DISSERTATION

# PLANT SPECIES EFFECTS ON SOIL ORGANIC MATTER TURNOVER AND NUTRIENT RELEASE IN FORESTS AND GRASSLANDS

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY NEAL A. SCOTT ENTITLED "PLANT SPECIES EFFECTS ON SOIL ORGANIC MATTER TURNOVER AND NUTRIENT RELEASE IN FORESTS AND GRASSLANDS" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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# ABSTRACT OF DISSERTATION

# PLANT SPECIES EFFECTS ON SOIL ORGANIC MATTER TURNOVER AND NUTRIENT RELEASE IN FORESTS AND GRASSLANDS

Although feedbacks between plant species and ecosystem dynamics have been demonstrated in a variety of terrestrial ecosystems, little research has examined the mechanistic relationship between plant species characteristics, the formation and turnover of soil carbon and nitrogen pools, and ecosystem processes such as net N mineralization. My objective was to examine two possible effects of species on soil C and N dynamics; changes in organic matter quality and changes in soil aggregation.

For several forest ecosystems, litter lignin:N ratio correlated negatively (non-linear) with net N mineralization, but the relationship did not apply to grass species. Climatic factors (temperature, precipitation) explained little of the variation in net N mineralization. The relationship between litter lignin:N ratio and net N mineralization from mineral soil and the forest floor was similar, suggesting that plant litter quality affects both forest floor and mineral soil organic matter quality.

For tree species monocultures in Wisconsin, net N mineralization during 387 day laboratory incubations indicated that species alter the quality of readily decomposable pools of soil N, and have little effect on more recalcitrant soil N. Changes in the quality of soil N correlated positively with *in situ* net N mineralization. Grass species did not influence N mineralization. Neither grass nor tree species influenced soil C dynamics, but differences in soil characteristics between sites influenced soil C dynamics. Soil microbes appear to act as a "decay filter", converting heterogeneous plant material into relatively homogeneous soil humus.

Changes in soil aggregate size distribution should alter whole-soil C and N quality because different size aggregates contain organic matter of different quality. Although tree species slightly altered aggregate size distribution, aggregate size distribution related poorly to whole-soil C and net N mineralization. Tree species had no effect on the physical protection of organic matter in soil aggregates or on organic matter quality of different size aggregates.

Species characteristics had little effect on soil C mineralization, but species-related changes in the quality of readily decomposable soil N pools (not the pool size) influenced net N mineralization. This suggests that the feedbacks between plant species and soil N cycling occur rapidly, ensuring an adequate nutrient supply when plant community structure changes.

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# Chapter 1

## Introduction

During litter decomposition, plant material is converted from recognizable plant fragments into amorphous organic material referred to as soil humus. Soil humus consists of a variety of organic compounds with turnover times ranging from tens to hundreds of years. Several studies have addressed the effect of plant species characteristics on rates of litter decomposition and nutrient dynamics during the early stages of decay (see for example Melillo et al. 1982; McClaugherty and Berg, 1987; Harmon et al. 1990; Aber et al. 1990; Palm and Sanchez, 1991). Far fewer studies have examined plant species effects on soil humus quality, especially the distribution of organic material in labile and recalcitrant fractions. This soil humus pool contains a large reservoir of nutrients required for plant growth (Tate 1987), so an understanding of the dynamics and control over this pool is essential to understanding soil fertility.

Two hypotheses have been proposed for the effect of plants on soil humus (referred to as soil organic matter (SOM)) turnover. Melillo et al. (1989), suggested that plant species have no effect on SOM quality. Soil microbial biomass functions as a "decay filter", converting heterogeneous plant material into homogeneous SOM. This hypothesis is supported by data from a 77 month decomposition experiment, where litter with a range of lignocellulose index values (0.2-0.6) was converted into SOM with a similar C:N ratio and a lignocellulose index ranging from 0.7-0.8. Alternatively, Berg and McClaugherty

(1987) and McClaugherty and Berg (1987) proposed that plant litter characteristics alter soil humus quality (specifically N release). They found that litter lignin concentration strongly affected the timing and quantity of N released from SOM. Higher lignin content led to greater N retention and delayed the onset of net N release. In both cases, no mechanistic relationships were examined linking plant species characteristics, formation of SOM fractions, and subsequent whole soil organic matter mineralization.

Soil organic matter may or may not contain discrete pools of organic material with different turnover times. In simulation models, soil organic matter has been represented by one to four discrete fractions with different turnover times (Jenkinson and Rayner, 1977; Paul 1984; Pastor and Post, 1985; Parton et al. 1987). An alternative representation is that organic matter turnover is a continuum ranging from very labile to very recalcitrant material (Duxbury et al. 1989; Bosatta and Ågren, 1991). Until methods are developed to measure the discrete fractions (if they exist), it is difficult to know whether they are realistic or simply there for mathematical convenience. Several fractionation methods are used to divide SOM into discrete fractions, based on chemical (Stevenson 1982) and physical characteristics (reviewed in Stevenson and Elliott, 1989). The biological and ecological significance of these chemical and physical fractions remains unclear. Notable exceptions include work on particulate organic matter (Cambardella and Elliott, 1992) and soil aggregation (Cambardella and Elliott, 1994). Even if we are able to attribute ecological significance to measurable SOM fractions, nothing is known about differences in the effects of species on these fractions, and whether these interactions alter the nutrient supply rate of a soil.

Plants might alter SOM turnover by several mechanisms. The distribution of organic material can be altered between relatively labile and recalcitrant pools of SOM. Alternatively, plants could alter SOM dynamics by changing soil aggregation or the physical protection of SOM. By changing the physical or chemical protection of SOM, plants could modify soil N supply and soil C turnover. Finally, species effects on the soil microflora and fauna community composition could influence organic matter turnover.

The objective of the work described in the next four chapters was to examine the relationship between plant species characteristics (litter quality and quantity) and the size and turnover of physically defined fractions of SOM. The effects of these fractions on whole-soil C and N turnover, in particular *in situ* rates of net N mineralization, were also examined.

In Chapter 2, I examined the relationship between litter chemistry, specifically litter lignin and nitrogen content, and *in situ* measurements of net N mineralization. Several studies have demonstrated that litter lignin content, or the ratio between lignin and N, correlates negatively with litter decomposition rates (for example see Melillo et al. 1982; Harmon et al. 1990). Far fewer studies have examined the relationship between litter chemistry and N release from soil. Individual site studies (e.g. Stump and Binkley, 1993; van Cleve et al. 1993) have demonstrated a relationship between litter quality and total net N mineralization (mineral soil plus forest floor). These individual studies occurred under conditions of uniform climate and soil type. I collated data from both forests and grasslands across a wide range of soil types, climate types, and plant species composition.

I used this information to test whether site-specific relationships between plant litter quality could be extrapolated across sites with different soils and climate.

Across a range of forest ecosystems with different climate and soil types, I found that tree species litter lignin:N ratio correlated strongly (non-linear) with *in situ* net N mineralization ($R^2$=0.74), and furthermore that the relationship between net N mineralization from either the forest floor or the mineral soil and litter lignin:N was similar. However, the relationship between lignin:N ratio and net N mineralization for several grass species was different than for the tree species. Climatic factors did influence net N mineralization, but did not explain nearly as much of the variation in net N mineralization as did litter lignin:N ratio.

Chapter 3 explores in detail the relationship between plant species characteristics and kinetically defined fractions of SOM. Some studies have demonstrated a relationship between mineralization of labile soil N and plant litter quality (Wedin and Pastor, 1993). Little work has addressed whether these same species characteristics alter C or N mineralization from more recalcitrant soil C and N pools. I collected soils from common garden experiments, including both tree and grass species, and conducted long-term laboratory incubations on the mineral soil to test the hypothesis that plant species alter the turnover of recalcitrant SOM. Based on the kinetics of carbon and nitrogen mineralization through time, I defined the size and turnover rate of labile and more recalcitrant SOM fractions in the mineral soil. I then examined correlations between the size and mineralization of the different pools and initial litter quality and quantity.

In spite of large differences in tissue chemistry, grass and tree species had no effect on soil C mineralization. In all cases, C mineralization was best described by a two-pool model: a labile pool with exponential decay, and a more recalcitrant pool with a constant decay rate. Differences in soil physical properties had a greater effect on soil C mineralization than did plant species. Nitrogen mineralization was best described by a single pool model (with exponential decay). For grass species, tissue chemistry was unrelated to differences in net N mineralization. For the tree species, litter lignin:N ratio correlated negatively with the mineralization rate constant of soil N, which correlated positively with *in situ* net N mineralization. This supports the idea that plant species do not affect the quality of more recalcitrant forms of soil C and N (i.e. soil humus).

Differences in soil aggregation might also explain species effects on SOM turnover. Conceptual models of soil aggregation suggest that aggregates of different size contain organic matter of different quality (C/N ratio) (Tisdall and Oades, 1982). Small microaggregates (<250 μm) contain low C/N organic matter, whereas macroaggregates (>250 μm), made up of microaggregates bound together with fungal hyphae and fine roots, contain higher C/N organic material. Whole-soil organic matter turnover would be altered if species characteristics (such as fine root biomass or mycorrhizal infection) altered the amount or distribution of organic matter in the different aggregate size classes. In Chapters 4 and 5, using the same soils used in Chapter 3, I examined the interactions between tree and grass species, soil aggregation, and whole-soil C and N mineralization. In Chapter 4, I examined whether species characteristics altered aggregate size distribution, and whether changes in aggregate size distribution altered whole-soil C and N mineralization. Then, in Chapter 5, I explored whether species effects on organic matter quality or the physical protection of intra-aggregate organic matter explains tree species effects on whole-soil SOM turnover.

Although plant tissue chemistry and root biomass differed greatly for the tree and grass species, aggregate size distribution did not differ for the grass species. Mean aggregate diameter was slightly higher for Norway spruce and lowest for white pine. Aggregate diameter correlated negatively with net N mineralization during aerobic laboratory incubations, but did not explain much of the variation in net N mineralization. Tree species had no effect on the physical protection of soil organic matter in soil aggregates, or on the quality of organic matter contained in different size aggregates. Overall then, it appears that the effect of species on soil aggregation is not an important mechanism by which species alter whole-soil organic matter dynamics.

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# Chapter 2

# Litter quality effects and annual net N mineralization: comparison across sites and species

## Abstract

The feedback between plant litterfall and nutrient cycling processes plays a major role in the regulation of nutrient availability and net primary production in terrestrial ecosystems. While several studies have examined site-specific feedbacks between litter chemistry and nitrogen (N) availability, little is known about the interaction between climate, litter chemistry, and N availability across different ecosystems. I assembled data from several studies spanning a wide range of vegetation, soils, and climatic regimes to examine the relationship between aboveground litter chemistry and annual net N mineralization. Net N mineralization declined strongly and non-linearly as litter lignin:N ratio increased in forest ecosystems ($R^2=0.74$, $p<0.01$). Net N mineralization decreased linearly as litter lignin concentration increased, but the relationship was significant ($R^2=0.63$, $p<0.01$) only for tree species. Litterfall quantity, N concentration, and N content correlated poorly with net N mineralization across this range of sites ($R^2<0.03$, $p=0.17$ to $0.26$). The relationships between litter lignin:N ratio and net N mineralization from both forest floor and mineral soil were similar. Litter lignin:N ratio explained more of the variation in net N mineralization than climatic factors, suggesting that litter quality

in forest ecosystems may alter patterns of net N mineralization by changing the quality of soil organic matter throughout the soil profile independent of climate.

## Introduction

Important feedbacks exist between plant characteristics and nutrient availability in terrestrial ecosystems (Stone 1975; Chapin 1980; Vitousek 1982; Vitousek 1984; Pastor et al. 1984; Shaver and Melillo 1984; Miles 1985). Most of the studies examining species effects on nutrient cycling occur at single sites with uniform climate and vegetation. Few researchers have examined litter quality effects on ecosystem processes across gradients of climate or vegetation. Meentemeyer (1978) found that litter lignin concentration had a greater effect on litter decomposition rates at higher actual evapotranspiration (AET). In contrast, Aber et al. (1993) suggested that the interaction between species-specific nutrient-use-efficiency and nutrient availability, not litter quality or climate, determines steady-state rates of net N mineralization. Litter quality can alter how quickly steady-state is reached. To fully understand feedbacks between litter quality and ecosystem processes, patterns across sites with different climate and vegetation need to be examined.

This study examines the hypothesis that net N mineralization is related to litter quality across sites with different climate, soil type, and total litter inputs. If so, litter quality should be a good, general predictor of net N mineralization rates independent of site-specific climoedaphic factors.

## Background

Site-specific studies have found strong relationships between plant species characteristics and soil N dynamics. Stump and Binkley (1993) found a negative, non-linear relationship between litter lignin:N ratio and annual net N mineralization in Rocky Mountain forests ($R^2$=0.64). Van Cleve et al. (1993) also found a negative, non-linear relationship between forest floor lignin:N ratio and net N mineralization in the forest floor of Alaskan forests ($R^2$=0.88). For these two examples, the lignin:N ratio where no further changes in net N mineralization occurred differed significantly (55 and 25, respectively), possibly due to site factors such as climate or soil type.

Two important processes contribute to the available N pool: N release during litter decomposition and soil humus mineralization. Litter decomposition rates generally vary inversely to litter lignin concentration (Fogel and Cromack 1977; Aber and Melillo 1982; Melillo et al. 1982; Harmon et al. 1990; Aber et al. 1990), and polyphenolic content (Palm and Sanchez 1991). Litter lignin content may also influence the timing of N release during litter decay (Berg and McClaugherty 1987; Aber et al. 1990). Changes in soil humus dynamics are less clearly linked to species characteristics. Melillo et al. (1989) suggested that during litter decay, the litter lignocellulose index converges on a common value; soil microbes act as a decay filter, converting heterogeneous plant material (in terms of carbon) into homogeneous soil humus. Alternatively, N release from soil humus can be influenced strongly by differences in the concentration of lignin-like compounds in the humus fraction (Berg and McClaugherty 1987; McClaugherty and Berg 1987). Additionally, litter lignin can influence long-term (10 year) accumulation of soil humus (de Haan 1977). Feedbacks may exist between litter chemistry and soil humus dynamics, but their effects on net N mineralization are poorly understood.

Climate is an important control over nutrient availability, and may exaggerate or dampen the effect of plant species characteristics on ecosystem processes. Meentemeyer (1978) suggested that as AET increases, the influence of litter lignin on litter decomposition decreases. Powers (1990) demonstrated that changes in temperature across an elevational gradient override species effects on net N mineralization. At regional scales, Yin (1992) found that total soil N and temperature predicted variation in N availability. In contrast, substrate chemistry appears to be the most important factor regulating litter decomposition and N availability in boreal forests (Flanagan and Van Cleve 1983; Van Cleve et al. 1993). Likewise, in arctic soils, substrate quality appeared to influence carbon © and net N mineralization more than differences in temperature (Nadelhoffer et al. 1991). Based on these studies, it is unclear whether litter quality affects nutrient availability similarly across gradients of temperature and moisture.

## Methods

I assembled data from 11 published and unpublished studies that examined the relationship between plant species and annual net N mineralization. In most cases, I limited my selection to data sets containing all variables (see Appendix 1). This included values for annual net N mineralization (both mineral soil and organic horizons when available), litterfall mass, and litter N and lignin concentration. I included 2 data sets that did not contain all the variables. The data (Table 2.1, Appendix 2.1) for the Rocky Mountain region (Stump and Binkley 1993) did not include litterfall mass, but I included them because they represented an extensive data set on low fertility (low net N mineralization) sites. The other incomplete data set (Table 2.1, Appendix 2.1) was from the Cedar Creek Natural History area (Grigal and Homann 1994) (Table 2.1), where no information on litter lignin concentration was available. This was, however, an extensive data set examining litterfall mass, N content, and annual net N mineralization.

Several techniques are available for measuring net N mineralization in the field. Some of the studies included in this analysis utilized the buried bag technique (Eno 1960), while others used the intact core method (Raison et al. 1987). There is no consensus on a "best" method for measuring net N mineralization, and in some cases the best method depends on climatic factors and soil type (Binkley and Hart 1989). When compared directly, there is no evidence of a systematic bias between these two methods in estimates of net N mineralization (Zou et al. 1990; Binkley et al. 1992). While differences in measurement techniques for net N mineralization might introduce error into cross-study comparisons, there is no way to "correct" one technique to compare results between methods. For this reason I made no attempt to screen data sets in order to include only those using identical methods, and likewise I did not try to correct for differences in methodology.

Several techniques are also available for measuring litter lignin content. Most of the studies included in this analysis utilized wet chemical lignin extraction methods developed for forage fiber analysis (van Soest and Wine 1968) and forest product analysis (Effland 1977). Ryan et al. (1990) compared these two lignin extraction methods and found little difference (c.f. Fig. 3 in Ryan et al. 1990). The remaining studies utilized near infrared (NIR) reflectance techniques to measure litter lignin concentration (Wessman et al. 1988; McLellan et al. 1991a). Multiple regression, using wavelengths corresponding to structural features of lignin as well as ones correlated with litter lignin concentration, was used to predict litter lignin concentration from NIR reflectance spectra (McClellan et al. 1991a ). Subsequent NIR measurements of litter lignin concentration suggest a small bias between wet chemical and NIR determinations of lignin concentration (McClellan et al. 1991b), but it is not clear whether this results from operator-related differences in wet digest procedures or a real bias between the methods (McLellan et al. 1991b). Although some error is likely to be associated with the use of different methods, there is no way to correct for differences related to use of different methods. Therefore, I used the published lignin values in this analysis without any correction.

Belowground litter inputs are an important component of total organic matter inputs to terrestrial ecosystems, but too few data were available for species differences in root chemistry and turnover to extend my analysis beyond aboveground "litterfall."

To examine the effects of climate on net N mineralization, mean annual precipitation and mean annual temperature were combined into one index value (Brown and Lugo 1982) where

$$\text{climate index}=(1000*\text{mean annual temperature})/\text{mean annual precipitation (mm)} \qquad \text{(Eq. 1)}$$

The interaction of these two factors has been shown to influence net N mineralization (Kladivko and Keeney 1987), so it was reasonable to combine them into one predictive variable.

One final caveat involves the use of individual plot data versus mean values for several plots. For most of the studies used in this comparison, one point represents a result from one independent plot. Four of the studies included were based on replicated experimental treatments (Binkley and Valentine 1991; Wedin and Tilman 1990; Gower and Son 1992; Pastor et al. 1993). In these cases, only mean values (for field blocks) were available.

## Statistical Techniques

Regression techniques were used to examine the relationship between litter quantity or quality and net N mineralization across sites. The relationship between net N mineralization and litter lignin:N ratio appeared to be non-linear, so I fit the non-linear model

$$\text{net N mineralization} = Ae^{(\pm b*\text{lignin:N})} \qquad \text{Eq. 2}$$

(procedure NLR, SPSS Inc. 1988) where "b" is a constant and "A" is the maximum net N mineralization value at a lignin:N ratio of zero. For the other litter quality parameters, the data did not suggest a need for non-linear models.

Stepwise multiple linear regression (SPSS Inc. 1988) using log-transformed values for net N mineralization was used to examine the relative importance of litter chemistry parameters and climate on net N mineralization.

## Results

### Aboveground litter chemistry

The negative, non-linear relationship between litter lignin:N ratio and net N mineralization explained more of the variation in net N mineralization for the forest ecosystems ($R^2=0.74$) than any of the other litter quantity or quality parameters (litter lignin, total litterfall, litterfall N content) (Fig. 2.1). Litter lignin concentration related negatively to net N mineralization for the forest sites, explaining over half of the variation in net N mineralization ($R^2=0.63$, $p<0.01$) (Fig. 2.2). Multiple regression analysis including litter lignin, N, and lignin:N indicated that litter lignin:N ratio explained the greatest proportion of the variation in net N mineralization (log transformed, $R^2=0.78$, $p<0.01$). Neither litter lignin or N concentration significantly improved the goodness of fit ($p>0.05$).

Total ecosystem net N mineralization includes N release/immobilization during two processes, litter decomposition and soil humus mineralization. I found that the relationship between litter lignin:N ratio and net N mineralization was identical from both the forest floor and from the mineral soil (Fig. 2.3), suggesting that initial litter chemistry alters not only N dynamics during litter decomposition, but also N release from soil humus.

The relationship between aboveground litter lignin, lignin:N and net N mineralization was noticeably different for the one grassland site included in this analysis ("b" points, Figs. 2.1 and 2.2). There was no significant relationship between litter lignin concentration or lignin:N ratio and net N mineralization for the grass species alone ($p=0.93$ and $0.23$, respectively). Substituting root chemistry for aboveground litter did not improve the relationships between litter chemistry and net N mineralization for the grass species.

### Litter quantity

Litterfall mass showed no correlation with net N mineralization ($R^2=0.01$, $p=0.26$, Fig. 2.3), with no apparent difference between forest and grassland species.

Litterfall N content has been linked to site N availability in forest ecosystems (Rommel 1935; Vitousek 1982), but across these sites I found no significant relationship ($R^2=0.03$, $p=0.17$) between litter N content and net N mineralization (Fig. 2.4). Once again, there was no apparent difference between forest and grassland species.

### Climate and litter quality effects on net N mineralization

To examine whether litter quality, climate, or a combination of both explained most of the variation in net N mineralization (log-transformed), I used stepwise multiple regression including percent litter lignin and N, lignin:N ratio, mean annual precipitation, mean annual temperature, and the combined climatic factor (Eq. 1). In the forest ecosystems, litter lignin:N ratio accounted for the greatest amount of variation in net N mineralization ($R^2=0.78$). Adding the combined climate factor improved the goodness of it of the model ($p<0.05$) while explaining slightly more of the variation in net N mineralization ($R^2=0.82$). This suggests that the effect of litter lignin:N ratio on net N mineralization is not affected greatly by climate, and that litter lignin:N ratio is the most important predictor of net N mineralization in forest ecosystems.

## Discussion

Several site-specific studies have demonstrated a negative relationship between litter lignin or lignin:N ratio and net N mineralization (Gower and Son 1992; Stump and Binkley 1993; van Cleve et al. 1993). My results also indicate a negative, non-linear relationship between litter lignin:N ratio and net N mineralization in forest ecosystems, and that litter lignin:N ratio is a good predictor of net N mineralization across a range of forest sites. The combined effects of litter lignin:N ratio and climatic factors explains only slightly more of the variation in net N mineralization. Interestingly, the relationship between litterfall lignin or lignin:N and net N mineralization appears to differ in forests and grasslands (Figs. 2.1 and 2.2).

Because the results from the grassland site are based on one site, they should be interpreted with caution. The common garden experiment at Cedar Creek (Wedin and Tilman 1990) had been in place for four years prior to net N mineralization measurements. Differences in net N mineralization appeared related to changes in a labile fraction of soil organic matter that responded rapidly to changes in species composition (Wedin and Tilman 1993). In the longer run the grass species may have greater effects on N release from soil humus. In ecosystem models, the effects of litter chemistry on litter decomposition and N mineralization are similar in forests and grasslands (i.e. CENTURY, Parton et al. 1987). The relationship between litter chemistry and net N mineralization in grasslands requires further study across a greater range of sites.

Site-specific studies on uniform soils have shown that species characteristics (such as litter lignin or lignin:N ratio) modify net N mineralization rates under uniform climate (Binkley and Valentine 1991; Wedin and Tilman 1990; Gower and Son 1992). Although several laboratory (Marion et al. 1981 and Kladivko and Keeney 1987, for example) and field (Schimel and Parton 1986; Burke 1989, for example) studies have demonstrated the importance of microclimate as a control over net N mineralization, seldom do these studies include large variation in litter quality. Nadelhoffer (1991) found that during laboratory incubations, variation in substrate quality controlled organic matter mineralization in arctic tundra soils more than variation in temperature. Binkley et al (1994) found that site factors influenced net N mineralization during laboratory incubations of tundra soils more than variation in temperature and moisture. However, in both studies no connection was made between litter quality and substrate (soil organic matter) quality. Alternatively, Powers (1990) found that over altitudinal gradients of temperature, moisture, and plant species that variation in climatic factors (temperature and moisture) influenced annual net N mineralization more than differences in substrate quality. Once again variation in soil substrate quality was not linked to differences in litter quality. My results suggest that differences in litter quality relate strongly to differences in annual net N mineralization, and whether these differences are related to differences in substrate quality (soil organic matter quality) requires further study. Studies examining net N mineralization should include measurements of litter lignin and N concentration.

In ecosystem models, the size and turnover of the soil humus pool is often unrelated to initial litter chemistry (Pastor and Post 1985; Rastetter et al. 1991). I found that the relationship between initial litter lignin:N ratio and net N mineralization from both the forest floor and soil humus pool was similar (Fig. 2.3). Based on simulated results, Aber et al. (1993) proposed that differences in litter chemistry do not determine steady-state net N mineralization rates. They suggested that differences in nutrient-use-efficiency ultimately determine rates of N cycling, and that litter chemistry affects how quickly an ecosystem reaches steady-state rates of net N mineralization. Based on my results (Fig.

2.3), mineralization of N from the forest soil humus fraction relates strongly to differences in litter chemistry, specifically litter lignin:N ratio. The forests included in this analysis ranged in age from 31-150+ years, suggesting that initial litter quality does influence rates of net N mineralization from soil humus regardless of whether an ecosystem is at steady-state.

Site-specific studies have used both linear and non-linear regression models to express the relationship between litter quality and net N mineralization. Stump and Binkley (1993) and van Cleve et al. (1993) found that a negative logarithmic function best characterized the relationship between litter lignin:N and net N mineralization and forest floor lignin:N and net N mineralization, respectively. However, Gower and Son (1992) used a linear function to express the relationship between litter lignin:N and net N mineralization at the Coullee Experimental Forest (cf. Fig. 6 in Gower and Son 1992, $R^2$=0.75). If a negative logarithmic function were fit to these data (Gower and Son 1992), the variability in net N mineralization explained by litter lignin:N ratios would be similar to the linear fit ($R^2$=0.74); they had too few points to distinguish clearly between linear and non-linear models. It appears that a negative logarithmic function describes the relationship between litter lignin:N ratio and net N mineralization both at individual sites and between several sites. The shape of the negative logarithmic function suggests that at high values of litter lignin:N ratio, other factors besides litter quality may influence net N mineralization.

During litter decomposition, litter N concentration may influence litter decomposition rate and net N mineralization in the forest floor (Berendse et al. 1987).

