The influence of basswood (*Tilia americana*) and soil chemistry on soil nitrate concentrations in a northern hardwood forest

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Abstract: In the Arbutus Lake Watershed in the Adirondack Mountains, New York, two nearly adjacent catchments (14 and 15) varied significantly in volume-weighted stream water nitrate (NO_3) export (54 and 17 μequiv.·L^{-1}, respectively; $P < 0.001$). The most notable differences between the catchments were that Catchment 14 had significantly higher soil Ca concentrations and patches of basswood (*Tilia americana* L.). We evaluated the possible contributions of basswood and soil Ca concentrations to soil water NO_3 concentrations. Among the major overstory tree species, basswood leaf litter had the lowest C:N ratios, highest Ca concentrations, and among the lowest lignin:N ratios. Basswood basal area was significantly related to soil water NO_3 concentrations ($R = 0.46$, $P = 0.01$). Forest floor and mineral soil Ca concentrations were positively correlated with basswood basal area and negatively correlated with American beech (*Fagus grandifolia* Ehrh.) basal area. Our results suggest that a relatively low-density, calciphilic species such as basswood may create, given the proper soil conditions, hotspots with elevated soil water NO_3 concentrations. These hotspots result from the convergence of high soil Ca concentrations, due mostly to soil geology, with relatively labile litter substrate available for N mineralization and nitrification.

Résumé : Dans le bassin du lac Arbutus situé dans les monts Adirondacks, dans l'État de New York, aux États-Unis, deux bassins adjacents (14 et 15) étaient significativement différents en ce qui concerne l'exportation de nitrate (NO_3) pondérée par le volume d'eau dans les cours d'eau (respectivement 54 et 17 μequiv.·L^{-1}; $P < 0,001$). Les différences les plus notables entre les deux bassins venaient du fait que le sol dans le bassin 14 avait une concentration en Ca significativement plus grande et supportait des bouquets de tilleul d'Amérique (*Tilia americana* L.). Nous avons évalué les contributions possibles du tilleul et de la concentration de Ca dans le sol sur la concentration de NO_3 dans l'eau du sol. Parmi les principales espèces formant le couvert dominant, la litière de tilleul était caractérisée par le plus faible rapport C:N, la plus forte concentration en Ca et parmi les plus faibles rapports lignine:N. La surface terrière du tilleul était significativement corrélée à la concentration de NO_3 dans l'eau du sol ($R = 0,46$, $P = 0,01$). Les concentrations de Ca dans la litière et le sol minéral étaient positivement corrélées à la surface terrière du tilleul et négativement corrélées à la surface terrière du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.). Nos résultats indiquent qu'à une densité relativement faible, les espèces calciphiles, comme le tilleul d'Amérique, peuvent provoquer localement la présence de fortes concentrations de NO_3 dans l'eau du sol si les conditions du sol sont propices. Ces concentrations localisées sont causées par la convergence de fortes concentrations de Ca dans le sol, dues surtout à la géologie du sol, et d'un substrat de litière relativement labile disponible pour la minéralisation et la nitrification de N.

[Traduit par la Rédaction]

Introduction

Long-term trends of acidic deposition and base cation depletion have been raising concerns about the health of forest ecosystems through much of North America and Europe (Jandl et al. 2004; Bailey et al. 2005; Watmough et al. 2005). As mobile acid anions such as nitrate (NO_3) and sulfate (SO_4) are leached from the soil with a charge-equivalent loss of base cations (Currie et al. 1999), the potential for acidification of terrestrial and aquatic ecosystems increases as base cations become depleted and are replaced by acidic cations including monomeric Al (Driscoll et al. 2003). Some of the possible consequences of acidification include the declining productivity of sugar maple (*Acer saccharum* Marsh.) and red spruce (*Picea rubens* Sarg.) (Lawrence et al. 1997; Bailey et al. 2004), the decline of biotic diversity in freshwater ecosystems (Likens et al. 1996; Vitousek et al. 1997), and the slow recovery of acidified lakes and streams (Driscoll et al. 2003).

In addition to acidic deposition, the availability of inorganic N in a watershed for vegetation uptake or potential export is also influenced by the quality and quantity of the organic substrate available for mineralization (Melillo et al. 1982; McClaugherty et al. 1985; Scott and Binkley 1997). Previous research has shown that the quality of litter substrate, and consequently the mineralization rates, can vary with species (Lovett et al. 2002; Mitchell et al. 2003) and soil fertility indices including base cation concentrations (Finzi et al. 1998*a*; Likens et al. 1998; Sariyildiz and Anderson 2003).

