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Comparison of the litterfall and forest floor organic matter and nitrogen dynamics of upland forest ecosystems in north central Wisconsin

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Abstract. It has been suggested that a feedback exists between the vegetation and soil whereby fertile (vs infertile) sites support species with shorter leaf life spans and higher quality litter which promotes rapid decomposition and higher soil nutrient availability. The objectives of this study were to (1) characterize and compare the C and N dynamics of dominant upland forest ecosystems in north central Wisconsin, (2) compare the nutrient use efficiency (NUE) of these forests, and (3) examine the relationship between NUE and site characteristics. Analyzing data from 24 stands spanning a moisture / nutrient gradient, we found that resource-poor stands transferred less C and N from the vegetation to the forest floor, and that N remained in the forest floor at least four times longer than in more resource-rich stands. Analyzing data by leaf habit, we found that less N was transferred to the forest floor annually via litterfall in conifer stands, and that N remained in the forest floor of these stands nearly three times longer than in hardwood stands. NUE did not differ among forests with different resource availabilities, but was greater for conifers than for hardwoods. Vitousek's (1982) index of nutrient use efficiency (I_{NUE1} = leaf litterfall biomass / leaf litterfall N) was most closely correlated to litterfall specific leaf area and percent hardwood leaf area index, suggesting that differences in species composition may have been responsible for the differences in NUE among our stands. NUE2, defined as ANPP / leaf litterfall N, was not closely correlated to any of the site characteristics included in this analysis.

Introduction

Nitrogen (N) commonly limits growth in many temperate forest ecosystems (Vitousek & Howarth 1991). In nonpolluted forests, the majority of N required by trees is provided by mineralization of nutrients from decomposing forest floor matter (Melillo 1981). The rate of decay and amount of nutrients mineralized are influenced by the quantity and quality of litterfall

(Gosz 1981; Gower & Son 1992), which in turn are strongly influenced by site resource availability (Pastor et al. 1984) and species composition (McClaugherty et al. 1985). It has been suggested that a feedback exists between the soil and the vegetation whereby fertile sites support species with high quality litter that decays rapidly, maintaining high soil nutrient availability, while less fertile sites are dominated by species with recalcitrant litter that decays slowly, maintaining low nutrient availability (Gosz 1981; Hobbie 1992).

It has further been suggested that leaf longevity is an adaptation to resource availability, with evergreen species being suited to harsh environments (Aber & Melillo 1991). Greater leaf longevity reduces annual nutrient requirements (Son & Gower 1991) and increases the amount of carbon evergreen species can fix for a given input of N invested in foliage (Small 1972). In addition, the needle-leaf morphology of many temperate and boreal evergreen species provides added efficiency by increasing the foliage N concentration on an area basis (perhaps compensating for lower mass-basis concentrations; Gosz 1981) and reducing the transpirational surface area per volume of leaf. Studies comparing the nutrient use efficiency (NUE) of evergreen and deciduous species have been inconclusive, however. Evergreen (e.g., Vitousek 1982), deciduous (e.g., Son & Gower 1991) and neither (Tyrrell & Boerner 1987) leaf habit have been determined to be more efficient.

The objectives of this study were to (1) characterize and compare the carbon (C) and N dynamics of dominant upland forests in north central Wisconsin, (2) compare the NUE of these forests, and (3) examine the relationship between NUE and site characteristics.

Methods

Research design

This research was part of a larger study to compare the soil and stand characteristics of the major forest habitat types in north central Wisconsin (Fassnacht et al. 1997; Fassnacht & Gower 1997, 1998). A study area description as well as criteria used in site selection can be found in Fassnacht & Gower (1997). The experimental design consisted of four replicate stands from each of six forest habitat types for a total of 24 stands. Because some forests of similar habitat types were comprised of tree species with different leaf habit (i.e., conifer, mixed, hardwood), we also analyzed the data on the basis of leaf habit, with 4,7, and 13 stands per treatment, respectively. Leaf habit categories were defined as follows: conifer: 0–25% of overstory and shrub LAI in hardwood species; mixed: 26–74% hardwood LAI; hardwood:

75–100% hardwood LAI. Key stand characteristics are provided by Fassnacht & Gower (1997).

Kotar et al. (1988) suggested that the six habitat types used in this study fall along nutrient and moisture gradients in the order *Quercus rubra – Acer rubrum / Epigaea repens* (QAE) < *Acer rubrum – Quercus rubra / Vaccinium angustifolium* (AQV) < *Pinus strobus / Maianthemum canadense – Vaccinium angustifolium* (PMV) < *Acer saccharum / Vaccinium angustifolium – Viburnum acerifolium* (AVVib) < *Acer saccharum – Tsuga canadensis / Dryopteris spinulosa* (ATD) < *Acer saccharum / Viola pennsylvanica – Viola pubescens – Osmorhiza claytoni* (AViO). Results reported in Fassnacht & Gower (1998) support this hypothesis. The forest types used in this study fall along an edaphic gradient as well, ranging from coarse-textured, excessively drained soil, to finer-textured, more mesic soils. In the present study, therefore, C and N cycling characteristics were compared using habitat type as a surrogate for a general resource availability gradient in the order QAE, AQV < PMV < AVVib < ATD < AViO.

The results from analyses by general resource availability and by leaf habit should be viewed with caution because they are not entirely independent. Nutrient cycling characteristics may have been responding to differences in both resource availability and leaf habit, consequently the assumption of independent errors for some of the analyses may have been violated.

Litterfall

Leaf area index (LAI; projected leaf area per unit ground area) was estimated using leaf litterfall with six to ten 1 × 1 m litter screens at each site. Leaf area was calculated by multiplying litterfall specific leaf area by leaf biomass for each species. For conifer species, LAI was estimated as the product of litter biomass and average leaf longevity (Barnes & Wagner 1981). Site LAI was calculated as the sum of monthly average leaf area divided by the plot area. For a more detailed description of LAI determination, see Fassnacht et al. (1997).