However, at high litter N concentrations, litter lignin appears to be the most important control on litter decomposition (Cromack 1973; Berg and Ågren 1984). My results indicate that the ratio of litter lignin:N strongly influences net N mineralization from the forest floor more than either factor alone. When litter N concentration is low, litter lignin concentration is high, and litter lignin:N is also high. When N concentration is high, litter lignin is low, litter lignin:N is low, and net N mineralization is high. I found a significant ($R^2=0.32$, $p<0.01$) negative relationship between litter lignin and N concentration, which suggests that site N availability is related to tissue lignin concentrations. This inverse relationship between N and lignin may be mechanistic; changes in resource availability (N) have been shown to influence tissue lignin concentrations (Waring et al. 1985). Other work suggests that N mineralization from the soil humus pool is controlled by the interaction between N concentration and the mineralization of lignin-like complexes (Berg 1986; McClaugherty and Berg 1987), further supporting the idea that the ratio between litter lignin and N directly influences net N mineralization rates in forest soils.

When (if) an ecosystem reaches steady state, litterfall N should approximate net N mineralization (assuming no major losses of N). I found no significant relationship between litterfall N and net N mineralization (Fig. 2.5). Several of the studies included in this analysis reported only leaf litterfall (Nadelhoffer et al. 1983; Pastor et al. 1984; Gower and Son 1992). Other N inputs, including root and herbaceous materials, were not measured. Unless all N inputs are accounted for, it is unlikely that leaf litterfall N content will be an accurate predictor of net N mineralization rates unless leaf litterfall is the predominant N input.

## Conclusions

Species characteristics such as litter lignin concentration and lignin:N ratio are strongly related to differences in net N mineralization across a wide range of forest ecosystems. Litter lignin:N ratio accounted for over 70% of the variation in net N mineralization for forests. However, the relationship between litter quality and net N mineralization differed in forest and grassland ecosystems. Litter lignin:N ratio influences not only net N mineralization from the forest floor, but also from soil humus. Differences in litter lignin:N ratio explain more of the variation in net N mineralization than site-specific differences in temperature and precipitation. Whether differences in litter quality directly alter net N mineralization by changing substrate quality or some other soil factor is not known. Species effects on N release from soil humus should be incorporated in ecosystem models because soil humus is potentially a large source of mineral N utilizable by plants.

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Table 2.1. Site information. The letter following the site name is used to represent that site in all graphs.

| Site | Vegetation | Precipation mm | Temperature[1] C | Reference |
|---|---|---|---|---|
| Rocky Mountain Region CO (a) | Aspen, Lodgepole pine, Subalpine fir, Engelmann spruce | 700-840 | -10 / 13 | Stump and Binkley 1993 |
| Cedar Creek Natural History Area MN (b) | Big bluestem, Little bluestem, Switchgrass, Indiangrass | 660 | -10 / 22.2 | Wedin and Tilman 1990 |
| Coullee Exp. Forest WI (c) | Norway spruce, European larch, White pine, Red pine, Red oak | 780 | -10.4 / 22.8 | Gower and Son 1992 |
| Univ. Wisconsin Arboretum WI (e) | Black oak, White oak, Red oak, Sugar maple, Paper birch, White pine, Red pine, White spruce | 953 | -5.2 / 21.2 | Nadelhoffer et al. 1983 |
| Harvard Forest MA (f) | Mixed hardwood, Red pine | 1100 | -7 / 20 | Aber et al. 1993 |
| Eli Whitney Forest CT (g) | White ash, White pine, Norway spruce | 1134 | -1.1 / 23.5 | Binkley and Valentine 1984 |
| Blackhawk Island WI (h) | Red pine, White pine, Red oak, White oak, Sugar maple, Hemlock | 800 | -9.1 / 26 | Pastor et al. 1984 |
| Blodgett Res. For. CA (i) | Old growth mixed conifer forest | 1700 | 4.5 / 20.5 | Hart and Firestone 1991 |

Table 2.1 (cont.)

| | | | | |
|---|---|---|---|---|
| Isle Royale National Park MI, exclosures (j) | White spruce outside exclosure<br>Aspen, Paper birch, Balsam fir inside | 622 | -11.4 / 15.8 | Pastor et al. 1993<br>McInnes et al. 1992 |
| Cedar Creek Natural History Area MN (k) | Oak forest, Lowland forest, Cedar, Mixed hardwoods | 660 | -10 / 22.2 | Grigal and Homann 1994 |

[1] Mean January / July temperature

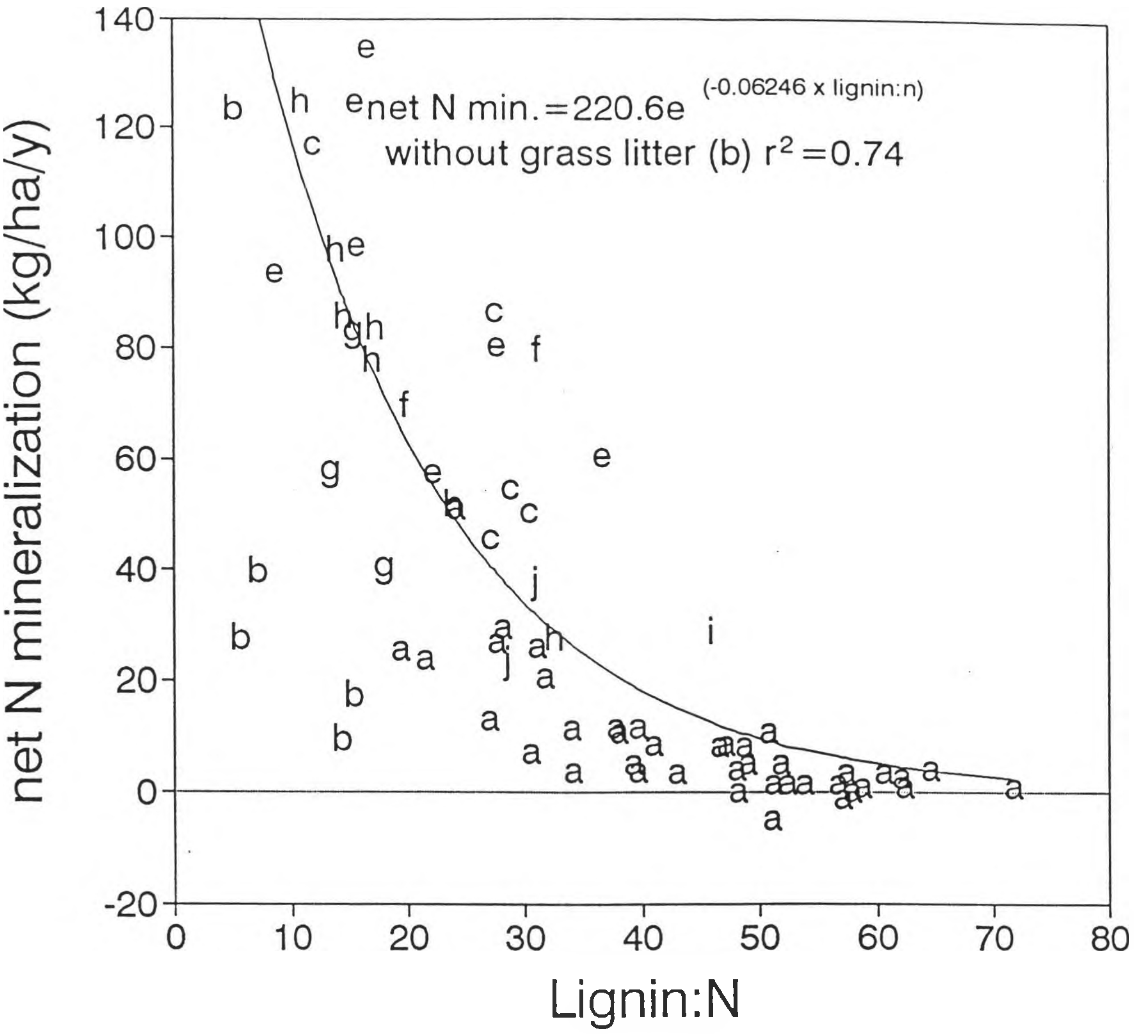

Figure 2.1. Relationship between litter lignin:N ratio and net annual N mineralization. Regression line (and equation) does not include data for grassland site ("b" points). Sites are coded in the following manner: "a" - Rocky Mountain region, "b" - grass plots at Cedar Creek Natural History area, "c" - Coullee Experimental Forest, "e" - University of Wisconsin Arboretum, "f" - Harvard Forest, "g" - Eli Whitney forest, "h" - Blackhawk Island (different site than "d"), "i" - Blodgett Research Forest, "j" - Isle Royale National Park, "k" - Cedar Creek Natural History Area. See Table 2.1 for more site detail.

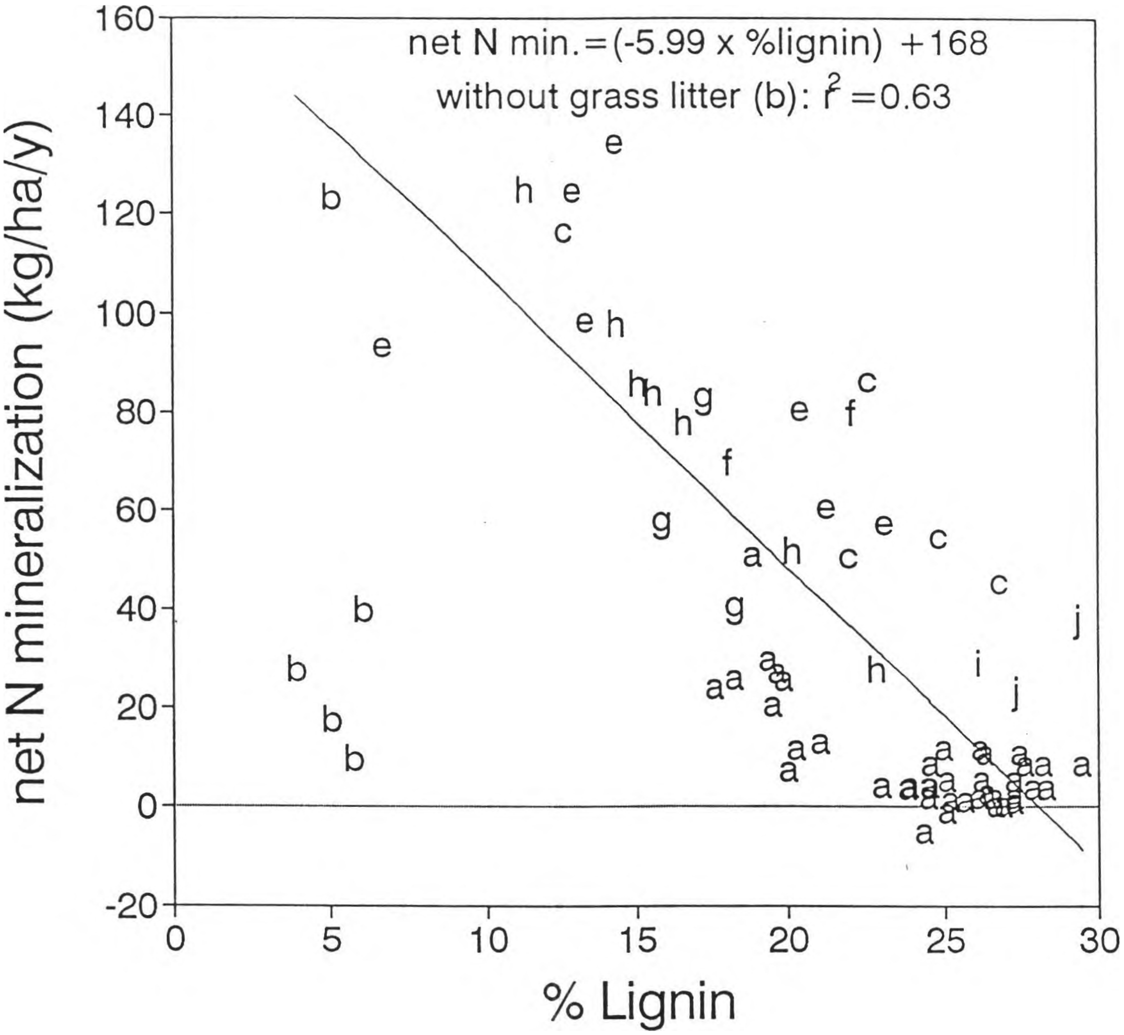

Figure 2.2. Relationship between litter lignin concentration and net annual N mineralization. Regression line and equation do not include data from grass plots. See Figure 2.1 for symbol definitions.

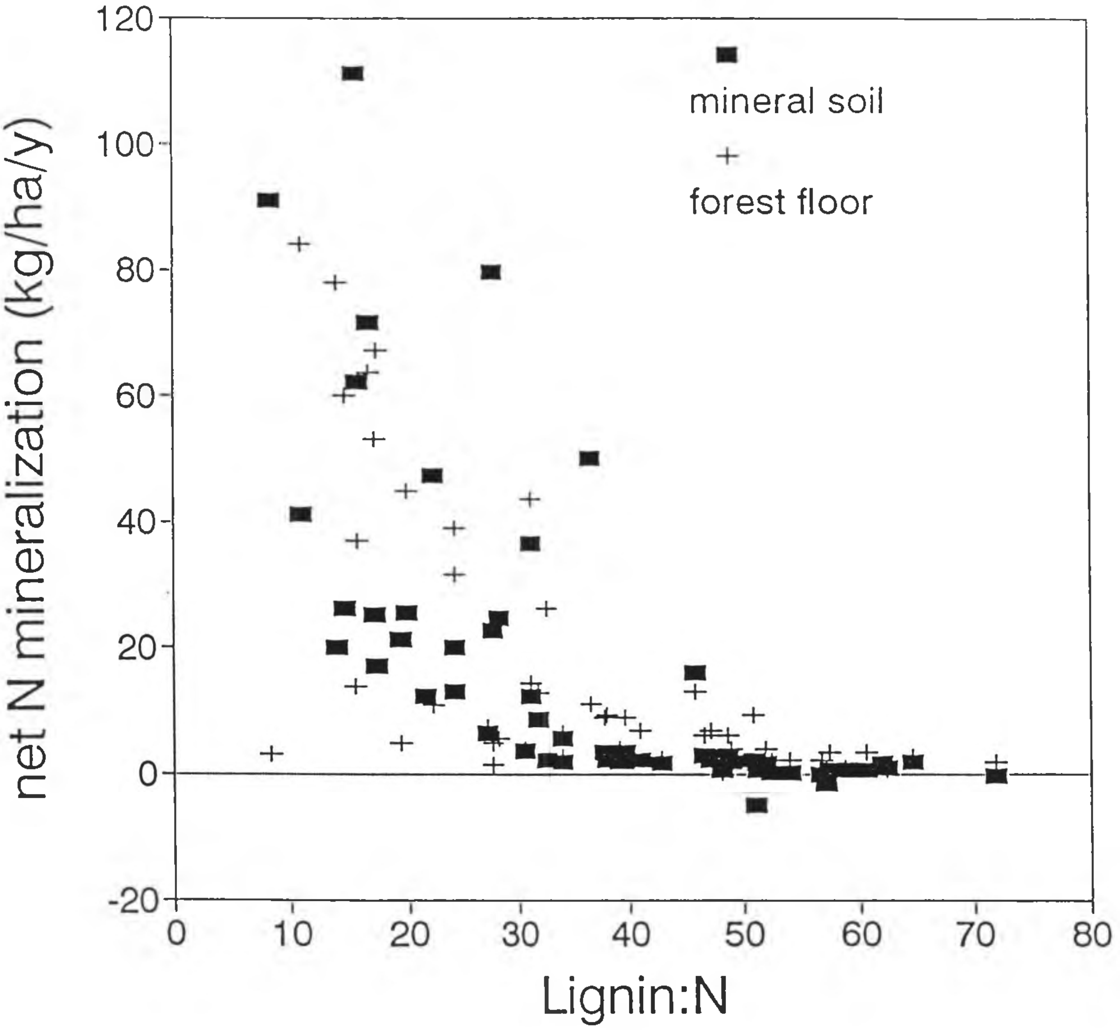

Figure 2.3. Annual net N mineralization from forest floor and mineral soil as a function of litter lignin:N ratio. Five forest sites were used for this comparison (Blackhawk Island, U. Wisconsin Arboretum, Isle Royale National Park, Blodgett Research Forest, Harvard Forest).

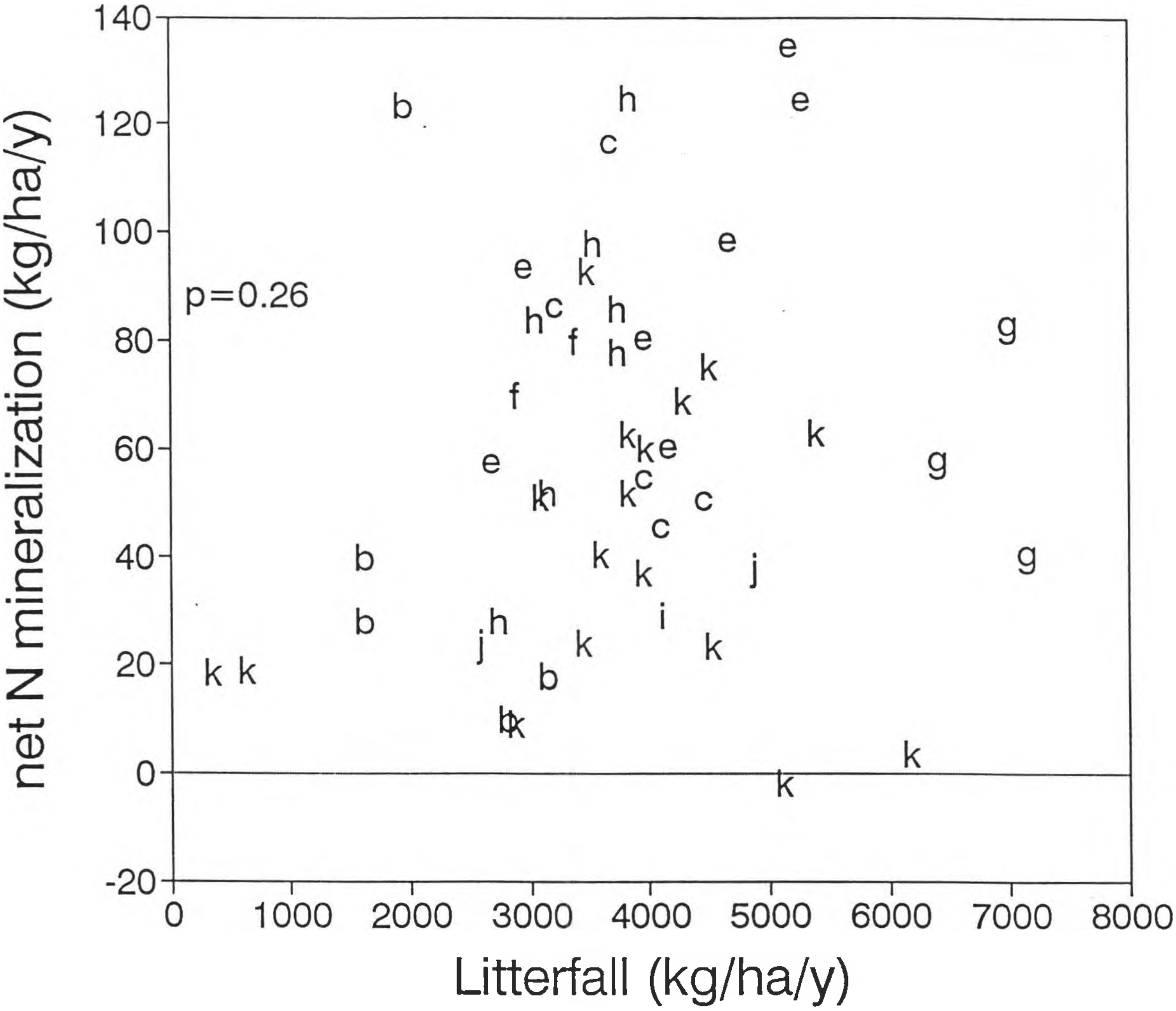

Figure 2.4. Relationship between total litterfall and net N mineralization. There was no significant relationship between these two variables. See Figure 2.1 for symbol definitions.

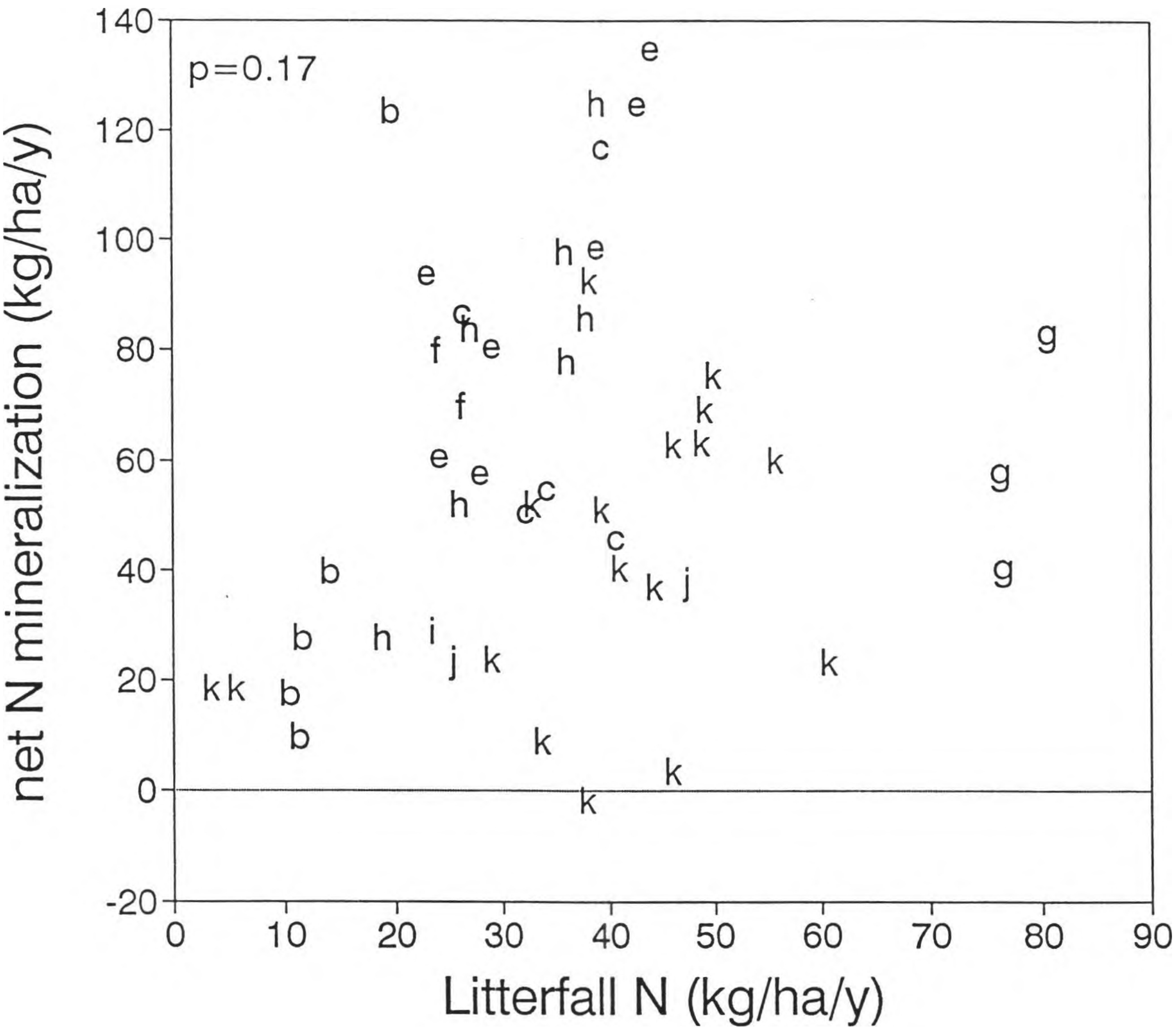

Figure 2.5. Relationship between litterfall N content and net N mineralization. There was no significant relationship between these two variables. See Figure 2.1 for symbol definitions.

