Oecologia (1993) 96:186–192

Oecologia

Nitrogen mineralization dynamics in grass monocultures

David A. Wedin*, John Pastor

Natural Resources Research Institute, University of Minnesota, Duluth, MN 55811, USA

Received: 7 October 1992 / Accepted: 19 July 1993

Abstract. Although Wedin and Tilman (1990) observed large differences in in situ N mineralization among monocultures of five grass species, the mechanisms responsible were unclear. In this study, we found that the species did not change total soil C or N, and soil C: N ratio (range 12.9–14.1) was only slightly, but significantly, changed after four years. Nor did the species significantly affect the total amount of N mineralized (per g soil N) in year-long aerobic laboratory incubations. However, short-term N mineralization rates in the incubations (day 1–day 17) differed significantly among species and were significantly correlated with annual in situ mineralization. When pool sizes and turnover rates of potentially mineralizable N (N_0) were estimated, the best model treated N_0 as two pools: a labile pool, which differed among species in size (N_l, range 2–3% of total N) and rate constant (h. range 0.04–0.26 wk^{-1}), and a larger recalcitrant pool with a constant mineralization rate across species. The rate constant of the labile pool (h) was highly correlated with annual in situ N mineralization (+0.96). Therefore, plant species need only change the dynamics of a small fraction of soil organic matter, in this case estimated to be less than 3%, to have large effects on overall system N dynamics.

Key words: N mineralization – Monocultures – Soil organic matter – Grasses

Vegetation along with climate, relief, and soil parent material, can have a major influence on soil development and soil nutrient cycles through time (Jenny 1941). Recent research suggests that feedbacks between plant species and soil nitrogen dynamics are stronger than previously thought (Pastor and Post 1986; Vitousek et al. 1987; Wedin and Tilman 1990; Berendse 1990; Hobbie 1992). If such feedbacks are strong, then relatively small, continuous changes in driving variables (such as climate or atmospheric N inputs) may cause large, discontinuous, and even chaotic responses in vegetation structure, primary productivity, soil carbon storage and other ecosystem attributes (Pastor and Post 1986; Cohen and Pastor 1991; Tilman and Wedin 1991a; DeAngelis 1992).

Wedin and Tilman (1990) found that in situ N mineralization diverged significantly among monocultures of five perennial grass species, ranging from 2 g N m^{-2} $year^{-1}$ to 12 g N m^{-2} $year^{-1}$ on initially homogeneous soils by year 3. This divergence was highly correlated with species differences in litter N and lignin concentration and belowground productivity. Field measures of net N mineralization have potential problems however, including artificial incubation conditions caused by the inclusion of severed roots or altered soil moisture levels (Binkley and Hart 1989). Furthermore, in situ incubations may reflect treatment differences in microclimate rather than differences in the quality or quantity of soil organic matter.

To further examine the mechanisms driving the divergence among these five grass species, we measured changes in potential N mineralization, total C and N, and C: N ratio in soils from four-year-old monocultures. Laboratory incubations were used to estimate potential N mineralization and to control for the effects of microclimate and severed roots, which can confound interpretation of field incubations. More importantly, long-term aerobic incubations with repeated measurements can be used to estimate the pool sizes of hypothetical fractions of soil organic matter and the turnover rates of these various pools (e.g. Stanford and Smith 1972; Deans et al. 1986; Bonde and Rosswall 1987).

Materials and methods

The perennial grass monocultures used in this study are part of an experimental garden at the Cedar Creek Natural History Area in east-central Minnesota, U.S.A. *Schizachyrium scoparium* (Michx.) Nash-Gould (formerly *Andropogon scoparius)* and *Andropogon*

* *Present address:* Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Canada M5S 3B2

Correspondence to: D. Wedin

gerardi Vitm. are native C_4 bunchgrasses that usually dominate tallgrass prairie, oak savannah, and late-successional grasslands at CCNHA. *Agrostis scabra* Willd. is a native C_3 bunchgrass with peak abundance in early successional grasslands. *Agropyron repens* (L.) Beauv. and *Poa pratensis* L. are rhizomatous C_3 grasses native to Eurasia and have peak abundance at CCNHA in early and mid-successional grasslands respectively (Tilman 1988). These five species are the most abundant species in successional grasslands on the glacial outwash sandplain at CCNHA and have been used in numerous studies of succession, competition and nitrogen dynamics at CCNHA (Tilman 1988; Wedin and Tilman 1990; Tilman and Wedin 1991b; Wedin and Tilman 1993).

