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Relationships among forest age, composition and elemental dynamics of Adirondack northern hardwood forests[1]

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McGee, G. G., M. J. Mitchell, D. J. Leopold and D. J. Raynal (SUNY, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210-2778) and M. Mbila (Alabama A&M University, School of Agricultural and Environmental Sciences, Normal, AL, 35762-0700). Relationships among forest age, composition and elemental dynamics of Adirondack northern hardwood forests. J. Torrey Bot. Soc. 134: 253–268. 2007.—We conducted a biogeochemical analysis of four Adirondack northern hardwood forests (two old-growth and two maturing second-growth) to elucidate correlations among stand age, site conditions and several nutrient cycling processes. One each of the old-growth and maturing forests were located on base-rich sites, while the other two were on base-poor sites. At each site we analyzed soil solution chemistry and estimated nutrient flux rates; measured annual litter production, and nutrient and lignin content; measured annual N mineralization and nitrification rates; and characterized herb- and canopy-layer vegetation, and coarse woody debris volumes. Vascular plant communities of the two base-rich sites were dominated by several rich-site indicator species, while such indicators were lacking at the base-poor sites. Tree basal areas and annual litter production did not differ among the study sites, but the old-growth stands contained 3-fold more coarse woody debris than the maturing stands. Foliar litter N concentrations did not differ among the study sites, but foliar litter from the base-rich sites had higher Ca^{2+} and lower lignin concentrations than the base-poor sites. Differences in foliar litter quality among the sites were due, in part, to intraspecific variation in litter chemistry. There were no consistent differences between the old-growth and maturing stands in soil solution nutrient concentrations or fluxes. Soil solution H^+ concentrations were higher and Ca:Al ratios lower at the two base-poor sites. Annual, net N mineralization rates did not differ among the sites, but net nitrification rates in the organic soil horizons at the rich old-growth site were more than twice those at the other sites. High levels of net nitrification and N leaching were observed only in the base-rich old-growth site. Our data suggest that net forest nutrient retention may be a function of interacting mechanisms associated with forest developmental stage, community composition and site conditions.

Key words: lignin, litter quality, nitrification, nitrogen, nutrient cycling, old-growth, stand development.

A complete understanding of temporal and spatial patterns of nutrient cycling in forest ecosystems requires consideration of forest maturation and site conditions. Some investigators have suggested that old-growth forests should exhibit zero net nutrient retention, while younger, aggrading forests should have a greater capability to retain nutrients, especially nitrogen (N) (e.g., Vitousek and Reiners 1975). When forest primary productivity is N-limited, net nitrification and nitrate (NO_3^-) leaching rates from forests should be low because either (1) plants out-compete nitrifying bacteria for ammonium (NH_4^+) thereby leading to lower gross nitrification rates; or (2) gross nitrification rates are equally high under N-limited conditions, but microbial assimilation of NO_3^- reduces net nitrification rates and NO_3^- leaching losses (Fenn et al. 1998). Several studies have corroborated that nutrient retention decreases as forests mature (Vitousek and Reiners 1975, Leak and Martin 1975, Peet 1992, Pardo et al. 1995, Perakis and Hedin 2001), while others have not (e.g., Martin 1979, Fisk et al. 2002). In particular, recent research has suggested that greater detrital biomass pools (primarily due to greater amounts of coarse woody debris) in

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old-growth forests result in greater microbial N immobilization compared to second-growth forests (Fisk et al. 2002). Furthermore, declines in surface water NO_3^- concentrations have recently been observed in the northeast U.S. (Goodale et al. 2003) including watersheds composed mostly of old-growth forests (Martin et al. 2000), thereby further confusing the relationships between forest development and nutrient retention.

Factors other than forest age/development also affect forest N retention. For instance, low forest floor C:N ratios (< 25) have been correlated with increased NO_3^- leaching rates (Johnson and Linberg 1992, Fenn et al. 1998). Litter decomposition and N turnover rates are further affected by foliar litter "quality" (the decomposability of carbon compounds). Litter high in lignin decomposes slowly thereby limiting mineralization rates (Aber and Melillo 1982, Ferrari 1999). Nitrification rates, and subsequent NO_3^- leaching potential, also appear to be affected by soil pH, base saturation and/or calcium (Ca) availability (Geary and Driscoll 1996, Bailey et al. 2004). In addition, nutrient cycling processes are influenced by forest overstory composition (e.g., Finzi et al. 1998a). For instance, Lovett and Rueth (1999) and Lovett et al. (2000, 2004) reported greater N leaching and nitrification rates from *Acer saccharum* Marsh. dominated forests, relative to forests dominated by *Fagus grandifolia* Ehrh. The presence of *A. saccharum* likely plays a key role in affecting nutrient cycling in hardwood forests of the northeast U.S. (Templer et al. 2003, Lovett and Mitchell 2004) and southeast Canada (Mitchell et al. 1992a). Mechanisms leading to greater nitrification and NO_3^- leaching rates in *A. saccharum*-dominated forests may be related to differences in litter quality, thereby suggesting that plant species can influence nutrient cycling processes (Finzi et al. 1998a). Conversely, some observed differences in nutrient cycling processes may covary with site requirements among species. *Fagus grandifolia* often dominates dry mesic, base-poor sites, while *Fraxinus americana* L., *Tilia americana* L., and *A. saccharum* dominate base-rich, mesic sites (Heimburger 1934, Burns and Honkala 1990, Kobe et al. 1995, Bakken and Cook 1998). Therefore, where rich-site indicator species dominate, site conditions happen to permit greater nitrification rates, leading to higher NO_3^- leaching rates.

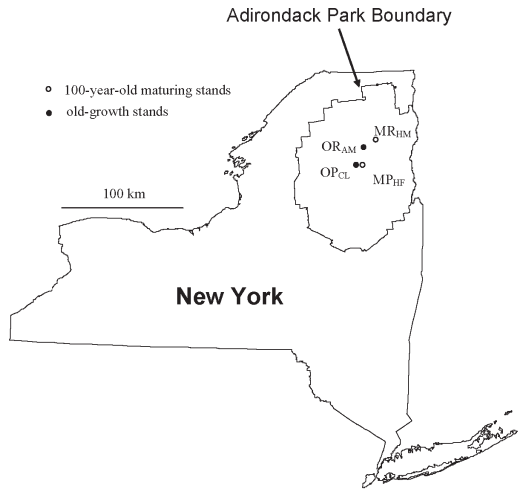

FIG. 1. Location of the four northern hardwood forest study sites in Adirondack Park, New York: Ampersand Mountain (OR_{AM}), Hennessy Mountain (MR_{HM}), Catlin Lake (OP_{CL}), and Huntington Forest (MP_{HF}). Subscripts are explained in Methods: Research Setting and Study Sites.

Thus vegetation alone may not control the nutrient cycling processes, but rather microbially mediated nutrient fluxes along with vascular plant species composition are correlated with site conditions.