Leaf and nonleaf tissues were composited (separately) across species and collection date for each year and ground in a Wiley mill to pass a 2 mm sieve. Litterfall N concentration was determined from a 0.300 g subsample of each tissue (leaf or nonleaf) per site per year. Samples were digested using a wet digestion technique (Parkinson & Allen 1975) and analyzed for total Kjeldahl N on a Lachat continuous flow ion analyzer (Lachat Instruments, Mequon, WI). Litterfall N content was calculated as the product of litterfall N concentration and biomass. Litterfall C content of leaf and nonleaf components was calculated by multiplying the dry mass of each component by 0.45

and 0.50, respectively (Atjay et al. 1977). Annual C input was calculated as the sum of periodic inputs.

Edaphic factors

Three soil samples (59 cm depth) were collected along three randomly oriented transects at each site. Each sample was thoroughly mixed, and soil moisture content and dry weight determined. Organic matter content, available P, available K, total N concentration, pH, and particle size content were determined at the University of Wisconsin Soils and Plant Analysis Laboratory on transect composites (Page 1982; Gee & Bauder 1986). Available soil water content (by volume) was estimated as the difference between soil water content at field capacity and permanent wilting point (soil water $\text{potential}_{\text{pwp}}$ = –1500 kPa). These two values were calculated using equations from Campbell (1985) (see Fassnacht 1996 for calculation). Because these calculations do not take into account the amount of incoming water lost to runoff, the values should be considered as *potential* available water.

Forest floor

Forest floor samples were collected to mineral soil from within a 25.2 cm diameter cylinder at eight random locations in each stand. Samples were oven dried at 70 °C to a constant mass, weighed to the nearest 0.01 g, and ground in a Wiley mill to pass a 2 mm sieve. A 2 g subsample was weighed to the nearest 0.1 mg, dry ashed at 450 °C in a muffle furnace (Type 6000 furnace; Thermolyne Inc.) for 24 hr, and reweighed. Fraction weight loss was multiplied by forest floor dry mass to correct forest floor dry weight for mineral content. A subsample of each of the eight ground forest floor samples from each site was digested and analyzed for N using the technique described for litter. The N content of the forest floor was calculated as the product of N concentration and forest floor dry mass (ash corrected).

Mean residence times (MRT) for organic matter and N in the forest floor were estimated as annual total (i.e., in leaf + nonleaf) litterfall organic matter or N content divided by forest floor organic matter or N content (Gosz et al. 1976; Landsberg & Gower 1997). This commonly used method of estimating MRT assumes that the ecosystem was in steady state (i.e., annual litterfall input = annual forest floor decay). We recognize that it is likely that the forest floors of our stands were aggrading (i.e., litterfall rate > efflux rate) to some degree; consequently, our estimates of MRT for organic matter and nitrogen content represent lower bounds for the true values of mean residence times. In this document, we have referred to our estimates of MRT as "mean residence time index", "index of mean residence time", or I_{MRT} in order to remind the reader of the likely discrepancy between our estimates and the true MRT values.

NUE and aboveground net primary productivity (ANPP)

Two definitions of NUE were used in this study. The first was actually an index of nutrient use efficiency (I_{NUE1}) calculated as the inverse of leaf litter N concentration (g leaf litter mass / g leaf litter N; Vitousek 1982). NUE2 was calculated as ANPP divided by leaf litter N content (Boerner 1984). ANPP was calculated as biomass increment plus detritus production (Fassnacht & Gower 1997).

Statistical analysis

All statistical analyses were performed using Statistical Analysis Software v.6.09 (SAS Institute, Inc., 1990). Nutrient cycling characteristics were compared by forest type or by leaf habit using analysis of variance (ANOVA; GLM procedure) and a Fisher's protected Least Significant Difference (LSD) comparison of means. For variables measured for more than one year (i.e., LAI and all nutrient cycling variables except those involving the forest floor), a year-by-treatment interaction was calculated to determine if the effect of the treatment was year dependent. If the interaction term was significant, separate ANOVAs were performed for each year.

Levene's Method (alpha = 0.05; H_O: all variances equal; Snedecor & Cochran 1989) was used to test for homogeneity of variance by treatment (forest type or leaf habit) before ANOVAs were computed. Square root or natural logarithm transformations were used, if necessary, to correct for nonhomogeneous variance. In some cases, transformations did not correct for variance heteroscedasticity, in which case ANOVAs were performed on observation ranks (vs actual values), thereby removing the assumption of normality and homogenous variance. For variables with Levene's p-value between 0.01 and 0.05 and habitat type as the treatment, the results of the rank ANOVA were compared to those of the standard ANOVA. If they were essentially the same, results from the standard ANOVA were used because they are easier to understand and interpret, and because if the design is balanced (as it was for the habitat types), ANOVA is robust against violations of the normality and heterogeneity of variance assumptions (Snedecor & Cochran 1989). For variables with Levene's p-values less than 0.01, or with Levene's p-value between 0.01 and 0.05 and leaf habit as the treatment, the results of the rank ANOVA were used.

To determine which site characteristics were related to I_{NUE1} or NUE2, each dependent variable was regressed individually against nonleaf litterfall C content, N concentration, N content, and C:N ratio; forest floor ash-corrected weight, N concentration, and N content; soil pH, organic matter content, available P, available K, total N concentration, plant available water, and texture; SLA, stand percent hardwood (by LAI), LAI, and ANPP. Residual plots were used to identify model violations, and MSE and r^2 were used to evaluate model fit. Many of the variables calculated in the present study were not independent of I_{NUE1} or NUE2 (e.g., leaf N content and NUE2 both use leaf biomass and leaf N concentration in their derivation) and were not included in the regression analysis.

