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Forest Ecology and Management 105 (1998) 129–136

Forest Ecology
and
Management

Non-additive effects of litter mixtures on net N mineralization in a southern New England forest

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Received 14 April 1997; accepted 4 September 1997

Abstract

In this study, we developed simple, phenomenological models that enabled us to examine whether litter mixtures of differing quality increased, decreased, or had no effect on the rate of net N mineralization relative to a model that extrapolated the expected result assuming no interaction among litters of differing quality. We found that the presence of low quality litter (e.g., litter with a high lignin:N ratio) held the rate of net N mineralization to a uniformly low level until $> 70\%$ of the litter mixture was dominated by species of high litter quality. After this point, there was a rapid increase in the rate of net N mineralization. Although there was a relatively small difference in the predicted rate of net N mineralization (1 kg ha^{-1} 28 d^{-1}) between the two models (one assuming an interaction among litter types and the second, no interaction), applied over larger spatial and temporal scales, this relatively subtle difference could lead to considerably different estimated rates of N supply to saplings and canopy trees over the course of forest succession. © 1998 Elsevier Science B.V.

Keywords: Forest dynamics; Nitrogen cycling; Litter quality

1. Introduction

The mechanisms controlling nitrogen (N) immobilization and mineralization in forest soils have important implications for processes ranging from forest productivity to the potential contamination of groundwater and surface water by nitrate (Keeney, 1987; Aber et al., 1989; Murdoch and Stoddard, 1992). While research on system-specific controls over litter decomposition and N transformations continue (Keenan et al., 1996; Hobbie, 1996; Knops et al., 1996), it is clear that rates of litter decomposition and net N mineralization are influenced by a combination of (1) site-level physical factors such as soil temperature and moisture (e.g., Stanford and Epstein, 1974; Meentemeyer, 1978; Matson and Vitousek, 1981; Hobbie, 1996); and (2) intrinsic chemical properties of plant litter including initial N content, C:N ratio, lignin:N ratio, and lignocellulose index (Aber and Melillo, 1980, 1982; Melillo et al., 1982; Taylor et al., 1989; Melillo et al., 1989; Aber et al., 1990).

Several studies suggest that the N dynamics of mixed-species forests cannot be predicted by extrapolating from the patterns observed in single species stands because the co-occurrence of tree species with

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PII S0378-1127(97)00277-6

different litter quality alters decomposition and N mineralization processes of the component litter (e.g., Nihlgard, 1971; Carlyle and Malcolm, 1986; Kelly and Beauchamp, 1987; Klemmedson, 1987; Chapman et al., 1988; Blair et al., 1990; Binkley et al., 1992; Briones and Ineson, 1996; Knops et al., 1996; Sulkava et al., 1996; Wardle et al., 1997). Consequently, the mixture of species at a site and their corresponding litter qualities may represent a third general class of controls over litter decomposition and the rate of N mineralization in forest soils. For example, Chapman et al. (1988) found higher than expected rates of N mineralization in the soils found in mixtures of Norway spruce and Scots pine plantations. The rate of N mineralization in the mixed-species stands was accompanied by higher rates of faunal respiration than expected from extrapolations from pure stands. They suggested that inhibitory compounds released in pure Norway spruce stands were partially offset by the presence of the relatively higher quality Scots pine litter. Blair et al. (1990) measured the decomposition rate of deciduous leaf litter and found that the weighted average amount of N immobilization in single-species litter bags would significantly over-estimate the aggregate immobilization of N in mixed-species litter bags.They attributed this to differences in the composition of the soil decomposer community found in mixed species litter bags.

