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Base-cation cycling by individual tree species in old-growth forests of Upper Michigan, USA

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Abstract. The influence of individual tree species on base-cation (Ca, Mg, K, Na) distribution and cycling was examined in sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), and hemlock (*Tsuga canadensis* L.) in old-growth northern hardwood – hemlock forests on a sandy, mixed, frigid, Typic Haplorthod over two growing seasons in northwestern Michigan. Base cations in biomass, forest floor, and mineral soil (0–15 cm and 15–40 cm) pools were estimated for five replicated trees of each species; measured fluxes included bulk precipitation, throughfall, stemflow, litterfall, forest-floor leachate, mineralization + weathering, shallow-soil leachate, and deep-soil leachate. The three species differed in where base cations had accumulated within the single-tree ecosystems. Within these three single-tree ecosystems, the greatest quantity of base cations in woody biomass was found in sugar maple, whereas hemlock and basswood displayed the greatest amount in the upper 40 cm of mineral soil. Base-cation pools were ranked: sugar maple > basswood, hemlock in woody biomass; sugar maple, basswood > hemlock in foliage; hemlock > sugar maple, basswood in the forest floor, and basswood > sugar maple, hemlock in the mineral soil. Base-cation fluxes in throughfall, stemflow, the forest-floor leachate, and the deep-soil leachate (2000 only) were ranked: basswood > sugar maple > hemlock. Our measurements suggest that species-related differences in nutrient cycling are sufficient to produce significant differences in base-cation contents of the soil over short time intervals (< 65 years). Moreover, these species-mediated differences may be important controls over the spatial pattern and edaphic processes of northern hardwood-hemlock ecosystems in the upper Great Lakes region.

Introduction

Individual tree species play an important role in the nutrient dynamics that influence community structure, ecosystem function, biodiversity, and sustainability of mixed stands (Chapin et al. 1997). Individual species affect the distribution and cycling of nutrients in biomass, the forest floor, and the mineral soil (Boettcher and Kalisz 1990; Pelletier et al. 1999; Rauland-Rasmussen and Vejre 1995; Finzi et al. 1998a, b; Neirynck et al. 2000). This single-tree effect on soils has been referred to as 'single-tree influence circles' (Zinke 1962; Boettcher and Kalisz 1990). Because individual species can create positive feedbacks to patterns of nutrient distribution and cycling of natural ecosystems (Hobbie 1992; van Breemen 1995; Chapin et al. 1997), the role of individual trees in forest ecosystems may be important to enhancing spatial heterogeneity and biodiversity (van Breemen et al. 1997; Finzi et al. 1998b).

Two predominant theories describe the longevity of pedogenic effects from single species. The ‘shifting mosaic’ theory argues that the diverse mosaic of individual species and patches of trees is temporary and that each part of the landscape undergoes a succession of developmental stages (Clark 1991; Frelich et al. 1993; Zhang et al. 1999). In contrast, the influence of individual trees or patches of trees may extend for repeated generations (i.e., ‘pedological memory’) because of the ‘self-reinforcing pedologic influence of trees’ (Miles 1985; Phillips and Marion 2004). The longevity of pedogenic effects from different species can be estimated by comparing annual inputs of nutrients with outputs and accretion of nutrients in biomass (Clayton 1979).

The objectives of this study were to quantify and compare the effects of individual tree species on base-cation cycling and distribution in old-growth northern hardwood – hemlock (*Tsuga canadensis* L.) forests of the upper Great Lakes region. We hypothesized that: (1) individual species in northern hardwood stands will store and influence the movement of base cations differently due to species-specific differences in nutrient transfers and transformations; and (2) significant differences in base-cation fluxes among species may be sufficient to result in species-related differences in base-cation content of the soil within one lifespan.

Materials and methods

Experimental site

The study was conducted in the Sylvania Wilderness-Recreation Area (SWRA) of the Ottawa National Forest (46°13′ N, 88°18′ W) in western Upper Michigan. The dominant landform of the area is the Winegar Moraine, which was deposited by the south-flowing Ontonagon ice lobe during the late Wisconsin approximately 10,000 years ago (Peterson 1982). The moraine is hummocky, contains till and debris-flow sediments capped in places with windblown sediments, and has a mean elevation of about 500 m above sea level. The soils of the SWRA were studied in detail by Bockheim (1997, 2003) and mapped by Bockheim and Jordan (2004).

The climate of the SWRA is cool continental. Mean annual precipitation is 860 mm, of which about half (420 mm) falls during the growing season (May through October) (National Oceanic and Atmospheric Administration 1980; National Atmospheric Deposition Program 2001). Snowfall accounts for 215 mm of water-equivalent precipitation annually. The mean annual temperature is 4.3 °C; the frost-free period averages 61 days. The soil temperature and moisture regimes are frigid and udic, respectively.

Pollen assemblages from Sylvania record a forest dominated by white pine, oak, and red maple until about 3200 years before present, at which time hemlock invaded the area, particularly in landscape depressions (Davis et al. 1998). At present, the dominant tree species are sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britt)., and hemlock (*Tsuga canadensis*); common associates are red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), and white cedar (*Thuja occidentalis* L.). The forest cover distribution at Sylvania is 37% hemlock, 12% northern hardwoods, 17% mixed hemlock-northern hardwoods, 13% wetlands, and 21% lakes (Pastor and Broschart 1990). The average basal area of old-growth northern hardwood – hemlock forests is 34 m^2 ha^{-1}, and species composition is sugar maple 70%, basswood 14%, yellow birch 10%, and hemlock 5.3% (Goodburn and Lorimer 1999).