Results and discussion

Comparison of nutrient dynamics

Resource availability gradient

Results from forest-type comparisons of litterfall and forest floor characteristics are shown in Figures 1–3. Our findings suggest that within a similar climate, forests cycle nitrogen and organic matter more slowly on sites with low compared to high resource availability. Litterfall C and N content were lower (Figure 1A, B) and the I_{MRT} of these nutrients were higher (Figure 3D, E) for resource-poor compared to resource-rich sites. A positive relationship between litterfall N content and site resources has also been noted by other scientists for both fertilized (e.g., Miller et al. 1976; Bockheim et al. 1986) and natural forests (e.g., Reich et al. 1997). For example, Pastor et al. (1984) reported a strong quadratic relationship between total litterfall N and N mineralization (r^2 = 0.69; $p < 0.01$) for six forest ecosystems occurring along a natural N-availability gradient in southern Wisconsin. This relationship plateaued at about 40 kg N ha^{-1} yr^{-1} of total litterfall N. Reich et al. (1997) observed a similar quadratic relationship (r^2 = 0.31) that also plateaued near 40 kg N ha^{-1} yr^{-1} for 50 stands in the Lake States. The quadratic form of these relationships suggests that litterfall N is more sensitive to changes in soil N availability on sites with low compared to high fertility. Furthermore, the similar "saturation" level of these models indicates that a resource(s) other than N (e.g., light) limits litterfall N content in these fertile forests.

The higher litterfall N content for more resource-rich stands in this study (Figure 1B) resulted from increases in both litterfall biomass and N concentration (Figure 1A; Figure 2A), although the former was the dominant effect. This is consistent with the results from fertilization studies which have shown that biomass allocation to foliage is directly related to soil water and N availability (Gower et al. 1992). There is no agreement, however, on the relative

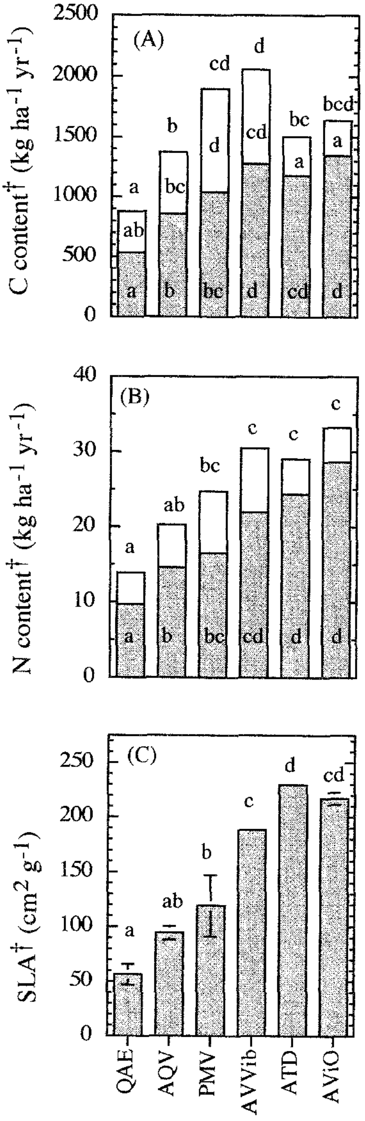

Figure 1. Comparison of litterfall (A) carbon content, (B) nitrogen content and (C) specific leaf area (SLA) by habitat type. Habitat type abbreviations are defined in the text (p. 3). Shaded bars represent the leaf litter component; white bars, the nonleaf litter component. Columns with the same letter are not significantly different at alpha = 0.05 using Fischer's protected LSD comparison. Columns having no letters did not differ among habitat types. Letters above the stacked columns are statistics for total litterfall (i.e., leaf + nonleaf litterfall). The bars in (C) represent one standard error. †ANOVAs for nonleaf and total carbon content and leaf nitrogen content were performed on natural logarithm transformed variables. The ANOVA for nonleaf nitrogen content was performed on a square root transformed variable. In all cases, the original variables are shown. Nonleaf carbon content and SLA data had Levene's *p*-values between 0.01 and 0.05. Rank ANOVA results were similar enough to regular ANOVAs that the latter were used.