The objective of our study was to examine the relationships between forest age, species composition, site conditions and nutrient retention with particular focus on N. Our study focused on (1) whether old-growth northern hardwood forests exhibit greater nitrification and nutrient leaching rates than younger, aggrading forests and (2) whether forests on base-rich sites exhibit greater nitrification and nutrient leaching rates than those on more acidic sites.

Methods. RESEARCH SETTING AND STUDY SITES. We conducted our study in northern hardwood forests in the Adirondack Mountains, New York, USA (Fig. 1). Forests within Adirondack Park are a mosaic of stands of varying maturity and anthropogenic disturbance. But as a whole, forests of this region are advancing in age since the Park's establishment in the 1890's. Rates of atmospheric NO_3^- and NH_4^+ deposition to this region are among the highest in North America (Stoddard 1994, National Atmospheric Deposition Program/National Trends Network 2005), and high NO_3^- leaching rates and surface water

NO_3^- concentrations in some watersheds suggest that forests here are becoming N-saturated (Stoddard 1994, Mitchell et al. 2003).

The study sites are characterized as Adirondack northern hardwood forests (Braun 1950), which occur below 980 m and are generally dominated by *A. saccharum, F. grandifolia*, and *Betula alleghaniensis* Britton. Common canopy associates include *Picea rubens* Sarg., *Tsuga canadensis* (L.) Carr., *Acer rubrum* (L.), *F. americana*, *T. americana*, and *Prunus serotina* Ehrh. Understory trees and shrubs include *Acer pensylvanicum* (L.), *Ostrya virginiana* (Mill.) Koch, and *Viburnum lantanoides* Michx. (nomenclature follows Mitchell and Tucker 1997).

The Adirondack climate is humid and continental. Weather stations in Tupper Lake (elevation 966 m), Lake Placid (591 m) and Indian Lake (506 m), which bound the limits of the study sites, have recorded mean January temperatures of -9 to -10 °C and mean July temperatures of 17 to 18 °C for periods spanning 1897–1996 (Hoare 2005). Average annual precipitation during approximately the same time period at the three weather stations ranged from 96–103 cm (Hoare 2005). The soils at the sites are spodosols that developed from glacial till overlaying Precambrian granite (Cline and Marshall 1992).

Two of the four study sites, Ampersand Mountain and Catlin Lake, have previously been described as old-growth forests (Woods and Cogbill 1994, McGee et al. 1999), having an uneven-aged canopy with dominant trees averaging 198 and 209 years, respectively (McGee 1998). The Catlin Lake site was never logged (SUNY-ESF Huntington Forest Wildlife Research Station records), but it is likely that the Ampersand Mt. site was selectively logged $\sim$ 1850–1890 for large-diameter *P. rubens, T. canadensis*, and/or *Pinus strobus* L. prior to its incorporation into Adirondack Park (McMartin 1994). The other two sites, Hennessy Mt. and the Huntington Forest Integrated Forest Study site, are maturing, 100-year-old, second-growth forests that regenerated following catastrophic wildfires during the early 1900s and have not been logged since their establishment (McGee 1998, SUNY-ESF Huntington Forest Wildlife Research Station records). Increment core data confirmed that the oldest trees of the post-disturbance cohorts at Hennessy and Huntington were 97 and 95 years, respectively, in 1999 (McGee 1998 for Hennessy, McGee unpublished data for Huntington).

All four study sites have been extensively researched (e.g., Johnson and Lindberg 1992, Mitchell et al. 1992b, Woods and Cogbill 1994, McGee et al. 1999) and were selected from a set of previously studied Adirondack old-growth and maturing forest stands (McGee et al. 1999) based upon their stand histories and site conditions. We considered the Ampersand Mt. old-growth and Hennessy Mt. maturing stands to be base-rich, mesic sites given their topographic positions (mid- to lower slopes), and the presence/abundance of species indicative of rich, moist site conditions (following Heimburger 1934). In addition to Heimburger's forest type indicator species, we included *Acer saccharum* as a base-rich site indicator. Although *A. saccharum* occurs across a range of soil textures pH and fertility, it is sensitive to decline on soils having low base saturation (Horsley et al. 2002), has demonstrated more vigorous positive growth response to experimental liming (Long et al. 1997), and dominates regeneration in mesic/rich habitat types (Kobe et al. 1995, Bakken and Cook 1998). Conversely, the absence of indicator species and the positions of stands at mid and upper slopes led us to consider the Catlin Lake old-growth and Huntington Forest maturing forests to be less mesic and base poor. Hereafter, we refer to the Ampersand Mt., Catlin Lake, Hennessy Mt., and Huntington Forest sites as OR_{AM}, OP_{CL}, MR_{HM}, and MP_{HF}, respectively. The abbreviations reference each stand's age (old growth versus maturing) and site conditions (base rich versus base poor).

Soil Solution Sampling. Soil solution samples were collected from porous cup tension lysimeters placed below the forest floor (15 cm deep) and below the maximum rooting depth (50 cm deep). Similar tension lysimeters have been used extensively to study relationships between soil solution and elemental cycling in forest ecosystems (Shepard et al. 1990, Mitchell et al. 2001a). Twelve lysimeter clusters were installed at each site during summer, 1999. Each cluster consisted of two pairs of 15 cm and 50 cm lysimeters. The two lysimeters in each pair were placed 30–40 cm apart. The pairs within each cluster were $\sim$ 1–2 m from each other. The lysimeters

were installed at a 45° angle to minimize preferential flow of surface water to the lysimeter porous cup (Mitchell et al. 2001a). Soil solution was collected from the lysimeters after setting the vacuum overnight at 40 kPa. At this tension both interstitial soil solution that is available to plants via transpiration (Brady and Weil 2002: 208–210) and gravitational water were sampled. Lysimeters were sampled monthly between May and November, 2000. Soil solution samples were bulked by depth for each lysimeter cluster.

All samples were transported on ice and stored at 4 °C prior to analyses. Samples were analyzed for NO_3^-, Cl^- and SO_4^{2-} (detection limit 0.2 μeq L^{-1}) on a Dionex 2000 ion chromatograph and for NH_4^+ (detection limit 0.003 μeq L^{-1}) on a Bran Luebbe AA3 auto analyzer. Total dissolved nitrogen (TDN) was determined on a Bran Luebbe AA3 auto analyzer after persulfate oxidation (Ameel et al. 1993), and dissolved organic nitrogen (DON) was calculated as the TDN (total dissolved nitrogen) – (NO_3^- + NH_4^+). Soil solution pH was determined potentiometrically. Exchangeable cations were analyzed using a Perkin Elmer 3300 DV ICP-AES. Many samples were analyzed in duplicate to monitor precision. Certified solutions were included in each run for quality control.