Field methods

We chose five dominant canopy trees from three major species in old-growth stands of the SWRA: sugar maple, basswood, and hemlock. Each tree was of similar size, with a mean diameter of 51 cm at breast height (1.37 m; DBH), and of comparable age (~200–250 years) (Table 1). The selected trees did not have canopies that overlapped with adjacent canopies. Sugar maple and basswood trees were selected within a 1-ha area south of Clark Lake and the hemlock trees were chosen from a 0.5-ha area near the west end of the lake. On average, the hemlocks were 2.0 km away from the northern hardwood trees. Care was taken to ensure that sample trees occurred on the same soil taxon and parent material: a sandy, mixed, frigid Typic Haplorthod (Pence sandy loam) on glacial outwash. Although the soils were similar morphologically and taxonomically, we hypothesized differences in soil chemical properties in response to individual tree species.

To investigate the effect of individual tree species on base-cation cycling, the drip line from the canopy edge of each tree was projected to the ground surface, i.e., the concept of 'single-tree influence circles' (Zinke 1962) and the

Table 1. Description of sample-tree species in Sylvania Recreational Area, Michigan, Sample age from 200 to 250 years.

Tree species	DBH		Height		Canopy area		Sapwood growth		Sapwood density
	Mean (m)	s.e.	Mean (m)	s.e.	Mean (m^2)	s.e.	Mean (mm)	s.e.	Mean (g/cm^3)
Sugar Maple	0.57^{a}	0.052	35^{a}	4.2	29.9^{ab}	3.05	2.18^{a}	0.23	0.56^{a}
Basswood	0.51^{a}	0.053	29^{a}	2.3	36.7^{a}	1.81	2.22^{a}	0.37	0.35^{b}
Hemlock	0.46^{a}	0.030	28^{a}	1.1	28.4^{b}	3.01	2.08^{a}	0.37	0.45^{ab}

Differences in small-case letters indicate differences within each compartment (leaf litterfall, throughfall and stemflow, mineralization, uptake, forest floor leachate, shallow leachate, and deep leachate) at the 0.05 probability level.

'pipe model theory' (Shinozaki et al. 1964). All samplers were located randomly around each tree midway between the drip line of the canopy edge and the stem; we assumed that samples from these positions represented mean fluxes and pool sizes for each species. The samplers were installed at least 1-m apart to avoid interactions.

Solution and litterfall samples were collected every other week from July 22, 2000 through October 15, 2000 and May 15, 2001 through October 15, 2001. No samples were collected during the dormant season because of limited access, low temperatures, and heavy snow. In addition, we assumed measurements during the growing season would capture species-related differences.

Bulk precipitation and throughfall were collected with 20-cm diameter funnels attached to plastic 4.3-l bottles (Likens and Bormann 1995). Two throughfall collectors were installed beneath each tree; and two precipitation collectors were installed in open areas sufficiently large enough to avoid the influence from adjacent canopies. Stemflow was collected using a 10-cm diameter flexible, plastic vent pipe from which a quarter of the circumference was removed. The vent pipe was stapled in a slightly descending spiral around the stem and sealed with silicone caulk. Stemflow was not sampled during the growing season of 2001 because of concerns that its collection may affect soil water chemistry.

The forest floor leachate was collected with zero-tension lysimeters constructed from 30-cm long PVC tubing with a 6-cm-wide screen over the opening (Jordan 1968). One collector was installed beneath the forest floor within the sampling area at a location where the forest floor was of mean thickness. Leachates from the upper mineral soil (15 cm) and below the rooting zone (85 cm) were collected using ceramic, porous-cup samplers (Soil Moisture Equipment Inc., Model #1900). Bentonite clay was inserted around each sampler above the suction cup to minimize preferential flow along the PVC neck. Each sampler was evacuated to negative pressure of 70 kPa using a hand vacuum pump following each sample collection.

The volumes of bulk precipitation, throughfall, stemflow, and the forest floor leachate were measured in the field, and 125-ml subsamples were collected for chemical analysis. All sampling equipment was rinsed with de-ionized water between each sample. Sample bottles were never reuseds.

The sum of mineralization and weathering was estimated using open-top cores 20 cm long by 5.2 cm inside diameter containing bags of cation exchange resin placed at the bottom to recover base cations released by weathering and mineralization (DiStefano and Gholz 1986). Understanding that these cores also capture base cations from the throughfall flux, we subtracted our throughfall measurements for the mineralization + weathering base-cation totals. Cores extended to the bottom of the A or A/E horizon at a mean depth of 10 cm below the mineral soil surface. Resin bags were replaced once a month from July 20 through October 15, 2000. We did not measure base-cation flux from mineralization and weathering in 2001.

One representative forest floor sample having a mean thickness within the sample area was collected from each single-tree plot using a 20-cm diameter circular frame. Ten samples of mineral soil were randomly collected using an Oakfield corer from two depths, 0–15 cm and 15–40 cm. All soil samples from around a sample tree and from a given depth interval were put in a bucket, mixed, and sub-sampled for chemical analysis.

Litterfall was collected in a 40 by 60 cm plastic laundry basket with the bottom replaced with 1-mm mesh fiberglass. Litterfall was collected bimonthly; each collector represented one of five replicates per species. Before drying and further processing, all leaf litter was separated by species and only the foliage from the sample tree was retained for analysis. At no sample date were significant amounts of foliage from adjacent species found in the collectors, nor were any twigs found in our collectors over the duration of this study.

For scaling purposes, the total canopy projected area of each tree was calculated using the method by Goodburn and Lorimer (1999). Eight crown radii were measured with a tape along eight cardinal directions from each tree's center to the drip line. Canopy area (CA; m^2) was then determined from a summation of those eight triangles using the equation:

$$CA = \sum_{n=1}^{8} \left(\frac{1}{2} \times \frac{r_n}{\sqrt{2}} \times r_{n+1} \right) \tag{1}$$

In this equation r_n is a radius (m) of each direction (e.g. r_1 = north, and r_2 = northeast). For sugar maple and basswood total litterfall mass per unit ground area over the growing season was then multiplied by total projected canopy area Eq. (1) to obtain total crown biomass per tree. For hemlock, total canopy biomass was obtained by multiplying litterfall mass per unit ground area by total projected crown area Eq. (1) and average leaf longevity (4 years) measured for each sample tree.