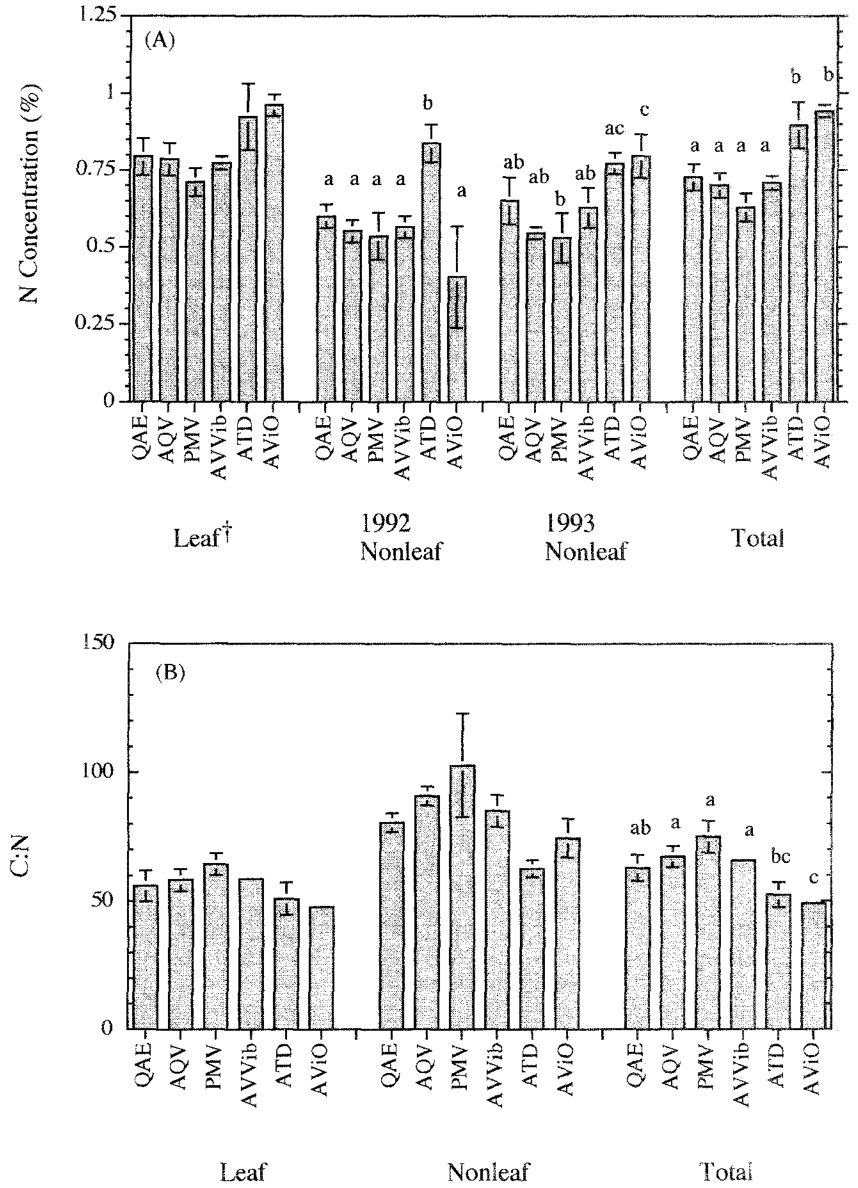

Figure 2. Comparison of litterfall (A) nitrogen concentration, and (B) carbon:nitrogen ratio (C:N) by habitat type. Habitat type abbreviations are defined in the text (p. 3). Leaf, nonleaf, and total (i.e., leaf + nonleaf) litterfall components are identified on the x-axis. Columns with the same letter are not significantly different at alpha = 0.05 using Fischer's protected LSD comparison. Columns having no letters did not differ among habitat types. In cases where results are shown for years separately, there was a significant year-by-treatment interaction. In all other cases, data were pooled across years. The bars represent one standard error. †The ANOVA for leaf nitrogen concentration was performed on a natural logarithm transformation of the variable. The original variable is shown.

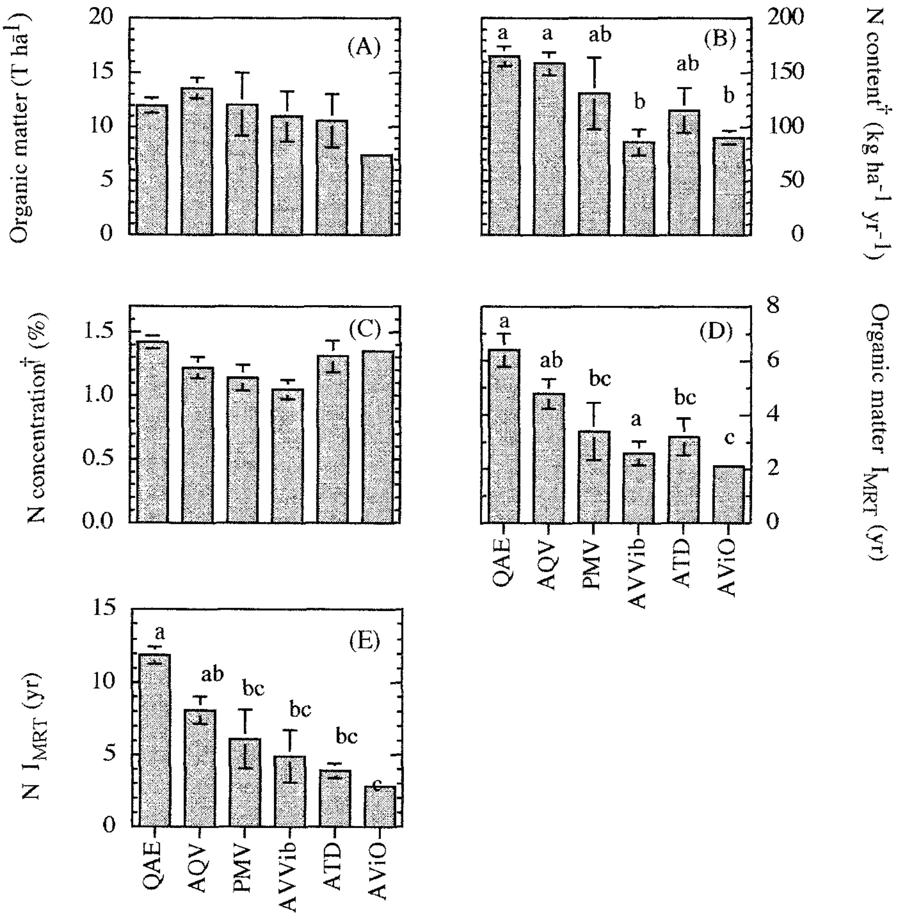

Figure 3. Comparison of forest floor (A) organic matter, (B) nitrogen content, (C) nitrogen concentration, (D) organic matter index of mean residence time (I_{MRT}; forest floor organic matter / annual total litterfall organic matter), and (E) nitrogen I_{MRT} (forest floor N / annual total litterfall N) by habitat type. Habitat type abbreviations are defined in the text (p. 3). Bars and column letters are explained in Figure 1. †Nitrogen content and concentration data had Levene's *p*-values less than 0.01. ANOVAs were performed on ranks of the original data. Original values are shown. A statistical outlier was removed from the nitrogen I_{MRT} data.

importance of changes in litterfall N concentration (Trofymow et al. 1991; Nihlgård & Lindgren 1977; Bockheim et al. 1986).

In addition to the litterfall quality and quantity, the residence times of organic matter and N in the forest floor are important factors controlling nutrient cycling in forest ecosystems. Indices of forest floor organic matter and N mean residence time varied by a factor of three to four across the resource availability gradient (Figure 3D, E) despite a relatively small range in C:N ratio of the litterfall (Figure 2B). One explanation for this apparent discrepancy is that on resource-poor sites, litterfall C and/or N was more recalcitrant than on more resource-rich sites (Birk & Vitousek 1986), increasing residence time indices on more resource-limited sites. Alternatively, on the more resource-rich sites, forest floor matter may have been incorporated into the soil still in organic form by soil fauna (Pastor & Bockheim 1984).