SOIL NUTRIENT FLUX ESTIMATION. Solution flux rates were estimated by combining the monthly solution concentrations obtained from tension lysimeters with monthly water flux estimates using the BROOK90 simulation model (Federer 1995). We have successfully used the BROOK2 and BROOK90 models to estimate water fluxes in several Adirondack watersheds and forest stands (Mitchell et al. 1996, 2001b). For this study water flux was estimated using inputs of daily precipitation and minimum and maximum temperatures. For OP_{CL} and MP_{HF} weather data were used from Newcomb, NY, which is 1 and 4 km, respectively, from these sites. For OR_{AMP} and MR_{HM} weather data were used from the Saranac Lake, NY weather station, which is 12 and 6 km, respectively, from each of these sites. Monthly soil water fluxes at 15 and 50 cm were multiplied by concentrations to obtain monthly solute fluxes. Monthly fluxes were summed over the soil solution sampling period (May–November, 2000) to estimate total nutrient fluxes.

VEGETATION AND WOODY DEBRIS SAMPLING. Trees (≥5 cm diameter at breast height, dbh) were inventoried at each site on two randomly-placed 0.1 ha quadrats. Understory vegetation (> 1 m tall; < 5.0 cm dbh) was sampled in four 25 m^2 subplots located within each 0.1 ha quadrat. Stems were identified and their diameters measured at breast height (1.4 m), or in the case of understory stems 1.0–1.4 m tall, at the base of the current year's growth. Relative Importance Values (RIV) were calculated at each site for trees and for understory vegetation where:

$$\text{RIV} = [\text{relative density}] + [\text{relative basal area}]/2.$$

Percent cover of each herb layer species (herbaceous and woody stems ≤ 1.0 m tall) was estimated on twenty-five 1 m^2 plots placed randomly in each of the 0.1 ha quadrats. In addition, the entire 0.1 ha quadrats were surveyed to list all vascular plant species present on the quadrats but not included in the sample. Tree species were characterized based upon their tolerance for understory competition (Burns and Honkala 1990). Tree, shrub, and herbaceous species were characterized as "base-rich" site indicators, "acid" site indicators, or non-indicators (Heimburger 1933, Burns and Honkala 1990, Kobe et al. 1995, Bakken and Cook 1998).

Decaying logs ≥ 10 cm diameter were measured on each 0.1 ha plot. The OR_{AM}, MR_{HM}, and OP_{CL} sites were sampled during an earlier study (McGee et al. 1999) and the MP_{HF} site was sampled in 1999. Total log volumes were estimated for each site as per McGee et al. (1999).

LEAF LITTER SAMPLING AND NUTRIENT ANALYSES. Litter was collected monthly during snow-free periods (October 1998–August 2000) using twenty randomly-placed 0.25 m^2 litter traps. Litter collections were dried at 65 °C to a constant mass. The litter was sorted into deciduous hardwood leaves, twigs (< 1 cm diameter) and other material. During the first year's collection only (October 1998–September 1999) deciduous hardwood leaves were further sorted by species. After dry mass was determined for each litter component from each litter trap, like litter material was composited for each site for chemical analyses. A subsample of the composited litter was

ground in a Wiley® mill to pass a 2 mm screen prior to microwave digestion for mineral nutrient determination, and further pulverized in a Wiggle-L-Bug® amalgamator prior to total C and N analyses. Carbon and N concentrations were determined using a Perkin-Elmer 2400 CHN Analyzer. Leaf litter cation concentrations were determined using ICP spectroscopy following microwave digestion of 0.25 g tissue sample in 1 ml 37% HCl and 4 ml 70% HNO_3. Leaf litter lignin concentrations were determined through acid-detergent digestion using a Daisy II Incubator system (Ankom Technology 2002). Nutrient and lignin concentrations were determined for individual hardwood species for the first year's collection, and on bulked hardwood leaf litter for the second year's collection.

Nitrogen Mineralization and Nitrification Determinations. Net N mineralization and nitrification rates were estimated for the forest floor (Oe + Oa horizons) and upper 10 cm of mineral soil at each study site using in situ incubations in buried polyethylene bags (Nadelhoffer et al. 1983). Eight 25 m transects were constructed at each site. One set of buried bags was incubated at a random location along each transect during each incubation period. Soil bags were incubated at seven monthly intervals from May–November 2000, with a final incubation conducted over the winter until May 2001. Incubations were prepared by removing a 10×10 cm area of forest floor and placing it in a bag, which was folded closed, but not sealed. Similarly, a sample of the underlying mineral soil was removed and placed in a bag. The bag with mineral soil was then returned to the hole, the bag containing the forest floor placed on top, and both were covered with leaf litter. Adjacent to these bags similarly sized samples of forest floor and mineral soil were removed, placed in bags, stored on ice, and taken directly to the laboratory for immediate analyses. Samples were retrieved for analyses following each incubation. At the time the samples were retrieved, new incubations were initiated. Net mineralization rates (g^{-1} soil dry mass) were calculated by finding the difference between initial and final $NH_4^+ + NO_3^-$ concentrations of each incubation. Net nitrification rates (g^{-1} soil dry mass) were calculated by finding the differences between initial and final NO_3^- concentrations for each incubation.

Statistical Design and Analyses. Twelve replicates of bulked soil solution from the 15- and 50-cm lysimeter clusters were obtained during each monthly sampling period at each study site. Monthly soil solution solute concentrations were averaged across the 2000 snow-free season (May–November) for each of the lysimeter clusters. These snow-free season averages were then compared among the four study sites using one-way ANOVA (PROC GLM, SAS Institute 2001). Differences in mean solute concentrations among the four study sites were determined using Tukey's studentized range test to control experiment-wise error rates.

Eight replicate estimates of N mineralization and nitrification were obtained at each study site during each incubation period for the organic and mineral soil horizons. Rates were summed across the entire annual incubation period (May 2000–May 2001) for each of the eight transects at each study site. Annual N mineralization and nitrification rates were then compared among the four study sites using one-way ANOVA (PROC GLM, SAS Institute 2001). Differences in mean annual rates among the four study sites were determined using Tukey's studentized range test to control experiment-wise error rates.

Weighted averages of litter chemistry were determined for each of two sampling periods, Oct. 1998 to Sept. 1999, and Oct. 1999 to Sept. 2000. Weighted averages for the first period were based upon biomass and litter chemistry determinations for leaves of each deciduous hardwood species, twigs, and other miscellaneous litter. Weighted averages for the second sample period were based upon the same categories except leaves from all deciduous species were combined. The two annual weighted averages served as replicate observations of litter quality (%N, %lignin, %C, C:N, lignin:N, base cation concentrations) at each site. Litter chemistries were compared among the sites using one-way ANOVA (PROC GLM, SAS Institute 2001). Differences in mean annual rates of litter elemental and mass fluxes among the four study sites were determined using Tukey's studentized range test to control experiment-wise error rates. Statistical comparisons of litter quality for the respective hardwood species could not be conducted since species-level analyses were conducted only in the first year.

It should be noted that each stand condition, old-base rich, old-base poor, maturing-base rich, and maturing-base poor is represented only once. Therefore conclusions regarding differences in nutrient cycling processes and retention rates due to stand developmental stage and site condition cannot be extended beyond the respective case studies. Even so, these data will help inform a growing understanding of processes regulating forest nutrient retention.

