative beginning by fitting first or second degree binomial regressions to all 18 trees and by determining a 95% confidence interval. If a species had two trees outside the 95% confidence interval, that species was removed from the data and another general regression was calculated. This process was repeated until no species was found to have two trees outside the confidence interval. Individual regressions

were derived for species that were not included in the general models. The approach allowed us to develop robust site-specific general models of stem K, Ca and Mg content while allowing for the development of species-specific models for some base-cations when significant differences warranted their development.

The rate of nutrient immobilization ($g\ m^{-2}\ yr^{-1}$) of individual trees (20–25 per species) was calculated by dividing the total nutrient content of the tree, estimated with the allometric equations, by its crown area and age at breast height. Linear regressions were used to assess relationships between rates of nutrient immobilization and DBH and tree age.

Homogeneity of variance for ANOVA analysis was assessed with the Bartlett test and logarithmic transformations were used when required. No variable transformations could eliminate the lack of homogeneity of variance of nutrient concentrations among stem component within species. Therefore, ANOVA and multiple comparison of means were used to assess differences between species within a component only. Species effects on rates of immobilization were assessed by means of ANOVA using DBH as a covariable. Duncan's critical range was used for multiple comparisons of means. All statistics were calculated with Statistica Software [36].

3. RESULTS

3.1. Stem tissue characteristics

Largest interspecific differences in concentrations of base elements in tissues were generally observed in heartwood and bark components (*figure 1*). Heartwood Ca and Mg concentrations were highest in basswood and sugar maple, whereas K was highest in basswood; red oak heartwood was lowest in Mg. Transition-zone wood K was highest in white ash; Ca was lowest in white ash although no differences were observed for Mg. Except for the high K concentration of basswood, sapwood showed no significant differences among species. Bark K was highest in white ash and sugar maple, Ca was lowest in red maple, and Mg was highest in white ash and lowest in beech, red oak and red maple. Red maple was consistently among the lowest in bark K, Ca and Mg concentrations.

Calcium concentrations were more than ten times higher in the bark than in other tissues (*figure 1*). Most species showed high K and Mg concentrations in the bark

and heartwood. In red oak, heartwood Mg concentrations were one tenth of that in other tissues. Differences in base-cation concentrations between the transition zone and the sapwood were generally small and no general trend could be identified (*figure 1*).

Wood density (g cm^{-3}) was high in beech (0.72), white ash (0.71) and sugar maple (0.70), intermediate in red oak (0.64) and red maple (0.60) and low in basswood