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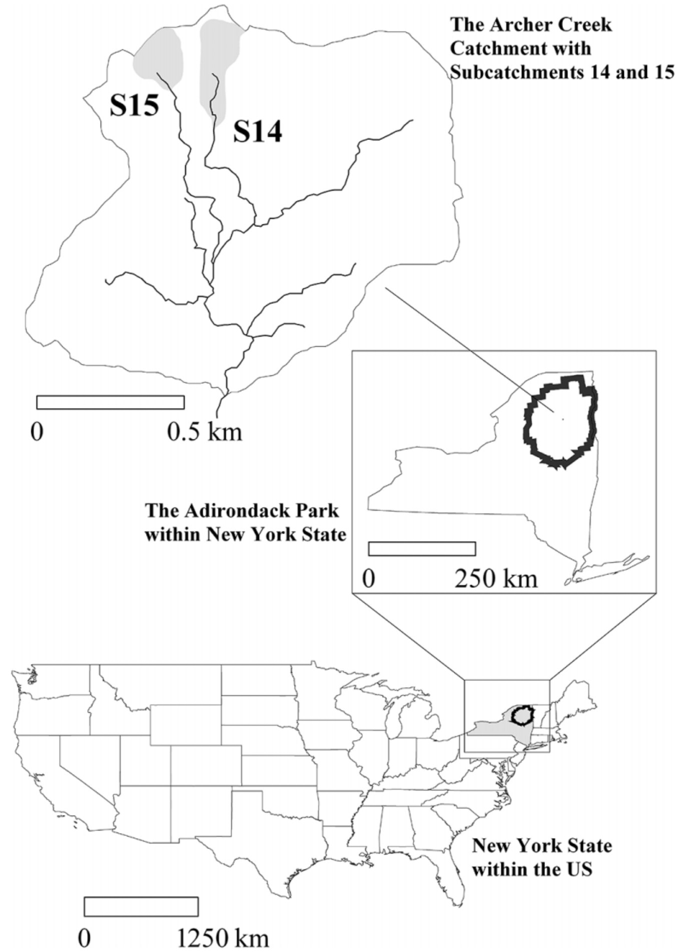
Studies that compared N mineralization rates among sites in New York and Ontario (Mitchell et al. 1992) and within the northeastern United States (Lovett and Rueth 1999) found that soil NO_3 and potential nitrification rates were higher in stands dominated by sugar maple as compared with those with a higher proportion of American beech (*Fagus grandifolia* Ehrh.). The differences among these groups are often attributed to the relatively higher lignin and phenolic content in trees from the Fagaceae (beech) family (Pastor and Post 1986; Finzi et al. 1998*b*). Scott and Binkley (1997) reported that lignin:N ratios were more important than other litter quality or quantity variables for explaining differences in N mineralization rates.

Because microorganisms are ultimately responsible for much of the mineralization of organic matter and release of organically bound N, variables that affect their metabolic rates such as temperature, moisture, and pH collectively have great influence on the availability and potential leaching of N (Meentemeyer 1978; Preston et al. 2000; Bohlen et al. 2001). Elevated concentrations of base cations including Ca and Mg have been shown to be positively correlated with decomposition and nitrification rates (Wolters and Joergensen 1991; Ohrui et al. 1999). Fujinuma et al. (2005) indicated that individual tree species can have variable effects on the distribution of base cations in forested ecosystems. For example, they reported that basswood (*Tilia americana* L.) tended to accumulate base cations resulting in elevated Ca concentrations in the upper 40 cm of the soil profile.

Our objectives were to evaluate the influences of basswood and soil Ca concentrations on concentrations of NO_3 in soil solution and to compare litter chemistry and decomposition rates among the dominant hardwood species in two nearly adjacent catchments.

Fig. 1. Map of Catchments 14 and 15 within the Archer Creek Catchment of the Arbutus Lake Watershed in the Central Adirondack Mountains, New York.



Methods

Site description

The Arbutus Lake Watershed (43°59′N, 74°14′W) is located in the Huntington Wildlife Forest in the central Adirondack Mountains, New York, and is within the Hudson River drainage (Fig. 1). Elevation ranges from 513 to 748 m within the watershed and mean annual temperature and total annual precipitation were 4.8 °C and 1080 mm, respectively, from 1981 to 2000 (Park et al. 2003). The Adirondack Mountains are part of the Grenville Province with bedrock composed primarily of granitic gneisses and metasedimentary rock. The Huntington Wildlife Forest and Arbutus Lake Watershed are within the Anorthosite Massif, a large igneous intrusion composed of up to 90% Ca-rich feldspar. The surficial geology is dominated by glacial till (Driscoll et al. 1991). The soils in Catchments 14 and 15 in the Arbutus Lake Watershed are Becket–Mundal associations (coarse-loamy, mixed, frigid, typic Haplorthods). Both catchments have similar elevation, aspect, and slope, with Catchment 14 having greater surface area compared with Catchment 15 (3.5 and 2.5 ha, respectively). Both catchments have a single surface water stream that flows throughout the year in the lowest third of each catchment. A detailed comparison of the hydrology of these two catchments is presented in Christopher et al. (2008).

Sampling

Stream water

Grab samples of stream water were collected on 39 occasions in each month throughout the year from May 2003 to October 2004 with the exceptions of December 2003, February 2004, and August 2004 when samples were not collected. At each collection period, the stage height of the stream was recorded and used to calculate flow to determine discharge-weighted stream concentrations. Samples were kept refrigerated at 4 °C until analysis.

Vegetation and soil

Vegetation surveys were conducted during summer 2002. Each catchment was divided into a grid of 20 m × 20 m plots with six horizontal 20 m transects (two lower, two middle, and two upper slope) randomly selected for vegetation sampling accounting for approximately 34% and 37% of the area of Catchments 14 and 15, respectively. Within these transects, the species and diameter at 1.4 m above the ground (diameter at breast height) were recorded for every tree ≥5 cm in diameter.

The forest floor (Oe (F) / Oa (H)) and upper mineral soil (0–10 cm) were sampled in approximately 20% of the plots in Catchments 14 and 15 (16 and 13 plots, respectively) during October 2002 and May, July, September, and November 2003. The forest floor was sampled by removing the Oi (L) horizon and cutting a small square approximately 20 cm × 20 cm into the Oe (F) / Oa (H) horizon with a knife. The upper mineral soil was sampled using a “bulb planter corer” under the location of the forest floor sample. From each horizon, the collected sample was homogenized by hand and sealed in a polyethylene bag. All collected samples were kept refrigerated at 4 °C until further analysis.