Variation in the composition of northeastern forests can produce dramatic changes in rates and patterns of nitrogen cycling (e.g., Pastor et al., 1984; Pastor and Post, 1986) because tree species differ so dramatically in litter quality (e.g., Gosz et al., 1973). Therefore, the potential for the synergistic effects of multi-species, multi-chemistry litter mixtures on net N mineralization may be important to our understanding of N availability in these forests. There are few studies which examine this possibility in these types of forests (e.g., Blair et al., 1990). In this study, we developed simple, phenomenological models that enabled us to examine whether litter mixtures of differing quality increased, decreased, or had no effect on the rate of net N mineralization relative to a model that extrapolated the expected results assuming no interaction among litters of differing quality. These models used data on leaf litterfall quality and the species composition of local tree neighborhoods as predictors of the rate of net N mineralization in a mixed-species, transition oak–hemlock–northern hardwood forest in Connecticut.

2. Methods and materials

2.1. Study sites and tree species

This research was conducted at two sites on the Canaan Mountain Plateau at elevations of 300–500 m in northwestern Connecticut (42°N, 73°15′W). One site was located on land belonging to the Bridgeport Hydraulic Company (BHC) near Wangum Reservoir. The second stand was located within the Great Mountain Forest (GMF) east of Wampee pond. Soils in both sites, hereafter referred as Wampee and Wangum, are well-drained, sandy loams classified as Typic Dystrochrepts (Hill et al., 1980). Within each stand, we randomly located 6 replicate canopy trees of each of the following 6 species: beech (*Fagus grandifolia*, Ehrh.), eastern hemlock (*Tsuga canadensis*, Carr.), sugar maple (*Acer saccharum*, Marsh.), red maple (*Acer rubrum*, L.), white ash (*Fraxinus americana*, L.), and northern red oak (*Quercus rubra*, L.).

2.2. Leaf litter collection and neighborhood species composition

Leaf litterfall was collected beneath 20 of the 36 target trees at the Wampee site only. Leaf litter was collected in 0.28 m^{-2} litter baskets beginning on September 15, 1994. Litter baskets were placed directly beneath the crowns of different species ($\sim$ 2–3 m from tree boles) to ensure representation of the full range of variation in litter inputs at this site. There were 2 litter baskets placed beneath hemlock, and red maple, 3 litter baskets placed beneath beech and sugar maple, and 5 litter baskets placed beneath white ash and red oak ($n = 20$ litter baskets total). Leaf litterfall was collected every two weeks through mid-November. Leaf samples were returned to the laboratory and dried at 70°C for 4 days. Leaves were sorted to species and weighed to the nearest 0.01 g. Although the duration of litter collection underestimates hemlock leaf litterfall, a majority of the leaves from hemlock trees fall during this period of time providing a good index of the relative contribution of hemlock leaves to the litter mixture at each litter basket.

At both stands, we mapped all the trees within a 15-m radius of the target tree ($n = 72$). Each 'neighborhood' map consisted of the diameter, distance and species identity of each tree > 10.0 cm diameter at breast height (DBH) within the 15-m radius.

2.3. Net N mineralization

The data on mid-summer net N mineralization are taken from a previous study where we measured in situ rates of net N mineralization beneath each of the replicate canopy tree species at both sites for a 28-day period from mid-July to mid-August, 1991, using a modification of the buried bag procedure ($n = 72$, Finzi et al., submitted; Finzi, 1996; Eno, 1960). Net N mineralization in those studies was calculated as the difference between NH_4^+ and NO_3^- concentrations in the incubated and initial sample. The rate of net N mineralization is expressed as kg ha^{-1} 28 d^{-1}.

2.4. Model development

The logic behind using leaf litter chemistry and neighborhood canopy tree composition as predictors of and as a means of assessing the potential for synergistic effects of litter mixtures on N mineralization is as follows. First, the lignin:N ratio of leaf litterfall accurately predicts the rate of leaf litter decomposition in northern hardwood forests (Melillo et al., 1982). The rate of leaf litter decomposition is also positively correlated with the loss of N from litter-bags and the rate of net N mineralization from soil organic matter (Stump and Binkley, 1993; Keenan et al., 1996). Therefore, leaf litter quality (e.g., lignin:N ratios) can be used to assess the effects of leaf litter mixtures on the rate of net N mineralization. Second, all the trees at our study sites are 80–150 years of age. Because litter production occurs both above- and belowground, and decomposition occurs over time scales of decades to centuries (e.g., Parton et al., 1987), we used the basal area of the dominant canopy tree species as a surrogate for the spatial and temporal scales of litter production and decomposition not accounted for by the leaf litterfall-only model.