Appendix 1. Litter and net N mineralization data from all sites used in site comparison.

| Site | Species | net N mineralization kg ha$^{-1}$ y$^{-1}$ | Lignin g kg$^{-1}$ | Nitrogen g kg$^{-1}$ | Litterfall kg ha$^{-1}$y$^{-1}$ |
|---|---|---|---|---|---|
| Rocky Mountain Region | Aspen | 24.3 | 176 | 8.2 | ---- |
| | | 26.3 | 182 | 5.9 | ---- |
| | | 21.1 | 195 | 6.1 | ---- |
| | | 7.6 | 200 | 6.6 | ---- |
| | | 11.9 | 203 | 6 | ---- |
| | | 29.9 | 193 | 6.9 | ---- |
| | | 25.9 | 198 | 10.2 | ---- |
| | | 51.4 | 188 | 7.8 | ---- |
| | | 27.4 | 196 | 7.1 | ---- |
| | | 13.4 | 210 | 7.8 | ---- |
| | Lodgepole pine | 2.1 | 244 | 4.8 | ---- |
| | | 5.6 | 250 | 4.8 | ---- |
| | | 1.5 | 256 | 4.4 | ---- |
| | | 4.1 | 237 | 5.5 | ---- |
| | | 3.1 | 263 | 4.3 | ---- |
| | | 1.5 | 251 | 4 | ---- |
| | | -4.6 | 243 | 4.8 | ---- |
| | | -0.6 | 250 | 4.4 | ---- |
| | | 2.1 | 261 | 4.6 | ---- |
| | | 1.4 | 273 | 3.8 | ---- |
| | Subalpine fir | 8.9 | 295 | 6.3 | ---- |
| | | 4.1 | 283 | 4.7 | ---- |
| | | 5.8 | 262 | 6.7 | ---- |
| | | 12.2 | 249 | 6.6 | ---- |
| | | 9 | 276 | 6.7 | ---- |
| | | 4.6 | 238 | 5 | ---- |
| | | 0.7 | 269 | 5.6 | ---- |
| | | 11.2 | 274 | 5.4 | ---- |
| | | 2.1 | 266 | 5.1 | ---- |
| | | 4.4 | 244 | 6.2 | ---- |
| | Engelmann spruce | 8.9 | 245 | 5 | ---- |
| | | 4.1 | 278 | 4.9 | ---- |
| | | 5.8 | 273 | 5.6 | ---- |
| | | 12.2 | 261 | 6.6 | ---- |
| | | 9 | 282 | 6 | ---- |
| | | 4.6 | 245 | 3.8 | ---- |

| | | | | | |
|---|---|---|---|---|---|
| | | 0.7 | 266 | 4.6 | ---- |
| | | 11.2 | 263 | 6.9 | ---- |
| | | 2.1 | 272 | 5.1 | ---- |
| | | 4.4 | 22.9 | 6.7 | ---- |
| Cedar Creek Natural Hist. Area | Ticklegrass | 123.6 | 51 | 10.1 | 1964 |
| | Quackgrass | 40 | 61 | 8.7 | 1622 |
| | Unknown | 28 | 39.8 | 7.1 | 1630 |
| | Little bluestem | 9.8 | 57.5 | 4 | 2800 |
| | Big bluestem | 17.8 | 50.8 | 3.3 | 3137 |
| Coullee Experimental Forest | European larch | 117 | 126 | 10.7 | 3680 |
| | White pine | 87 | 225 | 8.2 | 3210 |
| | Red pine | 51 | 219 | 7.2 | 4460 |
| | Norway spruce | 46 | 268 | 9.9 | 4100 |
| | Red oak | 55 | 248 | 8.6 | 3960 |
| University Wisconsin Arboretum | Black oak | 125 | 129 | 8.1 | 5280 |
| | Red oak | 135 | 143 | 8.5 | 5182 |
| | White oak | 94 | 67 | 7.8 | 2946 |
| | Sugar maple | 99 | 133 | 8.3 | 4674 |
| | White pine | 81 | 204 | 7.3 | 3692 |
| | Red/White pine | 61 | 212 | 5.8 | 4166 |
| | Norway spruce | 58 | 230 | 10.4 | 2680 |
| Harvard Forest | Red pine | 80 | 220 | 7.1 | 3370 |
| | Mixed hardwoods | 70 | 180 | 9.1 | 2870 |
| Eli Whitney Forest | Green ash | 41.1 | 183 | 10.7 | 7160 |
| | White pine | 83.7 | 173 | 11.5 | 7004 |
| | Norway spruce | 58.5 | 159 | 11.9 | 6416 |
| Blackhawk Island | Red pine | 28 | 228 | 6.9 | 2743 |
| | White pine | 52 | 202 | 8.3 | 3150 |
| | Red oak (1) | 78 | 166 | 9.6 | 3759 |
| | Red oak (2) | 86 | 151 | 10.1 | 3759 |
| | White oak | 84 | 156 | 8.9 | 3048 |
| | Sugar maple (1) | 98 | 144 | 10.1 | 3556 |
| | Sugar maple (2) | 125 | 113 | 10.1 | 3861 |
| Blodgett Res. Forest | Old growth mixed conifer forest | 29 | 261 | 5.7 | 4120 |
| Isle Royale Natl. Park | Deciduous | 38.3 | 293 | 9.7 | 4872 |
| | Coniferous | 23.8 | 273 | 9.8 | 2580 |

| | | | | | |
|---|---|---|---|---|---|
| Cedar Creek Nat. History Area | Mixed oak | 40.6 | ---- | 11.4 | 3605 |
| | | 51.1 | ---- | 12.7 | 3089 |
| | | 60.2 | ---- | 14 | 3990 |
| | | 52.1 | ---- | 8.6 | 3835 |
| | | 23.8 | ---- | 8.4 | 3445 |
| | | 75.5 | ---- | 11.1 | 4509 |
| | | 92.8 | ---- | 10.9 | 3492 |
| | Mix oak/pine | 69.3 | ---- | 11.5 | 4295 |
| | | 63.1 | ---- | 9 | 5398 |
| | Mesic hardwoods | 63 | ---- | 12 | 3835 |
| | | 37.2 | ---- | 11.2 | 3961 |
| | White cedar | 3.7 | ---- | 7.4 | 6186 |
| | | -1.7 | ---- | 7.4 | 5136 |
| | Lowland hardwoods | 9 | ---- | 11.7 | 2870 |
| | | 23.4 | ---- | 13.4 | 4538 |
| | Savanna | 18.6 | ---- | 10.1 | 349 |

# Chapter 3

# Soil carbon and nitrogen dynamics in forests and grasslands: effects of plant species

## ABSTRACT

Plant species characteristics strongly affect soil organic matter (SOM) turnover and soil fertility, but the relative impact of plant species on the dynamics of labile and more recalcitrant SOM fractions is poorly understood. Using long-term laboratory incubations (387 d), I examined the effects of 5 tree species (*Larix decidua*, *Quercus rubra*, *Pinus resinosa*, *Pinus strobus*, *Picea abies*), 6 grass species (*Andropogon gerardi*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Calamovilfa longifolia*, *Bouteloua curtipendula*, *Panicum virgatum*), and a mixed forest and grassland on kinetically-defined fractions of soil C and N. For all species, net N mineralization was best described using a single pool model ($N_t$=$N_o$(1-$e^{-kt}$)), suggesting that recalcitrant forms of soil N contribute little to net N mineralization. At the Coullee Experimental Forest (La Crosse, Wisc.), *L. decidua* had the highest net mineralization rate constant (0.019 $d^{-1}$), and litter lignin:N correlated negatively with the mineralization rate constant (r=-0.58). In the grass monocultures (Fergus Falls, MN), root lignin:N ratios ranged from 31-60, but grass species had little effect on net N mineralization (aboveground biomass is burned annually). Net N mineralization was lower for the grass species and the mixed grassland compared to the tree species and mixed forest. Carbon mineralization was best described by a two pool model ($C_t=(C_1(1-e^{-ht}))+(c*t)$, but species had no effect on mineralization of either labile C ($C_1$, h) or recalcitrant C ($c*t$). Soil and climatic factors that differed between sites (e.g. soil texture or temperature) affected C mineralization more than differences in vegetation. Plant litter quality did influence soil N dynamics, primarily as a result of plant-soil feedbacks altering the quality of labile soil N pools. This supports the hypothesis that soil microbes act as a "decay filter", converting heterogeneous plant litter into relatively homogeneous, more recalcitrant soil humus.

## INTRODUCTION

Ecologists and soil scientists have studied extensively the connections between nutrient availability, soil characteristics and net primary production (NPP) (reviewed by Mahendrappa et al. 1986). In terrestrial ecosystems, plant soil feedbacks affect soil characteristics such as pH (Binkley and Valentine, 1991; Binkley and Sollins, 1990), cation exchange capacity (Binkley and Sollins, 1990; Homann et al. 1992), and SOM quantity (Handley 1955; Son and Gower, 1992). Nutrient supply, specifically the rate of net N mineralization, is also affected by plant/soil feedbacks (Stone 1975; Pastor et al. 1984; Nadelhoffer et al. 1983; Miles 1985; Hobbie 1992; Binkley 1995). Many studies have addressed the effect of plant litter quality on N release during litter decomposition (Fogel and Cromack, 1977; Melillo et al. 1982; Aber et al. 1990; Harmon et al. 1990). Far fewer studies have examined the relationship between plant litter quality and nutrient release from mineral soil, especially from more recalcitrant pools of SOM. In a recent review, Scott and Binkley (1996) found that tree species altered *in situ* net N mineralization from both the forest floor and mineral soil, suggesting that species might alter N release from the more recalcitrant SOM found in the mineral soil.

Recalcitrant forms of SOM represent a large pool of critical plant nutrients, but are largely unavailable to soil microbes or plants (Mahendrappa et al. 1986; Tate 1987). Studies examining the effects of plant species on SOM turnover often focus on short-term SOM dynamics. Based on 30 day incubations, Wood et al. (1992) demonstrated that in the absence of understory vegetation, loblolly pine depressed C and N mineralization rates 7 years following plantation establishment. Nadelhoffer et al. (1991) also found significant differences in SOM mineralization in soils representing several arctic plant communities. These studies did not quantify the relative contribution of labile and recalcitrant forms of C and N to whole-soil C and N mineralization. Wedin and Pastor (1993) found that differences in *in situ* net N mineralization in a grassland common garden experiment correlated positively with the quality of the labile fraction of soil N, which could be linked to differences in litter quality (Wedin and Tilman, 1990). Research on primary succession and species monocultures suggests that, in addition to labile fractions of SOM (Halvorson et al. 1991), species can alter the rate of total SOM accumulation (due primarily to the presence of nitrogen-fixing trees) (Vitousek et al. 1987; Walker 1989). None of these studies provide evidence for a mechanistic connection between plant litter quality and more recalcitrant SOM formation and turnover.

Plants might alter N release from recalcitrant SOM three ways: changing the total pool size, the relative distribution of SOM between labile and recalcitrant fractions (quality), or the physical protection of SOM (Tate 1987). Based on results from a 77 month litter decomposition study, Melillo et al. (1989) suggested that initial litter chemistry influenced litter decay rates, but has little effect on the lignocellulose index ("quality") of SOM formed after litter decomposes. They proposed that litter passes through a "decay filter", converting heterogeneous plant litter to qualitatively homogeneous SOM. An alternative hypothesis suggests that initial litter chemistry (particularly lignin content) affects N release from more recalcitrant pools of SOM (Berg and McClaugherty, 1987; McClaugherty and Berg, 1987). In the CENTURY model (Parton et al. 1987), litter lignin content controls the accumulation of both C and N in the intermediate (40 year turnover time) pool. This suggests that plant species characteristics can alter the quality and nutrient release from more recalcitrant SOM fractions.

The response of ecosystems to disturbances such as fire, deforestation, or climate-induced changes in species composition depends in part on whether plants modify labile or recalcitrant pools of SOM. If plants modify the large, recalcitrant SOM pool, the signature of previous species might influence site fertility for some time after that species has been replaced. Alternatively, if species alter only labile pools with short turnover times, plant/soil feedbacks will quickly modify nutrient supply based on the litter quality of the new species.

The objective of this work was to examine the effects of tree and grass species on kinetically defined SOM fractions based on long-term laboratory incubations. I tested the hypothesis that plant species, through differences in litter quality and/or quantity, alter C and net N mineralization from more recalcitrant fractions of SOM. I also examined the relative importance of recalcitrant SOM to whole-soil C and N mineralization.

## METHODS

Common garden experiments, with multiple species at single sites, are ideal for addressing species effects on soil processes. Two common garden experiments were identified for this experiment, one containing five tree species and one with six grass species. I also selected one site where both trees and grasses occurred on similar soils with similar climate (not a common garden). Species effects on C and N mineralization were examined using long-term laboratory incubations and non-linear regression to quantify the size and quality of kinetically-defined organic matter pools.

### Site descriptions

#### Forest site

The plantations in the Coullee Experimental Forest (CEF) in La Crosse, WI, were established in 1960 by the Wisconsin Department of Natural Resources to examine the effects of landscape position and vegetation type on soil erosion (Sartz 1978). Four blocks were established on different landscape positions, each containing monocultures of five tree species in 45 m x 45 m plots. Tree species included: European larch (*Larix decidua* Miller), red oak (*Quercus rubra* L.), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L. and Norway spruce (*Picea abies* (L.) Karst.). Soils are predominantly silt loam Typic Hapludalfs. Mean January and July temperatures are -9.1°C and 23.3°C, and annual precipitation averages 780 mm. One of the ridge blocks did not contain red oak, but otherwise the design was a randomized complete block.

In each monoculture plot, five soil cores (5.4 cm diameter by 15 cm deep) were collected in June 1992 along transects (X-shaped) that represented within-plot topographic variation. In addition, three cores were collected along a diagonal transect for root analysis. Soils were stored at 3° C for 2 weeks prior to incubation.

Litterfall and net N mineralization were measured in 1988 and 1989 (Gower and Son, 1992). Litter lignin was not measured for this site, but values for the five tree species were obtained from Aber et al. (1984) and Gower et al. (1989). For further information on vegetation characteristics and site history see Son and Gower (1991).

### Grass site

Grass species monocultures were established in 1982 by the Minnesota Department of Fish and Wildlife and the USDA Soil Conservation Service. Located in Fergus Falls, MN (FF), the site contains several varieties of six grass species (big bluestem (*Andropogon gerardi* Vitm.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash.), Indiangrass (*Sorghastrum nutans* (L.) Nash.), prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and switchgrass (*Panicum virgatum* L.)) in three randomized field blocks. The plots are burned annually to reduce invasion of the monocultures. Soils are classified as Barnes Loams. Mean annual precipitation is 620 mm and mean annual temperature is 5.7°C (see Olson (1984) for additional site information).

In June 1992, two varieties of six species were selected for sampling where invasion by unwanted grass species and other plants was minimal. Four soil cores (5.4 cm diameter by 15 cm deep) were taken from each plot at 2 m intervals along a transect down the center of the plot. Two cores were composited for incubation studies and two were composited for root analysis. Again, soils were stored for 2 weeks at 3°C prior to incubation.

Aboveground production and annual net N mineralization were measured in 1991 by Dr. Dave Wedin (Wedin unpublished data). Net N mineralization was measured using the buried resin bag technique (Binkley and Matson, 1983).

### Forest and grassland site

The University of Wisconsin Arboretum (UWA) contains a collection of ecological communities native to Wisconsin. The Curtis Prairie was restored from degraded pasture in the late 1930's (Sachse 1974). Vegetation is characteristic of tallgrass prairie ecosystems. Soils are predominantly silt-loam or silty clay loam Typic Hapludalfs that are gradually developing a mollic epipedon. Four independent sample sites with similar soil texture were located within the Curtis Prairie, but no attempt was made to standardize species composition between the sites.

Forest sites were located in three different stands around the Arboretum. Noe Woods is characteristic of a northern oak forest, dominated by northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.). Wingra Woods is a northern mesic forest, again dominated by red oak and white oak. Gallistel Woods is a southern mesic forest, with white oak dominating the overstory. Dominant trees on all these sites are at least 125 years old. Soils range from silt-loam to silty clay loam Typic Hapludalfs.

Four sample sites within the three forests were selected to minimize differences in soil texture between the forest and grassland sites (see Table 3.1). At each site, five soil cores (5.4 cm diameter by 15 cm deep) were collected in June 1992, three for incubation studies and two for root analysis. All litter was removed from the surface soil before soil coring. Soils were stored under ice for 3 days and then refrigerated at 3°C for two weeks prior to incubation.

Mean July and January temperatures are 21.2 and -5.2°C (Wisconsin State Climatological Laboratory, Madison, WI), and annual precipitation for the period 1971-1980 averaged 95 cm.

Soil and litter data for all sites are summarized in Table 3.1.

## Laboratory methods

### Long-term laboratory incubations

I used microlysimeters to measure C and net N mineralization through time on single soil samples, with periodic leaching to remove inorganic N (Stanford and Smith, 1972; Nadelhoffer 1990). All soils were passed through a 2 mm sieve, then field moist soil (50 g) was mixed with 40 g of dry, acid washed sand, and the mixture was added to the top portion of a polystyrene filter unit (Falcon No. 7111, 150 mL bottle-top unit). The filter units were modified by placing a nylon screen glued to a PVC ring in the bottom of the filter unit to facilitate removal of the top portion of the filter unit to change filter paper during the incubation. A layer of glass wool was placed on top of the nylon screen to prevent soil from passing through the screen, and the sand/soil mixture was placed on top of the glass wool. Deionized water was then added to the mixture to approximate soil moisture at field capacity.

Although the lack of direct filter/soil contact in the incubation chamber might prevent accurate soil moisture control (Motavalli et al. 1995), this arrangement was necessary for two reasons; filters needed to be replaced during the incubation, and the filter units were not gas tight (R. Hubbard, unpublished data), so $CO_2$-C measurements had to be made in gas-tight containers. During leaching, the units were sealed so that the entire volume (not just the soil/filter paper contact) was evacuated to the required suction. Leachate recovery averaged 97.4% and 102.4% on the first two sample dates, suggesting that the soil/sand mixture remained relatively close to the calculated field capacity moisture content.

$CO_2$-C production was measured seven times (22, 61, 91, 151, 211, 307 and 387 days) by incubating the soil in a 1 L Mason jar and trapping $CO_2$ in alkaline base traps (2-5 mL of 1-5$\underline{N}$ NaOH, depending on respiration rates). $CO_2$-C production was quantified by adding 1 mL of 1.5$\underline{M}$ $BaCl_2$ to 1 mL of NaOH (to precipitate carbonates) and titrating the remaining NaOH with 1.000$\underline{N}$ HCl to a pH of 8.3. At each date, soils (filter units) were removed from the Mason jars, mounted on a filtration apparatus, and leached with 100 mL of a dilute salt solution (4 $\underline{mM}$ $CaCl_2$, 2 $\underline{mM}$ $KH_2PO_4$, 1 $\underline{mM}$ $K_2SO_4$ and $MgSO_4 \cdot 7H_2O$, 25 $\underline{\mu M}$ $H_3BO_3$, 2 $\underline{\mu M}$ $MnSO_4 \cdot H_2O$ and $ZnSO_4 \cdot 7H_2O$, and 0.5 $\underline{\mu M}$ $CuSO_4 \cdot 5H_2O$ and $Na_2MoO_4 \cdot 2H_2O$) (Nadelhoffer 1990) to measure net mineral-N production. I equilibrated soils with leaching solution for 40 minutes, then leached at -0.05 MPa suction until no further solution passed through the filter (≈15-20 minutes). Recovery of leaching solution ranged from 90-105% across all sample dates. Leachate was analyzed for $NO_3^-$-N and $NH_4^+$-N on a Lachat flow injection analyzer (Lachat Instruments 1988).

Soil and litter analyses

I collected roots by soaking soil cores in water for 30 minutes, then collected floating roots on a 1 mm sieve. Roots were dried at 55° C, ground to < 0.5 mm and analyzed for total C and N (Carlo Erba C/N analyzer) and lignin content (modified Van Soest digestion (Van Soest and Wine, 1968; Waldern 1971)).

Soil analysis included pH, total C and N, and texture. Soil pH was measured by mixing 10 g of soil with 50 mL of 0.01N $CaCl_2$, agitating briefly, and measuring pH in the supernatant using a glass electrode after 15 minutes of settling. I used the hydrometer method to measure soil texture (Gee and Bauder, 1986). Soils used for C and N measurement were sieved through a 2 mm sieve (all visible root fragments removed), dried at 60°C, and ground to pass through a 0.25 mm screen. Soil C and N determinations were done on a Carlo Erba C/N analyzer.

## Estimating labile and recalcitrant soil organic matter pools

Qualitative differences in SOM pools were assessed by fitting non-linear exponential decay models to cumulative C and N release. Depending on SOM characteristics, cumulative C and N release may be represented well by a single pool model

$$M_t=M_o(1-e^{-kt}) \qquad \text{(Eq. 1)}$$

where $M_t$ is cumulative C or N mineralization through time (potentially mineralizable C, N, Stanford and Smith, 1972), or by a two pool model

$$M_t=(M_1(1-e^{-ht}))+ct \qquad \text{(Eq. 2)}$$

where $M_1$ represents the labile C or N pool, "h" is the mineralization rate constant for the labile pool, and "c" is the constant mineralization of recalcitrant SOM (Bonde and Rosswall, 1987). Equation 2 assumes that one SOM fraction (more recalcitrant) mineralizes at a constant rate. Alternatively, C and N release could be represented by the two pool model

$$M_t=M_1*s(1-e^{-ht})+M_1*(1-s)(1-e^{-bt}) \qquad \text{(Eq. 3)}$$

with exponential decay of both pools. "S" is the proportion of $M_1$ in the labile pool, and "b" is the mineralization rate of recalcitrant SOM (Deans et al. 1986; Bonde and Rosswall, 1987).

### Statistical Analysis

Cumulative C and N mineralization results were fit to each of the three equations using procedure NLR (SPSS Inc. 1988). Default convergence criteria (reduction in sums of squares $\leq 1E^{-8}$) and maximum number of iterations (100) were used in all cases. Different initial conditions were used to ensure the non-linear curve-fit was robust. If convergence did not occur in the default number of iterations, the analysis was terminated. To evaluate which model gave the "best" fit, I examined residual distributions, parameter correlations, and reduction in residual sums of squares (Bates and Watts, 1988). If the simpler models (i.e. fewer parameters) gave a better fit, that model was assumed to be the "best" model describing C and net N mineralization. I fit the "best" non-linear model to each species/block combination, giving me a data set of regression parameters that could be used subsequently to examine species and ecosystem effects on C and N dynamics. In addition, the model was fit to the entire data set for each species (Table 3.2).

Species effects on C and N mineralization dynamics were examined within a site using procedure ANOVA (SPSS Inc. 1988). An F-protected LSD was used to compare species within sites. Within each site, species and block were the main factors, and the interaction term was used as the error term in the ANOVA.

## RESULTS

### Total soil carbon and nitrogen

At each site, species had no effect on total soil N ($p>0.45$, Fig. 3.1). At CEF, *Q. rubra* had significantly lower total soil C ($p=0.07$) and *P. abies* had the highest (Fig. 3.1). Soil C:N ratio was also significantly lower for *Q. rubra* (9.4, $p=0.01$) and highest for *P. abies* (11.9). Grass species had no significant effect on total soil C or C:N ratio ($p=0.98$ and 0.10, respectively), although soil C:N ratio was 26% higher for *B. curtipendula* than for *C. longifolia*). Forest and grassland at UWA did not differ in total soil C or C:N ratio ($p=0.90$ and 0.85, respectively). The grass monoculture plots at FF had the highest total soil C and N and tree species plots at CEF had the lowest (Fig. 3.1).

### Carbon mineralization

For all species and ecosystems, Eq. 2 best described cumulative C mineralization. In several cases, Eq. 3 did not converge on a solution before reaching the maximum number of iterations. Although statistical comparison of Eqs. 1 and 2 was not possible (because they are not nested models), other criteria (e.g. residual distribution) suggested that Eq. 2 better described cumulative C mineralization. This suggests that 2 pools of soil carbon contribute to C mineralization in these soils: a labile pool ($C_l$) that decays exponentially, and a more recalcitrant pool that decays at a constant rate ("$c_c$"). The influence of these two pools on cumulative C release is shown clearly in Figs. 3.2 and 3.3. Initially, C mineralization rates were high, but they decreased until day 151 (Fig. 3.3), after which they were relatively constant and did not approach zero.

Within each site, species had no effect on recalcitrant C mineralization ($p>0.41$) or the size of the labile C pool ($p>0.41$) (Table 3.2). At CEF, the mineralization rate of the labile C pool ($k_c$) was significantly higher ($p<0.01$) for *Q. rubra* (Table 3.2, Fig. 3.3), and correlated positively with root lignin:N ratio ($r=0.63$, $p<0.01$). Aboveground litter lignin or lignin:N ratio correlated weakly with $k_c$ ($p=0.08$ and 0.18, respectively).

Ecosystem type and species had less influence on soil C dynamics than site characteristics (Table 3.2, Figs. 3.2, 3.3). Although recalcitrant C mineralization rates were higher for the tree species than the grass species (Table 3.2), the forest and grassland at UWA did not differ. Total soil C correlated strongly with $c_c$ across all sites ($r=-0.72$, $p<0.01$) and at UWA ($r=-0.93$, $p<0.01$) in spite of no difference between the forest and grassland in total soil C. Soil clay content also correlated negatively with $c_c$ and total C mineralization across all sites ($r=-0.67$ and $-0.80$, respectively, $p<0.01$), while silt content correlated positively with $c_c$ and total C mineralization ($r=0.65$ and 0.78 respectively, $p<0.01$). Multiple regression on all soils ($n=45$) showed that total soil C was most closely related to differences in $c_c$ ($R^2=0.75$), and adding soil silt content to the model further increased the goodness of fit ($R^2=0.86$). Interestingly, if a subset of the data containing complete information for litterfall and litter N (tree and grass species information) were used for the multiple regression analysis (n=33), total soil C still explained most of the variation in $c_c$ ($R^2=0.85$). This suggests that in spite of large differences in litter chemistry and litter inputs between forests and grasslands (Table 3.1), soil factors such as total soil C and texture accounted for most of the variation in mineralization of recalcitrant soil C mineralization.

The size of the labile C pool was also smaller for the grass species than the tree species ($C_1$,Table 3.2), and correlated negatively with total soil C both within sites (r=-0.48 and -0.60 at CEF and FF) and across sites (r=-0.71); again, the forest and grassland at UWA did not differ (Table 3.2). Stepwise multiple regression analysis showed that total soil C explained the greatest proportion of the variation in $C_1$ ($R^2=0.49$ for all soils), and adding clay content to the model increased slightly the goodness of fit ($R^2=0.53$).

### Nitrogen mineralization

For all soils, Eq. 1 best described cumulative net N mineralization (Fig. 3.4). Residual sums of squares were similar for both Eq. 1 and 2, and estimates of $N_o$ and $N_1$ were similar. This suggests that: 1) net mineralization of N occurs primarily from a single pool with exponential decay and 2) more recalcitrant pools of organic matter contribute very little to available N pools. Net N mineralization rates approached zero for most of the soils in this experiment (Fig. 3.5).

Although net N mineralization differed by two-fold during the first 60 days, species had no significant effect on $N_o$ (p=0.86). Species altered the mineralization rate constant only slightly ($k_n$, p=0.10, Table 3.2). *L. decidua* had the highest net N mineralization rate between 0-30 days, and *Q. rubra* had the lowest (Fig. 3.5b). However, *Q. rubra* had the highest total net N mineralization of any of the tree species (Fig. 3.4b). The mineralization rate constant ($k_n$) correlated negatively with both aboveground litter lignin concentration ($r=-0.58$, $p=0.01$) and litter lignin:N ratio ($r=-0.67$, $p=0.01$), suggesting that litter quality alters the quality, not quantity, of mineralizable N.

Grass species had no significant effect on $N_o$ ($p=0.49$) or $k_n$ ($p=0.75$). However, species differences in $k_n$ and $N_o$ ranged from about two- to three-fold, respectively. Variation in $N_o$ was unrelated to differences in root lignin, lignin:N ratio and biomass ($p=0.49$, 0.46, and 0.73, respectively) or $k_n$ ($p=0.53$, 0.43, and 0.30, respectively). The grass monocultures at FF are burned annually, so aboveground litter inputs were not considered.