It is difficult to ascertain the generality of our site resource-availability-versus-mean residence-time-index relationships because few studies in the Lake States report both forest floor characteristics and resource availability. While a plot of mean residence time index for organic matter against N mineralization using data from Bockheim et al. (1983), McClaugherty et al. (1985) and Gower & Son (1992) (not shown) revealed no relationship, mean residence time of organic matter did differ between broad-leaved deciduous (0.8 to 4.7 yr) and needle-leaved evergreen stands (3.2 to 10.3 yr) using data from these and other studies (Pastor & Bockheim 1984; Gries 1995; this study). This result suggests that mean residence times may vary, in part, because of differences in species composition rather than in soil resource availability. This matter is further discussed below (see *Controls and feedbacks*).

Leaf habit

Results from leaf-habit comparisons of litterfall and forest floor characteristics are shown in Figures 4–6. We found that less N was transferred to the forest floor annually via litterfall in conifer compared to hardwood stands (Figure 4B, C), and that the forest floor N mean residence time index was nearly three times larger for the conifer than the hardwood stands (Figure 6E). Furthermore, because the litterfall was of poorer quality in the conifer than the hardwood stands (Figure 5B), additional N from the mineral soil was probably immobilized by microbes during litter decomposition (Gosz 1984). These trends, however, may not be general for all forests in the northern Lake States (Reich et al. 1997).

Mixed stands generally produced litter whose quality was intermediate to that of conifer and hardwood stands (Figure 5B); however, mixed stands occurred on soil with the lowest growing season N mineralization rates (H. Rueth, unpublished data) and had greater forest floor organic matter and N content than did either conifer or hardwood stands (Figure 6A, B). The mean residence time index of organic matter and N in the forest floor did not differ significantly between mixed and conifer stands (Figure 6D, E) likely because the fraction of the total LAI comprised of conifers exceeded 55% in all but two of the mixed stands (i.e., they were conifer-dominated vs hardwood-dominated mixed stands).

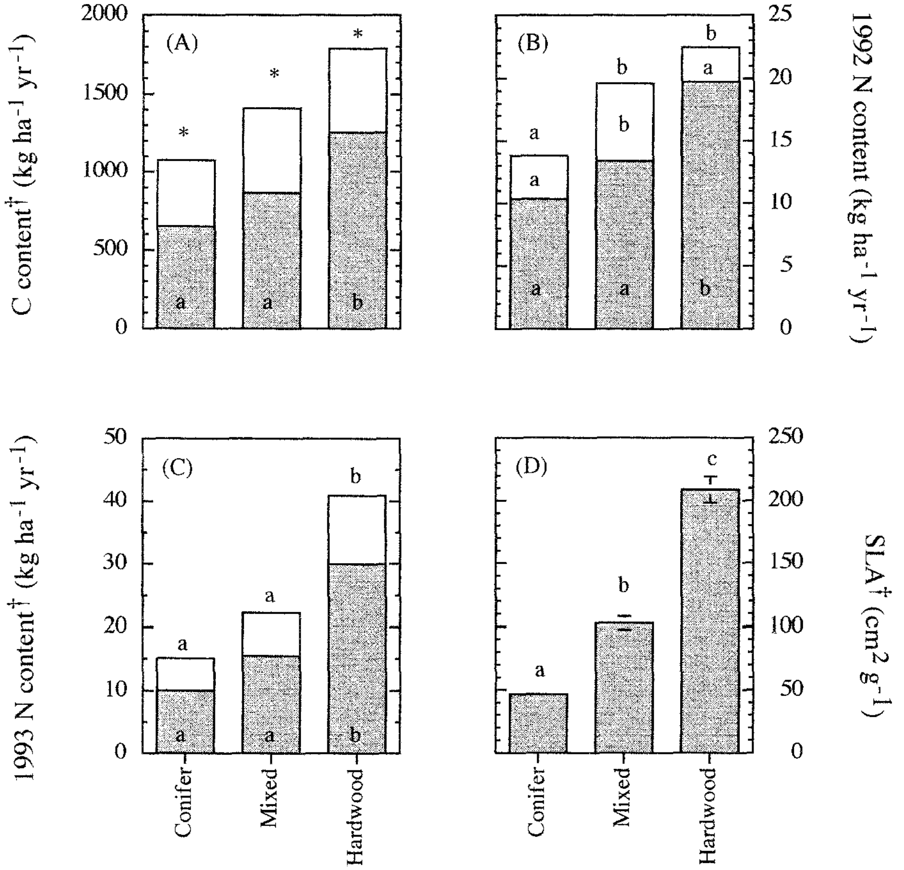

Figure 4. Comparison of litterfall (A) carbon content, (B) 1992 nitrogen content, (C) 1993 nitrogen content, and (D) specific leaf area (SLA) by leaf habit. Leaf habit categories are defined in the text (pp. 2–3). Column colors, bars, and letters are explained in Figure 1. The "*" above the columns in (A) denotes a year-by-treatment interaction for total litterfall. Letters are appropriate for the two components only. For total litterfall, individual year values are as follows: 1992: Conifer = 1006, Mixed = 1451, Hardwood = 1400; 1993: Conifer = 1142 (a), Mixed = 1406 (a), Hardwood = 2137(b). †ANOVAs for nonleaf and 1992 total carbon content, 1993 nonleaf nitrogen content and SLA were performed on natural logarithm transformed variables. In all cases, the original variables are shown or reported.