We divided the six study species into two litter quality groups based on leaf litter chemistry. The two groups were the high quality litter (HQL) species sugar maple, red maple, and white ash, and the low quality litter (LQL) species beech, red oak, and hemlock. The bases for this grouping are as follows. Rates of leaf litter decomposition in northern hardwood forests are negatively correlated with the lignin:N ratio of leaf litter and lignin:N ratios are lower for sugar maple, red maple, and white ash than they are for beech, red oak, and hemlock (Table 1) leading to more rapid rates of mass loss and N mineralization from mesh bags (Melillo et al., 1982; Aber et al., 1990). Consistent with these results, Finzi et al. (submitted) found that rates of mid-summer net N mineralization beneath sugar maple, red maple, and white ash were nearly 2-fold greater than those beneath beech, red oak, and hemlock (Table 1).

For statistical analysis, the data on leaf litterfall and tree abundance in the neighborhood plots are

Table 1
The mean rate of net N mineralization and lignin: N ratios for each of the six study species

Species	Net N mineralization (kg ha^{-1} 28 d^{-1})[a]	Lignin: N ratio
Sugar Maple	19	16.8[b] average = 15.7
		14.6[c]
White Ash	19	13.6[b]
Red Maple	20	14.4[b] average = 22.0
		26.2[d]
		25.3[e]
Beech	9	26.8[b]
Red Oak	11	30.2[c] average = 32.0
		32.2[d]
		33.6[e]
Hemlock	11	24.8[c]

[a] Values reported in Finzi et al. (submitted) for the Great Mountain Forest, CT.

[b] Values reported in Melillo et al., 1982 for the Hubbard Brook Experimental Forest, MA.

[c] Values reported in Aber et al., 1990 and taken from a study by McClaugherty et al. (1985) for Blackhawk Island, WI.

[d] Values reported in Aber et al., 1990 for the Harvard Forest hardwood stand, MA.

[e] Values reported in Aber et al., 1990 for the Harvard Forest red pine stand, MA.

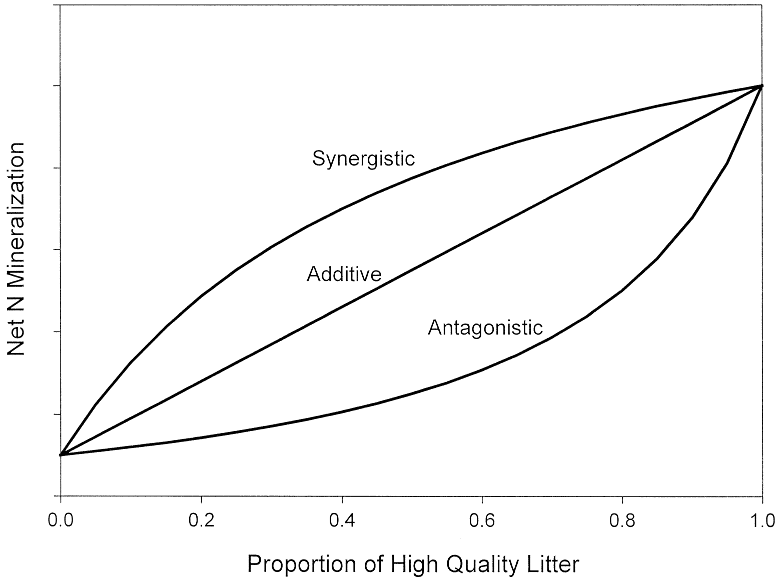

Fig. 1. The outcomes of the synergistic, additive, and antagonistic effects models of litter mixtures on the rate of net N mineralization using the proportion of high litter quality species present in a mixture as the *x*-axis and arbitrary units of net N mineralization on the *y*-axis.