Potentially mineralizable N was almost twice as high for the tree species than the grass species, with little difference in $k_n$ (Table 3.2). Similarly, at UWA, $N_o$ was almost seven-fold higher in the forest than in the grassland (Fig. 3.4, Table 3.2). Most of the net N mineralized in the forest ecosystem occurred between 0-151 days, supporting the idea that species effects on net N mineralization occur primarily in labile soil N pools. Root lignin content at UWA ranged from 137-344 mg $g^{-1}$, and correlated highly with $N_o$ ($r=0.93$, $p<0.01$). Across all sites, $N_o$ also correlated with root lignin concentration ($r=0.35$, $p=0.02$). However, regression analysis suggested that variation in both soil clay and N content explained the greatest proportion of the variation in $N_o$ across all sites ($R^2=0.21$), suggesting that as with C, site factors have a greater effect on C and N pool sizes across a range of sites. At CEF, soil clay content (15-21%) correlated negatively with $N_o$ ($r=-0.58$, $p=0.01$), further supporting the idea that variation in soil characteristics influences N pool sizes more than differences in vegetation.

Between 307-387 d, net N mineralization rates varied from 2 to 37 μg N $g^{-1}$ N $d^{-1}$, and correlated positively with potentially mineralizable N ($r=0.86$, $p<0.01$). This suggests that the amount of mineralizable N influences net N release from more recalcitrant soil N pools, possibly through the production of stable microbial metabolites. Both litter and root "quality" related poorly to net N mineralization rates after 307 d. This is further evidence that large differences in initial litter quality between species and ecosystems do not influence N release from more recalcitrant pools of organic matter, and furthermore that more recalcitrant N pools contribute little to annual net N mineralization.

### Laboratory and *in situ* net N mineralization

In spite of differences in $N_o$ and $k_n$ for both tree and grass species (Table 3.2), they related poorly to *in situ* net N mineralization (Fig. 3.7). Potentially mineralizable N ($N_o$) correlated poorly with *in situ* net N mineralization for tree species ($p=0.72$) and grass species ($p=0.44$), and $k_n$ also related poorly to *in situ* net N mineralization ($p=0.43$ for all species).

## DISCUSSION

Despite large differences in initial litter quality (Table 3.1), my results indicate that plant species can influence the mineralization of more labile forms of C and N, but have little impact on the mineralization of C and N from more recalcitrant pools. Fitting two pool regression models (Eqs. 2 and 3) did not explain more of the variation in cumulative net N mineralization than a single pool model (Eq. 1), suggesting that only one pool of soil

N contributes to net N mineralization during the incubation. In contrast, a two pool model (Eq. 2) predicted more of the variation in cumulative C mineralization, but species had little influence on C mineralization from the more recalcitrant pool (Table 3.2, Fig. 3.3). This supports the hypothesis that during litter decomposition, soil microbes act as a filter, converting heterogeneous plant litter into a more uniform soil humus pool (Melillo et al. 1989).

An alternate explanation for a lack of species effects on mineralization of recalcitrant SOM is that the monoculture plots had not been established long enough to modify more recalcitrant SOM pools. In the CENTURY model (Parton et al. 1987), the intermediate pool of SOM has a turnover time of 40 y. The tree species monocultures have been established for 34 years, and the forest/grassland plots at UWA are at least 60 y old. If a discrete, intermediate pool of SOM exists (turnover time of *ca.* 40 y), this pool should influence the mineralization of more recalcitrant forms of C and N from soils at CEF and UWA.

Results from this work indicate that a single soil N pool contributes significantly to net N mineralization during long-term laboratory incubations, and that recalcitrant forms of soil N contribute little to net N mineralization. This does not, however, mean that N cycling stops once labile N is completely mineralized. Gross N mineralization most likely continues throughout the incubation (Hart et al. 1994), but is offset by N immobilization, giving no net N mineralization. Previous work, primarily on agricultural soils, suggested that long-term N mineralization kinetics were best described by a two-pool model (Deans et al. 1986; Bonde and Rosswall, 1987). In addition, long-term net N mineralization from grass monoculture soils at the Cedar Creek Natural History Area was best described by a two pool model (Eq. 2) (Wedin and Pastor, 1993). Interestingly, all of the examples where two pool models best described cumulative N mineralization were in soils either currently being cultivated or heavily disturbed four years prior to sampling (Wedin and Pastor, 1993); therefore, it is unlikely that plant inputs, litter decomposition, soil organic matter mineralization, and N cycling rates were at steady-state. The time required for steady-state rates of net N mineralization to be achieved is not known, but the grass monoculture plots at FF may have come closer to steady state in 10 y. However, if the net N mineralization dynamics during the long-term laboratory incubations reflect a steady-state between litter inputs and OM quality, one would expect a relationship between laboratory net N mineralization kinetics and *in situ* net N mineralization. My results indicate that for these soils, laboratory net N mineralization dynamics ($N_o$, $k_n$, Eq. 1) correlated poorly with *in situ* net N mineralization, suggesting that laboratory determinations of potentially mineralizable N in relatively undisturbed ecosystems may not be a good predictor of N availability as has been shown for agriculture systems (Cabrera and Kissel, 1988).

Previous work suggests a greater accumulation of more recalcitrant SOM in grasslands compared to forests on uniform soils (Stevenson 1982; Tate et al. 1995). Across sites, total soil C was higher and recalcitrant C mineralization was lower in the grass monocultures at FF compared to the tree monoculture plots at CEF, suggesting a larger pool of more recalcitrant C in the grassland. However, at UWA, both total C (Fig. 3.1) and recalcitrant C mineralization rates (Table 3.2, Fig. 3.3) were similar in the forest and grassland on uniform soils. Besides the differences in vegetation between CEF and FF, soil clay content was two-fold higher at FF (Table 3.1). Higher clay content can lead to a greater stabilization of soil C (Sorenson 1981), and may increase the formation of more recalcitrant soil C (Parton et al. 1987). An alternative hypothesis is that the colder climate at FF (primarily winter temperatures) increased the formation of more recalcitrant forms of SOM. Models of soil C dynamics suggest that with a decrease in temperature (but similar vegetation), the formation of more recalcitrant forms of soil C increases (Potter et al. 1993). This suggest that in spite of large differences in aboveground litter and root tissue chemistry (Table 3.1), formation and turnover of more recalcitrant forms of soil C were probably influenced more by soil or climatic characteristics than by vegetation characteristics.

As with soil C mineralization, species had little influence on mineralization of N from more recalcitrant sources, and it appears that for these soils, recalcitrant sources of N contribute little to net N mineralization (Fig. 3.4). However, grassland soils had lower rates of net N mineralization than the forests both across sites and within sites, suggesting that grass species do lower rates of net N mineralization more than tree species. Other studies have also measured lower rates of net N mineralization in grasslands than in forests (Mazzarino et al. 1991; Hart et al. 1993), but these comparisons were not done on similar soils. Hart et al. (1993) found significantly higher N immobilization rates in annual grasslands compared to an adjacent coniferous forest as a result of larger higher labile C pools and (therefore) more rapid microbial biomass turnover in the grassland soil. This rapid microbial turnover could increase the rate of soil humus formation, and (possibly) faster formation of more recalcitrant forms of soil C and N. However, I observed that labile and recalcitrant C mineralization were similar when forests and grasslands were compared on similar soils (UWA, Fig. 3.2), suggesting that this hypothesis is incorrect. An alternative hypothesis is that increased fine root inputs in the grassland enhances N immobilization and decreases net N mineralization.

In spite of two-fold differences in root lignin:N ratios (31-60, Table 3.1), I found no significant species effect on *in situ* net N mineralization or C and N mineralization during laboratory incubations at Fergus Falls. Wedin and Tilman (1990) found that after 3 years, *in situ* net N mineralization in perennial grass monocultures was higher for the species with lower root biomass and low lignin:N ratio. The highest rates of *in situ* net N mineralization occurred under *Agrostis scabra* Wiild. (root lignin:N of 8.6) and the lowest rates under the two C4 species (*Schizachyrium scoparium* (Michx.) Nash-Gould and *Andropogon gerardi* Vitm. (lignin:N of 23.0 and 26.8, respectively). In subsequent work on the same species, Wedin and Pastor (1993) correlated changes in *in situ* net N mineralization with the mineralization rate of labile soil N, not the size of the pool (cf. Table 2, Wedin and Pastor, 1993). The two C4 species had the largest labile soil N pool but the lowest mineralization rate. This suggests that species effects on the quality of more labile SOM pools is the important determinant of field net N mineralization rates. However, my results showed no significant relationship between root lignin:N ratio and net N or C mineralization for the grass species at FF, but the lowest root lignin:N ratio for these grass species was 30 (Table 3.1) compared to 8.6 for *A. scabra*. Other research has demonstrated a negative, non-linear relationship between litter lignin:N ratios and *in situ* net N mineralization (Stump and Binkley, 1993; van Cleve et al. 1993; Scott and Binkley, 1996). It appears that for the grass species at FF, root lignin:N ratios were too high to greatly influence either *in situ* net N mineralization rates or laboratory rates of C and N mineralization.

Although tree species had little influence on the labile C pool and recalcitrant C mineralization, the mineralization rate constant for labile C was almost two-fold higher under *Q. rubra* (Table 3.2). Besides being more decomposable, total soil C was also lowest under *Q. rubra*. Several studies have shown that plant species can influence the size of earthworm populations (Boettcher and Kalisz, 1991; Zou 1993). Graham and Wood (1991) hypothesized that greater earthworm activity under scrub oak (*Quercus dumosa* Nutt.) compared to Coulter pine (*Pinus coulteri* B. Don) redistributed silt and clay particles from B to A horizons. Greater earthworm activity under *Q. rubra* may have redistributed organic matter deeper in the soil profile, and possibly enhanced soil C decomposability. Gower and Son (1992) found that between 0-30 cm, soil C was not lower under *Q. rubra* compared to the other tree species at CEF. This supports the hypothesis that soil C concentrations between 0-15 cm were lower for *Q. rubra* because of organic matter redistribution, not a depletion of soil C. Earthworm casts can contain stabilized residue fragments, making them physically unavailable to soil microbes (Lee 1985). These casts might have been broken when soil and sand were mixed prior to the long-term incubations, releasing a pool of readily decomposable organic matter (Figs. 3.2 and 3.3). Other work (Scott 1996) suggests that macroaggregate stabilization was greater under *Q. rubra*, but that the aggregates were highly unstable. This could also be explained by greater earthworm activity under *Q. rubra.* This suggests an indirect influence of plant species on soil organic matter dynamics as a result of litter quality effects on soil fauna populations.

Understanding species effects on SOM dynamics is important when developing management strategies that include changing species composition. Specifically, do plants modify soil nutrient cycles to meet their own nutritional requirements, and if so how quickly? It appears that this modification can happen fairly quickly, and that plant characteristics have a greater effect on the turnover of labile SOM pools than on more recalcitrant pools of OM. Soil characteristics such as texture appear to be important controls on recalcitrant SOM dynamics than plant characteristics. However, it is also important to remember that the monocultures used in this experiment (and others) are relatively young compared to the age of more recalcitrant SOM fractions present in SOM simulation models (Parton et al. 1987), and it could take several decades before species modify these more recalcitrant fractions.

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Table 3.1. Species and site characteristics for monoculture plots at Coullee Experimental Forest (CEF) and Fergus Falls (FF). Values for mixed forest and grassland plots at U. Wisconsin Arboretum (UWA). Values in Parentheses represent one standard deviation.

| Site/ Species | Leaf litter[v] | Leaf N[v] | Leaf lignin[v] | Root biomass | Root N | Root lignin | netNmin[z] | netNmin | SoilpH | %clay | %sand |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | g m$^{-2}$ | ----g kg$^{-1}$---- | | g m$^{-2}$ | -------g kg$^{-1}$-------- | | kg ha$^{-1}$y$^{-1}$ | µg N g$^{-1}$ resin y$^{-1}$ | | | |
| **CEF** | | | | | | | | | | | |
| *L. decidua* | 367 | 10.8 | 126 | 120 | 11.6 | 344 | 117[v] | ---- | 4.37 | 18 | 24.5 |
| | (2.4) | | | (35) | (2.7) | (60) | | | (.33) | (5.4) | (12.6) |
| *P. abies* | 411 | 9.9 | 268 | 196 | 8.7 | 328 | 46 | ---- | 4.12 | 19 | 16.8 |
| | (77) | | | (26) | (1.9) | (40) | | | (.18) | (1.6) | (3.4) |
| *Q. rubra* | 428 | 8.6 | 248 | 156 | 6.9 | 375 | 55 | ---- | 4.24 | 20.3 | 21.7 |
| | (215) | | | (56) | (.7) | (35) | | | (.17) | (.6) | (8.3) |
| *P. resinosa* | 446 | 7.2 | 219 | 165 | 11.3 | 369 | 51 | ---- | 4.34 | 18.3 | 23.5 |
| | (550) | | | (30) | (2.9) | (26) | | | (.1) | (3.1) | (6.6) |
| *P. strobus* | 321 | 8.3 | 225 | 166 | 10.2 | 363 | 87 | ---- | 4.59 | 18.8 | 32.5 |
| | (70) | | | (114) | (2) | (14) | | | (.16) | (2.6) | (18.7) |
| **FF** | | | | | | | | | | | |
| *A. gerardi* | ---- | 6.0 | ---- | 1116 | 3.0 | 180 | ---- | 58.2[y] | 7.46 | 32.2 | 35.2 |
| | | (.4) | | (620) | (.4) | (14) | | (18) | (.24) | (2.2) | (3.5) |
| *S. nutans* | ---- | 5.8 | ---- | 537 | 5.6 | 172 | ---- | 77.5 | 7.35 | 34.3 | 30.3 |
| | | (6) | | (137) | (1.3) | (31) | | (22) | (.33) | (2.3) | (1.5) |
| *C. longifolia* | ---- | 9.1 | ---- | 787 | 3.5 | 170 | ---- | 98 | 7.34 | 33.8 | 31.5 |
| | | (2) | | (263) | (.2) | (4.3) | | (37) | (.28) | (1.7) | (3.2) |
| *P. virgatum* | ---- | 6.0 | ---- | 1413 | 4.2 | 151 | ---- | 74.2 | 7.46 | 33.3 | 32.7 |
| | | (.3) | | (602) | (.6) | (13) | | (14) | (.3) | (1.5) | (4.6) |
| *S. scoparium* | ---- | 7.0 | ---- | 1068 | 3.8 | 140 | ---- | 97.4 | 7.5 | 32 | 32.5 |
| | | (1) | | (701) | (.6) | (14) | | (64) | (.16) | (1.1) | (3.9) |
| B. curtipendula | ---- | 8.1 | ---- | 660 | 4.8 | 181 | ---- | 98.5 | 7.6 | 32.5 | 34.3 |
| | | (.9) | | (243) | (.6) | (18) | | (42) | (.05) | (2) | (4.6) |

Table 3.1 continued

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **UWA** | | | | | | | | | | | |
| oak forest | ---- | ---- | 135[w] | 206 | 10.5 | 292 | 120[x] | ---- | 4.52 | 23.3 | 14.8 |
| | | | (7.2) | (91) | (1.8) | (67) | (19) | | (.37) | (2.9) | (3.4) |
| grassland | ---- | ---- | ---- | 637 | 5.0 | 163 | ---- | ---- | 4.98 | 22.5 | 12.5 |
| | | | | (267) | (.7) | (29) | | | (.37) | (1.7) | (2.5) |

[v] Gower and Son (1992) and Yowhan Son, unpublished data.
[w] John Aber unpublished data
[y] Dave Wedin unpublished data

Table 3.2. Parameter estimates (and 95% confidence interval) for cumulative C and N mineralization during 387 d laboratory incubations.

| | $N_o$ mg N | $k_n$ $g^{-1}N$ $day^{-1}$ | $C_1$ mg C $g^{-1}$ C | $k_c$ $day^{-1}$ | $c_c$ mg C $g^{-1}$ C $day^{-1}$ |
|---|---|---|---|---|---|
| **Coullee Experimental Forest** | | | | | |
| *Larix decidua* | 16.6 (4.86) | .0187 (.021) | 74.5 (29.6) | .0149 (.009) | .253 (.088) |
| *Picea abies* | 18.3 (7.49) | .012 (.015) | 58.3 (12.02) | .021 (.008) | .273 (.04) |
| *Quercus rubra* | 23.8 (15) | .0067 (.0096) | 65.9 (19.1) | .0379 (.031) | .274 (.073) |
| *Pinus resinosa* | 12.8 (6.61) | .011 (.017) | 62.8 (39) | .018 (.018) | .271 (.123) |
| *Pinus strobus* | 14.8 (16) | .0049 (.01) | 76.6 (66) | .0176 (.025) | .215 (.21) |
| **Fergus Falls** | | | | | |
| *Agropyron gerardi* | 10.4 (4.99) | .0099 (.013) | 42.3 (13.1) | .0181 (.009) | .101 (.042) |
| *Sorghastrum nutans* | 4.41 (1.75) | .0202 (.032) | 45.2 (11.2) | .0196 (.009) | .11 (.036) |
| *Calamovilfa longifolia* | 15.7 (4.12) | .011 (.008) | 37.1 (9.4) | .0213 (.01) | .109 (.032) |
| *Panicum virgatum* | 7.3 (1.2) | .026 (.02) | 38.1 (9.5) | .0208 (.009) | .106 (.031) |
| *Schizachyrium scoparium* | 8.4 (3.12) | .0104 (.011) | 42.7 (14.4) | .0177 (.01) | .079 (.045) |
| *Bouteloua curtipendula* | 7.2 (2.14) | .0138 (.014) | 39.8 (10.5) | .0197 (.009) | .099 (.034) |
| **U. Wisconsin Arboretum** | | | | | |
| Mixed oak forest | 22.7 (3.8) | .0203 (.14) | 45.6 (9.4) | .026 (.012) | .279 (.033) |
| Mixed species grassland | 4.41 (1.44) | .0111 (.011) | 57 (32) | .022 (.0244) | .253 (.107) |

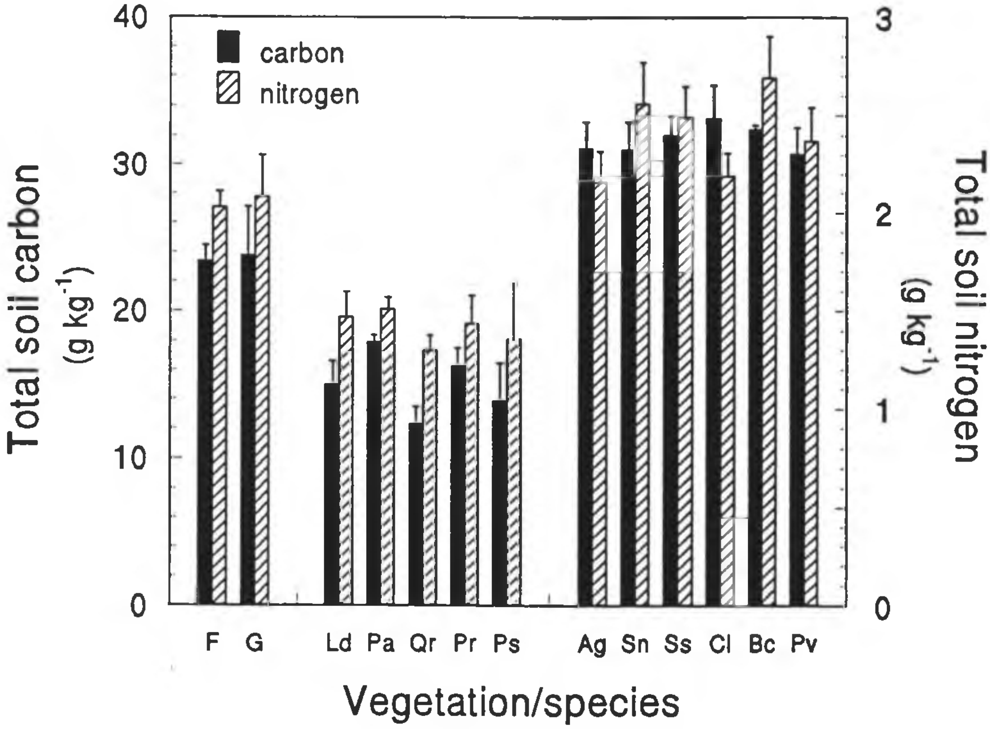

Figure 3.1. Total soil carbon and nitrogen (to 15 cm) for mixed forest and grassland, 5 tree species at Coullee Experimental Forest and 6 grass species at Fergus Falls. Bar labels are as follows: UWA site: F=forest, G=grassland. CEF site: Ld=*Larix decidua*, Pa=*Picea abies*, Qr= *Quercus rubra*, Pr=*Pinus resinosa*, Ps=*Pinus strobus*. FF site: Ag=*Andropogon gerardi*, Sn=*Sorghastrum nutans*, Ss=*Schizachrium scoparium*, Cl=*Calamovilfa longifolia*, Bc=*Bouteloua curtipendula*, and Pv=*Panicum virgatum*.

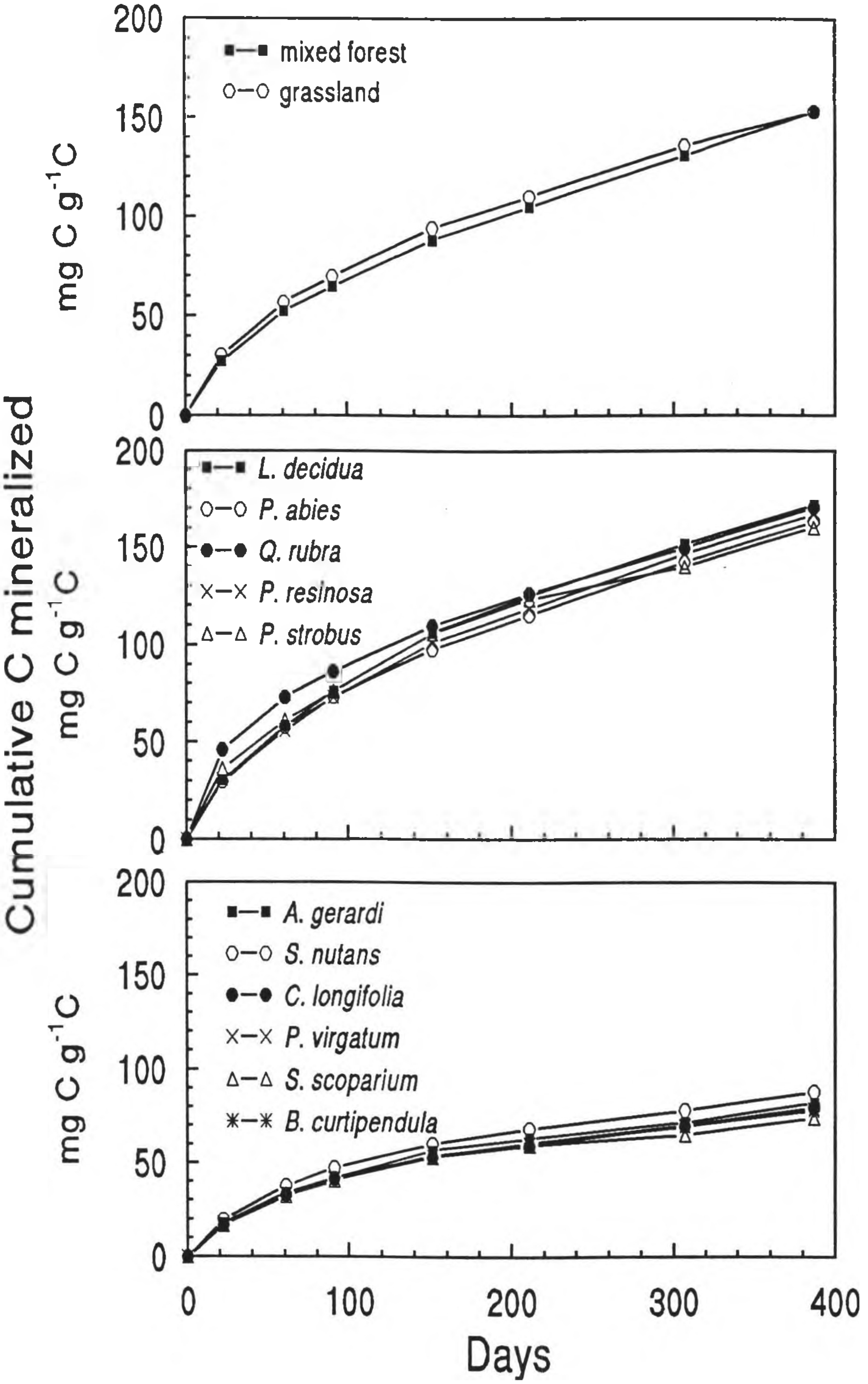

Figure 3.2. Cumulative C mineralization during 387 d laboratory incubations for a) forest and grassland on similar soils at U. Wisconsin Arboretum b) tree species at Coullee Experimental Forest and c) grass species at Fergus Falls.