Results. VEGETATION STRUCTURE AND COMPOSITION. Live tree basal areas ranged from 29.8–40.1 m^2 ha^{-1}, but did not differ between the old-growth (35.0 $\pm$ 5.2 m^2 ha^{-1}, average $\pm$ 1 S.E.) and maturing (35.0 $\pm$ 0.1 m^2 ha^{-1}) stands. The old-growth stands contained approximately 58 stems $>$ 55 cm dbh ha^{-1} compared to approximately 10 trees $>$ 55 cm dbh ha^{-1} in the maturing stands. Tree core data indicated that members of the post-fir cohorts in the maturing stands were approximately 30–45 cm dbh. The larger stems in the maturing stands were residuals that survived the stand-initiating fires (McGee 1998 for MR_{HM}, McGee unpublished data for MP_{HF}).

Acer saccharum (RIV range: 0.26–0.50) and *Fagus grandifolia* (RIV range: 0.21–0.61) attained the highest importance values of all tree species at the four sites. *A. saccharum* consistently had the highest basal area, while *F. grandifolia* had the greatest densities. Mid-successional species (i.e., *Acer rubrum, Betula alleghaniensis, Fraxinus americana, Prunus serotina*) were more important in the canopies of the maturing stands (cumulative RIV equaled 0.29 and 0.21 at MR_{HM} and MP_{HF}, respectively) than in the old-growth stands (cumulative RIV equaled 0.03 and 0.09 at OR_{AM} and OP_{CL}, respectively). The woody understories of all sites were dominated by shade-tolerant, late-successional species, but the sites differed in their dominance by understory base-rich site indicator species. The understories of the base-poor sites (OP_{CL} and MP_{HF}) were comprised solely of species tolerant of base-poor conditions (i.e., *Fagus grandifolia, Picea rubens, Viburnum lantanoides*), while base-rich site indicator species (*Acer saccharum, Fraxinus americana, Ostrya virginiana*) attained cumulative importance values of 0.27 and 0.30 at the base-rich sites (OR_{AM} and MR_{HM}).

The herbaceous layer species richness was lower at the base-poor sites (20 and 29 species in OP_{CL} and MP_{HF}) than at the base-rich sites (44 and 35 species in OR_{AM} and MR_{HM}). In addition, the herbaceous layers of the base-poor sites had fewer base-rich site indicator species (1 and 2 species at OP_{CL} and MP_{HF}) compared to the base-rich sites (11 and 5 species at OR_{AM} and MR_{HM}), and lower cumulative percent cover of rich-site indicator species (1 and 3 percent cover at OP_{CL} and MP_{HF}) compared to the base-rich sites (13 and 12 percent cover at OR_{AM} and MR_{HM}).

LITTER PRODUCTION AND NUTRIENT CONTENT. Coarse woody debris volumes were substantially greater at the two old-growth stands (range: 105–119 m^3 ha^{-1}) than at the maturing stands (range: 28–43 m^3 ha^{-1}). The annual, average total foliar litter production ranged from 4.6–5.0 Mg ha^{-1} at the four study sites, and did not differ significantly among sites (Table 1). Likewise, the total input of deciduous hardwood leaf litter did not differ among sites. The composition of the hardwood leaf litter component (determined only for October 1998–September 1999 sample period) was, however, consistent with the basal areas of the respective canopy species. *Acer saccharum* accounted for 73% of the foliage litter at OR_{AM}, but only 41%, 36%, and 31% at MR_{HM}, MP_{HF}, and OP_{CL}, respectively. *Fagus grandifolia* accounted for only 11% of the hardwood foliage litter mass at OR_{AM}, while contributing 26%, 39%, and 62% of the total at MR_{HM}, MP_{HF}, and OP_{CL}, respectively.

Nitrogen concentrations of bulked litter ranged from 1.1–1.2% and did not differ among the four study sites (Table 2). Bulked litter C concentration varied from 49.3–50.5%, but this slight difference was significant between the OR_{AM} and MP_{HF} sites. The resulting C:N ratios ranged from 43.4 to 44.8 and did not differ across the four sites. Litter Ca^{2+} concentrations were highest at the base-rich sites (16.4 and 12.5 mg Ca^{2+} per g dry weight at OR_{AM} and MR_{HM}, respectively) compared to the OP_{CL} and MP_{HF} sites (9.2–9.3 mg Ca^{2+} per g dry wt). The OP_{CL} site had the lowest litter Mg^{2+} concentrations of the four sites. Bulked litter at the base-rich sites had significantly lower lignin contents ($\sim$ 25% lignin at both OR_{AM} and MR_{HM}) than at the base-poor sites ($\sim$ 31% lignin at both OP_{CL}

Table 1. Average annual litter dry weight (Mg ha^{-1}) in four Adirondack northern hardwood forests. Values for bulked hardwood foliage, twigs, and miscellaneous components represent averages from two annual sampling periods: October 1998–September 1999; and October 1999–September 2000. *P*-values are presented for ANOVAs testing differences in mass of respective litter components among stands. Dry weight of individual hardwood species litter was determined only for the 1998–1999 sample, therefore no statistical comparisons were conducted on individual species components. Means with different superscripts are significantly different (Tukey's Studentized Range Test, $P < 0.05$).

	Maturing		Old growth		
	Base-rich (MR_{HM})	Base-poor (MP_{HF})	Base-rich (OR_{AM})	Base-poor (OP_{CL})	P
Hardwood foliage	3.65	3.18	3.16	3.01	0.21
Acer rubrum L.	0.44	0.45	0.00	0.00	
Acer saccharum Marsh.	1.48	1.13	2.30	0.92	
Betula alleghaniensis Britt.	0.17	0.26	0.08	0.21	
Fagus grandifolia Ehrh.	0.93	1.21	0.32	1.84	
Fraxinus americana L.	0.24	0.00	0.02	0.00	
Ostrya virginiana (Mill.) Koch	0.00	0.00	0.08	0.00	
Prunus serotina Ehrh.	0.30	0.04	0.00	0.00	
Tilia americana L.	0.00	0.00	0.02	0.00	
Viburnum lantanoides Michx.	0.00	0.04	0.00	0.02	
Twigs (< 1 cm dia.)	0.44	0.59	0.42	0.57	0.15
Miscellaneous†	0.65^{b}	0.78^{b}	1.37^{a}	1.17^{a}	0.004
Total	4.74	4.55	4.95	4.76	0.77

† Miscellaneous litter includes bark, branches (> 1.0 cm diameter), lichens, moss, conifer needles, bud scales, and flowers.

and MP_{HF}). The lignin:N ratios of bulked litter did not differ among sites.

Inter-species and Inter-site Variation in Litter Quality. *Acer saccharum, Betula alleghaniensis* and *Fagus grandifolia* were the only species occurring at all four study sites, therefore inter-site comparisons of species' litter quality were limited to these three species. Of these species, *B. alleghaniensis* consistently had greater leaf litter lignin (36.7%), N (1.7%), and total cation concentrations (25.6 mg g^{-1} dry weight) than *A. saccharum* and *F. grandifolia* (Table 3). *Acer saccharum* litter displayed the greatest variation in lignin (CV = 0.09) and base cation (CV = 0.12) concentrations across the sites, while *B. alleghaniensis* displayed the greatest variation in N concentrations (CV = 0.09). *Fagus grandifolia* consistently had the least inter-site variation in litter chemistry. Leaf litter produced by all three major tree species consistently contained lower lignin concentrations at the base rich sites (OR_{AM} and MR_{HM}) than at the base poor sites (OP_{CL} and MP_{HF}). Similarly, total cation concentrations in leaf litter of the three tree species were consistently greatest at the rich old-growth site (OR_{AM}). No significant differences were detected across the study sites in leaf litter N concentrations.