To construct the experimental garden, the top 0.7 m of soil was removed from a portion of an old field with a bulldozer. Nine large soil mixtures (each 3 × 12 m) were created by mixing different amounts of black soil with the subsurface sand left at the garden site. All mixtures were mixed thoroughly to an average depth of 23 cm by repeated passes with a rotortiller. The black soil, a Duelm sandy loam of the Hubbard-Isanti-Duelm association, was brought in from outside CCNHA and averaged 72% sand, 4% clay, 24% silt, 1.79% total C, 0.135% total N and pH 7.2. The subsurface sand averaged 93% sand, 3% clay, 4% silt, 0.09% total C, 0.013% total N, and pH 6.6. The resulting soil mixtures ranged from 100% sand to 100% black soil.

In each soil mixture, 64 plots (each 0.75 m × 0.75 m) were separated by 25-cm deep sheet metal. These plots were planted in May 1986 with either a monoculture of one of the five grass species or a competition treatment containing two or more species. The plots were fertilized annually with all nutrients except N and were watered to ensure that N was the only limiting soil resource (see Wedin and Tilman 1990; Tilman and Wedin 1991b for complete methods).

For this study, we used five monocultures for each of the five species from the high soil organic matter end of the soil mixture gradient (i.e. 90% to 100% black soil). In May 1986, prior to seeding and immediately following final mixing of the soils, four 20 cm deep by 2.5 cm diameter cores were taken from each plots, pooled, dried at 50° C, and passed through a 2 mm sieve. After four growing seasons (November 1989), the 25 plots in this study were resampled with three 2.5-cm diameter cores. To be consistent with the in situ mineralization study (Wedin and Tilman 1990), the 1989 cores were 16 cm deep. These samples were air-dried and passed through a 2 mm sieve. Although visible roots were removed, the samples may have contained fine root fragments. Subsamples from the 1986 and 1989 samples for each plot were dried at 60° C and ground with a coffee mill. The ground samples were analyzed for total soil C and total soil N (as %C and %N) with a Carlo-Erba NA1500 N/C analyzer. Estimates of 1986 total C and total N were adjusted to account for 0.5 cm of sand (total C and total N equal to zero) added to the plots during seeding. To avoid any bias introduced by using different soil sampling depths in 1986 and 1989, soil characteristics from the two sampling periods were not directly compared. The 1986 samples, however, do indicate the degree of pretreatment variance in total C, total N, and C:N ratio, and allow us to test if significant pretreatment differences existed that could confound interpretation of the posttreatment results.

For each of the 25 plots, we performed two replicate laboratory incubations. The aerobic incubation procedure followed the method of Stanford and Smith (1972) as modified by Nadelhoffer (1990), except that CO_2 evolution from the incubations was not measured. For each sample, 30 g of air-dried soil was placed on top of a glass-fiber filter and glass wool in the upper portion of a two-chambered plastic filter unit (150 ml Falcon Filter Model 7102). The experimental design allows repeated measurements of leachable N with minimal disturbance of the sample.

The samples were leached on day 1, 17, 39, 66, 102, 130, 164, 220, 295, 367. The initial leaching (d1) removed initial mineral N and was not included in the calculation of net N mineralization. Samples were leached with three increments of 0.01 M $CaCl_2$ (40 ml + 40 ml + 20 ml = 100 ml), followed by 25 ml of a dilute nutrient solution containing all required plant nutrients except N (complete description of nutrient solution in Nadelhoffer 1990). Approximately 0.5 h after its addition each successive increment of leaching solution was drawn through the sample with 75 kPa vacuum. The leachate was evacuated from the bottom chamber of each filter unit, brought up to 150 ml with 0.01 M $CaCl_2$, shaken, and a 20–30 ml subsample frozen for later analysis. The filter units were incubated in darkness at 30° C, and remoistened occasionally with deionized H_2O to maintain them at constant soil moisture content.