Controls and feedbacks

It is very difficult to distinguish the influence of resource availability and species composition on forest nutrient dynamics because both factors varied simultaneously along the gradient. While findings from experimental studies can be used to aid in the interpretation of our results, it is not possible to entirely uncouple resource availability and species effects since, in natural systems, differences in species requirements and competitive strategies will

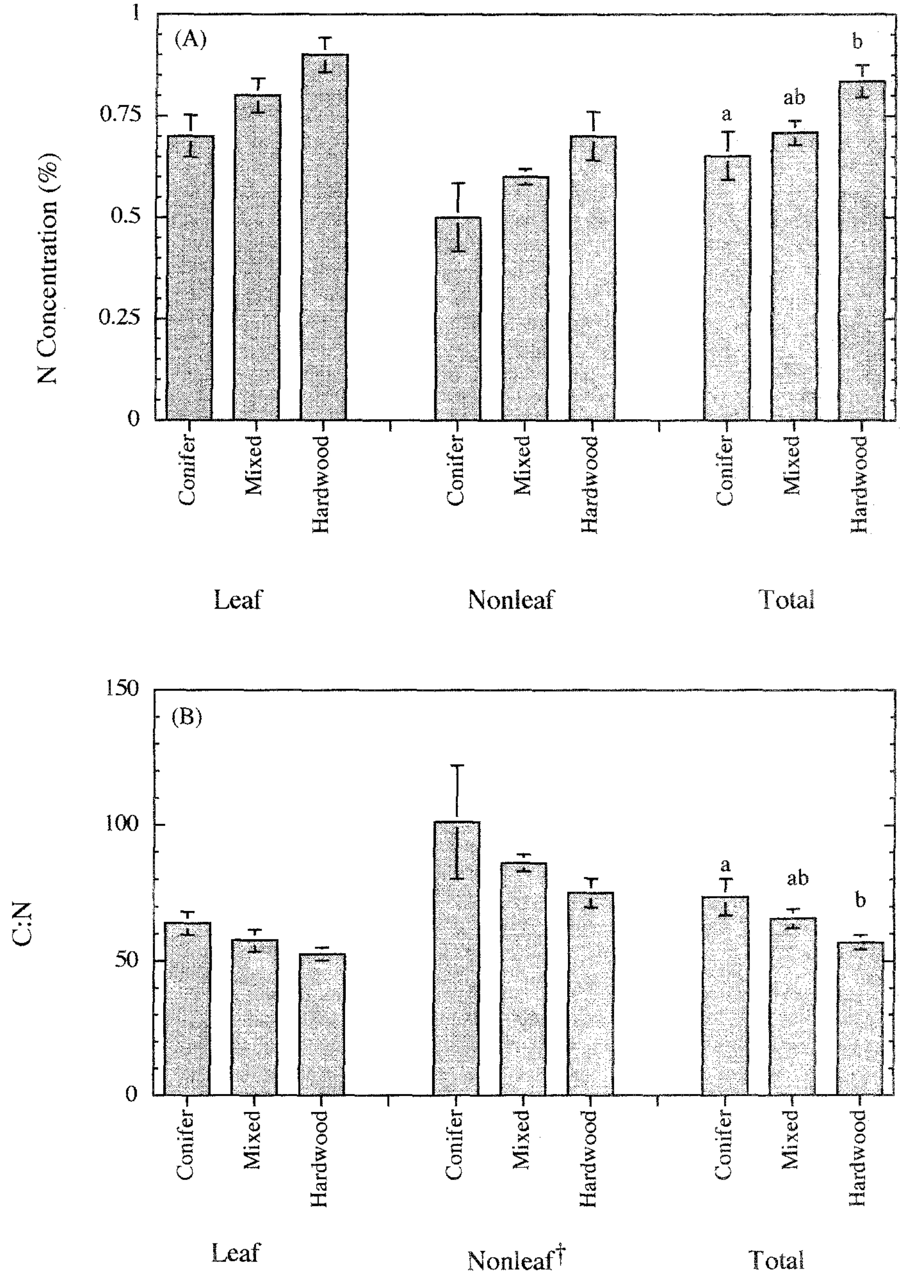

Figure 5. Comparison of litterfall (A) nitrogen concentration and (B) carbon: nitrogen ratio (C:N) by leaf habit. Leaf habit categories are defined in the text (pp. 2–3). Column colors, bars, and letters are explained in Figure 1. †The ANOVA for nonleaf C:N was performed on a natural logarithm transformed variable. The original variables is shown.

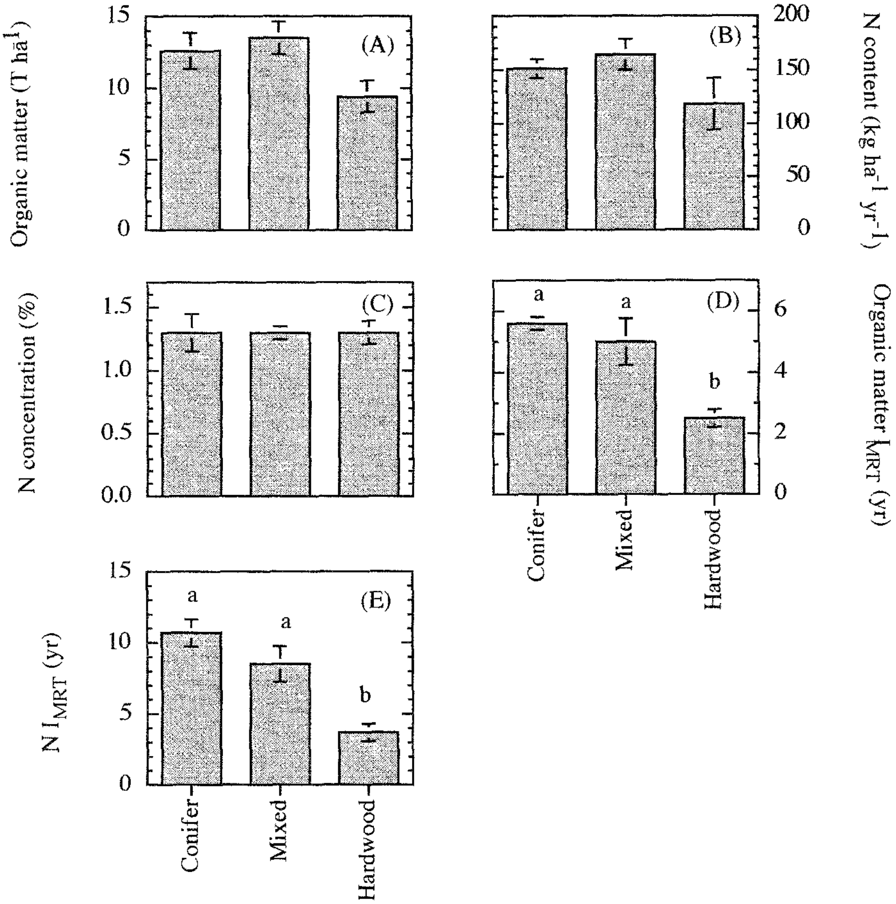

Figure 6. Comparison of forest floor (A) organic matter, (B) nitrogen content, (C) nitrogen concentration, (D) organic matter mean residence time index and (E) nitrogen mean resident time index by leaf habit. Mean residence time indices are defined in Figure 3. Leaf habit categories are defined in the text. Bars and column letters are explained in Figure 1.

lead to relatively consistent associations between soil and vegetation (e.g., pines on infertile sandy outwash and hardwoods on nutrient-rich moraines).