Because Sylvania is a protected wilderness, destructive sampling of trees for biomass determination was not permitted. Therefore, the DBH of each tree was used to estimate above- (excluding total leaf mass) and below-ground biomass using allometric equations developed for these species. The biomass of understory trees was not measured. Foliage and bolewood samples were collected from each tree. Two perpendicular bolewood samples were collected from each tree using a 5-mm inside diameter increment borer. We then measured the average diameter increment over the last five years growth to project the change in DBH over the duration of this study. Bark, live branches, coarse roots, and fine (<2 mm) roots were collected from recently wind-thrown trees of each species that still contained green foliage for tissue analysis.

Laboratory methods

Solution samples were passed through a 0.45-μm Millipore filter and sent to the University of Wisconsin, Soil and Plant Analysis Laboratory (SPAL) for measurement of base cations (potassium, calcium, magnesium, and sodium) using Inductively Coupled Plasma – Optical Emission Spectrometry (ICP-OES) (University of Wisconsin-Madison, Soil Testing Laboratory 2004).

Soil samples were air-dried at temperature (22 °C) for 5 days and passed through a 2-mm mesh teflon$^{\text{TM}}$ screen. Exchangeable cations were then extracted with 1 M ammonium acetate (pH 7.0) (Soil Survey Staff 1996, method 5B). Cations in resin bags for the mineralization plus weathering measurements were extracted with 75 ml 1 M $BaBr_2$.

Forest floor, bole wood, foliage, and litterfall samples were oven-dried at 60 °C for 10 days, measured for total dry weights, and ground to pass a 1-mm mesh before nutrient analysis by SPAL.

Computations and statistical analysis

Base-cation transfer from canopy exchange was estimated as the sum of throughfall and stemflow, minus bulk precipitation (Eaton et al. 1973). The transfer of base-cations in throughfall for a growing season was quantified from actual measurements during the period July 22 through October 15, 2000 and May 15 through October 15, 2001. Fluxes for the first part of the 2000 growing season (May 15 through July 22) were not directly measured at the study site. For this period, we used regressions between all remaining data collected during 2000 and 2001 growing seasons and bulk precipitation data over the same time period from the Trout Lake Research Station (Bowser et al. 2001) to estimate missing flux measurements ($r^2 = 0.69$). Trout Lake is located 20 km southwest of Sylvania. Stemflow for May 15 through July 22, 2000 was estimated from the ratio of throughfall and stemflow during the July 22 through October 15, 2000 period of data collection.

The volume of solution passing through the soil profile (0–15 cm and 15–85 cm) was estimated by the equation:

$$Lv = \mathrm{BP} - \mathrm{PET} - \mathrm{SW}_h \tag{2}$$

Lv represents the total cm of leachate at each depth (15 or 85 cm from mineral soil surface) during the growing season, BP is the cm of bulk precipitation, PET is cm of potential evapotranspiration during the growing season, and SW_h is the cm of water stored in the soil during that time period. PET was estimated by Thornthwaite's temperature-based equation (Pastor and Bockheim 1984; Dingman 1994).

All biomass components (above- and below-ground) were estimated from published allometric equations for each tree species. These allometrics use the diameter at 1.37 m aboveground to estimate the various above- and below-ground biomass pools of bolewood and canopy biomass including live branches and foliage. Specifically, we used equations from Ter-Mikelian and Korzukhin (1997) to estimate aboveground biomass of basswood and sugar maple and equations from Campbell and Gower (2000) for aboveground components of hemlock. Equations of Whittaker et al. (1974) were used to estimate belowground biomass for each species.

Nutrient uptake by individual trees was estimated from the equation:

$$U = \Delta B + LF + (TF + SF - BP) \qquad (3)$$

In this equation, U is uptake, ΔB is the change in above- and below-ground biomass, LF is leaf litterfall, TF is throughfall, SF is stemflow, and BP is bulk precipitation (Bockheim and Leide 1990). Retranslocation of base-cations was assumed to be negligible during the period measured in this study. Soil exchangeable base-cation pools were measured for the forest floor, upper mineral soil (0–15 cm) and lower mineral soil (15–40 cm).

The time required for nutrient fluxes by the individual species to produce differences in soil pools was determined using the equation of Clayton (1979):

$$\Delta S = BP + WM - (O_L + \Delta B) \qquad (4)$$

In this equation, BP is bulk precipitation, *Delta*S is change in soil storage of base cations, WM is release of base cations from weathering and mineralization, O_L is loss of base cations from the deep leachate, and ΔB is change in base-cation storage of perennial biomass.

We used a systematic random design to test our hypotheses and select each tree within each species group. Once a tree met our sampling criteria, as detailed earlier, the tree was treated as one of five replicates within each species. All base-cation pools and fluxes within a plot were expressed as $\text{mmol}_c\ \text{m}^{-2}$ for each growing season (2000 and 2001). Where necessary, we scaled these pools and fluxes to a per projected canopy area (i.e., 'pipe model theory'). We used a one-way analysis of variance using Statistical Analysis Systems GLM procedure (Statistical Analysis Systems 1999) to examine differences between base-cation pools and fluxes among species. Statistical differences are reported in the tables at the 0.05 probability level.

Results

Base-cation pools

Biomass. The mean base-cation contents of the woody (above- and belowground) and foliage per m^2 were significantly greater for sugar maple than for basswood or hemlock (Table 2), primarily because of the significantly greater foliar and woody biomass of sugar maple. These differences occurred despite the similarity in age of sample trees.

Forest floor. In general, forest-floor pools of individual and total base cations contents (sum of Ca, Mg, K, and Na) were significantly greater beneath hemlock than beneath sugar maple and basswood (Table 2), due in large part

Table 2. Average total extractable base-cation content by compartment in the Sylvania Recreation Area, Michigan.