Samples were analyzed colorimetrically with an Alpkem autoanalyzer for NO_3^- and NH_4^+. Solution concentrations were converted to mg N per kg dry soil, and net N mineralization for each sampling period was estimated as the sum of NO_3^--N and NH_4^+-N. Only net N mineralization, in contrast to gross N mineralization, was measured in this study and all references to mineralization imply net mineralization. Cumulative mineralization at each date was the sum of mineralization for that period and previous periods. Relative N mineralization was calculated by dividing cumulative N mineralization by soil total N. Results for the two replicate incubations for each plot on each sampling date were averaged prior to statistical analysis with ANOVA or curve fitting. For each incubation period, a weekly mineralization rate was also calculated as the net mineralization rate divided by the number of weeks for that period. Pairwise comparisons of mineralization and soil total C and N results were made with protected LSD comparisons at the $P = 0.05$ confidence level.

Estimation of potentially mineralizable N

Stanford and Smith (1972) proposed a first-order exponential function (Eq. 1) to estimate the amount of potentially mineralizable N in soils based on aerobic laboratory incubations.

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

N_t is the cumulative amount of N mineralized at time t, N_o is potentially mineralizable N, and k is the mineralization rate constant (per week).

Other researchers (e.g. Deans et al. 1986; Bonde and Rosswall 1987) have proposed using a model (Eq. 2) that considers two pools of potentially mineralizable N rather than one.

$$N_t = N_o s(1 - e^{-ht}) + N_o(1 - s)(1 - e^{-kt}) \qquad \text{(Eq. 2)}$$

$N_o s$ and h represent the pool size and rate constant of a labile or readily mineralizable pool of organic N, while $N_o(1\text{-}s)$ and k correspond to a recalcitrant pool of potentially mineralizable N. The remaining fraction of total soil N (i.e., total soil N minus N_o) can be considered the passive pool of organic N (Deans et al. 1986). However, the number of functional pools with which soil organic matter is considered, the names of those pools, and interpretation of their significance vary widely (see Paul 1984; Parton et al. 1988; Binkley and Hart 1989 for alternative treatments of soil organic N).

Equations (1) and (2) can only be fitted to experimental results if mineralization rates approach zero over the course of the incubation. Bonde and Rosswall (1987) observed that mineralization rates remained positive and failed to converge on zero during long-term aerobic incubations of agricultural soils. They proposed that mineralization of N from the recalcitrant pool of soil organic N was constant rather than decreasing over the course of their laboratory incubation. Thus, they presented a model with two pools of soil organic N mineralizing according to:

$$N_t = N_l(1 - e^{-ht}) + ct \qquad \text{(Eq. 3)}$$

where N_l and h are the pool size and rate constant for the labile pool, and c is the constant mineralization rate for the recalcitrant pool of potentially mineralizable N.

We fitted these three models to the incubation results for each of the five species using the non-linear curve fitting routine of SAS (Gauss-Newton method SAS 1988). All of our estimates of potential N mineralization are based on relative N mineralization results. Adequacy of curve fits was tested by observing residual plots (non-

random patterns in residuals indicate an inadequate model), as well as minimizing the residual sum of squares. Although we present 95% confidence intervals for the parameter estimates generated by SAS, comparisons among species using these intervals do not necessarily have the same statistical validity as comparable comparisons of parameter estimates from least-squares (linear) regression. To test the robustness of our parameter estimates, the models were fitted to the data a second time using both the highest and lowest parameter estimates from the set of five species as starting values for iterative curve fitting. In all cases, refitting gave essentially the same parameter estimates (differences between estimates less than 1×10^{-5}%).