Total elemental Ca concentrations from the Bs horizon (15 and 50 cm) and C horizon in Catchments 14 and 15 were determined previously using microwave digestion (Christopher et al. 2006). Samples were collected from two replicate plots in the upper half of each catchment. Each plot contained three pits in which the Bs horizon (15 and 50 cm) and C horizon were sampled for a total of 18 samples per catchment. Differences in Ca concentration by horizon between catchments were determined using ANOVA and Tukey’s means separation test (SAS Institute Inc. 1999).

Leaf litter

Leaf litter was collected from ten 2 m × 2 m nets suspended approximately 2 m above the ground in each catchment during autumn 2003. Samples from five nets in the upper half and five nets in the lower half of each catchment were pooled separately, yielding two aggregate collections per catchment. Litter decomposition rates were assessed using a transplant experiment for sugar maple, American beech, and white ash (*Fraxinus americana* L.) litter between Catchments 14 and 15. Basswood litter decomposition was also evaluated but incubated only in Catchment 14 because basswood was not present in Catchment 15.

Soil water

Two porous ceramic-cup tension lysimeters constructed of 5 cm diameter polyvinyl chloride were installed in October 2003 at 45° angles to vertical depths of 15 and 50 cm in each of the same plots where soil sampling was conducted. Samples were collected approximately once per month from March to October 2004 by evacuating lysimeters to –50 kPa and leaving under vacuum for 6–24 h. Samples were kept refrigerated at 4 °C prior to analysis.

Analysis

Stream water

NO_3, chloride, and SO_4 concentrations were determined using a Dionex DX-120® ion chromatograph. Determinations of Ca, Si, Na, K, Mg, and total Al were made using a Perkin-Elmer Optima DV 3300® inductively coupled plasma optical emission spectrophotometer (ICP-OES). Ammonium (NH_4) and dissolved organic N concentrations were determined using continuous-flow colorimetry on a Bran-Luebbe AutoAnalyzer3®. Dissolved organic C concentrations were determined through persulfate oxidation using a Tekmar Phoenix 8000® carbon analyzer. Water pH was determined potentiometrically.

Stage height was related to flow by developing regression equations based on data for the same streams presented in Christopher (2004). For Catchment 14, eq. 1 was used to calculate stream discharge:

$$[1] \quad \log Q = 11.5(\log S) + 3.84 \; (R^2 = 0.94, P < 0.001)$$

and eq. 2 was used for Catchment 15:

$$[2] \quad \log Q = 5.08(\log S) + 0.84 \; (R^2 = 0.86, P = 0.001)$$

where Q is discharge ($m^3 \cdot s^{-1}$) and S is stage height (m). Discharge-weighted stream chemistry means were then compared using ANOVA (SAS Institute Inc. 1999).

Vegetation and soil

Statistical comparisons of species basal areas between catchments were conducted using ANOVA (SAS Institute Inc. 1999). Fresh soils were homogenized and sieved to 6.4 mm to remove coarse fragments. Soil moisture was determined gravimetrically by oven-drying subsamples at 65 °C until mass remained constant. Soil pH for both horizons was determined potentiometrically in a 2:1 slurry of 0.01 $mol \cdot L^{-1}$ $CaCl_2$ – fresh sample.

Organic matter and soil Ca concentrations were analyzed using the October 2002 samples. Forest floor samples were oven-dried at 65 °C and ground in a Wiley Mill® using a No. 20 (0.85 mm) screen. Total Ca and percent organic matter were determined by ashing 1 g of homogenized sample at 470 °C for 16 h and dissolving the ash in 10 mL of 6 molar HCl. The acid solution was then evaporated to dryness on a hot plate and then the residual was re-dissolved in 10 mL of 6 $mol \cdot L^{-1}$ HCl. The solution was filtered through Whatman 42® ashless filter paper, rinsed three times with deionized, distilled water (ddH_2O), and raised to 100 mL with ddH_2O. Calcium concentrations were determined with a Perkin-Elmer Optima DV 3300® ICP-OES.

Upper mineral soil samples were air-dried and sieved to 2 mm to remove larger fragments. Exchangeable Ca was isolated by extracting approximately 15 g of dry soil in 50 mL of 2 $mol \cdot L^{-1}$ ammonium acetate, filtering through Whatman 42® ashless filter paper, rinsing three times, and raising the volume to 100 mL with ddH_2O. Samples were frozen until analyzed for Ca concentrations using a Perkin-Elmer Optima DV 3300® ICP-OES. Percent organic matter was calculated as loss-on-ignition at 470 °C for 16 h.

Pearson correlations were determined between forest floor and mineral soil Ca and lysimeter NO_3 concentrations with tree species basal areas. An ANOVA procedure was used to determine differences in Ca and organic matter values between catchments. Repeated-measures ANOVA was used for pH and soil moisture.

Leaf litter

After collection, leaves were air-dried, sorted by species, and subsamples ground in a Wiley Mill® using a No. 20 (0.85 mm) screen. Calcium concentrations were determined as detailed above for forest floor samples. Percent C and N were determined on a Thermo Electron Flash EA 1112® elemental analyzer. Percent lignin was determined by the Dairy One Forage Laboratory in Ithaca, New York, using an ANKOM A200® fiber analyzer. Comparisons of litter chemistry means among species and between samples were conducted using ANOVA and Tukey’s means separation test (SAS Institute Inc. 1999).