	Bulk density	Mass	Ca	Mg	K	Na	Total
	g/cm^{3}	kg/m^{2}	mmol$_{c}$/m^{2}				
Woody biomass (aboveground + belowground)							
Sugar maple		85^{a}	7051^{a}	2334^{a}	3777^{a}	683^{a}	13844^{a}
s.e.		14	1146	236	704	138	2122
Basswood		27^{b}	2732^{b}	949^{b}	1215^{b}	234^{b}	5130^{b}
s.e.		4	515	234	249	59	979
Hemlock		21^{b}	2191^{b}	618^{b}	1376^{b}	254^{b}	4440^{b}
s.e.		3	270	99	241	39	607
Foliage							
Sugar maple		1.18^{a}	883^{a}	147^{a}	91.1^{a}	4.04^{a}	1126^{a}
s.e.		0.15	109	21	10.5	0.71	139
Basswood		0.52^{b}	697^{a}	150^{a}	66.8^{ab}	1.66^{b}	916^{a}
s.e.		0.09	114	31	11.5	0.29	156
Hemlock		0.93^{a}	345^{b}	64^{b}	49.6^{b}	1.30^{b}	461^{b}
s.e.		0.13	37	10	7.9	0.18	54
Forest floor							
Sugar maple		0.78^{b}	633^{a}	57.5^{b}	18.5^{a}	0.09^{a}	709^{a}
s.e.		0.14	154	6.6	3.2	0.05	161
Basswood		0.62^{c}	521^{a}	80.5^{ab}	18.2^{a}	0.14^{a}	620^{a}
s.e.		0.15	109	21.1	2.8	0.08	131
Hemlock		2.03^{a}	1047^{b}	123.0^{a}	47.3^{b}	0.16^{a}	1218^{b}
s.e.		0.27	125	14.7	7.1	0.07	146
Upper mineral soil (0–15 cm)							
Sugar maple	0.89		4433^{b}	675^{b}	428^{a}	36.1^{a}	5572^{b}
s.e.			736	106	146	3.0	958
Basswood	0.89		9503^{a}	1639^{a}	330^{a}	37.4^{a}	11509^{a}
s.e.			1177	216	3^{a}	3.7	1369
Hemlock	1.23		3138 ^{b}	430^{b}	406^{a}	76.9^{a}	4051^{b}
s.e.			404	62	222	25.1	602
Lower mineral soil (150–40 cm)							
Sugar maple	1.31		2088^{b}	321^{b}	192^{a}	37.7^{a}	2638^{b}
s.e.			307	53	7	6.2	365
Basswood	1.31		3695^{a}	649^{a}	201^{a}	40.0^{a}	4586^{a}
s.e.			637	140	22	3.8	778
Hemlock	1.03		1151^{b}	219^{b}	129^{b}	51.8^{a}	1551^{b}
s.e.			321	51	13	6	370
Total base cation in the system							
Sugar maple			15088^{a}	3534^{a}	4506^{a}	761^{a}	23889^{a}
s.e.			1584	291	720	133	2463
Basswood			17149^{a}	3468 ^{a}	1832^{b}	313^{b}	22761^{a}
s.e.			2193	649	255	65	3094
Hemlock			7872^{b}	1455 ^{b}	2009^{b}	384^{b}	11720^{b}
s.e.			880	171	229	48	1050

Differences in small-case letters indicate differences within each compartment (woody biomass, foliage, forest floor, upper mineral soil, lower mineral soil) at the 0.05 probability level. # Each value is a mean (± s.e.) of 5 replicated trees.

to the significantly greater biomass of the forest floor beneath the hemlock. Calcium was the dominant cation in the forest floor regardless of tree species, followed by Mg, K, and Na. There were no significant differences in forest floor quantities of Ca and Mg between beneath sugar maple and basswood. The K content of the forest floor beneath hemlock was significantly greater than beneath sugar maple and basswood.

Mineral soil. Total base-cations, Ca, and Mg contents of the mineral soil were significantly greater beneath basswood than sugar maple and hemlock regardless of soil depth (Table 2). There were no significant differences in K contents among individual tree species for the upper mineral soil (0–15 cm). The K content of the lower mineral soil (15–40 cm) was significantly greater beneath basswood and sugar maple than beneath hemlock, although there was no difference when expressed over the entire sample depth (0–40 cm). Calcium was the most abundant cation averaging 80% of the total base cations for each tree species.

Single-tree systems. The total base-cation pool of the single-tree systems (i.e. sum of base cations in biomass, forest floor, and mineral soil) were significantly greater for sugar maple and basswood species than for hemlock (Table 2). System totals of K and Na were significantly greater for sugar maple than for basswood and hemlock.

Base-cation fluxes

Bulk precipitation. Base cations contributed by bulk precipitation were small relative to the other fluxes in the single-tree systems (Table 3). Calcium was the dominant base-cation contributed by bulk precipitation, followed by Mg, Na, and K. Volumes of bulk precipitation during the 2000 and 2001 growing seasons in Sylvania were 555 and 458 mm, respectively, similar to the 539 and 518 mm recorded at the Trout Lake research station.

Throughfall. Total base cations in throughfall for both growing seasons were ranked: basswood > sugar maple > hemlock (Table 3). Potassium was the dominant base-cation for all three species, comprising 64% of the base cations in sugar maple, 49% in hemlock, and 43% in basswood. Throughfall quantities of Ca and Mg were significantly greater beneath basswood than sugar maple and hemlock. No differences were detected in throughfall Na between species.

Stemflow. Total base cations in stemflow were significantly greater for sugar maple and basswood than for hemlock (Table 3). Calcium was the dominant cation in the stemflow of basswood, and K was most abundant in sugar maple and hemlock. Calcium and Mg were significantly greater in stemflow of basswood than in stemflow of sugar maple and hemlock. Stemflow K was significantly greater in sugar maple than in basswood and hemlock. No differences were detected in stemflow Na between species. Stemflow contributed less than 1% of the base-cations delivered to the forest floor around each species.