transformed to a relative scale (Blair et al., 1990). This transformation enables us to clearly define synergisms between litter and tree species mixtures and the rate of net N mineralization. If there are no effects of litter mixtures on the rate of net N mineralization, there should be a positive, linear relationship between the rate of net N mineralization and the percentage of HQL litterfall and neighborhood relative abundance (Fig. 1, additive model). In this case, the presence of LQL species has no effect on the rate of net N mineralization (because of the relativization) and does not enter into the simple linear regression. If there exist synergistic or antagonistic effects of litter mixtures on the rate of net N mineralization, the presence of LQL species will either increase or decrease the rate of net N mineralization to a greater or lesser extent than that predicted by the simple linear regression (Fig. 1). A synergistic effect of litter mixtures on net N mineralization implies that as the relative abundance of HQL increases, there is a greater than linear increase in the rate of net N mineralization. An antagonistic effect of litter mixtures on net N mineralization implies that the presence of LQL species decreases the rate of net N mineralization to a greater extent than predicted by the simple linear relationship.

The additive relationship between litter quality and the rate of mid-summer net N mineralization was modeled as a simple linear regression with the proportion of the litter contributed by HQL species as the independent variable (Fig. 1). The antagonistic relationship between litter quality and the rate of mid-summer net N mineralization was modeled by:

$$\text{Net N Mineralization} = P_1^{*}\,\%\text{LQL} + P_2^{*}\,\%\text{HQL} - \frac{\%\text{HQL}^{*}\,(P_2 - P_1)^{*}\,\%\text{LQL}}{P_3 + \%\text{LQL}} \qquad (1)$$

In Eq. (1), P_1 refers to the mean effect of LQL species on the rate N mineralization in the absence of any HQL while the converse is true of P_2. The third term in Eq. (1) reduces the rate of net N mineralization of the HQL as an asymptotic function of the abundance of LQL, with the shape of the asymptotic function determined by the parameter, P_3. The synergistic effect of litter mixtures on net N mineralization was modeled according to Eq. (1) with the exception that the third term in the equation was positive and the denominator included %HQL in the place of the %LQL. Differences in model r^2 and mean squared error (MSE) were used to assess the goodness-of-fit for the additive, antagonistic, and synergistic effects models.

3. Results

The relative proportion of leaf litterfall contributed by the high quality litter species was significantly and linearly related to the rate of mid-summer net N mineralization (Fig. 2a, Net N Min. = 2.8 + 13.8 × (%HQL), $p < 0.05$, $r^2 = 0.14$, MSE = 69.8). Goodness-of-fit increased only slightly by fitting the antagonistic effects model [Eq. (1)] relating leaf litterfall to the N mineralization data (Fig. 2a, $P_1 = 5.0$, $P_2 = 19.3$, $P_3 = 0.669$, $r^2 = 0.14$, MSE = 68.4). The largest difference between the predicted rate of net N mineralization using the linear, and the antagonistic model was 2.66 kg ha^{-1} 28 d^{-1}, corresponding to a relative error of 14%. The average difference in the predicted rate of net N mineralization between the two models was 0.62 kg ha^{-1} 28 d^{-1}. Visual inspection of the data suggested no synergistic effect of leaf litter mixtures on net N mineralization and no such model was fit to the data.