For the litter decomposition experiment, approximately 1.5–2.5 g of air-dried whole-leaf litter tissue was placed

Table 1. Volume-weighted stream water chemistry means (SD in parentheses) from Catchments 14 and 15 collected May 2003 to October 2004.

Variable	Catchment 14	Catchment 15	*F*	*P*
Ca^{2+} (μequiv.·L^{-1})	820 (97)	312 (67)	253	<0.001
Si (μmol·L^{-1})	457 (97)	159 (19)	125	<0.001
NO_3^- (μequiv.·L^{-1})	54 (13)	17 (3)	103	<0.001
Na^+ (μequiv.·L^{-1})	33 (5)	59 (11)	70	<0.001
pH (units)	7.4 (0.2)	6.9 (0.2)	33	<0.001
Total Al (μmol·L^{-1})	0.58 (0.51)	1.36 (0.46)	18	<0.001
Cl^- (μequiv.·L^{-1})	11.8 (3.2)	12.9 (2.0)	1.2	0.287
K^+ (μequiv.·L^{-1})	4.3 (4.4)	5.6 (1.9)	0.95	0.332
Dissolved organic C (μmol·L^{-1})	150 (56)	136 (25)	0.65	0.424
Dissolved organic N (μmol·L^{-1})	12.6 (15.9)	9.8 (6.9)	0.36	0.552
Mg^{2+} (μequiv.·L^{-1})	73 (5.7)	75 (16)	0.29	0.591
NH_4^+ (μequiv.·L^{-1})	1.3 (1.3)	1.4 (0.8)	0.10	0.758
SO_4^{2-} (μequiv.·L^{-1})	173 (29)	171 (21)	0.06	0.815

Note: *P* values from ANOVA with Tukey's means separation tests.

into 2 mm mesh, 15 cm × 15 cm fiberglass screen bags. From both catchments, 90 bags of litter were prepared for each of three species, sugar maple, American beech, and white ash, and 45 bags of basswood from Catchment 14. Three plots were selected in both catchments as the location for litter incubations based on similar forest floor moisture and canopy cover conditions. Each plot contained three incubation sets for three collection periods. Each incubation set consisted of 30 bags: five bags of sugar maple, American beech, and white ash litter native to that catchment and five bags of transplanted litter from each species. Each incubation set in Catchment 14 also contained five bags of basswood litter. Litter bags were distributed within the recent litterfall layer on 18 and 19 November 2003 with collection dates of 20 July 2004, 20 May 2005, and 20 August 2005. Upon collection, the litter bags were oven-dried at 65 °C and the mass recorded for comparison with each initial mass and to calculate the percentage of mass loss. A regression procedure using stepwise selection was conducted to identify which litter chemistry variables most significantly accounted for mass loss trends using mean data from the litter origin site. Mass loss was presented as the natural log (ln) of percentage of initial mass loss per day.

Soil water

Soil water was analyzed for pH, Ca, NO_3, and NH_4 concentrations using the same methods described previously for stream water samples.

Multivariate

Six variables were included in a principal components analysis (PCA) to evaluate the interactions of soil Ca concentrations, tree species, and soil NO_3 availability at the plot level. The variables used in the analysis were mean NO_3 concentrations from 50 cm lysimeters, forest floor Ca concentrations, and basal areas of sugar maple, American beech, white ash, and basswood. The PCA was conducted using Proc Factor in program SAS (SAS Institute Inc. 1999).

Results

Stream water

Volume-weighted stream chemistry means (Table 1) indicate that both Ca and NO_3 concentrations were approximately 2.5 times greater in stream water from Catchment 14 than in that from Catchment 15. Dissolved Si concentrations and pH were also significantly greater in stream water from Catchment 14. Total Al concentrations were approximately 2.5 times greater in the stream water in Catchment 15. Differences in stream water dissolved organic C, SO_4, and Mg concentrations were not significant between these two catchments. Discharge ranged from 0.10 to 6.43 L·s^{-1} (mean = 1.2 L·s^{-1}) for Catchment 14 and ranged from 0.01 to 1.13 L·s^{-1} (mean = 0.21 L·s^{-1}) for Catchment 15 during the sampling period.

Vegetation

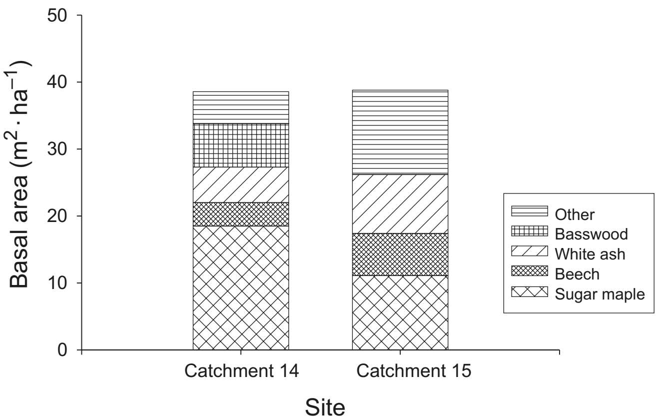
Vegetation sampling indicated almost identical total basal area in Catchments 14 and 15 (38.6 and 38.9 m^2·ha^{-1}, respectively). The basal area of sugar maple was greater in Catchment 14 relative to Catchment 15 (17.1 and 9.8 m^2·ha^{-1}, respectively, P = 0.01), while Catchment 15 relative to Catchment 14 had greater basal areas of American beech (6.4 and 4.1 m^2·ha^{-1}, respectively; P = 0.15) and white ash (9.2 and 6.3 m^2·ha^{-1}, respectively; P = 0.35) (Fig. 2). Basswood was found only in Catchment 14, generally clustered in the upper half of the catchment.