(0.43). These values are generally within 0.02 g cm^{-3} of published wood densities [22]; the only exception was for white ash which recorded a density 0.06 g cm^{-3} higher in our study. The proportion in volume of the different components ranged from 2 to 74% for the heartwood, 3 to 75% for the transition zone, 6 to 18% for the sapwood, and 4.9 to 11.7% for the bark. The proportion of heart-wood volume was low (< 10%) in basswood and sugar
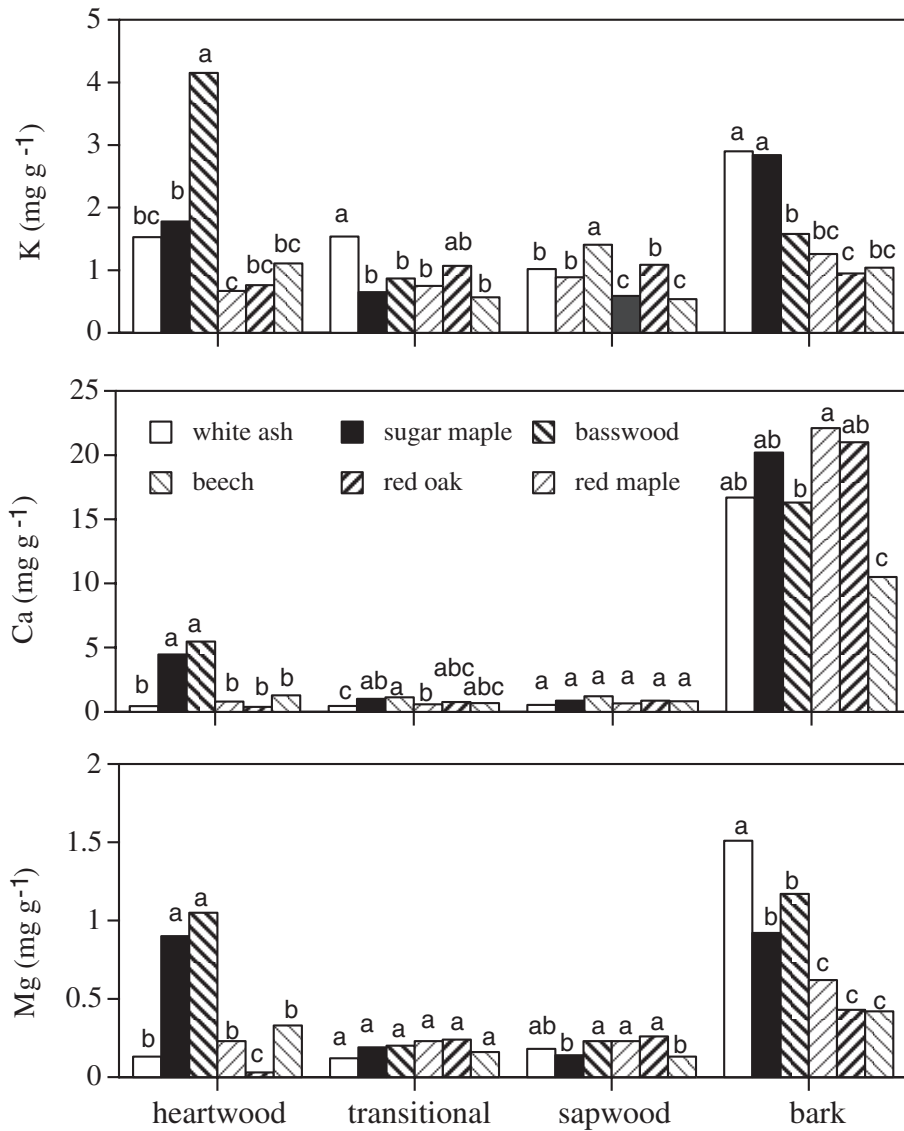

Figure 1. Interspecific comparisons of mean nutrient concentrations of each type of stem tissues. The concentration of 7 to 9 discs per tree was used to calculate the mean concentration of each tree; statistics are based on three trees per species. Means with different letters within a stem component are significantly different ($p < 0.05$).

maple, high in red oak (74%) and intermediate (21–31%) in the other species.

3.2. Nutrient content of the stem

Species-specific regression models were developed for white ash and sugar maple for K, for sugar maple and red oak for Ca, and for red oak for Mg (*table II*). Species ranking of stem nutrient content was as follows: for K, white ash > sugar maple > other species; for Ca, sugar maple > red oak > other species; and for Mg, red oak < other species (*table II*). Interspecific differences in stem nutrient content increased with DBH (*table II*).

3.3. Rates of nutrient immobilization

Linear relationships between rates of nutrient immobilization and tree age were significant in white ash, beech and red maple (*figure 2*). Nutrient immobilization rates decreased with age in white ash but increased with age in beech and red maple. Other species did not produce significant regressions between rates of nutrient immobilization and tree age.

Linear relationships between rates of nutrient immobilization and tree diameter were significant for all species except white ash (*figure 3*). Regressions showed increased rates of nutrient immobilization with increased tree diameter (*figure 3*).