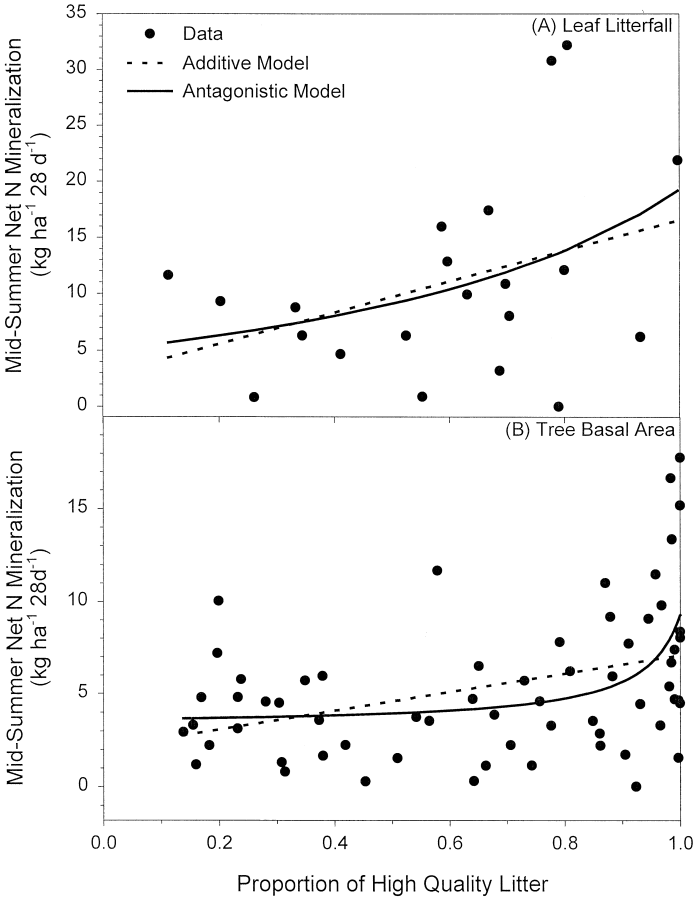

Fig. 2. (a) The relationship between the proportion of high quality leaf litter collected in leaf litter baskets at Wampee and the rate of mid-summer net N mineralization. The straight, dashed line is that of a simple linear regression of net N mineralization as a function of the proportion of HQL, and the curved, solid line is derived from the best estimates of P_1, P_2, and P_3 in Eq. (1). (b) As in (a) but with the proportion of HQL expressed as tree basal area.

There was also a significant linear relationship between the percent tree basal area accounted for by high quality litter species and the rate of mid-summer net N mineralization (Fig. 2b, $\text{Net N Min.} = 2.1 + 5.0 \times (\%\text{HQL})$, $p < 0.05$, $r^2 = 0.15$, $\text{MSE} = 13.7$). Goodness-of-fit increased by fitting the antagonistic effects model [Eq. (1)] to the net N mineralization data (Fig. 2b, $P_1 = 3.6$, $P_2 = 9.3$, $P_3 = 0.07$, $r^2 = 0.24$, $\text{MSE} = 12.2$). The largest difference in the predicted rate of net N mineralization between the two models was 2.2 kg ha^{-1} 28 d^{-1}, corresponding to a 16% relative error between models. The average absolute difference in the predicted rate of net N mineralization between the models was 1.0 kg ha^{-1} 28 d^{-1}.

4. Discussion

There was evidence for an antagonistic relationship between the rate of N mineralization and the relative abundance of tree species with high versus low quality litter (Fig. 2b). Although the scatter-plots are noisy, the presence of low quality litter species within 15-m of a sample location maintained the rate of net N mineralization at a uniformly low rate until $< 30\%$ of the tree basal area was comprised of low litter quality tree species. Beyond this point, there was an exponential increase in the rate of net N mineralization with a decrease in the relative abundance of low quality litter. Although the differences between the additive and antagonistic effects models were small (on average 1.0 kg ha^{-1} 28 d^{-1}), applied over larger spatial and temporal scales, these relatively small differences could lead to considerably different estimated rates of N supply to saplings and canopy trees over the course of forest succession.