Soil Solution Concentrations. *Nitrogen.* Concentrations of TDN in soil solution at OR_{AM} were more than 2-fold greater at 15 cm, and more than 3-fold greater at 50 cm than in the other three study sites

Table 2. Summary of litter characteristics at four Adirondack northern hardwood sites. Values represent means ($n = 2$) of two yearly sample periods at each site. Means were weighted by dry mass of constituent species and types of litter. Significant differences (Tukey's Studentized Range Test $P < 0.05$) in means among sites are denoted with different superscripts.

	Dry mass (Mg ha^{-1})	%C	%N	C:N	%lignin	lignin:N	mg g^{-1} dry weight litter				
							Al	Ca	K	Mg	Na
Old Growth											
Base-rich (OR_{AM})	4.94	49.3^{b}	1.1	44.6	25.1^{b}	24.2	.08	16.4^{a}	2.6	1.3^{a}	0.8
Base-poor (OP_{CL})	4.75	50.4^{ab}	1.2	43.4	30.6^{a}	26.0	.06	9.2^{c}	2.4	0.8^{b}	0.7
Maturing											
Base-rich (MR_{HM})	4.74	49.5^{ab}	1.1	44.8	25.0^{b}	23.8	.06	12.5^{b}	1.7	1.4^{a}	0.7
Base-poor (MP_{HF})	4.55	50.5^{a}	1.1	43.7	30.6^{a}	27.7	.06	9.3^{c}	1.6	1.2^{a}	0.6

Table 3. Summary of intraspecific variation in the leaf litter chemistry of dominant, deciduous broadleaf species among the four Adirondack northern hardwood sites. Base cations include Ca^{2+}, K^+, Mg^{2+}, Na^+. Values are bulked composites of 20 samples collected at each site during Sept.–Oct. 1998. Significant differences ($P < 0.05$, Tukey's Studentized Range Test; blocked by species) in litter chemistry constituents across the study sites are indicated with different letters in columns to the right. Significant differences ($P < 0.05$, Tukey's Studentized Range Test) in litter chemistry constituents between species are indicated with different superscript letters in the second to last row. Species abbreviations are *A.sac = A. saccharum, B.all = B. alleghaniensis*, and *F.gra = F. grandifolia.*

	Lignin percent			N percent			Σ base cations mg g^{-1} dry wt			Tukey test results		
	A.sac	*B.all*	*F.gra*	*A.sac*	*B.all*	*F.gra*	*A.sac*	*B.all*	*F.gra*	lignin	N	Σ cations
Old growth												
Base-rich (OR_{AM})	23.8	33.1	24.4	0.9	1.6	1.1	22.0	27.2	15.0	b	a	a
Base-poor (OP_{CL})	26.5	39.2	28.1	1.0	1.9	1.1	14.5	26.0	14.1	a	a	b
Maturing												
Base-rich (MR_{HM})	20.4	36.2	26.5	1.0	1.3	1.2	18.1	24.3	14.5	b	a	b
Base-poor (MP_{HF})	31.1	38.3	28.8	1.1	1.9	1.1	12.6	24.7	14.1	a	a	b
Mean	25.5^b	36.7^a	27.0^b	1.0^b	1.7^a	1.1^b	16.8^b	25.6^a	14.4^b			
Coefficient of variation	0.09	0.04	0.04	0.4	0.9	0.2	0.12	0.03	0.01			

(Table 4). In general, NH_4^+ contributed little to the TDN in soil solution at these sites. With the exception of OR_{AM}, DON represented the largest N fraction (generally > 50%) in soil solution. At OR_{AM}, NO_3^- was the dominant form of TDN with concentrations twice those of DON at both soil depths. Nitrate concentrations at OR_{AM} (129 μeq L^{-1}) were at least four times greater at 15 cm, and at least 5 times greater at 50 cm than those of the other three sites. There were no consistent relationships between soil solution NO_3^- or DON concentrations and forest stand age. In fact, soil solution NO_3^- and DON concentrations at OP_{CL} did not differ from those in the two maturing stands.

Anions. Total anion concentrations in soil solution were generally greater at 15-cm (ranging from 190–400 μeq L^{-1}) than at 50-cm (150–300 μeq L^{-1}) depths (Table 4). Soil solution at OR_{AM} contained the greatest total anion concentrations of all the study sites, but no consistent relationships existed between soil solution anion concentrations and stand age.

Base cations. In general, the pattern of total cation concentrations at the sites followed the pattern of the total anion concentrations, and charges were reasonably balanced at all sites at both depths (Table 4). Total soil solution base cation concentrations tended to be highest at the two base rich sites (OR_{AM} and MR_{HM}), but these differences were significant only for OR_{AM}. Total base cation concentrations at OR_{AM} were approximately twice those at the other three sites at both soil depths. Base cation concentrations at both 15-cm and 50-cm depths at all four sites were dominated by Ca^{2+} and Mg^{2+}. Concentrations of Ca^{2+}, Mg^{2+}, and Na^+ in soil leachate were all significantly higher at OR_{AM} than at the other three study sites. There were no consistent trends in soil leachate base cation concentrations relative to forest age as concentrations at OP_{CL} were indiscernible from those of the two maturing stands.

Acid cations. Soil solution H^+ concentrations tended to be higher at the two base poor sites (MP_{HF} and OP_{CL}) than at the base rich sites (MR_{HM} and OR_{AM}) (Table 4). While Al^{n+} concentrations were somewhat higher at the 15-cm depths at the two base poor sites compared to the base rich sites, these differences were not significant. Soil solution Ca:Al ratios in surface soils were higher at the base rich sites (4 to 7) than at the base poor sites (1 to 2).

N MINERALIZATION AND NITRIFICATION RATES. Annual net nitrogen mineralization rates ranged from 26–37 μmol N g^{-1} dry wt soil yr^{-1} in the upper mineral soils and from 124–173 μmol N per g^{-1} dry wt yr^{-1} in the organic (Oe + Oa) horizons at the four sites, but did not differ significantly among the sites (Table 5). Likewise, net nitrification rates in the upper mineral soils did not differ among stands, and ranged from 20–26 μmol N g^{-1} dry wt soil yr^{-1}. However, net nitrification rates in the organic horizons at OR_{AM} (55 μmol N g dry wt $soil^{-1}$ yr^{-1}) were more than twice those at the other three sites.

Table 4. Average (1 SE) soil solution ion concentrations at 15-cm and 50-cm depths in four Adirondack northern hardwood forest sites. Significant differences ($\alpha = 0.05$; Tukey's Studentized Range Test; $n = 12$) in means across the sites are denoted with different superscripts.