Litter chemistry and decomposition

Mean litter lignin:N ratios were significantly higher for beech relative to the other tree species, which did not differ significantly (P > 0.05) from each other. There were no significant differences in lignin:N ratios within litter samples for the same species between the catchments. The mean C:N ratio was lowest for basswood litter, highest for sugar maple, and intermediate for American beech and white ash with no significant differences between catchments. Litter Ca concentrations were highest for basswood (29.2 mg·g^{-1}) and similar for other species with means ranging from 8.2 to 19.2 mg Ca·g^{-1}. Mean Ca concentrations were significantly higher for both sugar maple and white ash litter in Catchment 14 relative to Catchment 15 (Table 2).

Although the effects of leaf litter origin and incubation site showed variable trends making within-species interpretation difficult, the mass loss data did clearly indicate that

Fig. 2. Basal area of tree species in Catchments 14 and 15 sampled during summer 2002. Species included as "other" were yellow birch (*Betula alleghaniensis* Britt.), red spruce, eastern white pine (*Pinus strobus* L.), and hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch), the latter found only in Catchment 14.



the greatest separation was among species rather than between catchments (Fig. 3). When analyzing mean daily mass loss among species without regard for catchment or collection period, white ash had significantly greater loss rates than sugar maple ($P < 0.001$) and sugar maple rates were significantly greater than American beech rates ($P < 0.001$). Basswood mass loss rates were intermediate between and not significantly different from white ash or sugar maple ($P = 0.15$ and 0.26, respectively). Regression analysis indicated that initial lignin:N ratios accounted for 86% of the variability in mass loss rates among species (Fig. 4):

$$[3] \quad \ln \% \text{ mass loss} \cdot \text{day}^{-1} = -1.54 - (0.05 \times \text{initial lignin : N ratio}) \quad (R^2 = 0.86, P = 0.003)$$

Soil

Soil chemistry means indicate significant differences between catchments in Ca concentrations and pH in the forest floor and upper mineral soil (Table 3) and elemental Ca concentrations in deep mineral soil (Table 4). There was also a larger percentage of organic matter in the forest floor samples of Catchment 14 compared with Catchment 15. Percent moisture values between catchments were not significantly different.

Forest floor Ca concentrations were significantly and positively correlated with sugar maple and basswood basal area and negatively correlated with American beech basal area. Correlations between species basal area and exchangeable Ca in the upper mineral soil followed the same trends but were not as strong as correlations with forest floor Ca (Table 5). Additionally, soil water NO_3 concentrations obtained from 50 cm deep lysimeters were positively correlated with basswood basal area.

Soil water

Soil water collected at both 15 and 50 cm depths had significantly higher concentrations of Ca and NO_3 in Catchment 14 relative to Catchment 15. Soil solution in Catchment 14 also had significantly higher pH than that in Catchment 15. Mean concentrations of NH_4 were higher in Catchment 14, but the differences were not significant at $\alpha = 0.05$ for either depth (Table 6).

Multivariate

The first two factors in the PCA accounted for 59% of the variability of the six considered variables. The factor pattens for the original variables and the first two factors are presented in Table 7. Variables with factor values furthest from zero are the most influential for their respective factors. The results indicate that those areas within the two catchments with the highest NO_3 concentrations (obtained from the lysimeters at 50 cm soil depth) generally had higher forest floor Ca, higher basswood and sugar maple basal areas, and lower American beech basal area (Fig. 5).

Discussion

Christopher et al. (2006) had previously identified substantial differences in stream water NO_3 and Ca concentrations in Catchments 14 and 15 of the Arbutus Lake Watershed. In addition to NO_3 and Ca, dissolved Si concentrations in stream water were also significantly greater in Catchment 14 (Table 1). Because atmospheric inputs of Si are generally minimal, the elevated concentrations of dissolved Si in Stream 14 may indicate more rapid mineral weathering in Catchment 14 (White and Blum 1995; Schlesinger 1997) or possible differences in groundwater contribution to stream flow (Scanlon et al. 2001; Rodgers et al. 2004). Increased weathering rates coupled with relatively Ca-rich minerals could account for the higher concentrations and greater availability of Ca in Catchment 14.

While the total tree basal areas of both catchments were nearly identical, the presence of basswood and greater basal area of sugar maple in Catchment 14 resulted in more labile litter (lower lignin:N ratios) than in Catchment 15 where American beech was more abundant. Low lignin:N ratios have been shown to be correlated with increased mineralization rates (Scott and Binkley 1997; Finzi and Canham 1998). In addition to its relatively high litter decomposition rate, basswood may also have had a significant role in maintaining elevated forest floor pH because it is a base-demanding species (Fujinuma et al. 2005) and its litter had higher Ca concentrations relative to the other species (Table 2). The large flux of Ca through basswood leaf litter to the forest floor may have further promoted high nitrification rates by helping to maintain a favorable pH for nitrifying bacteria (Haynes 1986). Vestin et al. (2006) also found a positive correlation between soil Ca and NO_3, suggesting that elevated Ca concentrations in alkaline soils promoted nitrification through higher pH values relative to less alkaline soils. Vestin et al. (2006) further suggested a cyclic pattern whereby increased nitrification and associated proton production leads to greater Ca dissolution, maintaining higher pH favorable for nitrifiers. Positive correlations between basswood basal area and Ca concentrations in the forest floor and upper mineral soil suggest a possible link between basswood and moderate soil pH (Table 5).