Comparisons of field and laboratory measurements

To compare estimates of in situ N mineralization measured in the monocultures in year 3 of the study (Wedin and Tilman 1990) with the laboratory incubation results, the in situ annual estimates for each plot were also converted to relative N mineralization (net mineralization per unit soil total N per year). Because parameters for Eq. 1–3 were estimated for each species rather than for individual replicate plots, correlations among various field and laboratory measures were made using mean values or estimates for each species ($n = 5$ for each correlation). Correlations were also calculated between in situ mineralization and both weekly mineralization rates and cumulative mineralization on a plot by plot basis. Because slightly different sets of monocultures were used in the field and laboratory studies, only 15 plots had both types of data for the plot by plot comparisons.

Results

Species effects on soil total C and N, and C:N ratio

After four growing seasons, total soil C and total soil N did not differ significantly among monocultures of the five grass species (1989 values of %C and %N in Table 1). In contrast, C:N ratio differed significantly ($P < 0.001$) among monocultures of the five species after four growing seasons, ranging from 12.9 for *Agrostis* to 14.1 for *Schizachyrium* (1989 values, Table 1).

N mineralization in laboratory incubations

The total amount of mineral N (NO_3^- plus NH_4^-) released per gram of soil during the 1 year laboratory incubation differed significantly among the five species (Table 2). However, these differences among species largely reflect random pretreatment differences in the initial quantity of soil organic matter in the plots (Table 1). Cumulative N mineralization after 1 year was significantly correlated with 1986 total soil C ($n = 25$, $r^2 = 0.491$, $P < 0.0001$) and 1986 total soil N ($r^2 = 0.501$). Therefore, we will focus on differences in relative N mineralization (i.e. mg N g^{-1} soil N) to correct for pretreatment plot differences in organic matter quantity and more accurately compare species effects on soil organic matter quality and N mineralization dynamics. After 1 year of incubation, soils from the five species' monocultures did not differ significantly in cumulative values for relative N mineralization (Table 2). For all species, cumulative N mineralization after 1 year was approximately 10% of total soil N. Over 99% of the N mineralized occurred as NO_3^-. Although all species converged on a comparable value for relative N mineralization by the end of the incubation, mineralization differed significantly among species from the beginning of the incubations through the fourth sampling date (102 d) (Fig. 1a).

The initial differences among species in cumulative N mineralization corresponded to large initial differences in weekly mineralization rates (mg N g^{-1} N $week^{-1}$) (Fig. 1b). The initial mineralization rates (period ending d17) were significantly higher for *Agrostis* than for *Agropyron* and *Poa*, which had significantly higher rates than *Schizachyrium* and *Andropogon* (Table 2). On d39 and d66 *Poa* had the highest mineralization rate, while after d102 *Schizachyrium* had the highest rate. By d66, *Agrostis* had dropped from the highest to the lowest rate. Thus between d17 and d102 there was a complete reversal in the species ranking for weekly N mineralization rate. By the fifth sampling date (d130) significant dif-

Table 1. Characteristics of monoculture soils used in incubations. Means and standard errors of total soil C (%C), total soil N (%N) and soil C:N ratio of five replicates for each of five perennial grass species prior to planting (May 1986) and after four growing seasons (November 1989). Means sharing the same lower case letter in rows do not differ significantly using PLSD multiple comparisons ($P \leq 0.05$). See text for details

	Agrostis scabra	*Agropyron repens*	*Poa pratensis*	*Schiz. scoparium*	*Andro. gerardi*	$F_{4,20}$
%C 1986	1.74 (0.08)a	1.64 (0.11)a	1.58 (0.13)a	1.56 (0.12)a	1.43 (0.19)a	0.78 n.s.
%N 1986	0.131 (0.006)a	0.126 (0.009)a	0.119 (0.010)a	0.115 (0.009)a	0.108 (0.014)a	0.83 n.s.
C:N Ratio 1986	13.29 (0.09)a	13.09 (0.16)a	13.30 (0.13)a	13.29 (0.09)a	13.21 (0.26)a	1.50 n.s.
%C 1989	1.63 (0.08)a	1.80 (0.13)a	1.57 (0.11)a	1.49 (0.12)a	1.42 (0.18)a	1.29 n.s.
%N 1989	0.126 (0.006)a	0.136 (0.010)a	0.121 (0.010)a	0.106 (0.006)a	0.103 (0.013)a	1.92 n.s.
C:N Ratio 1989	12.94 (0.06)a	13.22 (0.13)a	13.03 (0.21)a	14.06 (0.21)b	13.75 (0.12)b	9.36***