Site	Na^+	Mg^{2+}	K^+	Ca^{2+}	Al^{n+}	H^+	Cl^-	SO_4^{2-}	NO_3^-	NH_4^+	DON	TDN	DOC	Σ cations	Σ anions‡	Ca:Al
	μeq L^{-1}										μmol L^{-1}			μeq L^{-1}		
15-cm																
Old growth																
Base-rich (OR_{AM})	23[a] (2)	52[a] (5)	15[a] (3)	257[a] (23)	38 (8)	10[b] (2)	20 (5)	79[a] (6)	109[a] (25)	5 (2)	49 (6)	162[a] (28)	1726 (382)	400[a] (29)	362[a] (33)	6.8
Base-poor (OP_{CL})	16[b] (1)	28[b] (3)	12[ab] (2)	95[b] (17)	53 (8)	21[ab] (3)	11 (2)	63[ab] (6)	30[b] (6)	3 (1)	44 (5)	75[b] (10)	1610 (159)	227[b] (21)	204[b] (15)	1.8
Maturing																
Base-rich (MR_{HM})	17[b] (1)	33[b] (3)	7[b] (1)	155[b] (26)	37 (5)	10[b] (2)	15 (2)	66[ab] (6)	20[b] (6)	3 (1)	50 (7)	72[b] (9)	1608 (238)	262[b] (29)	261[b] (28)	4.2
Base-poor (MP_{HF})	16[b] (1)	32[b] (3)	6[b] (2)	80[b] (7)	56 (9)	30[a] (5)	12 (2)	56[b] (4)	28[b] (9)	4 (1)	38 (5)	68[b] (8)	1722 (260)	223[b] (18)	189[b] (9)	1.4
50-cm																
Old growth																
Base-rich (OR_{AM})	32[a] (2)	44[a] (5)	6 (1)	200[a] (18)	11 (2)	4[b] (1)	11 (2)	130[a] (7)	58[a] (19)	3 (1)	29[a] (6)	93[a] (20)	617[a] (87)	299[a] (21)	270[a] (18)	18.2
Base-poor (OP_{CL})	21[b] (1)	20[b] (1)	7 (2)	84[b] (6)	8 (2)	8[a] (2)	8 (1)	118[ab] (2)	11[b] (2)	1 (1)	12[b] (3)	24[b] (4)	236[c] (25)	150[b] (5)	159[b] (3)	10.5
Maturing																
Base-rich (MR_{HM})	28[ab] (1)	20[b] (2)	3 (1)	115[b] (5)	6 (1)	4[b] (1)	8 (1)	111[b] (4)	8[b] (2)	1 (1)	13[b] (2)	21[b] (4)	317[bc] (41)	177[b] (6)	170[b] (5)	19.2
Base-poor (MP_{HF})	24[b] (2)	30[b] (3)	6 (1)	80[b] (6)	11 (2)	5[ab] (1)	9 (1)	85[c] (5)	11[b] (4)	2 (1)	15[b] (2)	28[b] (4)	457[ab] (57)	159[b] (10)	163[b] (11)	7.3

‡ Total anions account for negative charges associated with dissolved organic carbon using parameters and equations of Mitchell et al. (2001b).

Table 5. Average (1 SE) annual net mineralization and nitrification rates (μmol N / g dry wt soil / year) in Oe+Oa and A soil horizons at four Adirondack northern hardwood forest sites. Values with different letters are significantly different (α = 0.05; Tukey's Studentized Range Test).

Site	Net mineralization	Net nitrification
Oe+Oa horizon		
Old growth		
Base-rich (OR_{AM})	124 (14)	55 (5)[a]
Base-poor (OP_{CL})	167 (17)	17 (5)[b]
Maturing		
Base-rich (MR_{HM})	164 (19)	23 (5)[b]
Base-poor (MP_{HF})	173 (15)	29 (8)[b]
A horizon		
Old growth		
Base-rich (OR_{AM})	26 (2)	26 (3)
Base-poor (OP_{CL})	34 (2)	24 (3)
Maturing		
Base-rich (MR_{HM})	33 (4)	20 (3)
Base-poor (MP_{HF})	37 (3)	27 (3)

NUTRIENT LEACHING ESTIMATES. Levels of precipitation differed at the two meteorological stations during the period of our study. The more southern Newcomb station and the northern Saranac Lake station recorded 844 and 597 mm of precipitation from May–November, 2000, respectively. The simulations estimated 436 and 247 mm of soil water flux for the sites near Newcomb (OP_{CL} and MP_{HF}) and Saranac Lake (OR_{AM} and MR_{HM}), respectively. Fluxes of TDN and NO_3^- were greatest at OR_{AM} (Table 6). In general, the flux rates of most other solutes tended to be greater at the two southern study sites (OP_{CL} and MP_{HF}) compared to the two northern sites (OR_{AM} and MR_{HM}) due to the higher water flux estimates. Estimated solute fluxes were not consistently greater in the two old-growth stands compared to the maturing stands.

Discussion. Past research suggests that old-growth forests display lower ecosystem N retention than aggrading and mature forests, due to elevated rates of canopy tree mortality and subsequent reduced phyto-autotrophic N demand (e.g., Vitousek and Reiners 1975, Leak and Martin 1975, Peet 1992, Pardo et al. 1995, Perakis and Hedin 2001). However, others have found that accumulations of recalcitrant woody detritus and/or foliar litter with high C:N and lignin:N ratios lead to greater microbial immobilization of N in woody debris and the forest floor, thereby leading to reduced nitrification rates, and lower NO_3^- leaching rates in old-growth forests (Gower et al. 1996, Fisk et al. 2002). Finally, canopy tree species composition (Finzi et al. 1998a, 1998b, Lovett and Rueth 1999, Lovett et al. 2000, 2004, Lovett and Mitchell 2004) and/or site conditions (Geary and Driscoll 1996, Bailey et al. 2004) have important influences on ecosystem nutrient cycling and retention processes.

None of these factors appeared to be singularly associated with nutrient cycling and retention processes at the four sites in our study. Rather, important interactions likely exist among ecosystem processes that vary in relation to forest development, site condition and species composition. Ours was a case study of four forest stands: two old-growth and two 100-year-old maturing forests that occurred on either base-rich or base-poor sites. It was not logistically feasible to conduct intensive measurements of soil leachate chemistry, litter quality, and N mineralization/nitrification in a manner that would adequately replicate for stand developmental stages and site conditions. Therefore, we opted to intensively study fewer locations that differed substantially in site conditions. Although care must be taken to limit conclusions to only those four sites that were studied, our findings should offer guidance to formulating further research to address interactions of forest development, site conditions and vegetation composition on nutrient cycling and retention processes. Another caveat to consider when interpreting our results is that the precipitation data used to estimate soil solute nutrient fluxes were obtained from weather stations 1–12 km from the study sites. Given the mountainous terrain of the region, this may have led to unquantified variation in our nutrient flux estimates.