Highest rates of immobilization were observed in white ash for K, Ca, and K+Ca+Mg, and in red oak for Ca, although the difference between red oak and white ash was not significant in this latter case (*table III*). Other interspecific differences in K and Ca immobilization rates were generally not significant. Both K and Mg showed a 3-fold difference between the lowest and the highest immobilization rates whereas Ca showed smaller variation among species. Overall (K+Ca+Mg) rates of immobilization ranked as follows: white ash > red oak ≥ sugar maple = basswood = red maple = beech.

Calculated weathering rates of Ca, Mg, K and Na for the St-Bernard soil were 3.2 ± 1.0 keq ha^{-1} y^{-1}, and 2.6 ± 0.7 keq ha^{-1} y^{-1} without Na. Weathering rates for the Ste-Sophie soil were 1.1 ± 0.4 keq ha^{-1} y^{-1} of Ca, Mg, K and Na, and 1.0 ± 0.3 keq ha^{-1} y^{-1} without Na (*table III*).

4. DISCUSSION

4.1. Stem tissue characteristics

Sugar maple and basswood, two of the three species with low heartwood volumes, had high Ca, and/or K

Table II. Allometric equations for K, Ca and Mg tree stem content (g tree^{-1}) based on DBH (cm).

Nutrient/species	Equation	N	R^2	prob.	[1]Content (g) per DBH class (cm)			
					20	30	40	SE[2]
K								
White ash	$1.4497*DBH^2 - 163.05$	3	0.9997	0.01	417	1142	2157	19
Sugar maple	$1.206*DBH^2 - 395.29$	3	0.9984	0.03	87	690	1534	30
Other species	$38.63*DBH - 651.9$	12	0.9173	0.00	121	507	893	107
Ca								
Sugar maple	$182.53*DBH - 3286.8$	3	0.9815	0.08	364	2189	4014	256
Red oak	$141.4*DBH - 2537.6$	3	0.9985	0.02	290	1704	3118	86
Other species	$100.73*DBH - 1730.5$	12	0.8794	0.00	284	1291	2299	335
Mg								
Red oak	$4.613*DBH - 78.668$	3	0.9406	0.15	17	80	144	18
Other species	$12.61*DBH - 204.16$	15	0.8557	0.00	48	174	300	44