In addition to buffering pH, Ca also appears to have important physical and metabolic functions in bacterial cells

Table 2. Litter chemistry means (SD in parentheses).

Species	Catchment	Lignin:N	C:N	Ca ($mg \cdot g^{-1}$)
Sugar maple	14	15.8 (1.9)b	52.9 (1.1)a	16.6 (2.0)*b
	15	16.1 (1.5)	50.4 (0.5)	8.6 (1.2)*
American beech	14	23.7 (6.7)a	44.5 (6.1)b	10.8 (1.4)b
	15	22.2 (1.5)	41.8 (1.8)	8.2 (0.8)
White ash	14	13.0 (1.4)b	43.2 (0.7)b	19.2 (3.0)*b
	15	11.7 (0.7)	44.3 (3.4)	9.2 (0.4)*
Basswood	14	9.9 (3.3)b	23.1 (1.4)c	29.2 (1.2)a
	15	na	na	na

Note: Different letters indicate significant differences (α = 0.05) among species when averaged between catchments. An asterisk indicates a significant difference within a species, between catchments at α = 0.05. na, not applicable.

Fig. 3. Mean cumulative mass loss as a proportion of initial mass from the leaf litter transplant experiment. Litter was collected and incubations begun during autumn 2003 in Catchments 14 and 15.

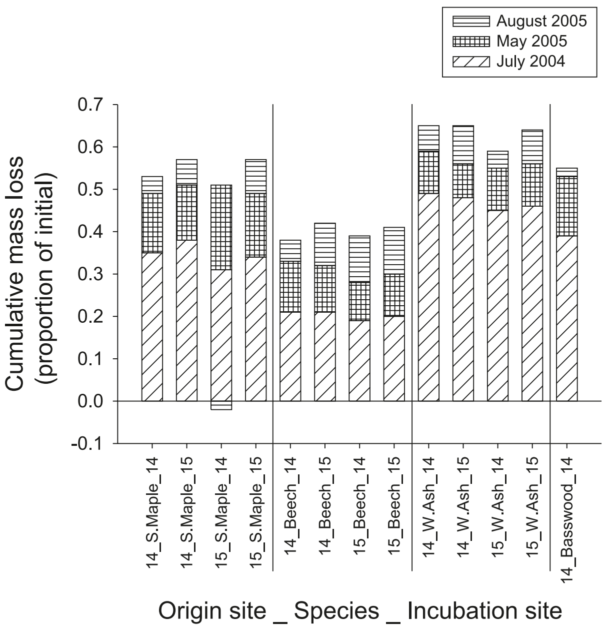
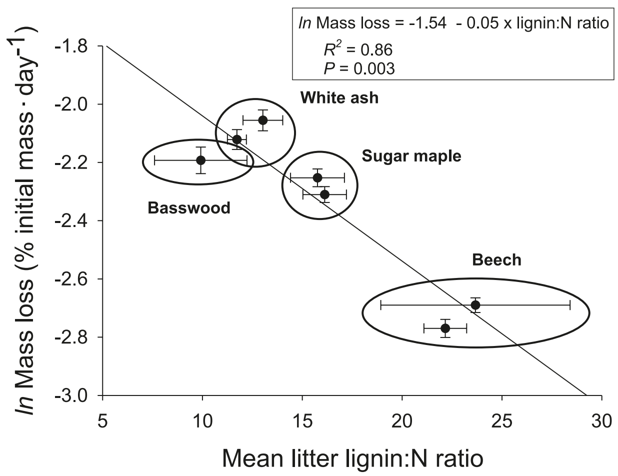


Fig. 4. Regression equation of mean mass loss per incubation day (November 2003 to August 2005) against initial lignin:N ratios from leaf litter transplant experiment in Catchments 14 and 15. Solid circles indicate litter origin = Catchment 14 and open circles indicate litter origin = Catchment 15. Error bars are 1 SE.



(Norris et al. 1991; Dominguez 2004). Norris and Jensen (1957) indicated that Ca is important for the growth of *Azotobacter*, an important group of N-fixing bacteria. Williard et al. (2005) suggested that low Ca concentrations could limit the growth of *Nitrosomonas* and *Nitrobacter* either directly through mechanisms detailed by Norris et al. (1991) or indirectly if reduced *Azotobacter* growth resulted in decreased availability of N for mineralization and nitrification. Although we do not have direct measurements on the microbial communities within these catchments, “acid-tolerant” nitrifiers (e.g., *Nitrosospira*), which may be more prevalent in forest soils (Robertson and Groffman 2007), could have similar physiological requirements for Ca. In a study of stone biodeterioration, Mansch and Bock (1998) reported that nitrifying bacteria showed a preference for calcareous materials. This apparent preference may be related jointly to pH as well as elemental Ca availability.

The presence of basswood in Catchment 14 and its absence in Catchment 15 together reflect the greater soil Ca availability in Catchment 14. Contributions of basswood litter with its relatively low C:N and lignin:N ratios result in more rapid C and N turnover. Conversely, American beech trees, with more recalcitrant litter, had basal areas that were highly negatively correlated with soil Ca concentrations. American beech litter had relatively high lignin:N ratios and had the lowest mass loss rates of any of the major tree species in these catchments. Working in the Appalachian Mountains, Williard et al. (2005) found that site geology ranging from Ca-rich limestone to a more base-poor sandstone could account for up to 49% of the variation in stream NO_3 concentrations. In agreement with our study, they suggested an indirect link whereby geology influenced soil fertility, which subsequently influenced tree species composition and N cycling rates.