FACTORS INFLUENCING NUTRIENT CYCLING AND RETENTION PROCESSES. *Stand Development and Disturbance History.* Although the base-rich old-growth stand (OR_{AM}) had the highest concentrations of total anions, total cations, NO_3^-, DON, and TDN in soil leachate (50 cm), and the highest estimated flux rates of TDN and NO_3^- of the four sites, the other old-growth site (OP_{CL}) had nitrification rates and soil solute concentrations that were indiscernible from the two maturing sites. Therefore, forest successional stage did not

Table 6. Average (1 SE) estimated soil solute flux rates from four Adirondack northern hardwood forest sites during the 7 month study period (May–November, 2000). Values are based upon measured, monthly soil solute concentrations below the rooting zones (50 cm) at twelve sample locations at each site and estimated monthly soil water fluxes (using the BROOK90 simulation model; see Methods for details). Significant differences among sites for each estimated mean solute flux are denoted with different superscripts ($\alpha = 0.05$; Tukey's Studentized Range Test; $n = 12$).

Site	Na^+	Mg^{2+}	K^+	Ca^{2+}	Al^{n+}	H^+	Cl^-	SO_4^{2-}	NO_3^-	NH_4^+	DON	TDN	DOC	Σ cations	Σ anions‡
	μeq ha^{-1}											μmol ha^{-1}		μeq ha^{-1}	
Old growth															
Base-rich (OR_{AM})	68^{b} (7)	91^{ab} (10)	14^{ab} (3)	428 (55)	21^{b} (2)	6^{b} (2)	26^{ab} (4)	272^{b} (22)	139^{a} (49)	3 (1)	56 (12)	187^{a} (40)	1119^{b} (130)	631^{ab} (69)	547^{ab} (58)
Base-poor (OP_{CL})	84^{ab} (5)	75^{bc} (6)	27^{a} (6)	341 (32)	30^{ab} (6)	31^{a} (9)	33^{ab} (3)	455^{a} (14)	55^{ab} (9)	2 (1)	40 (5)	96^{b} (11)	833^{b} (78)	589^{ab} (33)	618^{a} (24)
Maturing															
Base-rich (MR_{HM})	66^{b} (3)	49^{c} (5)	8^{b} (1)	303 (17)	14^{b} (3)	7^{b} (2)	22^{b} (1)	263^{b} (10)	20^{b} (5)	2 (1)	31 (4)	53^{b} (9)	782^{b} (133)	449^{b} (21)	410^{b} (20)
Base-poor (MP_{HF})	94^{a} (10)	122^{a} (16)	24^{a} (4)	381 (35)	44^{a} (8)	16^{a} (3)	36^{a} (3)	326^{b} (23)	45^{ab} (16)	7 (3)	63 (11)	115^{ab} (18)	1776^{a} (251)	689^{a} (60)	638^{a} (55)

‡ Total anions account for negative charges associated with dissolved organic carbon using parameters and equations of Mitchell et al. (2001b).

appear to be the single factor controlling nutrient retention in the four stands we studied.

Land use and disturbance histories can affect soil C:N ratios, thereby resulting in differences in ecosystem N retention. The two maturing stands we studied established following catastrophic wildfire. Therefore, our conclusions regarding the effects of stand development may be confounded by the nature of the stand-replacing disturbances. Some researchers have reported that fire volatizes N, thereby increasing soil C:N ratios and leading to lower mineralization and nitrification rates and greater N retention capacity (Fenn et al. 1998, but see Goodale and Aber 2001). Although it is possible that the two maturing forests had lower nitrification rates and lower nutrient concentrations in soil leachate than OR_{AM} due to the effects of past fires, fire history does not explain the similarities in nutrient cycling processes that the maturing stands had with the other old-growth stand (OP_{CL}).

The two old-growth sites contained volumes of coarse woody debris that were ~ 3-fold higher than in the maturing stands. If the accumulation of recalcitrant carbon in coarse woody debris led to greater heterotrophic immobilization rates (e.g., Fisk et al. 2002) then reduced nitrification and N leaching would be expected in both old-growth stands relative to the two maturing stands. This was not the case since OR_{AM} exhibited the highest nitrification and N leaching rates of all four sites.

Atmospheric Deposition Inputs. Experimental studies have illustrated that chronic N inputs can induce greater nitrification and NO_3^- leaching rates from forest ecosystems (e.g., Magill et al. 2000, Tietema et al. 1998, Kahl et al. 1999). Therefore, it is possible that differences in atmospheric N deposition could have accounted for some of the variation in nitrification rates and N export from these stands. Based upon modeled NO_3^- deposition rates in the Adirondack region (Ito et al. 2002), the range of NO_3^- deposition across our study sites (13.5 to 15 kg NO_3^- ha^{-1} yr^{-1}) does not appear sufficiently broad to induce measurable differences in nitrification and NO_3^- leaching (Magill et al. 2000, Tietema et al. 1998, Kahl et al. 1999).

Site Conditions and Species Composition. The interaction among site conditions (i.e., soil

fertility and moisture), vegetation composition, and N cycling process (particularly nitrification) are complex and interrelated. It has long been known that stand-level forest community composition is regulated by topo-edaphic conditions, and therefore site fertility can often be inferred through species composition (e.g., Heimburger 1934, Finzi et al. 1998b, Bigelow & Canham 2002). Our study sites were chosen to reflect a range of perceived topo-edaphic conditions within northern hardwood stand types. The OR_{AM} and MR_{HM} sites possessed species compositions indicative of Heimburger's (1934) rich "*Arisaema* type" northern hardwoods, which contain higher lime content in the organic soil horizons. The lower H^+ concentrations and higher Ca:Al ratios in soil solution at OR_{AM} and MR_{HM} reflect base-rich site conditions there. The other sites (OP_{CL} and MP_{HF}) were equated to Heimburger's more acidic "*Viburnum* type" northern hardwoods.

It remains unclear how soil fertility and vegetation influence nitrogen cycling processes, and in particular, nitrification and subsequent NO_3^- leaching rates. For instance, observational and experimental studies have demonstrated that nitrification rates are positively correlated with soil pH (Heimburger 1934, Zak et al. 1986, Williard et al. 1997, see also review by Haynes 1986) or phosphorus availability (Pastor et al. 1984). This relationship may reflect physiological ranges of tolerance for most nitrifying bacteria, bacterial limitation by P (which declines in solubility in soils of pH below pH 6.0) or bacterial Al toxicity under acidic soil conditions (Haynes 1986). Data from our study were consistent with this previous work. The OR_{AM} site, which had the lowest H^+ concentrations, highest Ca^{2+} and total cation concentrations and highest Ca:Al ratio in shallow (15 cm) soil solution of the four sites had significantly higher net nitrification rates in the organic soil horizons and the highest soil solution NO_3^- fluxes. Other studies that have measured ecosystem-level NO_3^- losses in relation to site conditions have reported positive correlations between soil pH and nitrification rates and NO_3^- leaching rates (e.g., Nyborg and Hoyt 1978, Vitousek and Matson 1985, Geary and Driscoll 1996, but see Finzi and others 1998b, Lovett et al. 2004).