[1] Mean content of a tree estimated from allometric equations.
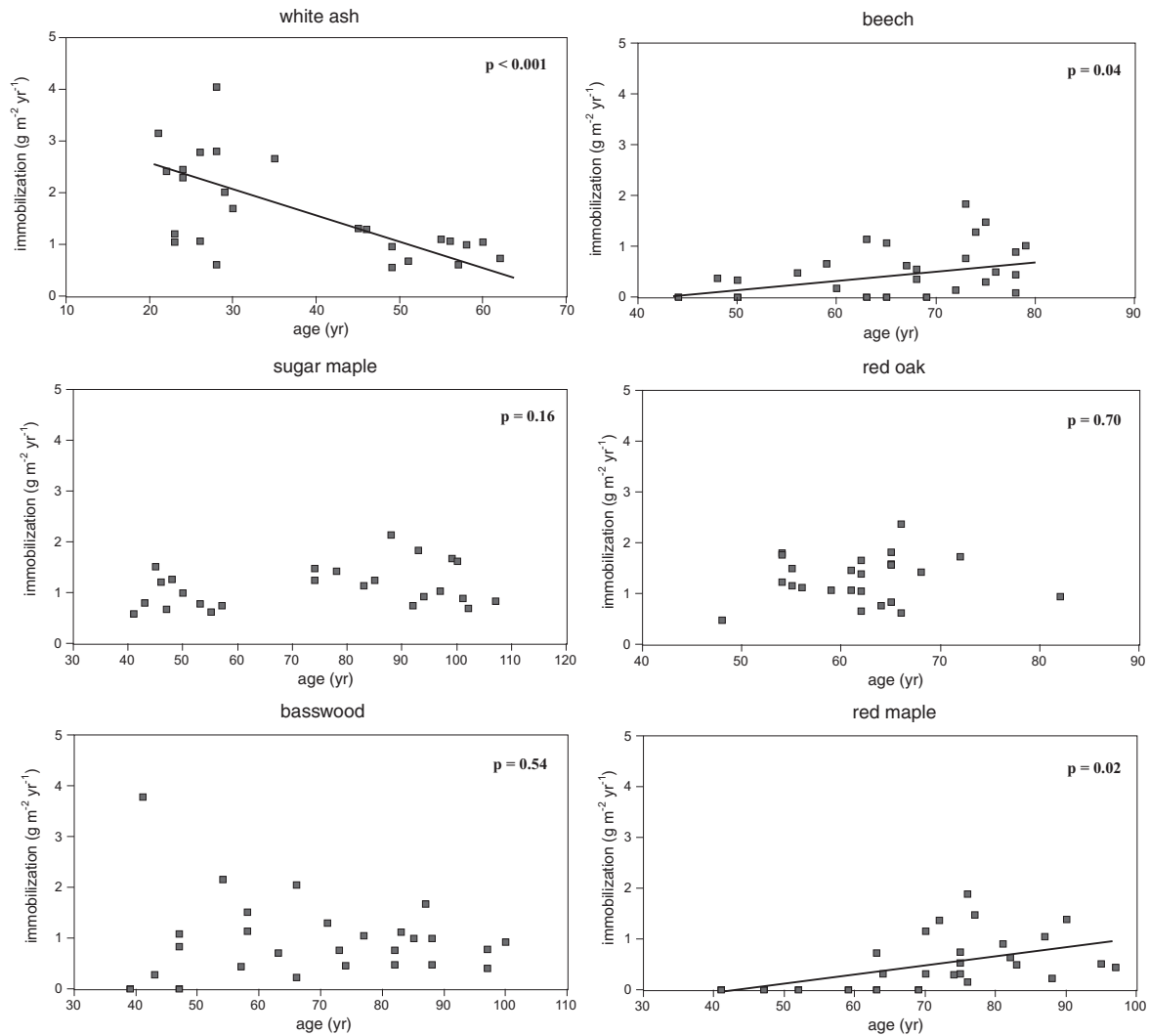[2] Standard error of the estimate.

Figure 2. Relationships between tree age and the sum of K, Ca and Mg stem immobilization rates of each species. Probabilities are for the linear regression of immobilization rate on age.

concentrations in the heartwood compared to the sapwood and the heartwood-sapwood transition. In contrast, red oak, the species with the highest proportion of heartwood, had low base-cation concentrations in the heartwood compared to sapwood and the heartwood-sapwood transition. These patterns suggest possible dilution effects in trees with thick heartwood and concentration effects in trees with proportionately more sapwood.

Base-cation concentrations tended to be highest in the bark and lowest in the sapwood and the heartwood-sapwood transition. Concentrations of mobile elements (N,