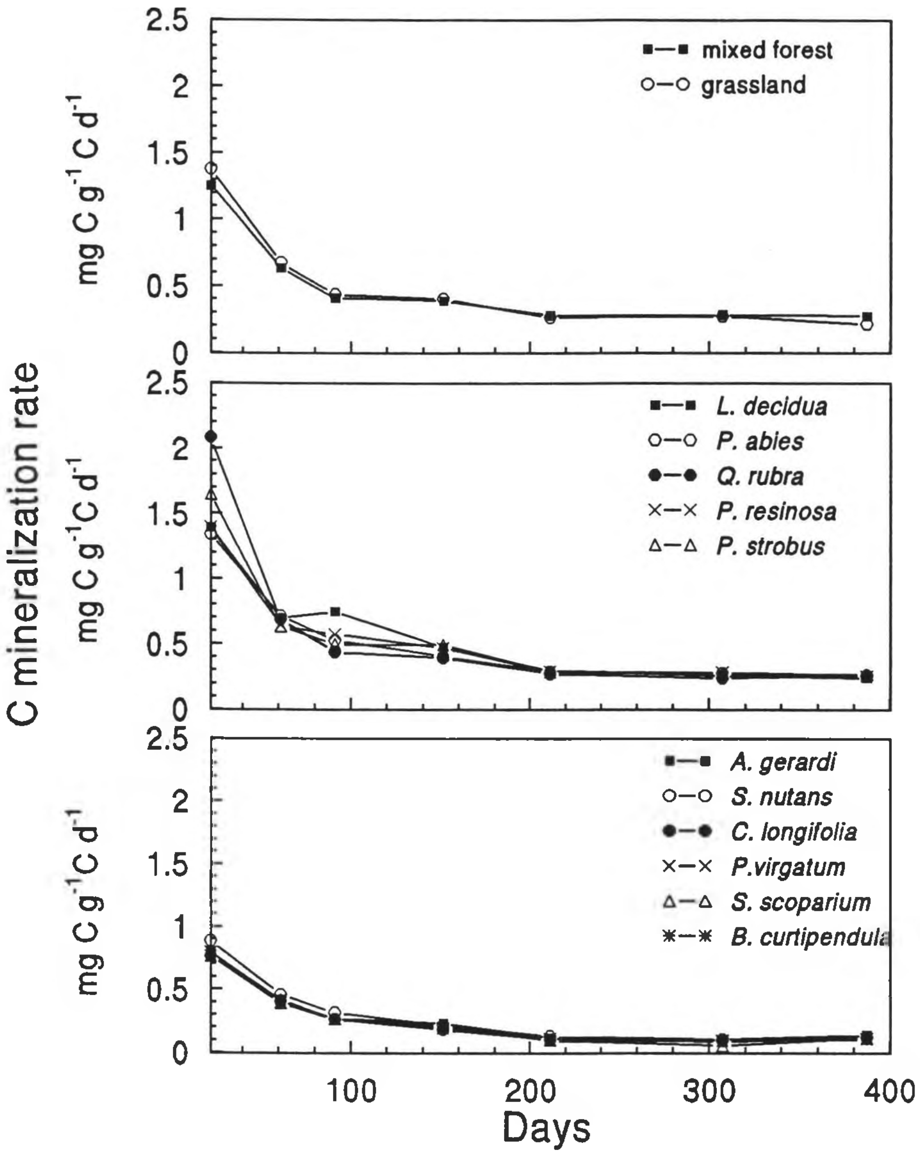

Figure 3.3. Carbon mineralization rates during 387 d laboratory incubations for a) forest and grassland on similar soils at U. Wisconsin Arboretum b) tree species at Coullee Experimental Forest and c) grass species at Fergus Falls.

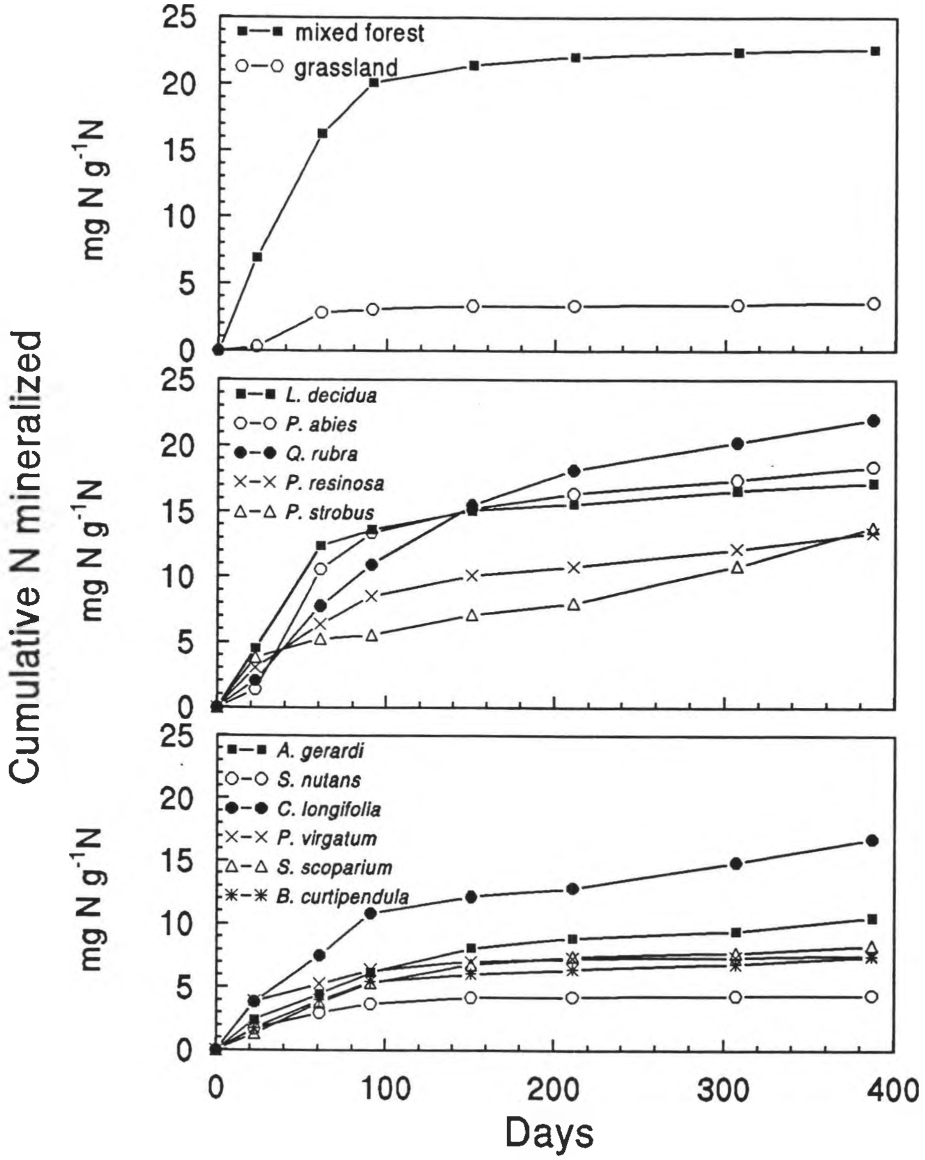

Figure 3.4. Cumulative N mineralization during 387 d laboratory incubations for a) forest and grassland on similar soils at U. Wisconsin Arboretum b) tree species at Coullee Experimental Forest and c) grass species at Fergus Falls.

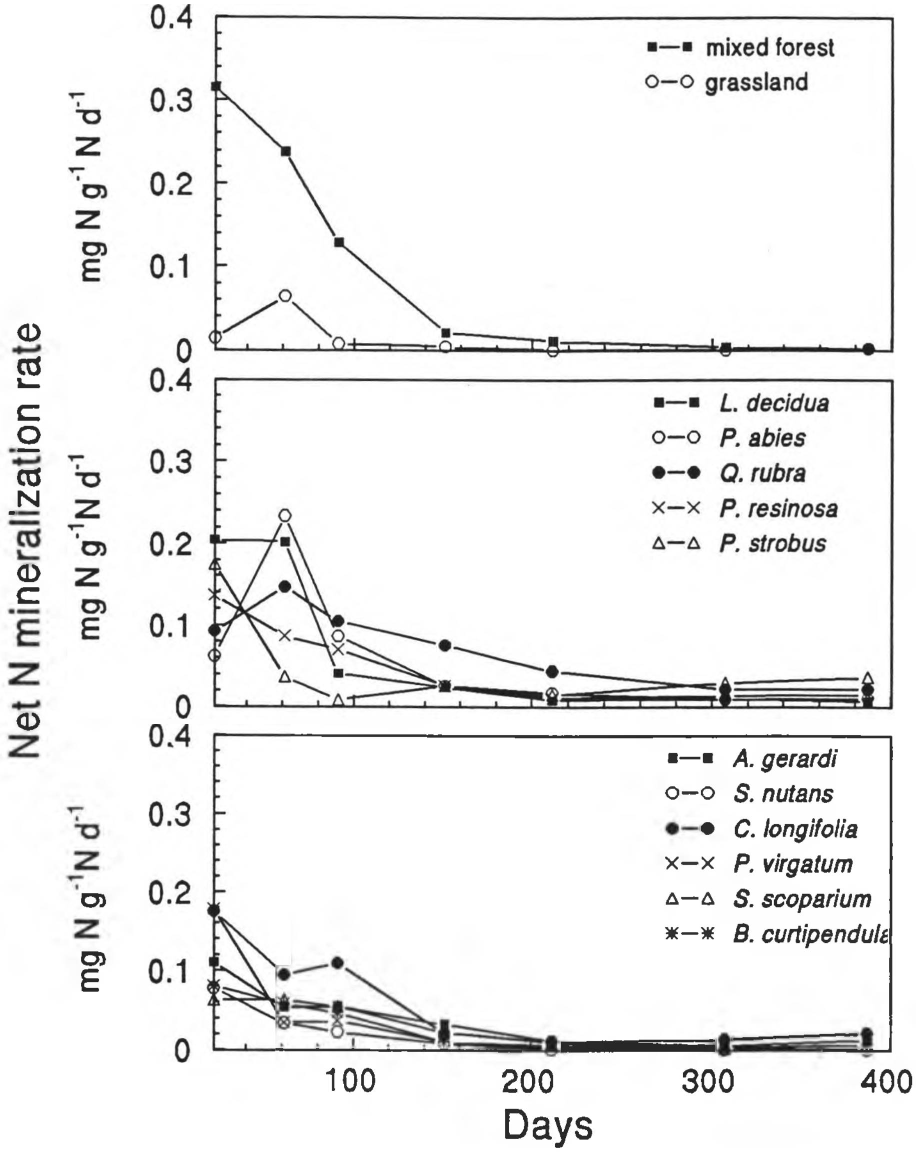

Figure 3.5. Nitrogen mineralization rates during 387 d laboratory incubations for a) forest and grassland on similar soils at U. Wisconsin Arboretum b) tree species at Coullee Experimental Forest and c) grass species at Fergus Falls.

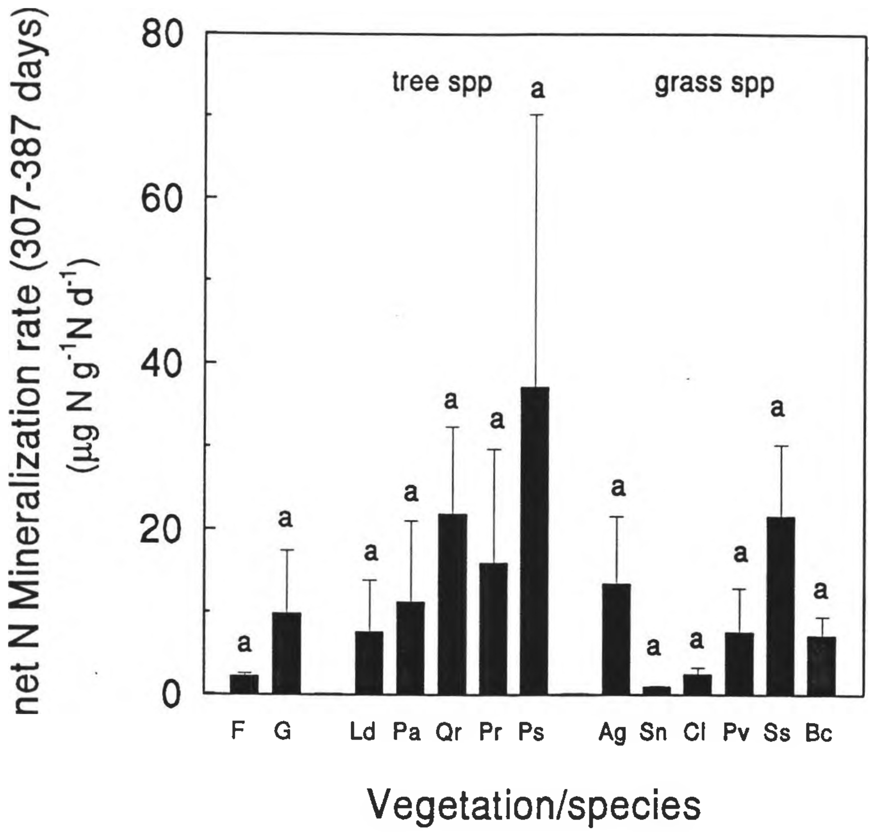

Figure 3.6. Nitrogen mineralization rates between 307-387 d during laboratory incubations. Bar labels as in Figure 1.

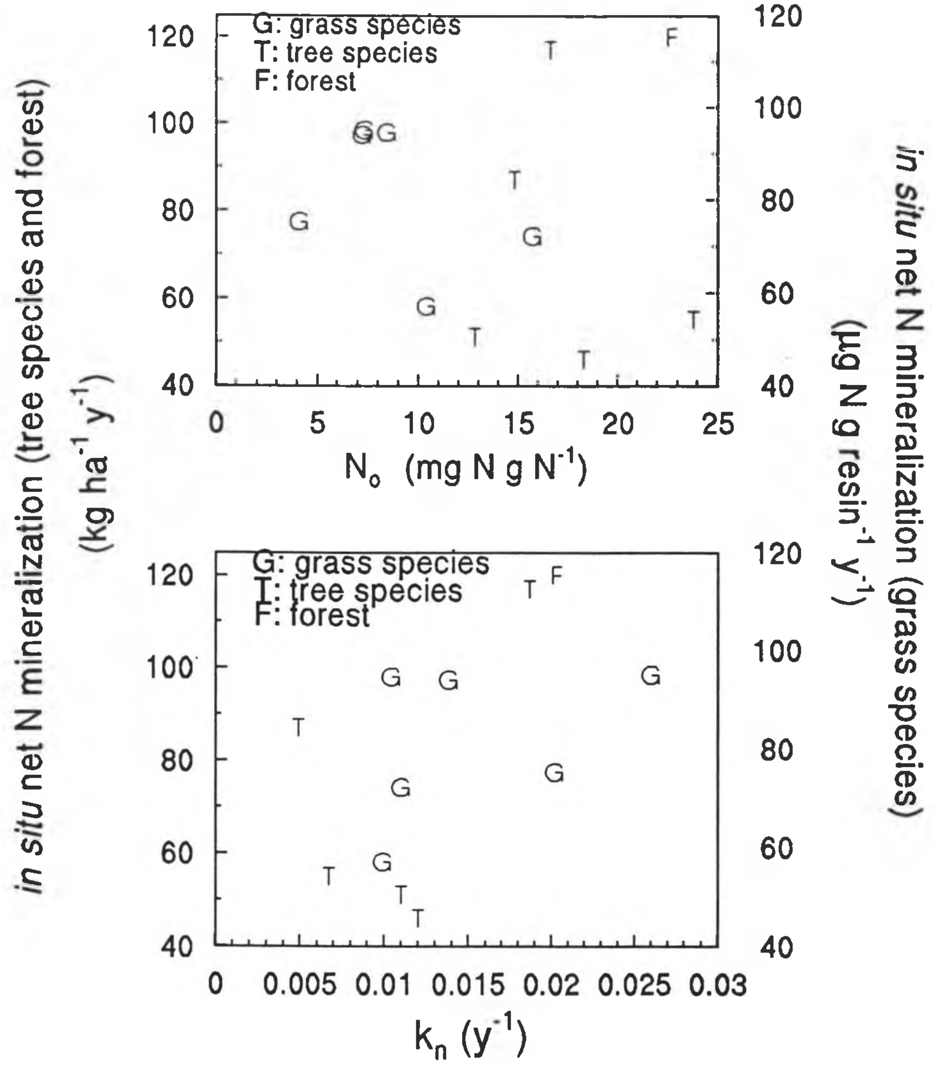

Figure 3.7. Relationship between *in situ* net N mineralization and potentially mineralizable nitrogen ($N_o$) and the rate constant for this pool ($k_n$) for all tree and grass species.

# Chapter 4

# Soil aggregation and organic matter mineralization in forests and grasslands: effects of plant species

## Abstract

Soil aggregation can affect C and N mineralization, and plant species may affect aggregate size distribution and organic matter concentration. These features were examined in common garden experiments. Tree species were European larch (*Larix decidua* Miller), red oak (*Quercus rubra* L.), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and Norway spruce (*Picea abies* (L.) Karst.), and grass species were big bluestem (*Andropogon gerardi* Vitm.), Indiangrass (*Sorghastrum nutans* (L.) Nash.), prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.), switchgrass (*Panicum virgatum* L.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash.), and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). For tree species, aggregate weighted mean diameter (WMD) ranged from 1.5-2.1 mm, and was significantly higher for *Picea abies* and *Q. rubra* than for *Pinus strobus* ($p=0.01$). Fungal biomass correlated positively with large macroaggregate formation for the tree species. The concentration of C in large macroaggregates ranged from 15 to 26 g $kg^{-1}$ for trees, and was lowest for *Picea abies* and *Q. rubra* ($p=0.07$). Grass species had no effect on aggregate size distribution or organic matter concentration in spite of two-fold differences in root biomass. Aggregate

size distribution correlated poorly with whole-soil C mineralization. For the tree and grass species, *in situ* net N mineralization was unrelated to differences in aggregate size distribution and N concentration, but correlated negatively with fungal biomass (tree species only). Net N mineralization differed more between sites than between species or ecosystem type, while species-induced patterns of aggregate size distribution had little effect on whole-soil C mineralization.

## Introduction

Although several studies have examined the effects of plant species on ecosystem processes such as net N mineralization (Stone, 1975; Nadelhoffer et al. 1983; Pastor et al. 1984; Miles, 1985; Hobbie, 1992, Van Cleve et al. 1993; Pastor et al. 1993; Binkley, 1995), none have examined the mechanistic relationship between plant species characteristics, soil characteristics (i.e. physical or chemical properties), and net N mineralization. Previous work suggests that changes in soil aggregation could influence functionally important pools of organic matter (Tisdall and Oades, 1982; Elliott, 1986; Cambardella and Elliott, 1994; Beare et al. 1994). However, a direct connection between species induced changes in soil aggregation and ecosystem processes such as net N mineralization and soil organic matter (SOM) turnover has never been demonstrated.

Conceptual models of soil aggregate formation suggest that changes in soil aggregation (size distribution or organic matter concentration) could influence whole-soil organic matter dynamics because of qualitative differences in organic matter in different sized aggregates. Tisdall and Oades (1982) and Oades (1984) proposed a hierarchical model of soil aggregation and SOM distribution in aggregate size classes for grassland soils. They divided aggregates into 3 size classes: primary particles (sand, silt and clay), microaggregates (53-250 µm) and macroaggregates (> 250 µm). Microaggregates contain transient OM (polysaccharides (not occluded) produced by plants and microbes) and persistent OM (humic material, possibly associated with amorphous Fe and Al compounds). Macroaggregates are held together by temporary organic material (roots and hyphae) that is readily decomposable when not protected inside the aggregate structure. Because of these qualitative differences in organic matter associated with different aggregate size classes, changes in aggregate size distribution or organic matter concentration could influence whole-soil SOM mineralization. However, no direct connection between plant species characteristics, soil aggregate formation, and SOM turnover has been demonstrated.

Plant species can influence soil aggregation by several mechanisms. Jastrow (1987) and Miller and Jastrow (1990) demonstrated that increased root production, root turnover, and root biomass enhanced macroaggregate formation in restored prairie ecosystems. Increased root length can also enhance macroaggregate formation (Reid and Goss, 1981; Tisdall and Oades, 1982; Lynch and Bragg, 1985), but interspecific differences in root length do not always correlate with macroaggregate formation (Monroe and Kladivko, 1987). Higher populations of mycorrhizal fungi can enhance macroaggregate formation (Tisdall and Oades, 1979). Increased litter or root decomposability (lower litter C/N or lignin/N ratio) can enhance microbial activity which, in turn, enhances aggregate formation (Martin and Waksman, 1941; Lynch and Bragg, 1985; Jastrow, 1987). Litter lignin:N ratios often correlates negatively with net N mineralization (Stump and Binkley, 1993; Van Cleve et al. 1993; Scott and Binkley, 1996), but whether this is a result of the interaction between litter quality, soil aggregation, and net N mineralization. Differences in the quality or quantity of root exudates can also influence microbial activity and aggregate formation in the rhizosphere (Klein et al. 1988). Finally, plant species can alter the density and activity of soil invertebrates such as earthworms (Boettcher and Kalisz, 1991; Graham and Wood, 1991; Zou, 1993), influencing the formation and nutrient concentration of macroaggregates (Shipitalo and Protz, 1988).

The objectives of this work were to 1) determine whether tree and grass species characteristics alter soil aggregation (size distribution and organic matter concentration) and 2) if so, do these changes in soil aggregation affect whole-soil C and N mineralization.

## Methods

I examined the relationship between species, soil aggregation and ecosystem processes by

1) selecting monoculture plots of tree and grass species growing in replicated common garden experiments to directly examine species effects on soil processes (Binkley, 1995)

2) measuring soil aggregate distribution and OM concentration for each of the monoculture plots and

3) examining relationships between soil aggregation and whole-soil C and net N mineralization.

In addition to the two common garden sites, an adjacent forest and grassland on uniform soils were also examined. All soils were collected in June 1992 and stored at 4° C prior to aggregate separation.

## Site and sampling information

### Grass species monocultures

The grassland common garden, located in Fergus Falls, MN, was established in 1982 by the Minnesota Department of Fish and Wildlife and the Soil Conservation Service. These plots are burned annually, removing the majority of aboveground biomass. Six grass species (2 varieties of each, randomly located in 3 blocks) native to northern Minnesota were selected: big bluestem (*Andropogon gerardi* Vitm.), Indiangrass (*Sorghastrum nutans* (L.) Nash.), prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.), switchgrass (*Panicum virgatum* L.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash.), and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). For all species, variety selection included those where invasion of the monoculture plots (3.7 m x 26 m) by other species or varieties was minimal (<10%, Dave Wedin personal communication). Soils are clay loams of the Barnes Loam soil series. Mean annual precipitation is 625 mm, mean annual temperature is 5.7°C (see Olson (1984) for additional site information).

Four soil cores (54 mm diameter by 150 mm deep) were collected along a transect from each of the 36 monoculture plots. Within each plot, two cores were composited for aggregate analysis and laboratory incubations and two were composited for root biomass measurements.

Aboveground production and annual net N mineralization (buried resin bags (Binkley and Matson, 1983)) were measured in 1991 by Dr. Dave Wedin (Wedin unpublished data).

### Tree species monocultures

The tree species monocultures were located in the Coullee Experimental Forest (CEF), La Crosse, WI. These plots (45 m x 45 m) were established in 1960 by the Wisconsin Department of Natural Resources, with four randomized complete blocks spread over two hillslope positions (top and bottom of a ridge) containing 5 tree species: European larch (*Larix decidua* Miller), red oak (*Quercus rubra* L.), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and Norway spruce (*Picea abies* (L.) Karst.). *Q. rubra* was missing from one of the blocks. Soils were silty loam Typic Hapludalfs. Mean July temperature is 23.3°C, and mean January temperature is -9.1°C. Annual precipitation averages 780 mm. For additional site information see Sartz (1978) and Son and Gower (1991).

Five cores (54 mm diameter by 150 mm deep) were collected from each monoculture plot in each block along a transect that represented topographic variability. Three of these five were composited for aggregate analysis and soil incubations, and two were composited for root separation.

Litterfall and *in situ* net N mineralization (buried bag method) measurements occurred over a three year period beginning in April 1988 and ending in May 1991 (Gower and Son, 1992).

### Mixed forest and prairie site

The University of Wisconsin Arboretum (UNA) contains a variety of restored ecological communities that were present in Wisconsin in the mid-1800s (Sachse, 1974). The Curtis Prairie, established in the late 1930s, contains over 350 tallgrass prairie plant species. Soils are predominantly silty clay loam Alfisols that are gradually developing a mollic epipedon. I selected 4 sites in different sections of the Curtis Prairie on soils with a silty clay texture.

Forest sampling locations were located in three different stands within the Arboretum less than one kilometer from Curtis prairie. Two of the stands were dominated by *Q. rubra*, and one contained co-dominant white oak (*Quercus alba* L.) and black oak (*Quercus velutina* Lam.). Understory vegetation varied between sites, but contributed little to stand biomass. Soils are silt loam to silty clay loam Typic Hapludalfs. Mean July and January temperatures are 21.2 and -5.2 °C, respectively. Annual precipitation is 950 mm (Wisconsin State Climatological Laboratory, Madison, WI). See Nadelhoffer et al. (1983) for further information on the forest stands at the Arboretum.

Three soil cores (54 mm diameter by 150 mm deep) were collected randomly from each location and composited for aggregate analysis, and two cores were collected for root analysis.

## Soil characteristics

### Aggregate separation

Aggregates were separated into size classes based on the general approach outlined by Tisdall and Oades (1982), with slight modifications (Elliott and Cambardella, 1991; Cambardella and Elliott, 1993). Field-moist soils were gently passed through an 8 mm sieve to remove large stones, root fragments, and twigs. Although air-drying soils prior to aggregate separation may increase aggregate stability (Elliott, 1986; Gollany et al. 1991), aggregate separation using field-moist soils is influenced strongly by antecedent soil moisture (Hofman and de Leenheer, 1975; Reid and Goss, 1981). All soils were, therefore, air-dried and stored for subsequent aggregate analysis.

Aggregates were wet-sieved into four size classes (>2000, 250-2000, 53-250, <53 μm) using a modified Yoder apparatus (Yoder, 1936). Forty grams of dry soil were placed on the 2000 μm sieve. Only two sieves (2000, 250 μm) were used in the initial separation. The sieves were submerged in a column of water, being careful not to allow water to pour in over the top of the 2000 μm sieve. After 10 minutes of soaking, soils were sieved for 5 minutes using a stroke length of 50 mm and a frequency of 26 strokes $min^{-1}$. Maximum stroke height was set so that the water level never fell below the 2000 μm screen. After sieving, aggregates drained freely until drainage was complete (2-4 minutes). Aggregates were then dried on the sieve for 30 minutes at 50°C (to permit removal from the sieve without disruption), placed in pans and oven-dried at 50°C for an additional 10-12 hours.

Dry soil aggregates can either be wetted gently prior to wet sieving (capillary wetting), or submerged directly in water (slaking) (Elliott and Cambardella, 1991). Capillary wetting gradually moistens a soil by absorbing water through capillary action, and is less destructive to macroaggregates (>250 μm) than slaking. Slaked soils are rapidly submerged in water (see previous paragraph), disrupting aggregates along weak fracture lines (Elliott and Cambardella, 1991). I compared aggregate distribution for both slaked and capillary-wetted soils. Soils were capillary wetted on -0.033 MPa ceramic plates for 2 hours prior to wet-sieving. Although aggregate distribution between size classes differed greatly as a result of wetting procedure, trends between species were similar. Therefore, only data from slaked soils are reported.

Soil and vegetation properties

Soil texture was measured using the hydrometer method after dispersing the soil in 5% sodium hexametaphosphate (Gee and Bauder, 1986). Aggregate sand content was measured by dispersing aggregates in 5% sodium hexametaphosphate and passing this material through a 53 μm sieve. All aggregates were finely ground using a mortar and pestle and analyzed for C and N (Carlo-Erba C/N analyzer). Aggregate C and N concentrations are expressed on a sand-free basis to increase the comparability between different treatments and soils. Soil pH was measured in the supernatant of 10 g of soil that had been mixed with 50 mL 0.005*M* $CaCl_2$, agitated briefly, and then allowed to settle for 15 minutes.