The litter transplant experiment between catchments indicated that there was relatively little difference in decomposition rates with regard to litter origin or incubation site but greater differences with respect to litter species. This result was somewhat surprising. We expected that leaf litter of each species from Catchment 14 would have lower lignin:N ratios relative to the same species from Catchment 15 due to the elevated soil solution NO_3 concentrations in Catchment 14. Therefore, we predicted that leaf litter originating from Catchment 14 would decompose more quickly than litter of

Table 3. Soil chemistry means (SD in parentheses) for forest floor and upper mineral soil (0–10 cm) samples from Catchments 14 and 15.

Variable	Catchment 14	Catchment 15	*F*	*P*
Forest floor				
Ca ($mg \cdot g^{-1}$)	15.2 (6.2)	3.37 (1.5)	45.3	<0.001
pH	5.17 (0.62)	4.06 (0.32)	46.7	<0.001
Organic matter (%)	64.5 (17.7)	46.6 (20.8)	6.52	0.016
Moisture (%)	68.7 (7.7)	67.6 (8.9)	0.22	0.642
Mineral soil (0–10 cm)				
Ca ($mg \cdot g^{-1}$)	2.22 (1.5)	0.32 (0.23)	21.7	<0.001
pH	4.46 (0.64)	3.71 (0.33)	15.9	0.001
Organic matter (%)	25.4 (17.1)	21.1 (14.6)	0.50	0.488
Moisture (%)	45.7 (12.2)	42.5 (10.2)	1.53	0.227

Note: Calcium and organic matter determined by total digestion of October 2002 samples. Percent moisture and pH means from all five sample periods. *P* values from ANOVA (repeated measures for moisture and pH) with Tukey's means separation tests.

Table 4. Mean elemental Ca ($mg \cdot g^{-1}$) (SD in parentheses) for Bs and C horizons in Catchments 14 and 15 (modified from Christopher et al. 2006).

Soil horizon	Catchment 14	Catchment 15	*F*	*P*
Bs horizon (15 cm)	52.3 (24.9)	16.9 (1.8)	12.09	0.006
Bs horizon (50 cm)	54.6 (16.3)	23.1 (3.2)	21.62	0.001
C horizon (~80 cm)	53.7 (19.0)	28.7 (2.3)	10.19	0.010

Note: *P* values from ANOVA with Tukey's means separation tests.

Table 5. Pearson's correlation coefficients (with *P* value) comparing tree species basal area with forest floor total Ca concentrations, mineral soil exchangeable Ca, and mean soil water NO_3 concentrations from 15 and 50 cm deep lysimeters at the plot level from Catchments 14 and 15.

	Sugar maple basal area	American beech basal area	White ash basal area	Basswood basal area
Forest floor Ca	0.38 (0.04)	–0.47 (0.01)	–0.04 (0.85)	0.52 (<0.01)
Mineral soil Ca	0.16 (0.43)	–0.41 (0.03)	–0.01 (0.97)	0.36 (0.06)
Lysimeter NO_3, 15 cm	0.14 (0.46)	–0.12 (0.55)	0.16 (0.40)	0.18 (0.34)
Lysimeter NO_3, 50 cm	0.35 (0.07)	–0.27 (0.16)	0.01 (0.94)	0.46 (0.01)

Table 6. Mean soil solution chemistry from lysimeters at 15 and 50 cm depth in Catchments 14 and 15 sampled from March to October 2004.

Variable	Catchment 14	Catchment 15	*F*	*P*
15 cm depth				
Ca^{2+} ($\mu equiv. \cdot L^{-1}$)	420	161	84	<0.001
pH	6.0	5.4	29	<0.001
NO_3^- ($\mu equiv. \cdot L^{-1}$)	252	128	11	0.003
NH_4^+ ($\mu equiv. \cdot L^{-1}$)	6.4	1.8	3.7	0.066
50 cm depth				
Ca^{2+} ($\mu equiv. \cdot L^{-1}$)	257	124	57	<0.001
pH	6.3	5.8	63	<0.001
NO_3^- ($\mu equiv. \cdot L^{-1}$)	44	29	6.6	0.016
NH_4^+ ($\mu equiv. \cdot L^{-1}$)	13	3.2	0.48	0.496

Note: Statistics calculated from mixed-model repeated ANOVA.

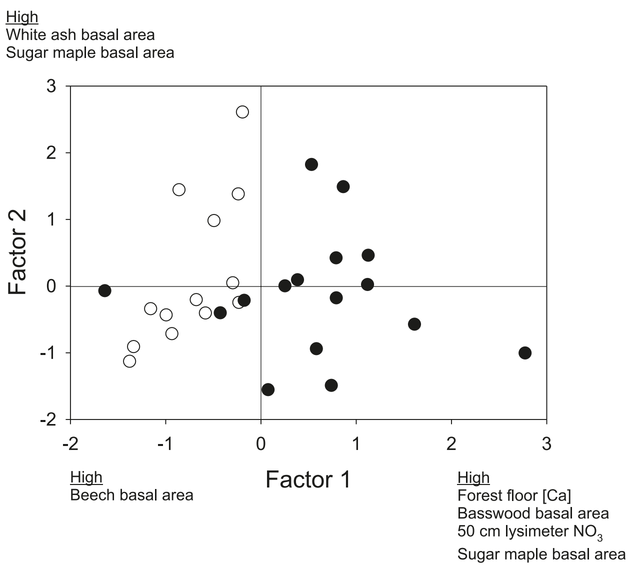
the same species that originated from Catchment 15. Additionally, we expected that edaphic conditions and microbial communities may have differed between catchments such that litter would decompose more rapidly in one catchment relative to the other. The results, however, showed no consistent trends in decomposition rates with litter origin or incubation sites, but instead a substantial species influence with American beech having the lowest mass loss rate of the species studied. The absence of a substantial site effect may have also been due to the relatively small amount of litter placed within the bags compared with the surrounding forest floor, and hence, the influence of the litter bag con-

Table 7. Factor pattern from PCA of data from Catchments 14 and 15.