P and K) are usually highest in the sapwood relative to other sections of the stem [4, 9, 13, 30, 33, 38]. Both autumnal retranslocation of N, P and K from the leaves and their uptake from the soil in the growing season can contribute to the high concentrations observed in the living sapwood [18]. In our study, K was found to be highest in the sapwood or the transition zone only in red oak. Sampling in mid-winter, when trees were not actively translocating nutrients, may have contributed to the generally low sapwood K concentrations observed in our study.
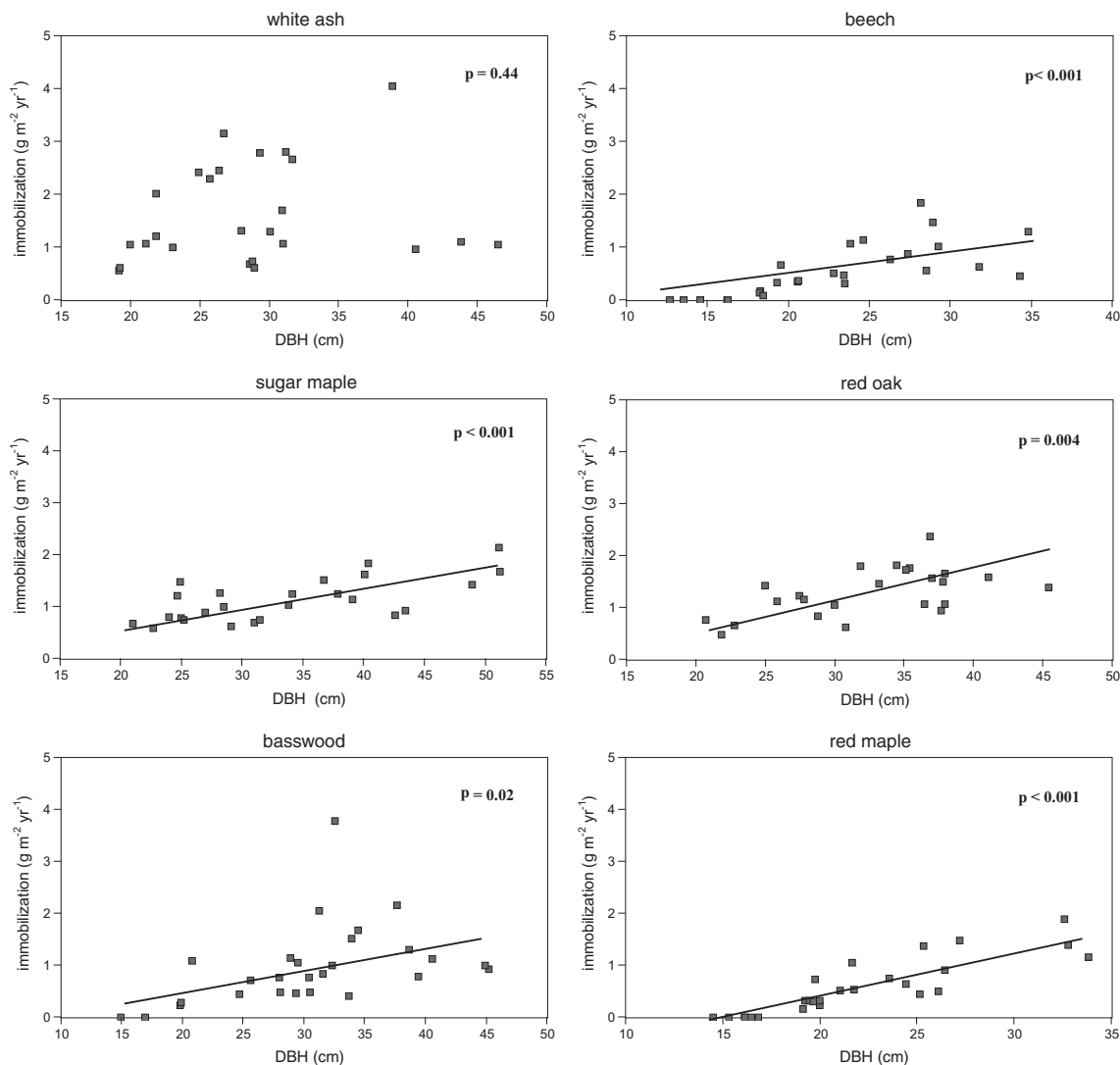
Figure 3. Relationships between DBH and the sum of K, Ca and Mg stem immobilization rates of each species. Probabilities are for the linear regression of immobilization rate on DBH.

4.2. Nutrient content of the stem

White ash ranked highest in K content in each diameter classes. The high K concentration of its bark, sapwood and transition wood coupled with its high wood density were important factors in making white ash stem highest in K content. High Ca concentrations of all stem tissues of sugar maple and a high wood density also contributed to the high Ca content of sugar maple relative to other species. In red oak, the low Mg

concentration of its heartwood, comprising 74% of its stem, and its intermediate wood density made it the lowest in stem Mg content per DBH class. The low Mg concentration and content of red-oak stems does not appear to be specific to our site. Stemwood Mg concentration of red oak are 4 to 6 times lower than in other hardwoods such as trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), sugar and red maple, and ironwood (*Ostrya virginiana* (Mill.) Koch) [8].