Table 3. Average base-cation flux in the Sylvania Wilderness Recreational Area, Michigan during the 2000 and 2001 growing seasons.

	2000					2001				
	Ca	Mg	K	Na	Total	Ca	Mg	K	Na	Total
						$mmol_c/m^2$				
Bulk precipitation	5	2	1	1	8	10	4	1	1	15
Throughfall										
Sugar maple	26^{b}	19^{b}	88^{a}	6^{a}	138^{b}	24^{b}	17^{b}	85^{a}	12^{a}	138^{a}
Basswood	71^{a}	69^{a}	111^{a}	7^{a}	258^{a}	64^{a}	60^{a}	95^{a}	5^{b}	224^{b}
Hemlock	9^{b}	6^{b}	19^{b}	5^{a}	38^{c}	9^{c}	5^{c}	17^{b}	3^{b}	34^{c}
Stemflow										
Sugar maple	0.33^{ab}	0.15^{ab}	0.77^{a}	0.02^{a}	1.28^{a}	0.36^{a}	0.16^{a}	0.75^{a}	0.06^{a}	1.33^{a}
Basswood	0.43^{a}	0.23^{a}	0.35^{b}	0.01^{a}	1.03^{a}	0.41^{a}	0.19^{a}	0.31^{b}	0.01^{b}	0.92^{ab}
Hemlock	0.13^{b}	0.04^{b}	0.16^{b}	0.01^{a}	0.33^{b}	0.16^{a}	0.04^{b}	0.15^{b}	0.01^{b}	0.36^{b}
Canopy exchange										
Sugar maple	21.4^{b}	17.0^{b}	88^{a}	4.4^{a}	131^{b}	14.7^{b}	12.7^{b}	85^{a}	11^{a}	124^{b}
Basswood	66.8^{a}	67.4^{a}	111^{a}	6.3^{a}	251^{a}	54.6^{a}	53.1^{a}	95^{a}	4^{b}	206^{a}
Hemlock	3.7^{b}	4.4^{b}	18^{b}	3.9^{a}	30^{c}	-0.3^{c}	0.8^{c}	16^{b}	3^{b}	19^{c}
Forest floor leachate										
Sugar maple	72^{b}	24^{b}	78^{a}	12^{a}	186^{b}	72^{b}	27^{b}	105^{a}	18^{a}	221^{ab}
Basswood	122^{a}	50^{a}	86^{a}	8^{a}	267^{a}	146^{a}	60^{a}	110^{a}	17^{a}	333^{a}
Hemlock	54^{b}	15^{b}	25^{b}	10^{a}	105^{c}	98^{ab}	23^{b}	24^{b}	9^{a}	155^{b}
Shallow leachate										
Sugar Maple	103^{b}	33^{a}	15^{a}	65^{b}	216^{b}	63^{b}	21^{b}	20^{a}	129^{b}	233^{b}

Basswood	212^{a}	49^{a}	58^{a}	84^{b}	403^{a}	138^{ab}	44^{ab}	127^{a}	136^{b}	445^{b}
Hemlock	165^{ab}	50^{a}	24^{a}	133^{a}	372^{a}	254^{a}	84^{a}	83^{a}	501^{a}	922^{a}
Deep leachate										
Sugar maple	70^{a}	28^{a}	7^{a}	34^{a}	139^{a}	76^{a}	28^{b}	14^{a}	49^{a}	168^{a}
Basswood	71^{a}	23^{a}	7^{a}	27^{a}	129^{a}	87^{a}	28^{b}	28^{a}	42^{a}	186^{a}
Hemlock	33^{a}	21^{a}	6^{a}	30^{a}	90^{a}	79^{a}	49^{a}	14^{a}	61^{a}	202^{a}
Leaf litterfall										
Sugar maple	889^{a}	148^{a}	92^{a}	4^{a}	1133^{a}	909^{a}	124^{a}	67^{a}	6^{a}	1107^{a}
Basswood	703^{a}	151^{a}	67^{a}	2^{b}	924^{a}	501^{b}	94^{a}	40^{b}	6^{a}	731^{b}
Hemlock	116^{b}	22^{b}	17^{b}	0^{b}	155^{b}	141^{c}	23^{b}	14^{b}	1^{b}	179^{c}
Mineralization and weathering										
Sugar Maple	67^{a}	55^{a}	0^{b}	132^{b}	255^{a}					
Basswood	95^{a}	101^{a}	0	159^{a}	354^{a}			n/a		
Hemlock	90^{a}	55^{a}	43^{a}	97^{c}	285^{a}					
ΔBiomass										
Sugar maple	62^{b}	21^{b}	33^{b}	6^{b}	121^{c}	159^{a}	36^{a}	46^{a}	3^{a}	243^{a}
Basswood	170^{a}	64^{a}	75^{b}	13^{b}	323^{b}	151^{a}	16^{b}	14^{b}	1^{b}	92^{b}
Hemlock	230^{a}	78^{a}	206^{a}	39^{a}	554^{a}	22^{b}	5^{c}	25^{b}	2^{a}	54^{b}
Uptake										
Sugar maple	973^{a}	186^{ab}	213^{a}	14^{b}	1386^{a}	1083^{a}	173^{a}	198^{a}	20^{a}	1474^{a}
Basswood	945^{a}	284^{a}	254^{a}	22^{b}	1506^{a}	716^{b}	170^{a}	150^{b}	12^{b}	1048^{b}
Hemlock	355^{b}	106^{b}	242^{a}	44^{a}	748^{b}	172^{c}	33^{b}	56^{c}	6^{b}	$267s^{c}$

Differences in small-case letters indicate differences in flux (leaf litterfall, throughfall and stemflow, mineralization, biomass increment, uptake, forest floor leachate, shallow leachate, and deep leachate) at the 0.05 probability level.