Results from experimental studies suggest that resource availability may be more important than species composition in determining litterfall N content. For example, fertilization of single-species stands commonly increased litterfall N content (Miller et al. 1976; Bockheim et al. 1986; Gholz et at. 1991; Gower et al. 1992), but litterfall N content often did not differ among a variety of species growing on similar soils (e.g., Perala & Alban 1982; Miller 1984; Gower & Son 1992).

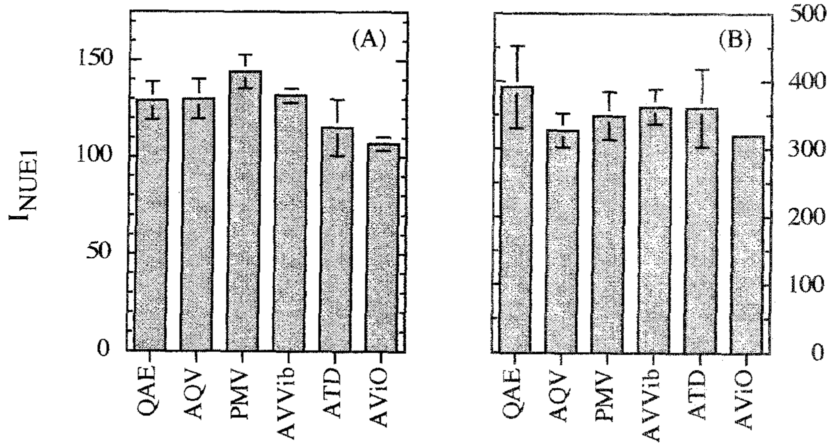

Figure 7. Comparison of (A) Vitousek's (1982) index of nutrient use efficiency (I_{NUE1} = grams leaf litter mass / grams leaf litter nitrogen), and (B) nutrient use efficiency defined as (aboveground net primary production / leaf litter nitrogen content) (Boerner 1984) by habitat type. Habitat type abbreviations are defined in the text. Bars and column letters are explained in Figure 1.

The observed differences in mean residence time indices of organic matter and N in the forest floor (Figure 3D, E; Figure 6D, E) were likely a result of species effects. In a study conducted on Blackhawk Island in south central Wisconsin, McClaugherty et al. (1985) found that leaf litter from white oak, white pine, aspen, and hemlock stands (which had increasingly lower N mineralization rates) decayed at different rates in a sugar maple stand (hemlock < white pine < aspen, white oak < sugar maple), but sugar maple leaf litter placed in each stand had a relatively constant decay rate. In McClaugherty's study, species effects were most important, and conifer litter decayed more slowly than hardwood litter. Additional support for the predominance of species composition versus resource availability in determining residence times was presented above (in *Resource availability gradient*).

In order for a feedback to exist between the soil and vegetation, influence must be exerted by the vegetation on the soil in addition to by the soil on the vegetation. Information discussed above has already demonstrated the potential of site resources to impact vegetation N dynamics (e.g. litterfall N content). Does the vegetation, in turn, impact soil N dynamics? Jenny (1980) proposed five factors which influence soil development: climate, relief, age, parent material, and biota. In order to determine whether vegetation impacts soil N dynamics, the other four factors must be relatively constant among sites. In the present study, differences existed in both parent material and

Table 1. Correlation coefficients (r) and p-values[1] from regressions between an index (I_{NUE1} = g leaf litter mass / g leaf litter N; Vitousek 1982) or a measure (NUE2 = ANPP / leaf litter N content; Boerner 1984) of stand nutrient use efficiency and site variables. Variables that were not independent of NUE were not included or are designated by a double dash (–).

	I_{NUE1}		NUE2	
Variable	r	p	r	p
Nonleaf litter C	0.217	0.309	—	—
Nonleaf litter %N	–0.219	0.303	–0.000	>0.999
Nonleaf litter N content	0.136	0.524	0.012	0.957
Nonleaf litter C:N	0.296	0.160	–0.046	0.830
SLA	–0.457	0.025	–0.060	0.780
% Hardwood (by LAI)	–0.446	0.029	–0.117	0.587
Forest floor weight	0.070	0.746	–0.278	0.188
Forest floor %N	–0.196	0.360	0.164	0.444
Forest floor N content	0.058	0.788	–0.013	0.951
Soil pH	–0.101	0.639	–0.191	0.371
Soil organic matter	–0.259	0.221	–0.229	0.283
Soil available P	0.091	0.672	–0.008	0.972
Soil available K	–0.397	0.055	–0.357	0.087
Soil Kjeldahl N	–0.269	0.203	–0.161	0.453
% Sand	0.284	0.179	0.023	0.914
% Silt	–0.270	0.202	–0.024	0.911
% Clay	–0.397	0.055	–0.012	0.955
Plant available water	–0.067	0.757	0.323[2]	0.133
LAI	–0.313	0.137	–0.114	0.594
ANPP	–0.355	0.089	—	—

[1] Due to the large number of regressions performed, it is likely that at least one regression is significant due to chance. To maintain an experiment-wise alpha of 0.10 or 0.05, comparison-wise alphas need to be 0.005 or 0.0025 respectively for I_{NUE1} regressions and 0.006 or 0.0028, respectively, for NUE2 regressions.