Table III. Mean nutrient immobilization rates in tree stems and estimates of nutrient inputs through atmospheric deposition and weathering.

Species/process	K	Ca	Mg	K+Ca+Mg
			(g m^{-2} yr^{-1})	
Maple/basswood				
White ash	0.75a[1]	0.77ab	0.11a	1.88a
Sugar maple	0.22b	0.64b	0.05cd	1.12bc
Basswood	0.23b	0.59bc	0.08b	1.06c
Weathering[2]	1.2	3.6	0.6	5.4
Beech/maple				
Beech	0.21b	0.51c	0.07bc	0.94c
Red oak	0.24b	0.86a	0.03d	1.40b
Red maple	0.23b	0.55c	0.07bc	1.00c
Weathering	0.45	1.3	0.22	1.97
Atmospheric deposition[3]	0.035	0.15	0.025	0.21

[1] Species means are adjusted for the covariable DBH; means of species within a nutrient with the same letter are not significantly different at $p = 0.05$.
[2] Weathering calculated with PROFILE [39] and adjusted for individual nutrients by allocating the same weight as measured in Likens et al. [29].
[3] Atmospheric deposition [5].

Stem Ca content was strongly dependent of bark Ca content. Estimates based on Ca concentrations averaging ten times higher than other tissues, and a mass accounting for one tenth of the total stem mass (based on a bark volume of 10% and a density 10% lower than wood), suggest that bark can account on average for at least 50% of total stem Ca in the studied species. Such a high proportion of stem Ca in stem bark is consistent with values for hardwoods of eastern Canada [8, 34].

4.3. Rates of nutrient immobilization

White ash in the sugar maple/basswood stand, and red oak in the red maple/beech stand, had high overall (K + Ca + Mg) rates of base-cation immobilization in the stemwood. Both are typical of early to mid successional hardwood forests in southern Quebec, and both are fast growers relative to other species included in this study [14]. Although both species had high overall rates of base-cation immobilization, their affinity for specific nutrients were not only different from one another but they also differed from the other species. Our results suggest that white ash has a high affinity for stem K and Mg, and red oak has a low affinity for stem Mg. The high K concentration of white ash leaf litter observed at that site in another study [10] coupled with its high affinity for stem K suggest a higher K uptake in white ash compared to other hardwoods. Other species in this study could be considered generalists in terms of their affinity for base-cations.

Rates of base-cation immobilization in white ash decreased with age but not with size whereas they increase with age ($p = 0.16$) and size in sugar maple. As a primary to mid-successional species commonly found in sugar maple forests of southern Quebec, white ash typically outgrows sugar maple in young stands [14] before loosing dominance to sugar maple later in the succession [6]. The known successional pattern of sugar maple gaining dominance over white ash over time might be the result of or the cause of the declining base-cation immobilization in older white ash. A similar situation may exist in the beech/maple stand where red oak is the mid-successional species. Although oak's rate of immobilization did not decrease with age like white ash, it did not increase either during the time red maple and beech rates of immobilization were increasing. These interspecific differences in base-cation immobilization rates over time are likely to result from a change in species competitiveness for site resources such as light, water and nutrients.

Comparing nutrient immobilization rates with weathering and inputs in the ecosystem show that it is a larger base-cation flux than wet atmospheric deposition and that it can account for more than 50% of weathering for some combination of nutrients and species such as K in white ash and Ca in red oak. These results suggest that stem nutrient immobilization is a significant component of the biogeochemical cycle of nutrients and that interspecific differences in rates of nutrient immobilization can develop as a result of forest growth during succession. Characterization of a larger number of commercial and non-commercial tree species for stem nutrient immobilization could lead to its integration in the planning of forest management in eastern Canada.