Canopy exchange. There were significant species-related differences in base-cations contributed to the forest floor by the interaction of bulk precipitation with the canopy (i.e., throughfall + stemflow − bulk precipitation); the ranking was basswood > sugar maple > hemlock (Table 3). Calcium and Mg were significantly greater beneath basswood than sugar maple and hemlock. Potassium was significantly greater beneath sugar maple and basswood than hemlock. There was no species-related difference in Na canopy exchange; however, the Na flux via the canopy was more than five times bulk precipitation.

Forest-floor leachate. The sum of base-cations in the forest floor leachate was greatest beneath basswood, followed by sugar maple and hemlock (Table 3). Calcium was the dominant cation in the forest floor leachate beneath basswood and hemlock, and K and Ca were equally abundant in the forest floor leachate beneath sugar maple. There were significantly greater amounts of Ca and Mg in the forest floor leachate beneath basswood than beneath sugar maple or hemlock. Potassium was significantly greater in sugar maple and basswood than beneath hemlock.

Soil leachates. Transfers of base cations in the shallow (0–15 cm) and deep (15–40 cm) leachates were greater beneath basswood and hemlock than beneath sugar maple except for the deep leachate in 2000 (Table 3). In general, Ca was the dominant base-cation in the shallow and deep leachates under all species, followed by Na, Mg, and K. No significant differences were detected in Mg and K contents in leachates among tree species.

Leaf litterfall. There were significant differences in base-cation contents of leaf litterfall among the three tree species; hemlock leaf litter had significantly less Ca, Mg, and K than sugar maple and basswood (Table 3). Base cations in litterfall were ranked: sugar maple > basswood > hemlock. The dominant base-cation in the litter was Ca, which comprised 76% of the total content over the two growing seasons. Calcium, Mg, and K contents were similar for sugar maple and basswood; however, they were significantly greater than for hemlock. Sodium was significantly greater for sugar maple than for basswood and hemlock.

Mineralization plus weathering. Although there were no species-related differences in total base cations contributed by mineralization plus weathering in the upper 15 cm of mineral soil, the general ranking was basswood > hemlock > sugar maple (Table 3). The dominant base-cation from mineralization plus weathering was Na, followed by Ca and Mg for all species. There was a significant difference in Na content of mineralization plus weathering, with the ranking being: basswood > hemlock > sugar maple. The K content in mineralization plus weathering beneath hemlock was significantly larger than beneath sugar maple and basswood. Potassium may be fixed by clay minerals in the soil, accounting for the apparent lack of K release from sugar maple and basswood. This is further evidenced by the low contents of K in deep leachates from all three species (Table 3).

Δ Biomass. Elements in annual production of perennial tissues generally were ranked: Ca > K, Mg > Na (Table 3). In 2000, hemlock had unusually

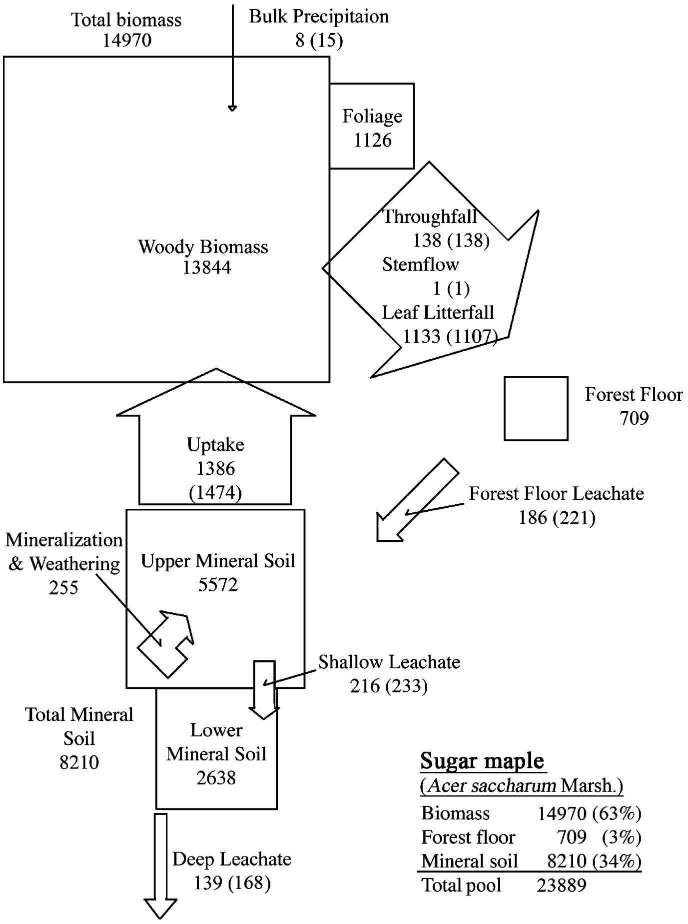

Figure 1. Base-cation distribution and cycling in sugar maple averaged for the years 2000 and 2001 growing seasons, Sylvania Wilderness, Upper Michigan (Note: the width of the arrows indicates the flux in mmol m^{-2} growing $season^{-1}$ and the size of the boxes indicates the pools in mmol m^{-2}).

large and a significantly greater amount of base cations in annual woody tissues than maple or basswood. However, in 2001 sugar maple had a significantly greater amount of base cations, with hemlock having the lowest quantity of bases. These extreme differences are most likely due to annual variations in ring widths, which were not captured in two increment cores and the technique of using allometric equations of DBH to predict biomass change.

Uptake. Based on Eq. (3), sugar maple and basswood took up significantly greater amounts of Ca and total base cations than did hemlock (Table 3). Potassium uptake was not significantly different among the three tree species, and Na uptake by hemlock was significantly greater than by sugar maple and beneath basswood.