Roots were collected by submerging soil cores in water, floating the roots to the surface, and collecting them on a 1 mm sieve. All roots (i.e. no separation of living and dead) were collected, dried at 50°C, and weighed for biomass. Root samples were ground to pass through a 0.5 mm sieve and analyzed for C and N on a Carlo-Erba C/N analyzer. Lignin content (ash corrected) was measured using a modified van Soest procedure (van Soest and Wine, 1968; Waldern 1971).

Total bacterial biomass was measured by the fluorescein isothiocyanate staining method (Babiuk and Paul, 1970). Fungal biomass was determined by fluorescein diacetate staining (Ingham and Klein, 1984). All microbial determinations (and methodological development) were done by the Soil Microbial Biomass Service at Oregon State University.

Aggregate weighted mean diameter (WMD)

Weighted mean diameter of aggregates was calculated as

$$\text{WMD} = (\Sigma\ d_i{*}w_i)/W \qquad \text{Eq. 1}$$

where "d" is the average aggregate diameter of a size class (in mm), "w" is the aggregate mass in that size class, and "W" is the overall sample mass (Capriel et al. 1990).

Laboratory measurements of C and net N mineralization

Thirty-day C and net N mineralization were measured by placing 10 g of unsieved soil (wetted to approximate field capacity) in a plastic specimen cup and incubating under aerobic conditions in a sealed 1L Mason jar. Carbon dioxide evolution was measured by capturing $CO_2$ in 2*M* NaOH. Total $CO_2$ evolved was measured by removing 1 mL of NaOH, adding 1 mL of 0.75*M* $BaCl_2$, then titrating excess NaOH with 1*M* HCl. After 30 days, soil was extracted with 100 mL of 2*M* KCl by shaking for 1 hour and removing 20 mL of supernatant after settling occurred. Extractable soil $NO_3^-$-N (diazotization following cadmium-reduction) and $NH_4^+$-N (salicylate/nitroprusside) was measured using a Lachat flow-injection system.

Potentially mineralizable C and N (Stanford and Smith, 1972) were measured during 385 day laboratory incubations. Forty grams of wet soil (sieved to 2 mm) were mixed with 50 g of acid-washed sand and placed in the top portion of a microlysimeter (Nadelhoffer, 1990). Soil $CO_2$ loss was measured using alkali absorption of $CO_2$ (similar methods to those used in 30 day incubations). Net N mineralization was measured by periodically leaching the sand/soil mixture with a 10 m*M* $CaCl_2$ solution containing other biologically important elements (Nadelhoffer, 1990). See Scott (1996; Chapter 3) for additional experimental details.

### Data analysis

Within each site, species and block effects on aggregate distribution, C and N content, C/N ratio, and whole soil C and net N mineralization were assessed using univariate tests in procedure MANOVA (SPSS Inc., 1988). No statistical comparisons were made across sites. An F-protected least significant difference test was used to compare means within a single aggregate size class. Significance values for all correlations are two-tailed p values.

## Results and Discussion

Soil pH, texture and organic matter concentration data are summarized for all sites in Table 4.1.

### Aggregate size distribution

In the monoculture plots, grass species did not affect mean aggregate diameter (p=0.40) (Table 4.1) or aggregate distribution (p>0.27 for all size classes) (Fig. 4.1a). In contrast, tree species at CEF did alter soil aggregate distribution. The proportion of large macroaggregates (Fig. 4.1b) and mean aggregate diameter (Table 4.1), were lower under *Pinus strobus* (p=0.02 and p=0.01, respectively). Macroaggregate formation was greater in soils under *Picea abies* and *Q. rubra* (Fig. 4.1b). *Picea abies* had the highest mean aggregate diameter, followed by *Q. rubra* (Table 4.1). Tree species did not affect the proportion of soil in the silt+clay fraction (<53 µm, p=0.81).

For the adjacent forest and grassland, the proportion of macroaggregates was slightly greater in the grassland ecosystem, whereas the forest soil had a greater proportion of soil in the microaggregate and silt+clay fraction (Fig. 4.1c). Aggregate diameter was significantly higher in the grassland soil (p=0.03, Table 4.1). Interestingly, the general pattern of aggregate size distribution at UNA was similar to that at CEF; small macroaggregates comprised the dominant fraction (Figs. 4.1b,c). In contrast, at FF a greater proportion of the soil was contained in large macroaggregates (Fig. 4.1a). This suggests that site factors had a greater influence over large macroaggregate formation than vegetation type between these sites.

Root biomass, fungal biomass, and macroaggregation were not consistently related in the different ecosystems. For the grass species, root biomass varied by almost three-fold (Table 4.2), but was unrelated to aggregate diameter (p=0.14). In the adjacent forest and grassland, root biomass was higher in the grassland (Table 4.2), but again unrelated to aggregate diameter (p=0.58). Tree species affected fungal biomass (Table 4.1), which correlated positively with aggregate WMD (p=0.01, r=0.56). Two-fold greater fungal biomass in the forest (compared to the adjacent grassland) did not increase mean aggregate diameter (Table 4.1). Although these results support the general concept of greater macroaggregate formation in grassland ecosystems (Fig. 4.1), species differences in total root biomass do not appear to be regulating macroaggregate formation. Site factors such as temperature, moisture, or mineralogy may have enhanced the formation of large macroaggregates at FF (Fig. 4.1a).

Although root and fungal biomass may influence macroaggregate formation (Reid and Goss, 1981; Tisdall and Oades, 1982; Jastrow, 1987; Miller and Jastrow, 1990), a three-fold difference in root biomass for the grass species monocultures did not alter the proportion of macroaggregates. For the forest/grassland comparison, macroaggregation was higher in the grassland ecosystem, but was unrelated to differences in root or fungal biomass. The greater proportion of fine roots observed in the grassland may be more important than total root biomass as a factor controlling macroaggregate formation in grasslands. Fungal biomass correlated positively with mean aggregate diameter for the tree species, suggesting that macroaggregate formation is related to fungal biomass in the forest soils, but is not important in the grassland soils.

Increased litter decomposability or litter production may stimulate microbial activity and macroaggregate formation (Martin and Waksman, 1941; Lynch and Bragg, 1985; Jastrow, 1987). I found no positive relationship between root biomass and macroaggregate formation (see above), nor was there a relationship between aboveground litter production and macroaggregate formation for the tree species. Root N concentrations varied significantly between grass species ($p<0.01$) (Table 4.2), but did not correlate with mean aggregate diameter. For the tree species, there were no significant relationships between litter chemistry (lignin concentration, N concentration) and aggregate WMD. Root lignin:N ratios of the tree species correlated positively (albeit weakly) with aggregate WMD ($r=0.46$, $p=0.05$). Fungal biomass correlated positively with litter lignin:N ratio (r=0.52, p=0.02) of the tree species, suggesting a possible relationship between litter quality, fungal biomass and soil aggregation for the tree species.

### Aggregate organic matter concentrations

Besides aggregate size distribution, species characteristics could also alter aggregate organic matter concentration, and consequently whole-soil organic matter dynamics. For the tree species monocultures, aggregate sand-free C and N concentrations generally decreased with decreasing aggregate diameter and were lowest in the *Q. rubra* soil (Figs. 4.2a,c). However, in *P. abies* soils, sand-free C and N concentrations were similar in macro- and microaggregates. Tree species had no effect on sand-free C and N concentration in the <53 µm fraction. Aggregate C:N ratios decreased with aggregate size and were unaffected by tree species except in the >2000 µm size class, where *P. resinosa* C:N ratio was significantly higher. Grass species had no effect on aggregate C and N concentrations. Aggregate organic matter concentration correlated negatively with aggregate WMD across all sites ($r^2$=0.34, p<0.01).

Macroaggregate sand-free C concentrations correlated positively with tree species root N concentrations (r=0.63, p<0.01) and negatively with root C:N ratios (r=-0.59, p<0.01). Sand-free N concentrations in this fraction also correlated significantly with root N concentrations (r=0.62, p<=0.01) and root C:N ratios (r=-0.59, p<0.01). There were no significant correlations (p>0.2) between the quality- or quantity of aboveground litter inputs and sand-free C or N concentrations in large macroaggregates. This suggest that although roots may not play a vital role in the process of soil aggregation for the tree species, they are an important source of soil organic matter incorporated into aggregate structure.

Hierarchical models of soil aggregation in arable soils predict that aggregate organic matter concentration and C:N ratio decrease with decreasing aggregate size (Tisdall and Oades, 1982; Oades and Waters, 1991). For the tree species monocultures, aggregate C concentration decreased significantly ($p<0.01$) from 21.7 g kg$^{-1}$ for macroaggregates to 15 g kg$^{-1}$ for microaggregates. Aggregate C:N ratio also decreased from 11.5 to 9.5. The change in aggregate organic matter concentration and C:N ratio varied greatly among species (Figs. 4.2a,c,e). A similar decrease in aggregate C and N concentration and C:N ratio was observed for the mixed forest at UNA (Figs. 4.2b,d,f), suggesting that in general, models of soil aggregate formation developed for arable soils are applicable to forest soils, but that individual species might alter the predicted patterns of soil aggregation. For the mixed prairie at UNA, neither aggregate organic matter concentration nor C:N ratio decreased with aggregate size (Figs. 4.2b,d,f), perhaps due to biannual burning of the prairie.

### Soil aggregation and whole-soil organic matter dynamics

In the monoculture plots, grass species did not affect rates of net N mineralization ($p=0.48$, Table 4.2). Potentially mineralizable N ($N_0$) varied by three-fold and was greatest for *C. longifolia* and lowest for *S. nutans*. Thirty day net N mineralization was significantly lower for *S. scoparium* and greatest for *P. virgatum*. Grass species had no effect on potentially mineralizable C ($C_0$) or 30 d C mineralization ($p=0.11$) (Table 4.3). *In situ* net N mineralization (Table 4.2) and potentially mineralizable N (Table 4.3) varied by more than two-fold for the tree species. Tree species had no effect on C mineralization (Table 4.3). Thirty day net N mineralization and potentially mineralizable N were nearly four-fold higher in the mixed forest than for the mixed prairie (Table 4.3).

The relationship between mean aggregate diameter and annual *in situ* net N mineralization was non-significant for the grass species ($p=0.34$) or the tree species ($p=0.22$). *In situ* net N mineralization for the tree species correlated poorly with aggregate N concentration and C:N ratio in every size class, except in the 250-2000 µm fraction ($r=0.79$, $p=0.11$). Fungal biomass related poorly to aggregate size distribution, but correlated negatively with *in situ* net N mineralization for the tree species ($r=-0.8?$).

For the grass species, 30 day net N mineralization and potentially mineralizable N were unrelated to aggregate WMD ($p=0.93$ and $p=0.35$, respectively). For the tree species, potentially mineralizable N correlated negatively (but weakly) with aggregate diameter ($r^2=0.29$, Fig. 4.3), but was unrelated to 30 day net N mineralization. Across all sites, potentially mineralizable N and 30 day net N mineralization related negatively to aggregate WMD. The grassland ecosystem at UNA had lower mean aggregate diameter than the grass species at FF, but similar levels of potentially mineralizable N (Fig. 4.3) and 30 d net N mineralization (Table 4.3). Net N mineralization and soil aggregation were similar for the tree species at CEF and the forest at UNA. This suggests that differences between ecosystem type and species (i.e. forest vs. grassland) affected the interaction between soil aggregation and net N mineralization less than differences between site, most likely related to differences in soil texture, pH, or total soil C and N. Grass(lands) species depressed N mineralization relative to forests, but not due to differences in soil aggregation.

For the tree species, potentially mineralizable C correlated positively (albeit weakly) with aggregate WMD ($r^2$=0.19, p=0.03, Fig. 4.4), but 30 day C mineralization was unrelated to aggregate WMD (p=0.87). For all soils combined, there was no significant relationship between potentially mineralizable C (Fig. 4.4) or 30 day C mineralization and aggregate WMD. However, potentially mineralizable C and 30 day C mineralization correlated negatively with macroaggregate sand-free C concentration for the combined data from the tree species (CEF), and mixed forest and prairie (UWA, Figs. 4.5a,b).

As macroaggregate formation increases, the relative amount of more decomposable C (i.e. potentially mineralizable C) should also increase (Tisdall and Oades, 1982). I found no significant relationship between aggregate mean diameter and soil C mineralization (Fig. 4.4), suggesting that qualitative differences in organic matter associated with soil aggregates (and soil aggregation processes) differed from those predicted by soil aggregation models (Tisdall and Oades, 1982). I also found that specific rates of net N mineralization correlated negatively (and weakly) with enhanced macroaggregate formation (higher aggregate WMD), but large differences in N mineralization between forests and grasslands were unrelated to differences in soil aggregation.

## Conclusions

Plant species and vegetation type can alter soil aggregate distribution and organic matter concentration, but these alterations are minor and not strongly linked to differences in root biomass, plant litter quality, or fungal biomass. Differences in the size distribution and organic matter concentration of soil aggregates explained too little of the variation in whole-soil C and N dynamics to be useful; only site differences in macroaggregate formation appeared to influence whole-soil net N mineralization. Aggregate C and N concentrations and C:N ratios tended to decrease with decreasing aggregate size as predicted by hierarchical models of soil aggregate formation (e.g. Tisdall and Oades, 1982); there were, however, several exceptions. These results suggest that hierarchical models of aggregate formation may not accurately describe changes in organic matter quality and aggregate formation across a range of plant species and ecosystem types, or that differences in organic matter quality associated with different size soil aggregates are not large enough to influence whole-soil organic matter turnover.

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Table 4.1. Soil characteristics for monoculture plots at Coullee Experimental Forest, Fergus Falls, and for mixed forest and grassland plots at U. Wisconsin Arboretum. Values in parentheses represent one standard deviation.

| Site/Species | pH | clay | silt | sand | $C_{org}$ | $N_{org}$ | Fungal biomass | Bacterial biomass | WMD[1] |
|---|---|---|---|---|---|---|---|---|---|
| | | ------------------------- g kg$^{-1}$ -------------------------- | | | | | -------mg kg$^{-1}$------ | | mm |
| **Coullee Experimental Forest** | | | | | | | | | |
| *Larix decidua* | 4.37 | 180 | 575 | 245 | 15 | 1.47 | 461 | 48.5 | 1.73 |
| | (.33) | (54) | (87) | (126) | (3.1) | (.25) | (205) | (26.4) | (.54) |
| *Picea abies* | 4.12 | 190 | 642 | 168 | 17.9 | 1.51 | 1181 | 38.5 | 2.13 |
| | (.18) | (16) | (32) | (34) | (.9) | (.12) | (589) | (7.3) | (.28) |
| *Quercus rubra* | 4.24 | 203 | 580 | 217 | 12.3 | 1.3 | 801 | 43.3 | 2.05 |
| | (.17) | (6) | (79) | (83) | (2.0) | (.14) | (399) | (10) | (.21) |
| *Pinus resinosa* | 4.34 | 183 | 582 | 235 | 16.3 | 1.44 | 861 | 40.6 | 1.81 |
| | (.1) | (31) | (67) | (66) | (2.5) | (.27) | (118) | (5.1) | (.35) |
| *Pinus strobus* | 4.59 | 188 | 492 | 320 | 13.9 | 1.36 | 534 | 50.8 | 1.49 |
| | (.16) | (26) | (190) | (187) | (5.1) | (.56) | (180) | (16.3) | (.49) |
| **Fergus Falls grass monocultures** | | | | | | | | | |
| *Andropogon gerardi* | 7.46 | 322 | 376 | 352 | 31.1 | 2.16 | ND | ND | 2.91 |
| | (.24) | (22) | (3) | (35) | (4.4) | (.38) | | | (.37) |
| *Sorghastrum nutans* | 7.35 | 343 | 352 | 303 | 31 | 2.56 | ND | ND | 3.14 |
| | (.33) | (23) | (21) | (15) | (4.6) | (.51) | | | (.29) |
| *Calamovilfa longifolia* | 7.34 | 338 | 347 | 315 | 32.4 | 2.69 | ND | ND | 2.79 |
| | (.28) | (17) | (21) | (32) | (6.5) | (.51) | | | (.32) |
| *Panicum virgatum* | 7.46 | 333 | 340 | 327 | 32 | 2.49 | ND | ND | 2.87 |
| | (.3) | (15) | (35) | (46) | (3.3) | (.40) | | | (.75) |
| *Schizachyrium scoparium* | 7.5 | 320 | 355 | 325 | 30.7 | 2.37 | ND | ND | 3.02 |
| | (.16) | (11) | (23) | (39) | (4.4) | (.14) | | | (.09) |
| *Bouteloua curtipendula* | 7.6 | 325 | 332 | 343 | 33.1 | 2.19 | ND | ND | 2.75 |
| | (.05) | (20) | (28) | (46) | (5.7) | (.30) | | | (.21) |

Table 4.1 continued

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **U. Wisconsin Arboretum** | | | | | | | | | |
| forest | 4.52 | 233 | 619 | 148 | 23.4 | 2.03 | 570 | 48.7 | 1.51 |
| | (.37) | (29) | (34) | (34) | (2.1) | (.16) | (24) | (5.1) | (.21) |
| grassland | 4.98 | 225 | 650 | 125 | 23.8 | 2.08 | 202 | 101.2 | 2.06 |
| | (.37) | (17) | (36) | (25) | (6.7) | (.44) | (17) | (21.4) | (.40) |

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[1] Weighted mean diameter (see Eq. 1).

Table 4.2. Characteristics of monoculture plots at Coullee Experimental Forest, Fergus Falls, and mixed forest and grassland plots at U. Wisconsin Arboretum. Values in parentheses represent one standard deviation.

| Site/Species | Leaf litterfall[1] | Leaf litter N[1] | Leaf litter lignin[1] | Root biomass | Root N | Root lignin | netNmin | netNmin |
|---|---|---|---|---|---|---|---|---|
| | $g\ m^{-2}$ | ------$g\ kg^{-1}$-------- | | $g\ m^{-2}$ | -------$g\ kg^{-1}$------- | | $kg\ ha^{-1}y^{-1}$ | $\mu g\ N\ g\ resin^{-1}y^{-1}$ |
| **Coullee Experimental Forest** | | | | | | | | |
| *Larix decidua* | 367 | 10.8 | 126 | 120 | 11.6 | 344 | 117[v] | ---- |
| | (2.4) | | | (35) | (2.7) | (60) | | |
| *Picea abies* | 411 | 9.9 | 268 | 196 | 8.7 | 328 | 46 | ---- |
| | (77) | | | (26) | (1.9) | (40) | | |
| *Quercus rubra* | 428 | 8.6 | 248 | 156 | 6.9 | 375 | 55 | ---- |
| | (215) | | | (56) | (.7) | (35) | | |
| *Pinus resinosa* | 446 | 7.2 | 219 | 165 | 11.3 | 369 | 51 | ---- |
| | (550) | | | (30) | (2.9) | (26) | | |
| *Pinus strobus* | 321 | 8.3 | 225 | 166 | 10.2 | 363 | 87 | ---- |
| | (70) | | | (114) | (2) | (14) | | |
| **Fergus Falls grass monocultures[4]** | | | | | | | | |
| *Andropogon gerardi* | ND | ND | ND | 1116 | 3.0 | 180 | ---- | 58.2[3] |
| | | | | (620) | (.4) | (14) | | (18) |
| *Sorghastrum nutans* | ND | ND | ND | 537 | 5.6 | 172 | ---- | 77.5 |
| | | | | (137) | (1.3) | (31) | | (22) |
| *Calamovilfa longifolia* | ND | ND | ND | 787 | 3.5 | 170 | ---- | 98 |
| | | | | (263) | (.2) | (4.3) | | (37) |
| *Panicum virgatum* | ND | ND | ND | 1413 | 4.2 | 151 | ---- | 74.2 |
| | | | | (602) | (.6) | (13) | | (14) |
| *Schizachyrium scoparium* | ND | ND | ND | 1068 | 3.8 | 140 | ---- | 97.4 |
| | | | | (701) | (.6) | (14) | | (64) |

Table 4.2 continued

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Bouteloua curtipendula* | ND | ND | ND | 660<br>(243) | 4.8<br>(.6) | 181<br>(18) | ---- | 98.5<br>(42) |
| **U. Wisconsin Arboretum** | | | | | | | | |
| forest | ND | ND | 135[2]<br>(7.2) | 206<br>(91) | 10.5<br>(1.8) | 292<br>(67) | 120<br>(19) | ---- |
| grassland | ND | ND | ND | 637<br>(267) | 5.0<br>(.7) | 163<br>(29) | ND | ND |

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[1] Gower and Son (1992) and Yowhan Son, unpublished data.

[2] John Aber unpublished data

[3] Dave Wedin unpublished data

[4] Aboveground litter characteristics not reported because of annual burning.

Table 4.3. Potentially mineralizable C and N and recalcitrant C mineralization (and 95% confidence interval) during 385 day laboratory incubations. See non-linear models used to estimate parameters at bottom of table. Also C and net N mineralization during 30 day laboratory incubations.

| Site/Species | $N_o$[a] | $C_o$[b] | $c_c$[b] | C min.(30 d) | net N min. (30 d) |
|---|---|---|---|---|---|
|  | mg N $g^{-1}$N | mg C $g^{-1}$C | mg C $g^{-1}$ C $d^{-1}$ | µg $gC^{-1}$ $d^{-1}$ | µg $gN^{-1}$ $d^{-1}$ |
| **Coullee Experimental Forest** |  |  |  |  |  |
| *Larix decidua* | 16.6 (4.86) | 74.5 (29.6) | 0.25 (.09) | 1461 (813) | 555 (110) |
| *Picea abies* | 18.3 (7.49) | 58.3 (12.02) | 0.27 (.04) | 1201 (450) | 476 (77) |
| *Quercus rubra* | 23.8 (15) | 65.9 (19.1) | 0.27 (.07) | 2006 (275) | 599 (279) |
| *Pinus resinosa* | 12.8 (6.61) | 62.8 (39) | 0.27 (.12) | 1387 (549) | 449 (73) |
| *Pinus strobus* | 14.8 (16) | 76.6 (66) | 0.22 (.21) | 2534 (1977) | 562 (172) |
| **Fergus Falls grass monocultures** |  |  |  |  |  |
| *Agropyron gerardi* | 10.4 (4.99) | 42.3 (13.1) | 0.10 (.04) | 560 (162) | 202 (63) |
| *Sorghastrum nutans* | 4.41 (1.75) | 45.2 (11.2) | 0.11 (.04) | 637 (139) | 224 (77) |
| *Calamovilfa longifolia* | 15.7 (4.12) | 37.1 (9.4) | 0.11 (.03) | 524 (136) | 241 (57) |
| *Panicum virgatum* | 7.3 (1.2) | 38.1 (9.5) | 0.11 (.03) | 623 (135) | 306 (118) |
| *Schizachyrium scoparium* | 8.4 (3.12) | 42.7 (14.4) | 0.08 (.05) | 540 (144) | 160 (55) |
| *Bouteloua curtipendula* | 7.2 (2.14) | 39.8 (10.5) | 0.10 (.03) | 625 (109) | 228 (66) |
| **U. Wisconsin Arboretum** |  |  |  |  |  |
| forest | 22.7 (3.8) | 45.6 (9.4) | 0.28 (.03) | 844 (239) | 525 (111) |
| grassland | 4.41 (1.44) | 57 (32) | 0.25 (.11) | 920 (290) | 119 (82) |

$N_t=N_o(1-e^{-kt})$ $(k=k_n)$

$C_t=C_o(1-e^{-kt}) + c_c t$ $(k=k_c)$

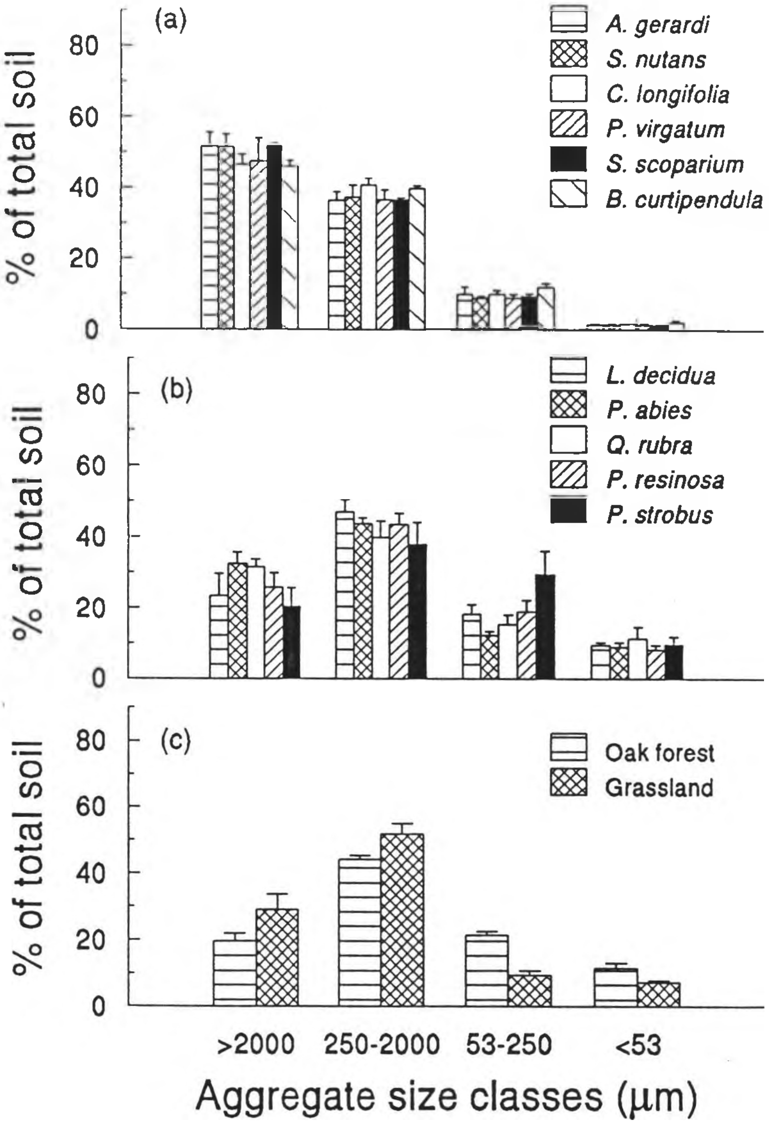

Figure 4.1. Effects of species and ecosystem type on aggregate size distribution after slaking. Error bar is one standard error.(a) grass monocultures at Fergus Falls (b) tree species monocultures at Coullee Experimental Forest (c) mixed forest and prairie and U. Wisconsin Arboretum.