As hypothesized, fast growing mid-successional species had the highest overall rates of base-cation immobilization in the stemwood. Our results suggest that both the rates of growth and tissue concentrations are important determinants of the rate of nutrient immobilization in stemwood. Unusually high or low concentrations of specific base-cations in the stem can be a good indicator of the species potential for fast or slow immobilization rates in tree stems, respectively.

REFERENCES

[1] Aber J., Melillo J., McClaugherty C., Predicting long-term patterns of mass loss, nitrogen dynamics and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems, Can. J. For. Res. 68 (1990) 2201–2208.

[2] Alban D., Effects of nutrient accumulation by aspen, spruce, and pine on soil properties, Soil Sc. Soc. Am. J. 46 (1982) 853–861.

[3] Attiwill P., The loss of elements from decomposing litter, Ecology 49 (1967) 142–145.

[4] Attiwill P., Nutrient cycling in a *Eucalyptus obliqua* (L'Hérit.) forest. IV Nutrient uptake and return, Aust. J. Bot. 28 (1980) 199–222.

[5] Boulet G., Jacques G., Programme d'échantillonnage des précipitations du Québec/Sommaire des données de la qualité des eaux de précipitations 1989. Direction des Réseaux Atmosphériques. Ministère de l'Environnement du Québec. Rapport QEN/PA-45, 1992.

[6] Brisson J., Bergeron Y., Bouchar A., Les successions secondaires sur sites mésiques dans le Haut-Saint-Laurent, Québec, Canada, Can. J. Bot. 66 (1988) 1192–1203.

[7] Castelle A.J., Galloway J.N., Carbon dioxide dynamics in acid forest soils in Shenandoah National Park, Virginia, Soil Sci. Soc. Am. J. 54 (1990) 252–257.

[8] Chatarpaul L., Burgess D., Methven I., Equations for estimating above-ground nutrient content of six eastern Canadian hardwoods, Can. For. Institute, Inf. Rep. PI-X-55, 1985.

[9] Colin-Belgrand M., Ranger J., Bouchon J., Internal nutrient retranslocation in chestnut tree stemwood. III. Dynamics across an age series of *Castanea sativa* (Miller), Ann. Bot. 78 (1996) 729–740.

[10] Côté B., Fyles J.W., Leaf litter disappearance of hardwood species of southern Quebec: interaction between litter quality and stand type, Ecoscience 1 (1994) 322–328.

[11] Côté B., Ouimet R., Decline of the maple-dominated forest in southern Quebec: impact of natural stresses and forest management, Environ. Rev. 4 (1996) 133–148.

[12] Crockford R., Richardson D., Sageman R., Chemistry of rainfall, throughfall and stemflow in a eucalypt forest and a pine plantation in south-eastern Australia. 3. Stemflow and total inputs, Hydrol. Processes 10 (1996) 25–42.

[13] De Visser P., The relations between chemical composition of oak tree rings, leaf, bark, and soil solution in a partly mixed stand, Can. J. For. Res. 22 (1992) 1824–1831.

[14] Doyon F., Bouchard A., Gagnon D., Tree productivity and successional status in Quebec northern hardwoods, Ecoscience 5 (1998) 222–231.

[15] Federer C.A., Hornbeck J.W., Tritton L.M., Martin C.W., Pierce R.S., Smith C.T., Long-term depletion of calcium and other nutrients in eastern US forests, Envir. Manag. 13 (1989) 593–601.

[16] Finzi A.C., Canham C.D., Vanbreemen N., Canopy tree soil interactions within temperate forests – species effects on pH and cations, Ecol. Appl. 8 (1998) 447–454.

[17] France E.A., Binkley D., Valentine D., Soil chemistry changes after 27 years under four tree species in southern Ontario, Can. J. For. Res. 19 (1989) 1648–1650.