Several hypotheses have been proposed to explain the non-additive (i.e., synergistic or antagonistic) effects of leaf litter mixtures on litter decomposition and the rate of N mineralization. Chapman et al. (1988) suggested that the rapid decomposition of high quality leaf litter produced high ambient N availability which stimulated the decomposition of lower quality litter by allowing the transfer of nutrients between litter, leading to a more rapid utilization of carbon substrates. In contrast, McClaugherty et al. (1985) and Prescott et al. (1993) found no clear relationship between site nutrient availability and the rate of leaf litter decomposition for a standard litter type transplanted into sites differing in N mineralization rates, and some studies have suggested that a high concentration of inorganic N may depress the rate of lignin decomposition leading to an overall decline in the rate of net N mineralization (Fenn and Kirk, 1981; Melillo et al., 1989).

Other studies have suggested that heterogeneous litter substrates change the abundance and composition of the soil fauna leading to increases or decreases in litter decomposition and N mineralization (Chapman et al., 1988; Blair et al., 1990; Prescott, 1996; Sulkava et al., 1996). For example, Blair et al. (1990) found that the abundance of fungi and bacteria in mixed-species litter bags was either similar to or lower than those in single-species litter bags, while the opposite was true of fungal- and bacterial-feeding nematodes. They suggested that greater resource heterogeneity present in the mixed species litter bags stimulated nematode populations, leading to increased rates of N mineralization during the initial phase of leaf litter decomposition.

The non-additive effects of litter mixtures on the rate of net N mineralization in multi-species stands could be caused by tree species effects on microclimate or soil physical properties: a species may contribute a relatively small quantity of litter, but significantly alter physical factors that determine overall rates of litter decomposition. While significant microclimate effects on litter decomposition and N mineralization have been found in gaps (Mladenoff, 1987) or clearcuts (Prescott et al., 1993), most studies in intact forests involving reciprocal litter or soil core transplants have found that organic matter quality (e.g., C:N ratio or Lignin:N ratios) is more important in determining rates of litter decomposition or N mineralization than are actual differences in microclimate between stands (e.g., Carlyle and Malcolm, 1988). Even in the case where there is a significant interaction between litter chemistry and incubation site, other sources of variation (e.g., changes in composition of the decomposer community) can confound any microclimate effects (Blair et al., 1990).

Secondary compounds such as polyphenols and monoterpenes present in either decomposing litter or root exudates of one or more species could decrease the rate of litter decomposition and N mineralization by inhibiting the activity of the decomposer community (e.g., White, 1986, 1991). A form of this hypothesis was first formulated by Rice and Pancholy (1972, 1973) to explain a decrease in nitrate production over the course of secondary forest succession, with further support from Anderson (1973), Lamb (1980), and White (1986, 1991). However, there exist no conclusive demonstrations of inhibition of ammonium or nitrate production by secondary compounds at concentrations found in field soils (Bremmer and McMarty, 1988; McCarty et al., 1991; White, 1991). In the absence of direct inhibitory effects, it is not clear that these secondary compounds would behave in a qualitatively different way than compounds such as lignin which decompose slowly and increase in concentration during the course of organic matter decomposition (Alexander, 1977; McClaugherty and Berg, 1987; Melillo et al., 1989).

Although there is no clear consensus on the factors responsible for the patterns of litter decomposition observed in multi-species litter bags and in rates of N mineralization in mixed species stands, it is clear that the dynamics of N immobilization and mineralization from multi-species leaf litter are different than the dynamics of single-species litter. As a result, extrapolations of the results of litter decomposition in single species litter studies is likely to lead to discrepancies in patterns of N immobilization and mineralization in multi-species stands. Additional studies will be required if we are to explain why the decomposition of litter mixtures in some cases lead to greater than expected rates of net N mineralization and in other cases lower than expected rates of net N mineralization relative to single species stands.

Acknowledgements

This research was supported by the National Science Foundation (grant BSR 9220620), the Department of Energy (grant DE-FG02-90ER60933), and by the National Aeronautics and Space Administration (NAGW-2088) to C.D.C. We would like to thank Bill Schlesinger and two anonymous reviewers for their comments on an earlier draft of this manuscript. This research is a contribution to the program of the Institute of Ecosystem Studies.

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