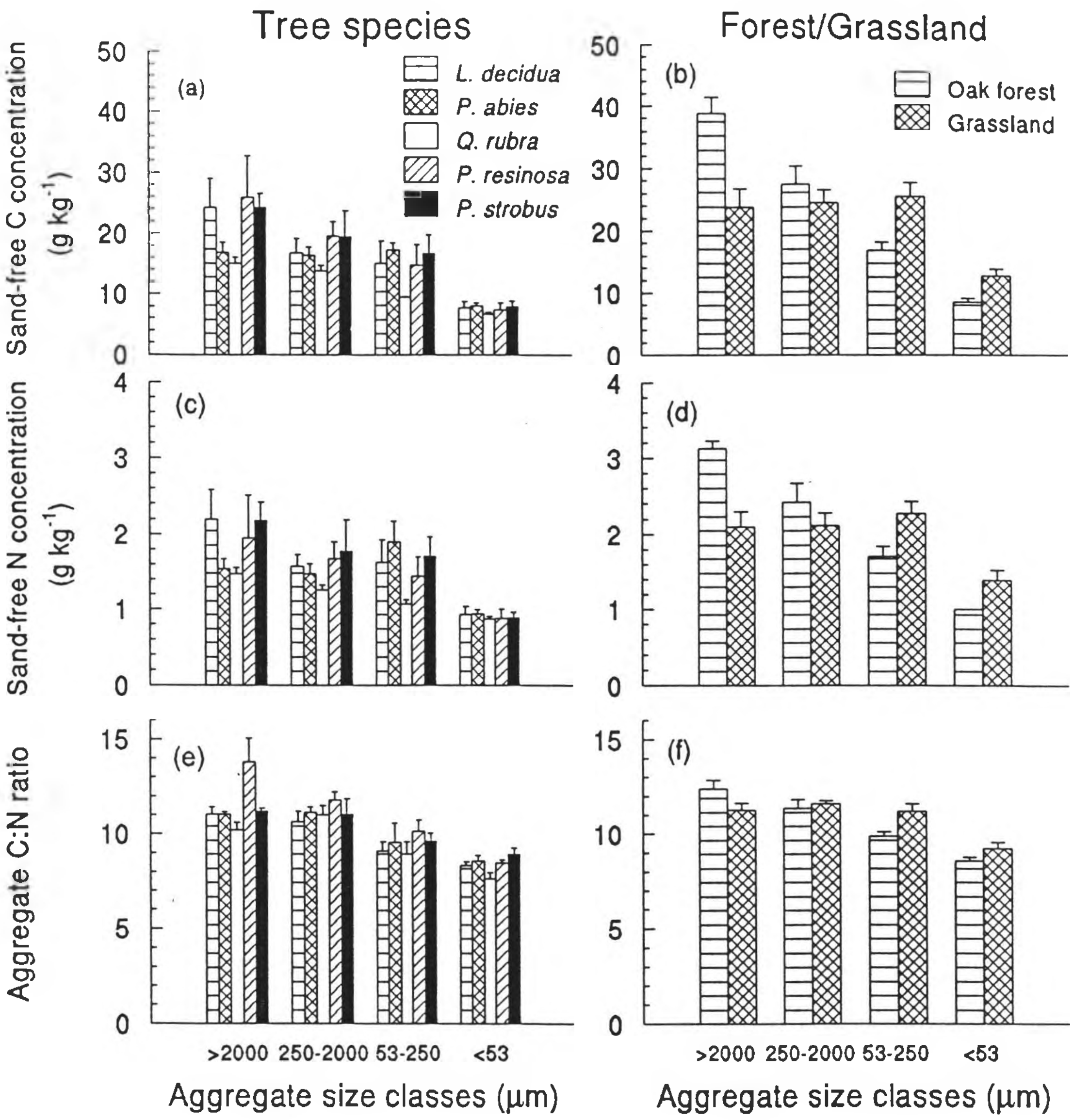

Figure 4.2. Effects of tree species and ecosystem type on aggregate organic matter concentrations and C:N ratios. Error bar is one standard error. (a,c,e) carbon, nitrogen, and C:N ratio for soil aggregates under tree species at Coullee Experimental Forest and (b,d,e) carbon, nitrogen, and C:N ratio for mixed forest and prairie at U. Wisconsin Arboretum.

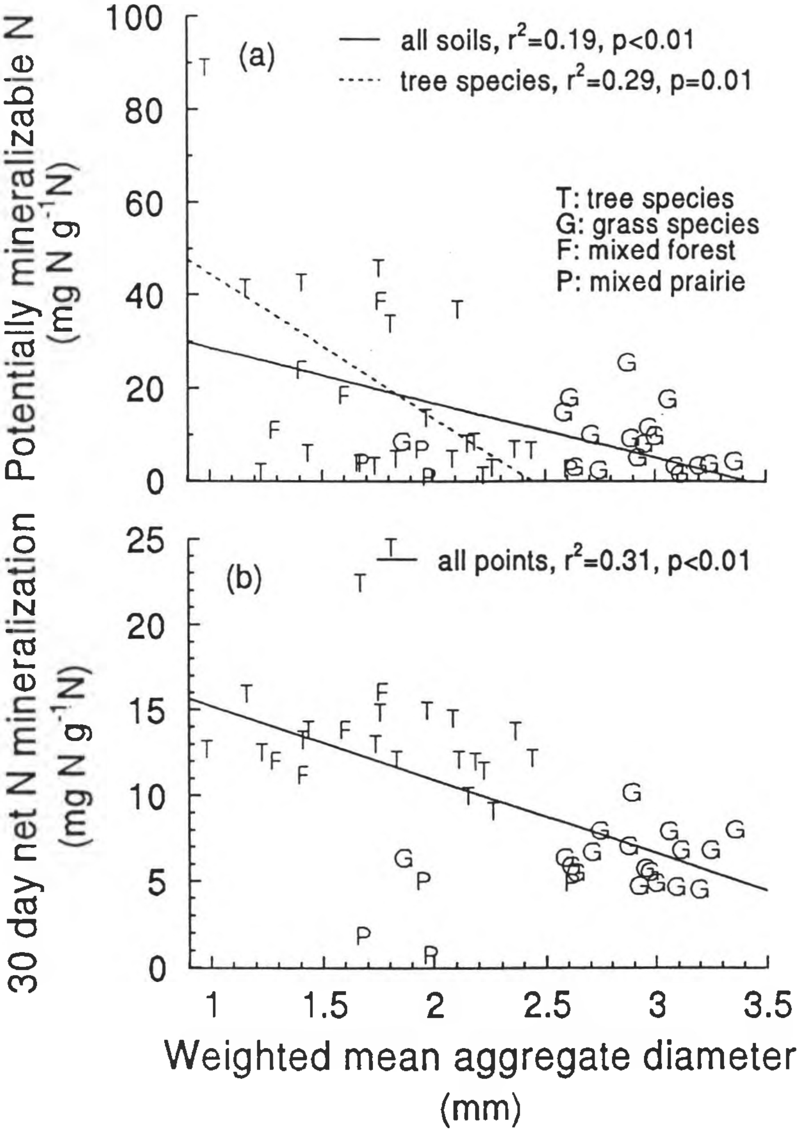

Figure 4.3. Relationships between net N mineralization and aggregate weighted mean diameter during (a)387 day laboratory incubations and (b) 30 day laboratory incubations.

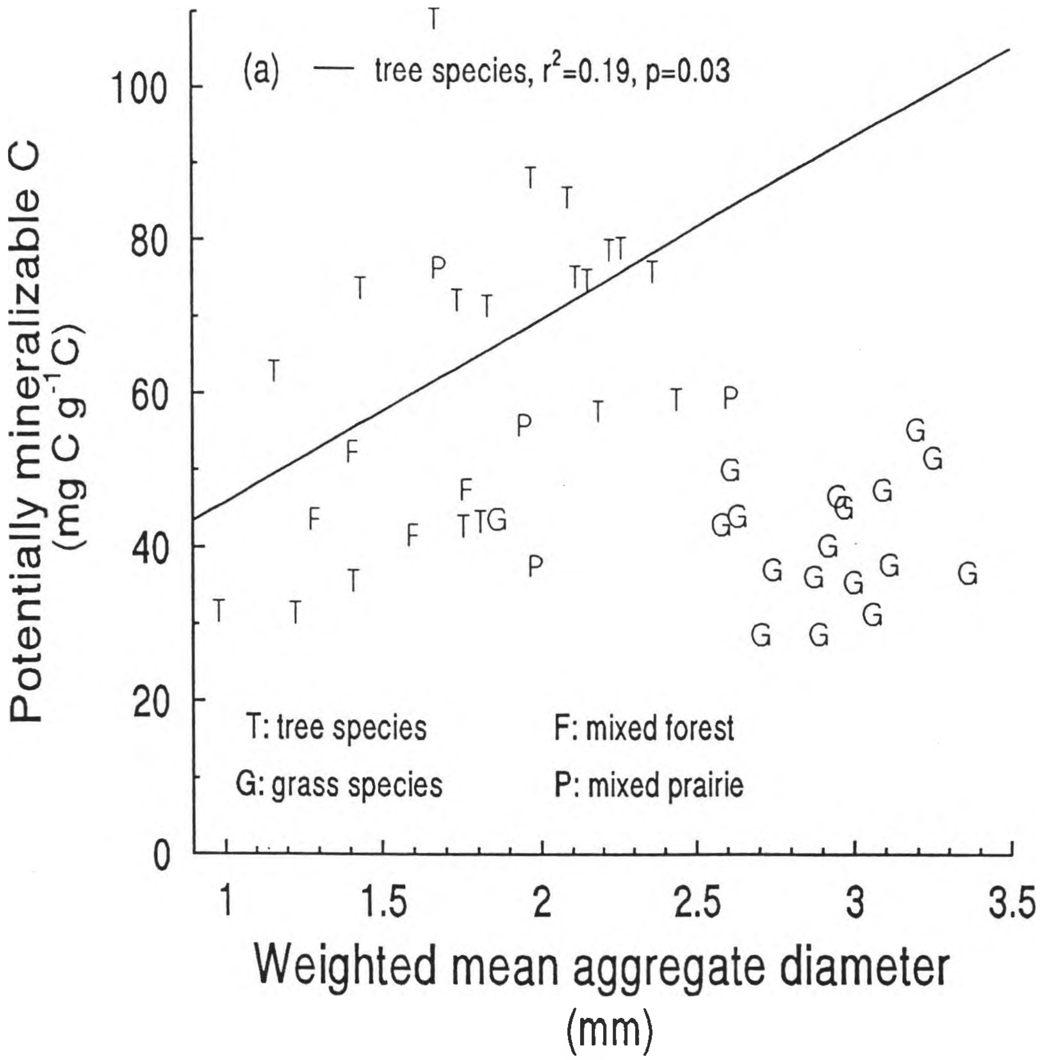

Figure 4.4. Relationships between potentially mineralizable C (see Table 3 for equation) and aggregate weighted mean diameter during 387 d laboratory incubations.

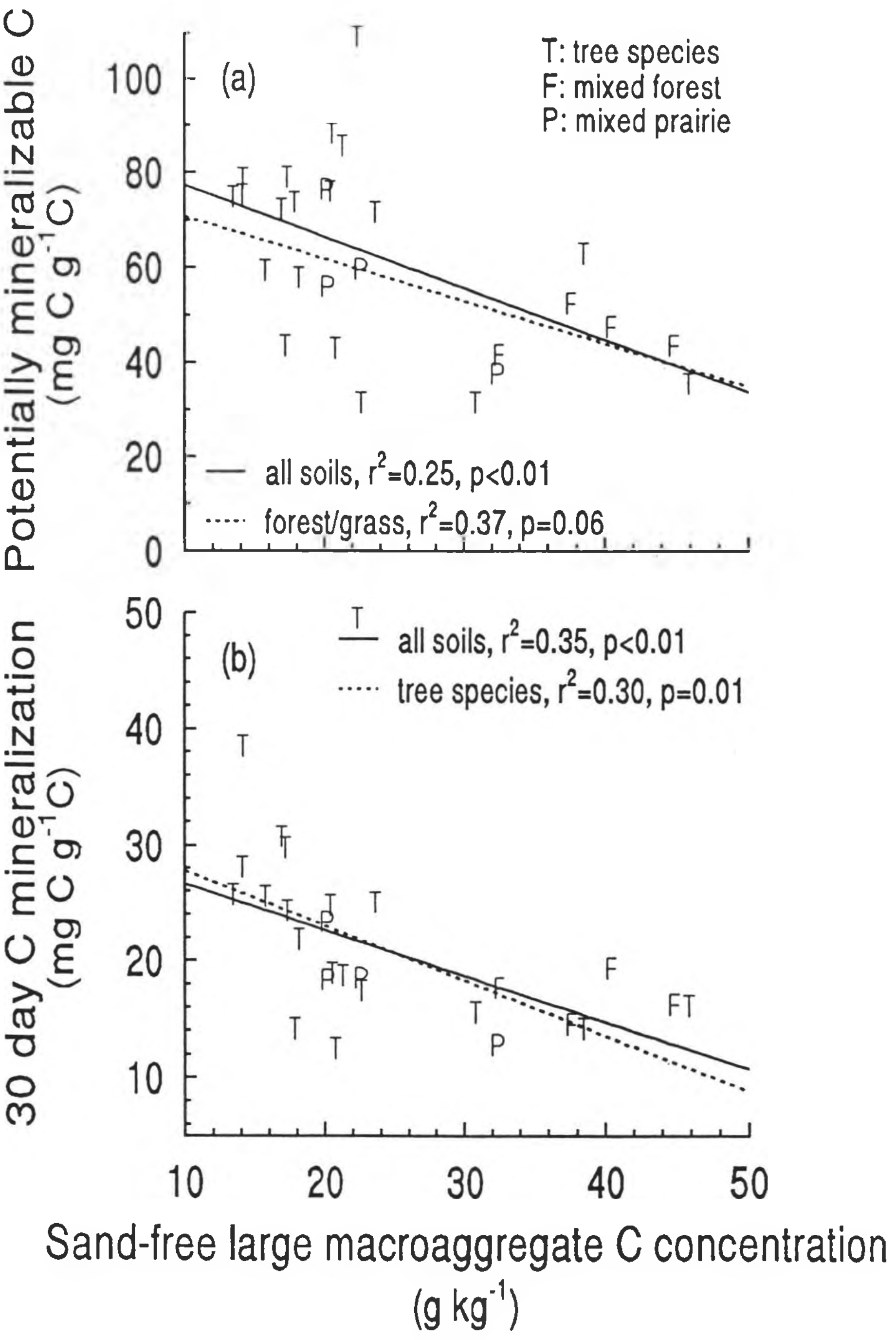

Figure 4.5. Relationship between C mineralization and large macroaggregate (>2000 µm) C concentration during (a) 387 day laboratory incubations and (b) 30 day laboratory incubations

# Chapter 5

# Carbon and nitrogen mineralization in soil aggregates: organic matter protection and tree species effects

## Abstract

Plant species could alter whole-soil organic matter dynamics by changing the quality or physical protection of organic matter in soil aggregates. Soils (0-150 mm) from monoculture plots of five tree species were wet-sieved to separate soil aggregates into three size classes. These aggregates were incubated aerobically at 25° C for 112 d as crushed or intact aggregates. Neither species or crushing influenced C or net N mineralization rates in macroaggregates (>250 μm). Initally, C mineralization rates were higher from macroaggregates than from microaggregates (<53 μm), but during the latter stages of the incubation mineralization rates were higher from microaggregates (p=0.07). Net N mineralization rates in microaggregates were slightly higher than in large macroaggregates (>2000 μm). Net N mineralization (83-112 d) in large macroaggregates was negatively correlated with litter lignin concentration and lignin:N ratio, as were *in situ* net N mineralization rates. Species effects on *in situ* net N mineralization appear to be related to changes in N mineralization in large macroaggregates, not with changes in aggregate size distribution. These results also suggest that macroaggregates may not be

composed of microaggregates held together by readily decomposable materials such as fungal hyphae and root fragments.

## Introduction

Changes in soil aggregation could influence whole-soil organic matter (OM) dynamics by changing soil physical attributes (i.e. pore-size distribution, bulk density, total porosity), organic matter quality and availability. Tisdall and Oades (1982) and Oades (1984) proposed a hierarchical model of soil aggregation where aggregates of different size classes contain organic matter with different degrees of recalcitrance. This model implies that changes in soil aggregate size distribution could alter whole-soil C and N dynamics, but Scott (1996) found that species-induced changes in aggregate size distribution and organic matter concentration were unrelated to soil C and net N mineralization (both *in situ* and laboratory incubations). This suggests either that organic matter quality in different size classes has little impact on whole-soil organic matter dynamics, or that the model proposed by Tisdall and Oades (1982) does not explain differences in organic matter quality associated with different size classes of soil aggregates.

Changes in soil aggregation can alter both SOM quality and the physical protection of SOM. Tisdall and Oades (1982) proposed a hierarchical model of soil aggregation that described qualitative differences in organic matter associated with different size aggregates. Transient and persistent OM (non-occluded polysaccharides and humic materials) are associated primarily with microaggregates (<250 µm), which usually have lower C and N mineralization rates than macroaggregates (>250 µm) (Elliott 1986; Gupta and Germida, 1988). Temporary OM (roots and hyphae), which stabilizes microaggregates into macroaggregates, has a higher C:N ratio than microaggregate-associated OM and is readily decomposable when not physically protected from microbial degradation. Alternatively, Oades (1984) proposed that microaggregates are formed at the center of macroaggregates when small fragments of particulate organic material (POM) become encrusted by microbial mucilages and clay particles. These microaggregates are relatively stable and enriched in organic matter. When soil aggregates are crushed, SOM mineralization rates generally increase both in microaggregates and macroaggregates (Craswell and Waring, 1972; Gupta and Germida, 1988; Gregorich et al. 1989; Beare et al. 1994; Cambardella and Elliott, 1994), suggesting that physical protection is an important control over organic matter turnover. The importance of physical protection of organic matter can vary depending on the process of aggregate formation (Beare et al. 1994; Cambardella and Elliott, 1994).

Plant species could modify SOM dynamics by altering soil aggregate size distribution, stability, intra-aggregate OM quality, and intra-aggregate OM protection (Lynch and Bragg, 1985; Jastrow, 1987). Variation in root biomass or length can enhance macroaggregate formation and stability (Reid and Goss, 1981; Jastrow 1987; Miller and Jastrow, 1990), although this is not always observed (Scott 1996). Species-dependent rates of vesicular-arbuscular mycorrhizal infection could also enhance macroaggregate formation and aggregate stability (Tisdall and Oades, 1979; Miller and Jastrow, 1990). Increased litter decomposability (both above- and belowground) may also enhance aggregate formation and intra-aggregate OM quality (Martin and Waksman, 1941; Lynch and Bragg, 1985; Jastrow 1987). Plant species can also influence soil invertebrates, including earthworms, which can greatly alter aggregate formation and stability (Shipitalo and Protz, 1988; Boettcher and Kalisz, 1991; Graham and Wood, 1991; Martin 1991). The effects of plant species on soil aggregation could provide a mechanistic explanation for the feedbacks between plant species characteristics and *in situ* C and N dynamics (Nadelhoffer et al. 1991; Hobbie 1992; Stump and Binkley, 1993; Scott and Binkley, 1996).

Scott (1996) found that whole-soil organic matter dynamics correlated poorly with changes in aggregate size distribution. This work addresses the hypotheses that 1) physical protection of organic matter influences whole-soil C and N mineralization 2) organic matter quality (i.e. decomposability) increases with increasing aggregate size and 3) species effects on intra-aggregate organic matter physical protection or organic matter quality explain species-induced changes in whole-soil organic matter dynamics (e.g. net N mineralization).

## Methods

Species and size-class effects on aggregate organic matter dynamics were examined by 1) selecting monoculture plots of tree species growing in replicated common garden experiments to directly examine species effects on soil processes (Binkley, 1995) 2) crushing aggregates to liberate physically isolated intra-aggregate organic matter and 3) examining C and N mineralization dynamics in both crushed and intact aggregates of different sizes.

### Site descriptions and sampling information

The Wisconsin Department of Natural Resources established the Coullee Experimental Forest in 1960 to examine the effects of tree species on soil water dynamics (Sartz 1978). The site includes monoculture plots (45 m by 45 m) of five tree species (European larch (*Larix decidua* Miller), red oak (*Quercus rubra* L.), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and Norway spruce (*Picea abies* L.) Karst.) arranged in a randomized complete block design. Two plots are located along a ridge-top, and two are in the adjacent valley bottom. Soils are silt loam Typic Hapludalfs. Mean July temperature is 23.3°C, mean January temperature is -9.1°C, and annual precipitation averages 780 mm. For additional site information see Sartz (1978) and Son and Gower (1991).

Previous work at this site indicates that *in situ* net N mineralization rates vary over two-fold for the different tree species (Table 5.1), most likely due to differences in litter chemistry (Gower and Son, 1992). Litter lignin and N content vary from 126 to 268 g $kg^{-1}$and 7.2 to 10.8 g $kg^{-1}$, respectively. Litter lignin:N ratio ranges from 12 for European larch to 31 for red pine (Gower and Son, 1992). Root N concentrations vary from 6.9 to 11.6 g $kg^{-1}$ with little variation in root lignin concentrations (Table 5.2). Soil organic carbon ranges from 12.3 mg $kg^{-1}$ for red oak to 17.9 mg $kg^{-1}$ for Norway spruce (Table 5.1).

Five soil cores (5.4 cm diameter by 15 cm deep) were collected along two transects representing topographic variability in both June and November 1992. Three cores were composited for aggregate analysis, and two were combined for root analysis. Aggregates from both dates were combined for subsequent incubations.

### Aggregate separation

Soil cores were carefully broken apart and passed through an 8 mm sieve to remove coarse roots, wood, and rocks, then air-dried. Drying soil can increase aggregate stability (Elliott 1986; Gollany et al. 1991), but antecedent soil water content also influences aggregate stability (Reid and Goss, 1981; Elliott 1986; Gollany et al. 1991). I decided it was better to remove variability due to differences in antecedent soil water content, so all soils were air-dried prior to aggregate separation.

Aggregates were separated into three size classes (> 2000 μm, 250-2000 μm, 53-250 μm) based on previous work with soil aggregate organic matter dynamics (Tisdall and Oades, 1982; Elliott and Cambardella, 1991; Cambardella and Elliott, 1993). Soil was wet-sieved using a modified Yoder apparatus (Yoder 1936) to separate aggregates into three size classes. Forty grams of dry soil were placed on a 2000 μm sieve (nested with the 250 μm sieve), and lowered into a column of water until the water level was approximately four cm above the soil. After 10 minutes of submersion, wet sieving began using a stroke length of 0.05 m and a frequency of 36 strokes min$^{-1}$. After five minutes, sieves were removed from the water and drained freely until no further drainage was observed (app. 3 minutes). Aggregates on the sieves were dried at 50°C for 30 minutes, after which aggregates were removed from the sieve and dried for 12 hours at 50°C. The material remaining in the water column (< 250 μm), was poured through a 53 μm sieve and hand sieved (Kemper and Rosenau, 1986) (50 strokes, 0.02 m stroke length). Aggregates remaining on the sieve were carefully rinsed into a pan and dried at 50°C. Both large (>2000 μm) and small (250-2000 μm) macroaggregates were crushed by forcing them through a 250 μm sieve. Coarse sand and large organic particles remaining on the 250 μm sieve were included in the crushed sample.

### C and N mineralization

To examine the effects of size class, crushing, and species on C and net N mineralization, aggregates (crushed and intact) were incubated aerobically for 16 weeks at 25°C. Four 5 g samples of aggregates were weighed into glass scintillation vials, and the water content adjusted to 55% water-filled porosity. All four samples were placed in a 1 L Mason jar with 1 *M* NaOH for soil respiration measurement. Total $CO_2$-C production was measured after 8, 17, 24, 40, 60, 83, and 112 days by titrating alkali traps with 1.000 *M* HCl. Net N mineralization was measured at 24, 40, 83, and 112 days by extracting one sample with 50 mL of 2 *M* KCl. Extracts were analyed for $NO_3^-$-N and $NH_4^+$-N using a Lachat automated flow-injection colorimetric system (Lachat Instruments, 1988).

In addition to examining total C and net N mineralization over the 112 day period, C and N mineralization were examined between 0-23 days (readily decomposable material) and between 83-112 days (more recalcitrant C and N).

### Soil and plant analysis

Aggregates were finely ground using a Tekmar grinder and mortar and pestle (when necessary) and analyzed for total C and N by thermal combustion on a Carlo-Erba CN analyzer. Soil texture was measured using the hydrometer method following dispersal with 50 g $L^{-1}$ sodium hexametaphosphate (HMP). To express mineralization rates on a sand-free weight basis, aggregate sand content was measured by dispersing aggregates with 50 g $L^{-1}$ sodium HMP and sieving (53 μm). Soil pH was measured in a 5:1 slurry of $0.01M$ $CaCl_2$ and soil.

Roots were collected by submerging soil cores in water, floating the roots to the surface, and collecting them on a 1 mm sieve. All roots (i.e no separation of living and dead) were collected, dried at 50°C, and weighed for biomass. Root samples were ground to pass through a 0.5 mm sieve and analyzed for C and N on a Carlo-Erba C/N analyzer. Lignin content (ash corrected) was measured using a modified van Soest procedure (van Soest and Wine, 1968; Waldern 1971).

### Statistical analysis

Since the aggregate treatments were repeated treatments on the original soil sample, I used repeated measures analysis of variance to examine the effects of species, size class and crushing on C and net N mineralization (MANOVA (SPSS Inc. 1988)). When significant interactions (species by size class or species by aggregate treatment (crushed vs. intact)) occurred, species were compared using paired t-tests. Species effects within a size class and aggregate treatment (crushed and intact) were analyzed using analysis of variance (procedure ANOVA, SPSS Inc. 1988) and an F-protected LSD for mean comparisons within a size class.