Leaf Litter Quality. Nitrification processes may not be regulated solely by abiotic, edaphic factors (e.g., soil pH). Rather, nitrification rates could be influenced by composition of the forest vegetation. Other studies have found important differences in N cycling processes in northern hardwood forests of differing composition and soil types (Nadelhoffer et al. 1983, Pastor et al. 1984, Zak et al. 1989, Reich et al. 1997). Lovett et al. (2000) found that vegetation composition in the Catkskill Mountains (New York, USA) was a major determinant of NO_3^- concentrations in stream water. Catskill sites in which *Quercus rubra* L. was the predominant overstory species had the lowest NO_3^- concentrations in stream water. Lovett and Rueth (1999) found that potential nitrification rates were significantly higher in *Acer saccharum* stands compared to *Fagus grandifolia* stands in the Catskills. These reported relationships between forest vegetation, nitrification rates, and N-retention capacity may be mediated by foliar litter quality.

Foliar litter chemistry differs among forest tree species (Pastor et al. 1984, Stump and Binkley 1993, Ferrari 1999, Lovett et al. 2000, 2004, this study), and these differences can influence N cycling processes. For instance, litter lignin:N ratios are negatively correlated with mineralization/nitrification rates (Pastor et al. 1984, Finzi et al. 1998a, Scott and Binkley 1997, Ferrari 1999). Although there were important differences among our sites in the dominance by base-rich site indicator species, and although the base-rich forests produced leaf litter having lower lignin concentrations than the acid site forests, the differences in litter quality could not be attributed solely to differences in species composition. Rather, all three common hardwood species (*Acer saccharum, Fagus grandifolia, Betula alleghaniensis*) exhibited a degree of plasticity in leaf litter chemistry. Leaf litter cation concentrations for these species were generally highest and lignin concentrations lowest at the two base-rich sites (OR_{AM} and MR_{HM}). *Fagus grandifolia*, a base-poor site and shade-tolerant species (Burns and Honkala 1990), was generally the least plastic of the three species. Bailey et al. (2004) also reported intraspecific variation in *A. saccharum* foliar Ca and Mg concentrations in association with soil exchangeable cations. This site-related plasticity in litter quality may be a function of nutrient stress. Cellular lignification in plants is a phenotypic response to nutrient stress, and decreasing soil fertility

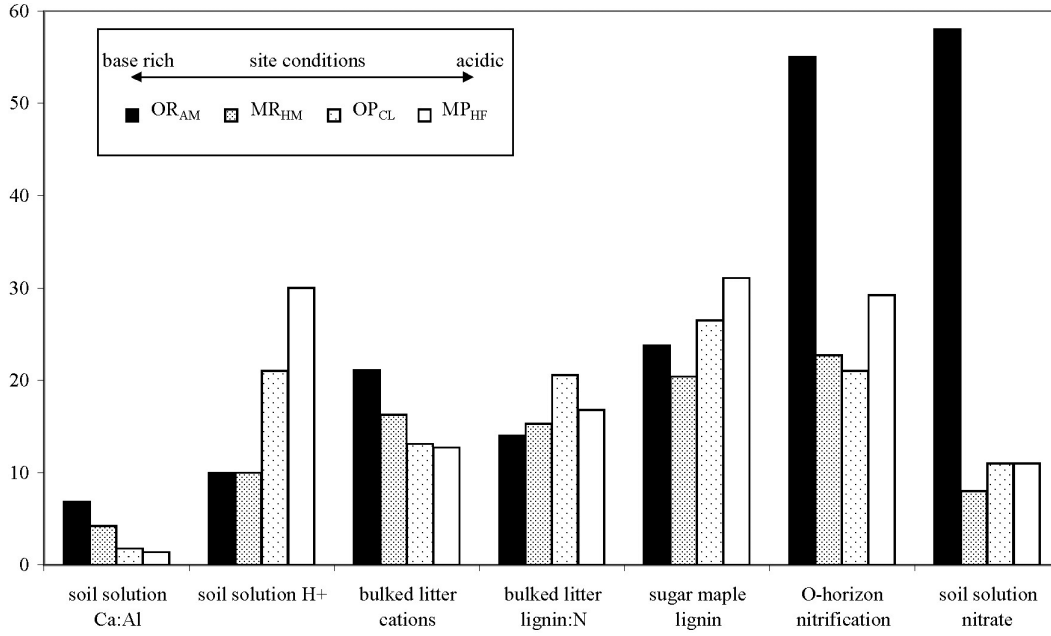

FIG. 2. Summary of site conditions, litter quality, and nutrient cycling processes at four Adirondack northern hardwood forest sites. Study sites have been ordered in relation to site conditions. Response variables are: Ca:Al in shallow (15 cm) soil solution; H^+ concentration in shallow soil solution (μeq L^{-1}); bulked leaf litter total cation content (mg g^{-1} dry wt); bulked leaf litter lignin:N; sugar maple litter lignin content (percent); O-horizon net nitrification rates (μmol N g^{-1} dry wt soil yr^{-1}); NO_3^- concentration (μeq L^{-1}) in soil solution below rooting zone (50 cm).

leads to increased foliar lignin content (Chapin 1991). This stress response may lead to ensuing positive feedback mechanisms by reducing mineralization and nitrification rates, and thereby reducing nutrient losses from the site.

POTENTIAL INTERACTIONS OF SITE AND FOREST DEVELOPMENT. Neither forest developmental stage nor site conditions/forest composition appeared to be solely associated with N cycling processes and nutrient retention in the four northern hardwood forests we studied. Rather the differences we observed in ecosystem N cycling and retention processes may be the result of several interacting biotic and abiotic factors. The more base-rich sites (OR_{AM} and MR_{HM}), which had higher Ca:Al ratios and lower H^+ concentrations in shallow (15 cm) soil solution, produced litter with higher base cation contents and lower lignin:N ratios (Fig. 2). The greater lignin content of foliar litter in the more acidic sites was not due to the greater abundance of species that tend to produce more lignified litter, but rather to intraspecific variation in lignin production by all three common deciduous hardwood species (Fig. 2 illustrates this pattern for *Acer saccharum* only). Higher quality litter is expected to decompose more rapidly and thereby lead to higher rates of mineralization and nitrification. But higher rates of nitrification were found only in the rich old-growth site (OR_{AM}) and not at the rich maturing site (MR_{HM}) (Fig. 2). It is possible that the aggrading overstory at MR_{HM} was able to retain mineralized N, thereby limiting activities of nitrifying bacteria. Reduced nitrification capacity due to either low quality litter (at the acid sites, OP_{CL}, and MP_{HF}) or to aggrading live forest biomass (at MR_{HM}) may have resulted in lower NO_3^- in soil solution below the rooting zone at these sites in compared to OR_{AM} (Fig. 2). Our study suggests that important relationships may exist between forest composition and chemistry of both the litter and soil solutions. These relationships need to be more thoroughly evaluated to understand both temporal and spatial patterns of nutrient dynamics of these forests.

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