Variable	Factor 1	Factor 2
Lysimeter NO_3 , 50 cm	0.64873	0.02216
Forest floor Ca	0.77301	–0.06883
Sugar maple basal area	0.53820	0.50499
American beech basal area	–0.69975	–0.07149
White ash basal area	0.02912	0.86107
Basswood basal area	0.75762	–0.40662

Note: Variables with factor values furthest from zero are the most influential for their respective factors.

Fig. 5. PCA. The factor pattern for this analysis is presented in Table 7. Solid circles indicate Catchment 14 and open circles indicate Catchment 15.



tents may have been dampened by surrounding chemical conditions. We did not analyze the chemistry of the postincubation litter samples, which may have indicated greater differences among species and between catchments than change in mass alone.

The litter chemistry results showed that common litter quality indices such as lignin:N ratios and C:N ratios differed more among species than between catchments. Among the litter chemistry variables, initial lignin:N ratios accounted for most of the differences in mass loss rates among tree species (Fig. 4). The relatively high lignin:N ratio of American beech litter coupled with its higher basal area may partly account for reduced N export in stream water from Catchment 15. Melillo et al. (1982) indicated that litter with relatively high initial lignin content resulted in greater N immobilization per unit C respired and potentially increased formation of humus with additional capacity for N retention. A link between increased American beech dominance in a stand and reduced N transformation rates has been described previously (Mitchell et al. 1992; Lovett and Rueth 1999).

Results from the PCA show a multivariate correlation where plots with elevated soil solution NO_3 tended also to have higher forest floor Ca concentrations and higher basswood basal area. Plots with lower Ca concentrations generally had greater American beech basal area and lower soil solution NO_3. While several studies have shown a positive correlation between pH and nitrification rates (Ste-Marie and Paré 1999; Venterea et al. 2003) and soil pH and Ca concentrations are generally highly correlated, we suggest that soil Ca concentrations can further influence the availability of soil NO_3 through affecting vegetation species composition and possibly as a requirement in the metabolism of nitrifying bacteria.

Our results suggest that basswood, as a base-demanding species (Fujinuma et al. 2005), likely promotes nitrification through its flux of Ca-rich, labile litter to the forest floor. The influence of basswood may be most notable when it occurs in fairly localized regions, thereby forming "hotspots." McClain et al. (2003) suggested that biogeochemical hotspots occur where there is a confluence of "complementary or missing reactants" that result in reaction rates that are disproportionately high relative to the surrounding area. Our results support the suggestion of Christopher et al. (2006) that soil Ca concentrations can play a substantial role in N mineralization through influencing the vegetation species composition and the associated litter quality. Page and Mitchell (2008) presented additional data showing a relationship between concentrations of soil Ca and inorganic N across 11 hardwood-dominated stands in the Adirondack Mountains.

Recently, two other studies also examined site variables associated with substantial differences in NO_3 export between two adjacent or nearly adjacent forested catchments. In the Fernow Experimental Forest in the Appalachian Mountains, Christ et al. (2002) attributed elevated NO_3 export to increased net nitrification potential associated with relatively high base cations and acid-neutralizing capacity, low C:N ratios, and high water-holding capacity. Schiff et al. (2002) concluded that steep slopes and relatively high water conductivity in the Harp Lake Watershed, Ontario, were the primary drivers behind an order of magnitude increase in stream NO_3 export between catchments. In the two catchments considered in this study, Christopher et al. (2008) indicated that streams from both catchments had similar relative contributions from soil and groundwater, although there were temporal variations in NO_3 concentrations from their respective sources.

Conclusions

Two nearly adjacent forested catchments with similar elevation, aspect, topography, and site history had stream water NO_3 and Ca export that differed by a factor of ≥ 2.5. The most marked differences between the two catchments were the presence of basswood clusters and higher mineral soil Ca concentrations in the upper half of Catchment 14, the catchment with the greater NO_3 and Ca export. Analysis of leaf litter chemistry showed that basswood had the lowest C:N ratio, highest Ca concentration, and among the lowest lignin:N ratios. Although soil water Ca, NO_3, and pH varied significantly between the two catchments, differences in leaf litter chemistry and decomposition rates were greater among species than between catchments. In correlation and PCA, basswood was highly associated with elevated soil Ca and soil water NO_3 concentrations. We suggest that the relatively Ca-rich geology of Catchment 14 enabled the establishment of basswood, a calciphilic species, which created hotspots of soil NO_3 through the production of leaf litter that was both relatively labile and high in Ca, providing for a highly mineralizable substrate at a favorable pH. Such conditions would be highly conducive for nitrification. Additional experimental work is required to identify the mechanistic links between calciphilic species such as basswood and N biogeochemistry.

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