## Results and Discussion

### Physical protection of organic matter

Crushing soil aggregates did not stimulate total C mineralization (Fig. 5.1a) or net N mineralization (Fig. 5.2a) from large macroaggregates (> 2000 μm). In fact, intact large macroaggregates had 5% higher C mineralization rates between 0-23 d compared to crushed large macroaggregates ($p = 0.09$) (Fig. 5.1b). Crushing did not affect C or net N mineralization rates between days 83-112 ($p=0.53$ and 0.20, respectively, Figs. 5.1c and 5.2c).

Crushing small macroaggregates (250-2000 μm) lowered total C and N mineralization (Figs. 5.1a and 5.2a) ($p < 0.01$), with the greatest difference between crushed and intact aggregate C mineralization occuring between 83 and 112 days (Fig. 5.1c). Species by crushing treatment interactions were not significant throughout the incubation ($p>0.10$).

Some studies have shown that crushing aggregates or grinding soil stimulates mineralization of C and N (Craswell and Waring, 1972; Gupta and Germida, 1988), but this response is not universal (Robinson 1967). In the present study, crushing soil aggregates did not appear to increase organic matter availability. Crasswell and Waring (1972) found that clay mineralogy played an important role in determining whether crushing soil increased SOM mineralization. In soils containing predominantly montmorillonite, net N mineralization increased after crushing, but a soil dominated by kaolinite showed no response. In soils dominated by montmorillonitic clays, organic matter is more strongly bound to clay particles than in soils dominated by 1:1 clays such as kaolinite because of the surface and inter-layer charge characteristics (Brown et al. 1978). Furthermore, both micro- and macroaggregate stability (and organic matter stabilization) are enhanced by 2:1 clay minerals (Edwards and Bremner, 1967; Churchman and Tate, 1986; Borchers and Perry, 1992). Although the mineralogy of the soil at the two

Wisconsin sites was not determined, the low pH (Table 5.1) suggests a significant portion of the clay fraction could be dominated by 1:1 clay minerals.

## Aggregate size class

For intact aggregates, aggregate size-class had no significant effect on total C and net N mineralization (Figs. 5.1a and 5.2a). Between 0-23 d, however, C mineralization rates were two-fold lower in microaggregates than in large macroaggregates and 30% lower than in small macroaggregates. C mineralization rates were 20% lower in small macroaggregates compared to large macroaggregates (Fig. 5.1b). Net N mineralization rates were 20% lower in microaggregates than either macroaggregate fraction ($p<0.01$) in spite of having a slightly higher C:N ratio. However, between days 83-112, C mineralization rates in microaggregates were two-fold higher than either class of macroaggregates ($p=0.07$) (Fig. 5.1c), but net N mineralization rates did not differ between microaggregates and small macroaggregates (0.44 vs 0.42 $\mu g\ g^{-1}\ d^{-1}$, respectively, Fig. 5.2c).

According to hierarchical models of soil aggregation (Tisdall and Oades, 1982), microaggregate-associated organic matter should be less decomposable than that associated with macroaggregates, due primarily to humification of microaggregate-associated organic matter (Edwards and Bremner, 1967). Other studies using short-term (14-20 d) laboratory incubations have verifid the lower decomposability of microaggregate-associated organic matter (Elliott 1986; Gupta and Germida, 1988; Gregorich et al. 1989). Field-based $^{14}C$ decomposition experiments suggested that the mean residence time of microaggregate C was seven-fold higher than macroaggregate C

(Buyanovsky et al. 1994). My results indicate that macroaggregates contain a small fraction of readily decomposable organic matter, but that most macroaggregate C is less decomposable than organic matter in microaggregates (and not physically protected). These results suggest that macroaggregates are not simply an amalgamation of microaggregates as proposed by Tisdall and Oades (1982), and that most of the organic matter in microaggregates is more decomposable than that contained in macroaggregates.

### Effects of plant species

In spite of large differences in root and litter lignin and N concentrations (Table 5.2), tree species had no effect on the physical protection of organic matter (no species by crushing interactions), suggesting that litter quality has little or no impact on the physical protection of intra-aggregate organic matter. Scott (1996) found that these tree species also had little effect on aggregate size distribution, and that any differences in aggregate size distribution were unrelated to litter chemistry. Therefore, it appears that these tree species have little impact on soil aggregate formation and stability.

For all size classes of intact aggregates, tree species had no effect on total C mineralization (Fig. 5.3) or C mineralization rates between 0-23 d and 83-112 d. Tree species also did not affect total net N mineralization (Fig. 5.4a), but did influence net N mineralization at different times during the incubation. Between 0-23 d, net N mineralization was lowest in macroaggregates from soils under Norway spruce and highest under white pine and red pine (Fig. 5.4b), but unrelated to litter quality ($p>0.10$). However, between 83-112 d, net N mineralization rates were highest for European larch in large macroaggregates and correlated negatively with litter lignin and lignin:N ratio

(Figs. 5.5a,b). *In situ* net N mineralization also correlated negatively with net N mineralization rate (83-112 d) from large macroaggregates ($r^2$=0.80, p=0.04).

Previous work at CEF (Gower and Son, 1992) indicated that annual *in situ* net N mineralization rates were highest for European larch (Table 5.1). They attributed higher net N mineralization rates to lower leaf litter lignin:N ratio (cf. Fig. 6 in Gower and Son, 1992). During 387 d laboratory incubations, Scott (1996) found that potentially mineralizable N was higher for red oak, but net N mineralization rates between 0-20 days were highest for European larch. This suggests that species effects on net N mineralization are related to the incorporation of relatively labile (more decomposable) aboveground plant litter fragments into large macroaggregates, and that the quality of the intra-aggregate organic matter influences net N mineralization, not the degree of soil aggregation. Differences in *in situ* net N mineralization related poorly to aggregate weighted mean diameter or aggregate organic matter concentration (Scott 1996).

Oades (1984) proposed a model of soil aggregation where microaggregates form inside macroaggregates, with small fragments of relatively undecomposed organic matter acting as the nucleus of aggregate formation. This would suggest that mineralization of C and N from microaggregates should be related to differences in the quality of the organic material around which microaggregates develop (assuming it is not physically isolated from soil organisms). I found no relationship between initial litter quality and C or net N mineralization from microaggregates, suggesting either that the material within microaggregates is physically protected from soil microorganisms (Cambardella and

Elliott, 1994) or that the quality of organic matter around which microaggregates form is unrelated to the quality of the plant litter.

## Conclusions

I found no evidence supporting the idea that physical protection of SOM influences whole-soil organic matter dynamics in these soils. Species characteristics had no influence on the physical protection of organic matter. Compared to microaggregates, C mineralization from macroaggregates was higher during the early stages of the incubation, but after 83 d C mineralization rates were higher in microaggregates, suggesting that macroaggregates are not simply a conglomeration of microaggregates as proposed by Tisdall and Oades (1982). Plant species modified net N mineralization from macroaggregates, which correlated negatively with litter lignin and lignin:N ratio and positively with *in situ* net N mineralization. This suggests that it is the quality of organic material in macroaggregates rather than the quantity that influences ecosystem processes such as net N mineralization.

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Table 5.1. Soil characteristics for monoculture plots at Coullee Experimental Forest. Values in parentheses represent one standard deviation.

| Site/Species | pH | $C_{org}$ | $N_{org}$ | Agg. WMD[1] | N min |
|---|---|---|---|---|---|
| | | ------- g $kg^{-1}$------- | | mm | kg $ha^{-1}y^{-1}$ |
| *Larix decidua* | 4.37 | 15 | 1.47 | 1.73 | 117 |
| | (.33) | (3.1) | (.25) | (.54) | |
| *Picea abies* | 4.12 | 17.9 | 1.51 | 2.13 | 46 |
| | (.18) | (.92) | (.12) | (.28) | |
| *Quercus rubra* | 4.24 | 12.3 | 1.3 | 2.05 | 55 |
| | (.17) | (2.0) | (.14) | (.21) | |
| *Pinus resinosa* | 4.34 | 16.3 | 1.44 | 1.81 | 51 |
| | (.1) | (2.48) | (.27) | (.35) | |
| *Pinus strobus* | 4.59 | 13.9 | 1.36 | 1.49 | 87 |
| | (.16) | (5.1) | (.56) | (.49) | |

[1] Aggregate weighted mean diameter ($WMD=(\Sigma d_i*w_i)/W$), d=average aggregate diameter of a size class (mm), w=aggregate size class mass, and W=overall sample mass (Capriel et al. 1990).

[2] Annual net N mineralization (values for Coullee Experimental Forest from Gower and Son, 1992)

Table 5.2. Species characteristics in the monoculture plots at Coullee Experimental Forest. Values in parentheses represent one standard deviation.

| Site/Species | Leaf litterfall[1] | Leaf litter N[1] | Litter lignin[1] | Root biomass | Root N | Root lignin |
|---|---|---|---|---|---|---|
| | g $m^{-2}$ | ------g $kg^{-1}$------ | | g $m^{-2}$ | -------g $kg^{-1}$------- | |
| *Larix decidua* | 367 | 10.8 | 126 | 120 | 11.6 | 344 |
| | (2.4) | | | (35) | (2.7) | (60) |
| *Picea abies* | 411 | 9.9 | 268 | 196 | 8.7 | 328 |
| | (77) | | | (26) | (1.9) | (40) |
| *Quercus rubra* | 428 | 8.6 | 248 | 156 | 6.9 | 375 |
| | (215) | | | (56) | (.7) | (35) |
| *Pinus resinosa* | 446 | 7.2 | 219 | 165 | 11.3 | 369 |
| | (550) | | | (30) | (2.9) | (26) |
| *Pinus strobus* | 321 | 8.3 | 225 | 166 | 10.2 | 363 |
| | (70) | | | (114) | (2) | (14) |

[1] Gower and Son (1992) and Yowhan Son, unpublished data.

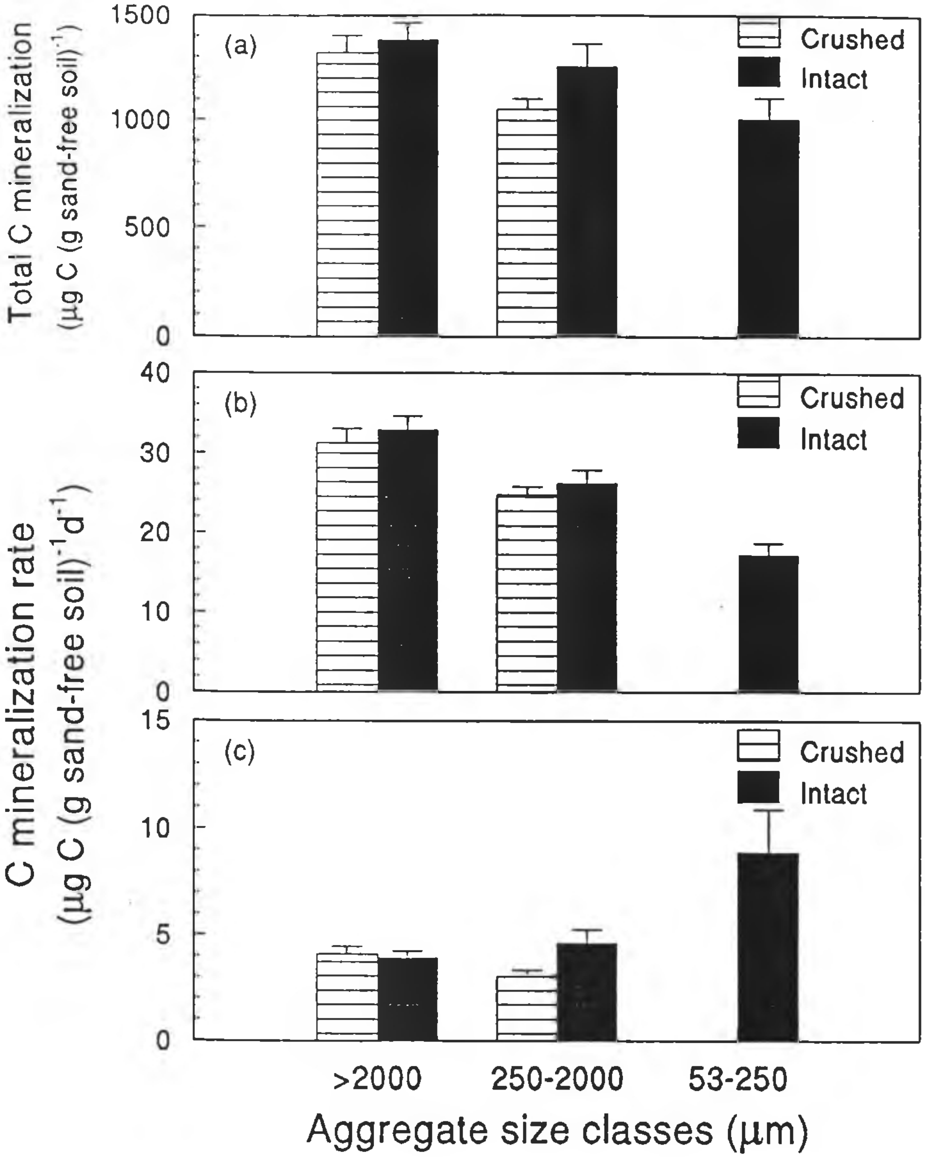

Fig. 5.1. Carbon mineralization from crushed and intact aggregates during 112 day laboratory incubations. Microaggregates (53-250 µm) were not crushed. (a) total C mineralization (b) 0-23 day C mineralization rate and (c) 83-112 day C mineralization rate. Error bars represent 1 SE.

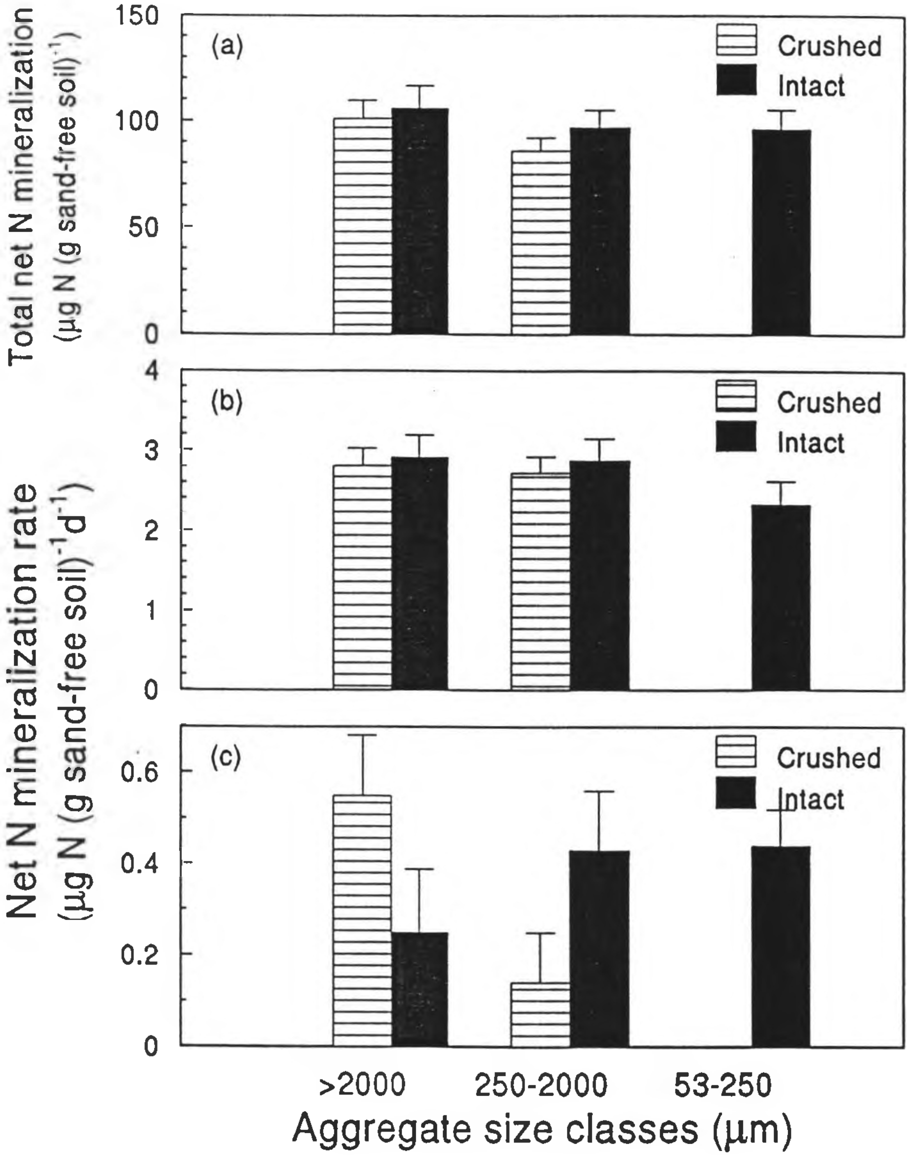

Fig. 5.2. Net N mineralization for crushed and intact aggregates during 112 day aggregate incubations. (a) Total N mineralization (b) 0-23 day net N mineralization rate (c) 83-112 day net N mineralization rate. Error bars represent 1 SE.

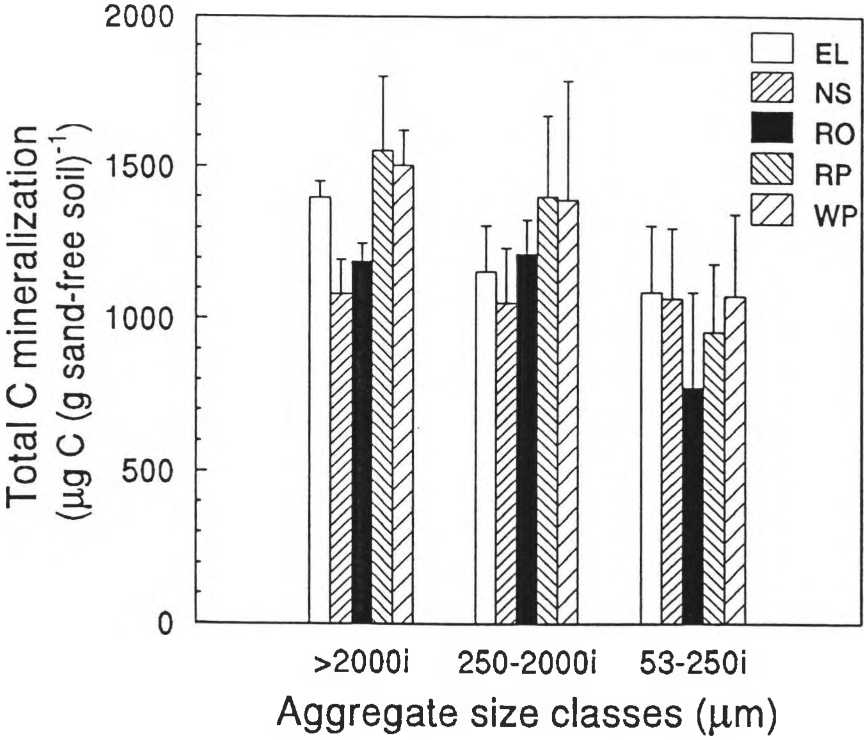

Figure 5.3. Comparison of C mineralization in 3 aggregate size classes (all intact) during 112 day laboratory incubations. Legend symbols: EL=European larch, NS=Norway spruce, RO=red oak, RP=red pine, WP=white pine. Error bars represent 1 SE.

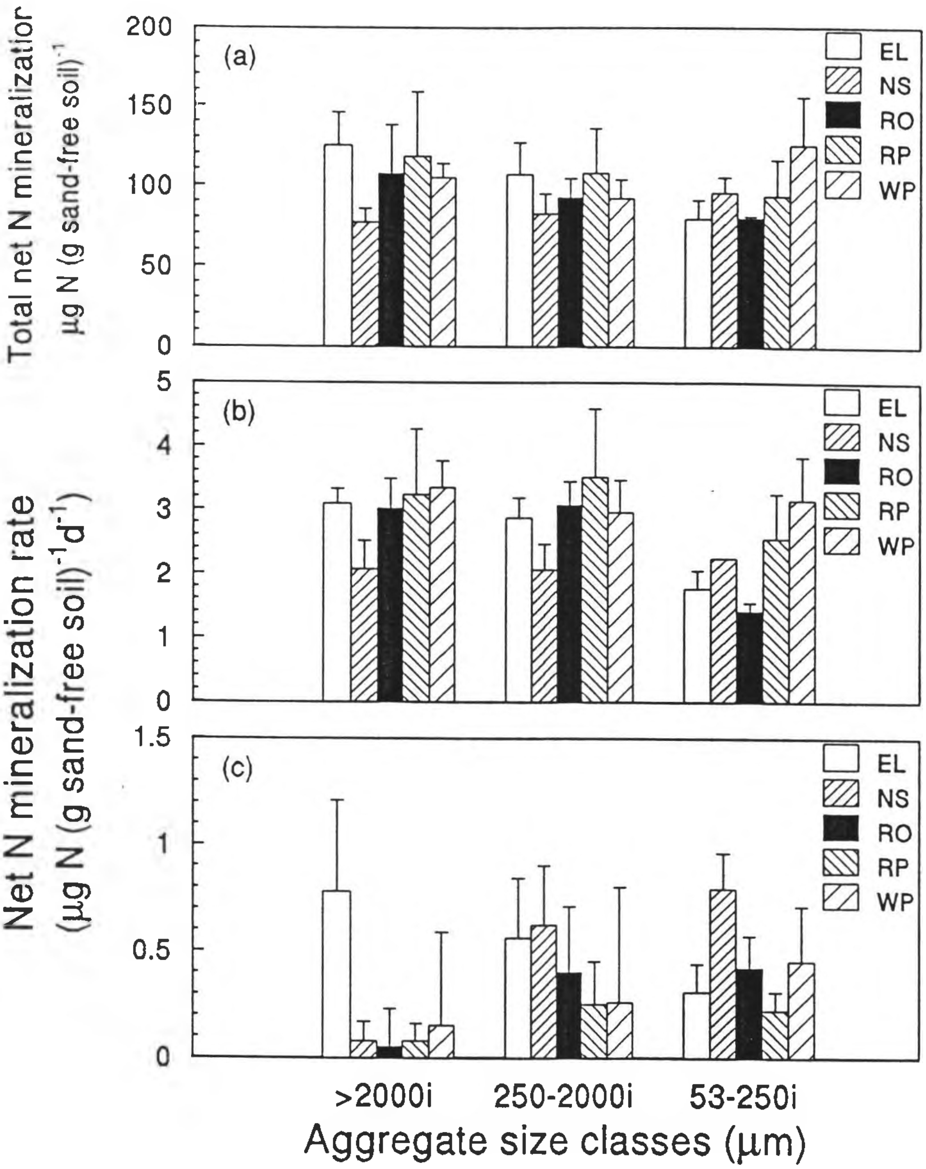

Figure 5.4. Comparison of N mineralization in 3 aggregate size classes (all intact) during 112 day laboratory incubations. (a) Total N mineralization (b) 0-23 day net N mineralization rate (c) 83-112 day net N mineralization rate. Legend symbols: EL=European larch, NS=Norway spruce, RO=red oak, RP=red pine, WP=white pine. Error bar represents 1 SE.

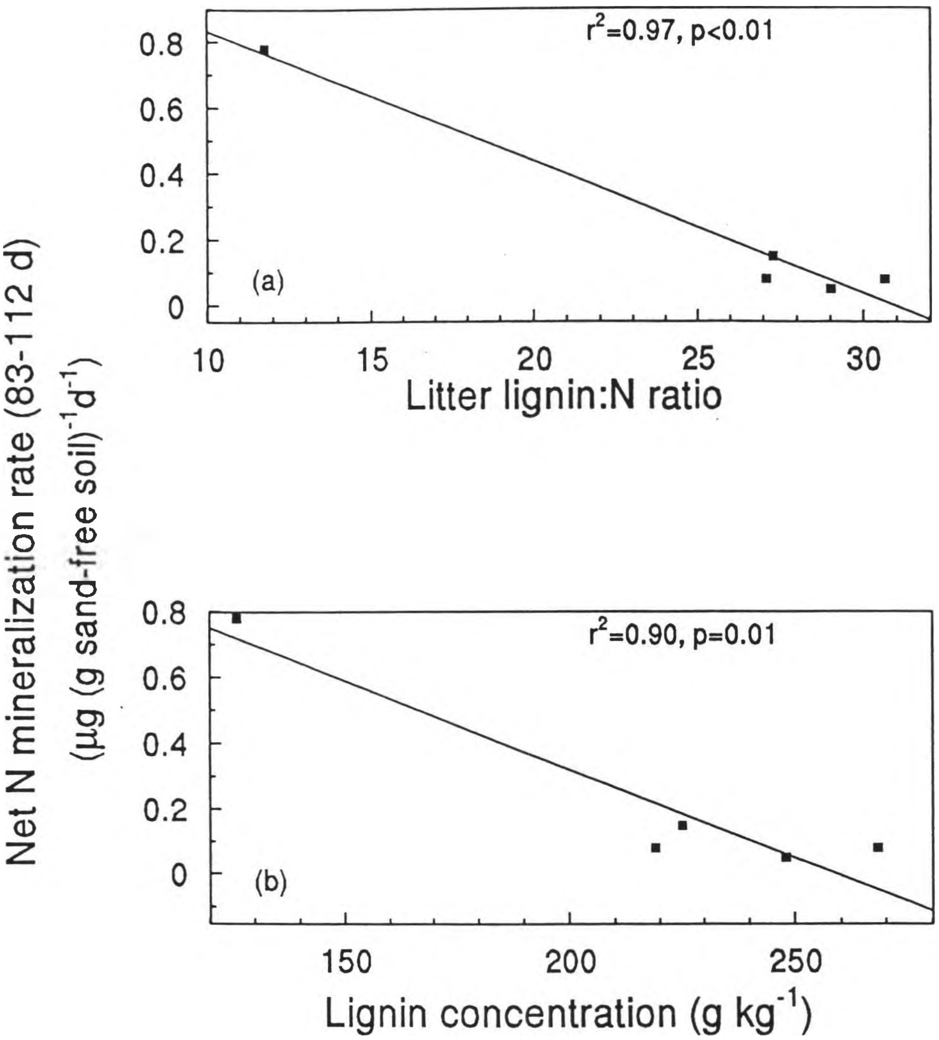

Fig. 5.5. Relationship between net N mineralization rate between 83-112 d and leaf litter lignin:N ratio and lignin concentration for five tree species at Coullee Experimental Forest.