[2] Statistical outlier removed.

vegetation making it difficult to implicate vegetation as the cause of the differences in soil characteristics. However, several studies which meet the aforementioned criterion do provide support for the notion that vegetation influences soil N dynamics (Wedin & Tilman 1990; Gower & Son 1992; Fisher 1995).

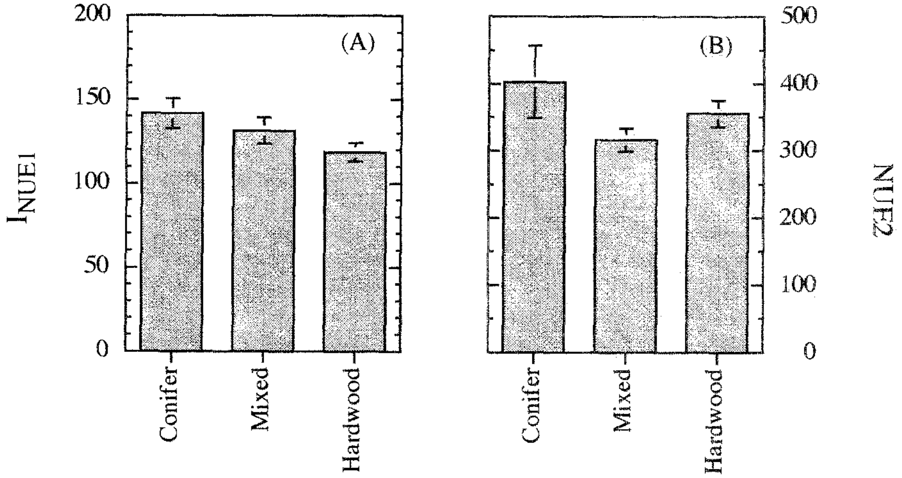

Figure 8. Comparison of (A) Vitousek's (1982) index of nutrient use efficiency, and (B) nutrient use efficiency (Boerner 1984) by leaf habit. NUE definitions are given in Figure 5. Leaf habit categories are defined in the text. Bars and column letters are explained in Figure 1.

Nutrient use efficiency

Vitousek (1982; 1984) concluded that forests use N less efficiently as N availability increases based on the inverse relationship between the ratio of litterfall dry mass to litterfall N content and litterfall N content. However, results from the current and other studies do not agree with this conclusion (Figure 7A; Pastor et al. 1984; Boerner 1985). Moreover, we found that very few variables were correlated to either I_{NUE1} or NUE2 (Figure 7A, B). Several explanations are possible for the discrepancy between the present and other studies and that of Vitousek (1982). First, the inverse relationship Vitousek (1982) observed between I_{NUE1} (i.e., ratio of litterfall mass to litterfall N content) and litterfall N content may have been a result of the lack of independence between the variables. This speculation is supported by Reich et al. (1997) who found no relationship between independent measures of NUE (ANPP: litterfall N) and N availability (N mineralization) even though correlated measures (i.e., ANPP: litterfall N vs litterfall N, or ANPP: N mineralization vs. N mineralization) demonstrated the "expected" inverse relationship. It is also plausible that the restricted range in litterfall N content for forests in the Lake States made it exceedingly difficult to detect a relationship in our study. This explanation, however, is not supported by Birk & Vitousek (1986), who found a significant relationship between NUE and N availability for loblolly pine forests that did not differ greatly in N availability.

We speculate that the observed differences in NUE among forests with differing resource availabilities may have been due, in part, to the substitution of species across the resource gradient (Pastor et al. 1984; this study). There are several lines of indirect evidence supporting this notion. First, in relating I_{NUE1} to site characteristics, we found that litterfall SLA (Figure 1C; Figure 4D) and percent hardwood LAI in our stands were the strongest and only significant correlates with I_{NUE1} (Table 1).[1] Second, Pastor et al. (1984) found that the I_{NUE1} of particular species did not vary with N mineralization. They concluded that the differences they observed in I_{NUE1} with N mineralization were a result of changes in species composition of the forest along the gradient. Finally, Prescott et al. (1989) suggested that the observed differences in NUE among pure or mixed stands of lodgepole pine (*Pinus contorta* Loudon), white spruce (*Picea glauca* Moench), Engelmann spruce (*Picea engelmannii* Parry ex Engelm) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) were due to intrinsic species characteristics rather than site differences.

In considering forests of different leaf habits, our results suggest that the NUE of conifers is greater than that of hardwoods (Figure 8A, B). Several scientists have reported similar results (e.g., Vitousek 1982; Reich et al. 1997). Only one of the two measures of NUE showed mixed stands to have efficiencies intermediate to that of conifers and hardwoods (I_{NUE1}; Figure 8A), however. NUE2 was minimum in mixed stands (Figure 8B). This latter result may be explained by the substantial contribution of oak to the productivity of some of the mixed stands (Reich et al. 1997).

Conclusions

The results from this study suggest that resource-limited forests have lower litterfall N content, lower litter quality (i.e., higher C:N ratio), and longer residence times for N and organic matter compared to more resource-rich sites. While results from other studies suggested that litterfall N patterns were general for Lake States forests, they indicated that the relationship observed between resource availability and residence time of organic matter and N in the forest floor were less broadly applicable.

The results of our study also suggest that evergreen forests have lower litterfall N content, lower litter quality, and longer residence times for N and organic matter compared to hardwood forests. Data from other forests in the Lake States region suggested that the relationships between leaf habit and residence times of N and organic matter in the forest floor were general.

Finally, the differences in NUE among stands appear to be due primarily to species substitution rather than differences in resource availability. NUE differed little among the major forest types, but was greater for conifers than hardwoods.

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Note

1. Due to the large number of regressions performed, it is likely that at least one regression was significant due to chance. The regressions between I_{NUE1} and SLA or percent hardwood would not be significant if Bonferoni adjustments were made. To maintain an experiment-wise alpha of 0.10 or 0.05, comparison-wise alphas need to be 0.005 or 0.0025 respectively for I_{NUE1} regressions and 0.006 or 0.0028 for NUE2 regressions.

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