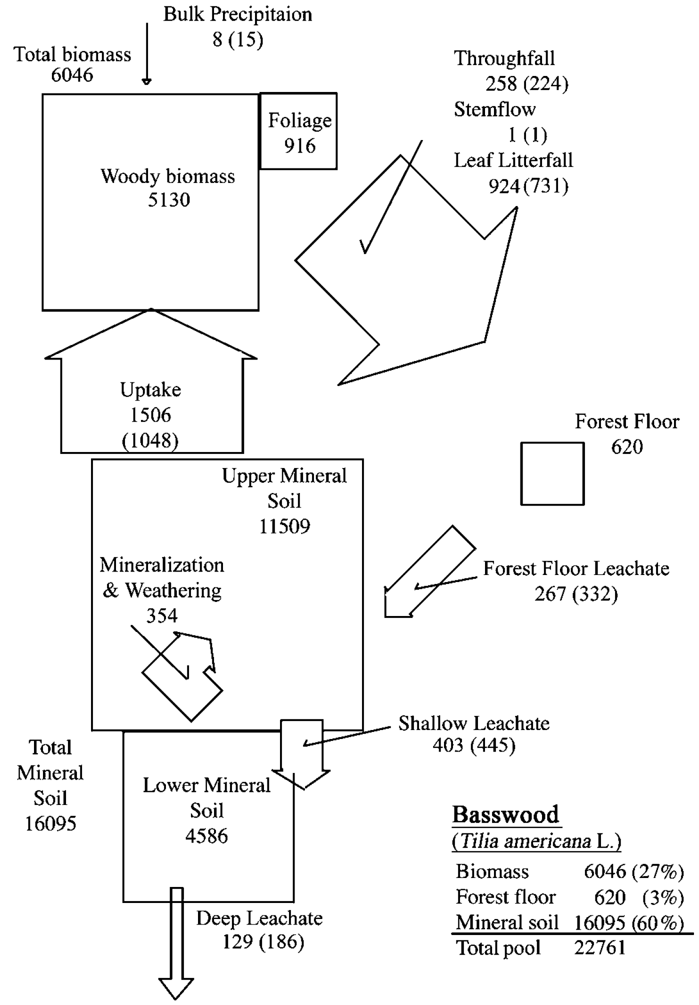

Figure 2. Base-cation distribution and cycling in basswood averaged for the years 2000 and 2001 growing seasons, Sylvania Wilderness, Upper Michigan (Note: the width of the arrows indicates the flux in mmol m^{-2} growing $season^{-1}$ and the size of the boxes indicates the pools in mmol m^{-2}).

Discussion

In this study, individual tree species had a profound influence on the distribution and cycling of base cations, supporting our first hypothesis. These findings are important with regards to the structure and functioning of northern hardwood-hemlock ecosystems in the upper Great Lakes region and suggest that species-mediated differences may be important controls over the spatial pattern and edaphic processes of northern hardwood-hemlock forests within this region.

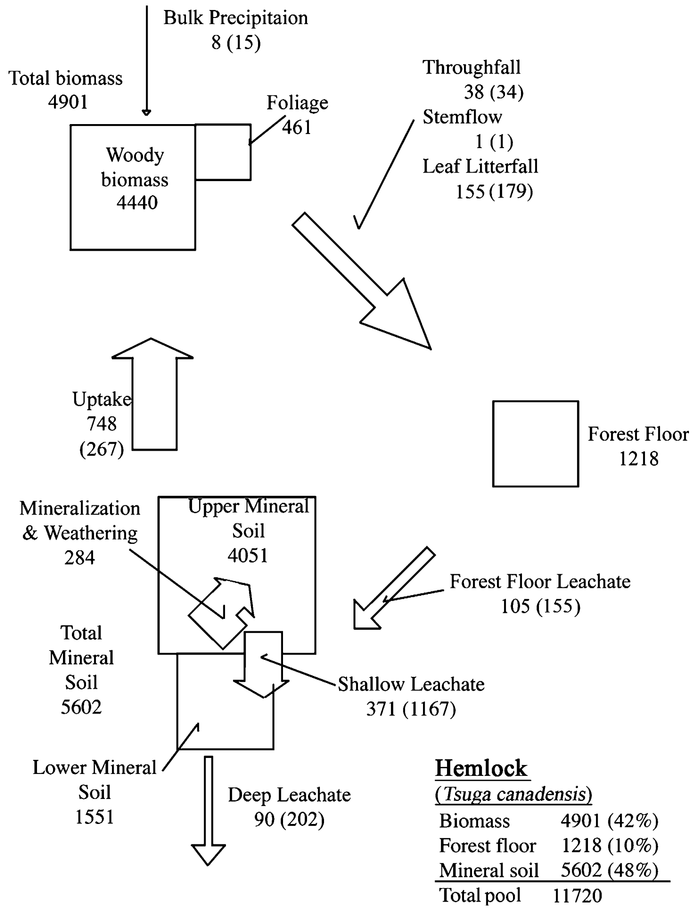

Figure 3. Base-cation distribution and cycling in hemlock averaged for the years 2000 and 2001 growing seasons, Sylvania Wilderness, Upper Michigan (Note: the width of the arrows indicates the flux in mmol m^{-2} growing $season^{-1}$ and the size of the boxes indicates the pools in mmol m^{-2}).

Individual tree species and the pattern of northern hardwood ecosystems

Contents of base cations in both foliage and woody biomass were ranked: sugar maple > basswood > hemlock. These findings are consistent with other studies that recognize basswood as a base-accumulator (i.e., ‘lime tree’) in forests (Piggott 1989; Côté and Fyles 1994; Neirynck et al. 2000). The low content of base cations in hemlock biomass is likewise consistent with studies comparing base-cation levels of this species with northern hardwood species (Young and Guinn 1967; Bockheim 1997).