[18] Frelich L.E., Bockheim J.G., Leide J.E., Historical trends in tree-ring growth and chemistry across an air-quality gradient in Wisconsin, Can. J. For. Res. 19 (1989) 113–121.

[19] Gosz J., Likens G., Bormann F., Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire, Ecol. Monogr. 43 (1973) 173–191.

[20] Hendershot W.H., Duquette M., A simple barium chloride method for determining cation exchange capacity and exchangeable cations, Soil Sci. Soc. Am. J. 50 (1986) 606–608.

[21] Holstener-Joergensen H., Krag M., Olsen H.C., The influence of twelve tree species on the acidification of the upper soil horizons, Forst. Forsoegsvaes. 17 (1988) 1–25.

[22] Hough R.B., The American Woods, 3rd edition. Weed, Parsons & Co., N.Y., 1910.

[23] Huettl R.F., Schaaf W., Nutrient supply of forest soils in relation to management and site history, Plant Soil 168–169 (1995) 31–41.

[24] Johnson D.W., Todd D.E., Nutrient cycling in forests of Walker Branch Watershed, Tennessee: Roles of uptake and leaching in causing soil changes, J. Environ. Qual. 19 (1990) 97–104.

[25] Jönsson C., Warfvinge P., Sverdrup H., Application of the SAFE model to the Solling spruce site, Ecol. Model. 83 (1995) 85–96.

[26] Kipkech F.C., The effects of sugar maple (*Acer saccharum* Marsh.) and black walnut (*Juglans nigra* L.) on soil fertility: preliminary assessment of their agroforestry potential. M.Sc. Thesis, McGill University, Montréal, Canada, 1995.

[27] Lajoie P.G., Les sols des comtés d'Argenteuil, Deux-Montagnes et Terrebonne (Québec). Service de recherches, Ministère de l'agriculture du Canada. A57-215/1960F, 1960.

[28] Lajoie P.G., Stobbe P., Étude des sols des comtés de Soulanges et Vaudreuil dans la province de Québec, Agric. Can., Ottawa, Ontario, 1951.

[29] Likens G.E., Bormann F.H., Pierce R.S. Eaton J.S., Johnson N., Biogeochemistry of a forested ecosystem, Springer-Verlag, N.Y., 1977.

[30] McClenahen J., Vimmerstedt J., Scherzer A., Elemental concentrations in tree rings by PIXE: statistical variability, mobility, and effects of altered soil chemistry, Can. J. For. Res. 19 (1989) 880–888.

[31] Miller R., Plant nutrient in hard beech. III. The cycle of nutrients, N. Z. J. Sci. 6 (1963) 388–413.

[32] Millette G., Soil map of the Morgan Arboretum. W.H. Brittain memorial forest science laboratory, Dept. Nat. Res. Sci., McGill University, Québec, 1948.

[33] Myre R., Camiré C., The establishment of stem nutrient distribution zones of European larch and tamarack using principal component analysis, Trees 9 (1994) 26–34.

[34] Rennie P., The uptake of nutrients by mature forest growth, Plant Soil 7 (1955) 49–95.

[35] Rowe J., Forest regions of Canada. Can. J. For. Serv. Publ. No. 1300. Ministry of Fisheries and the Environment, Ottawa, Ontario, 1972.

[36] StatSoft, Statistica for the Macintosh, Statsoft Inc., Tulsa OK, 1994.

[37] Thomas R., Sheard W., Moyer J., Comparison of conventional and automated procedures for nitrogen, phosphorus, and potassium analysis of plant material using a single digestion, Agron. J. 59 (1967) 240–243.

[38] Wardell J., Hart J., Radial gradients of elements in white oak wood, Wood Sci. 5 (1973) 298–303.

[39] Warfvinge P., Sverdrup H., Calculating critical loads of acid deposition with PROFILE – Steady state soil chemistry model, Water Air Soil Pollut. 63 (1992) 119–143.