Base-cation contents in the forest floor were ranked: hemlock > sugar maple, basswood (Table 2; Figures 1–3), primarily because the mass of the forest floor was greatest beneath hemlock. However, concentrations of base cations in the forest floor were greater for sugar maple and basswood relative to hemlock. These trends reflect differences in base-cation contents in leaf litterfall among the three species. Similar findings were reported for several northern hardwood species and hemlock in the SWRA (Ferrari 1999), Québec (Pelletier et al. 1999), and northwestern Connecticut (Finzi et al. 1998a). Litter decomposition of hemlock is much slower than sugar maple because of its lower litter quality (Elliott et al. 1993). The high base-cation leaching beneath hemlock may be explained by the significantly lower uptake of these cations (Table 3), which enables them to be leached beyond the effective rooting zone. The difference implies that hemlock has a slower rate of turnover of base cations than sugar maple and basswood.

The amounts of base cations in the mineral soil (0–15 cm and 15–40 cm) were significantly greater for basswood than for sugar maple and hemlock (Table 2; Figures 1–3), despite the similar morphology and taxon of soils beneath the various species (Bockheim 1997; Bockheim and Jordan 2004). Enrichment of base cations in soils under basswood may be attributed to greater canopy exchange and mineralization + weathering (Table 3). Although the differences were not significantly different, hemlock contained the least amount of base cations in the soil. Hemlock contributed lower amounts of bases in canopy exchange, and a larger proportion of these bases were retained in the forest floor than for sugar maple and basswood. Other studies also report fewer amounts of base cations in soils beneath hemlock than beneath northern hardwood species (Piggott 1989; Côté and Fyles 1994; Bockheim 1997; van Breemen et al. 1997; Finzi et al. 1998b; Nierynck et al. 2000).

These findings suggest a pattern of soil nutrients within northern hardwood-hemlock ecosystems in the SWRA. There are two likely explanations for this patterning: either local differences in the soil parent materials control the distribution of individual tree species (van Breemen 1995), or the trees themselves are able to initiate and maintain differences in soil fertility (Miles 1985; Phillips and Marion 2004). Support for the first explanation was obtained in northern hardwood stands of northwestern Connecticut. The distribution of canopy trees within these stands was attributed to subtle variations in the supply of mineral nutrients, in particular the plagioclase content of the parent material, which controlled the Ca weathering rate (van Breemen et al. 1997; Dijkstra et al. 2003).

Numerous studies have documented the control of individual tree species on soil properties both within plantations (Challinor 1968; Alban 1982) and by individual trees in mixed stands (Boettcher and Kalisz 1990; Finzi et al. 1998a, b; Boucher and Côté 2002; Dijkstra and Smits 2002; Dijkstra 2003). We likewise found significant species-related differences in transfer of base cations in canopy exchange and litterfall and transformation of base cations from mineralization + weathering (Table 3; Figures 1–3). Although we can not be certain that small-scale differences in base-cation content of the parent materials existed, it seems highly improbable that the distribution of individual trees species within a small (1 ha) area is dependent on this presumption.

We used data in Tables 2 and 3 and Eq. (4) to estimate the length of time for individual tree nutrient fluxes to produce differences in base-cation content of the soils beneath them. These calculations suggest that the species-related differences in base cations in the soil could occur in < 65 years. This finding is consistent with reported changes in base cations in soils of plantations (Challinor 1968; Alban 1982) and supports our second hypothesis that significant differences in single-tree ecosystems can occur within one lifespan of the species measured here. It is possible the individual tree species investigated in this study have occupied the same microsite for several generations, as has been suggested by Phillips and Marion (2004). For example, a base-poor soil such as that found beneath hemlock would not favor establishment by base-demanding species such as basswood and sugar maple. Phillips and Marion (2004) used this phenomenon, described as 'self-reinforcing pedologic influences of trees', to explain patterns of soil variability in the Ouachita Mountains, Arkansas. Although we cannot rule out the existence of a 'pedogenic memory' (Phillips and Marion 2004), our results suggest that the small-scale differences in soil fertility may be initiated by individual tree species in a short period of time.

Individual trees and sustainability of northern hardwood ecosystems

Input-output balances from bulk precipitation and leaching at the bottom of the rooting zone have been used to gauge the health of terrestrial ecosystems (Likens and Bormann 1995). In our study, the loss of base cations from the soil leachate at the base of the rooting zone exceeds inputs from atmospheric deposition for all three species (Table 3; Figures 1–3). A similar phenomenon was observed in northern hardwood ecosystems of north central (Foster et al. 1992; Bockheim and Crowley 2002) and northeastern US (Likens and Bormann 1995; Dijkstra and Smits 2002). However, this may not always have been the case in the upper Great Lakes region. Pastor and Bockheim (1984) reported a net gain in base cations (20 $\text{mmol}_c\ \text{m}^{-2}\ \text{year}^{-1}$) of a comparable ecosystem in the early 1980s. Timber harvesting accompanied by close utilization (e.g., removal of branches) could have a significant and negative effect on the long-term sustainability of these ecosystems by the removal of a large portion of the base cations from the biomass (Hix and Barnes 1984).

Conclusions

The relative pool sizes of base cations differed among the three species examined within a northern hardwood – hemlock ecosystem in the upper Great Lakes region. The majority of base cations for sugar maple were found in its biomass, the majority for basswood was in the mineral soil, and the majority for hemlock was in the forest floor (with the smallest base-cation pools in the biomass and mineral soils). Total base-cation contents in the single-tree systems were significantly greater beneath basswood and sugar maple relative to hemlock.

The species-related differences in base cations of the mineral soil can be explained by differences in the base-cation fluxes, such as canopy exchange and mineralization + weathering. The differences in base-cation fluxes among individual tree species during a growing season were small, but large enough to produce significant differences in the base cations amounts in the mineral soil within a single generation (ca. <65 years). The species-related differences in base-cation cycling may increase the heterogeneity of these soils. Because basswood concentrates base cations, especially calcium, in the mineral soil, basswood may be important in maintaining the long-term sustainability of northern hardwood – hemlock ecosystems.

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