Table 2. Various measures of net N mineralization in soils from monocultures of five grass species. Means ($n=5$), standard errors and pairwise comparisons (means sharing lower case letters do not differ significantly using PLSD at $P \leq 0.05$) are presented for cumulative N mineralization, relative N mineralization (cumulative), and initial N mineralization rate (average over days 1–17). Values of N_0 (potentially mineralizable N), k (rate constant for N_0), N_1 (labile fraction of potentially mineralizable N), and h (rate constant for N_1) are parameter estimates from non-linear curve fits with 95% confidence intervals. Means (with s.e. and pairwise comparisons) for in situ N min are based on Wedin and Tilman 1990. See text for details

	Agrostis scabra	*Agropyron repens*	*Poa pratensis*	*Schiz. scoparium*	*Andro. gerardi*
Cumulative N min. after 367d (mg N kg^{-1} soil)	116.04 (2.37)ab	132.28 (6.29)a	122.25 (2.04)ab	106.63 (6.71)bc	97.60 (9.73)c
Relative N min. after 367d (mg N g^{-1} N)	93.38 (5.21)a	97.73 (2.71)a	103.93 (8.20)a	101.59 (3.99)a	96.41 (3.13)a
Initial N min. rate (mg N g^{-1} N wk^{-1})	5.18 (0.42)a	4.41 (0.35)ab	3.92 (0.63)b	1.40 (0.2)c	1.61 (0.28)c
N_0 (mg N g^{-1} N)	118 (23)	128 (17)	148 (45)	214 (66)	200 (53)
k (wk^{-1})	0.027 (0.009)	0.025 (0.005)	0.022 (0.010)	0.012 (0.005)	0.012 (0.004)
N_1 (mg N g^{-1} N)	19.0 (2.3)	23.0 (1.7)	28.1 (5.8)	30.6 (7.0)	23.7 (4.4)
h (wk^{-1})	0.262 (0.160)	0.155 (0.048)	0.098 (0.064)	0.044 (0.021)	0.054 (0.023)
In situ N min. (mg N g^{-1} N yr^{-1})	31.95 (2.95)a	9.86 (1.61)b	8.60 (3.79)b	2.94 (0.99)c	3.99 (0.21)bc

ferences in weekly N mineralization rate among species had disappeared and all five species had converged on a N mineralization rate of approximately 1.4 mg N g^{-1} N wk^{-1} (Fig. 1b).

When the incubation results were fitted with equation 1, *Agrostis* and *Agropyron* had lower N_0 values and higher k values than *Schizachyrium* and *Andropogon* (compared using 95% confidence intervals, Table 2). However, because the soils were still mineralizing N after one year (Fig. 1a), the confidence intervals associated with the N_0 estimates were quite large. Non-random residual patterns from the curve fits also indicated lack of fit to the data: for *Agrostis, Poa* and *Agropyron* the single exponential model (Eq. 1) underestimated mineralization early in the incubation (i.e., positive residuals) and overestimated it during the middle of the incubation. Residuals for *Schizachyrium* and *Andropogon* showed the opposite pattern. The double exponential model (Eq. 2) fitted the data poorly, failing to converge on parameter estimates for three out of five species (Table 3).

Of all the models, Eq. 3 was the best fit to the data and had lower residual sums of squares and more randomly distributed residuals for all species (Table 3). This model assigns the recalcitrant pool a constant mineralization rate (c), which we defined as 1.4 mg N g^{-1} N $week^{-1}$. This is approximately the mineralization rate on which all species converged by the midpoint of the incubations (Fig. 1b). Figure 1c shows cumulative relative N mineralization results for the hypothesized labile pool following adjustment of mineralization rates by c. The adjustment essentially rescaled mineralization rates in Fig. 1b so that 1.4 became 0.0. The species differed in estimates of both N_1 and h (Table 2). In general, the rank order of the species estimates for N_1 and h paralleled those for N_0 and k from the single exponential model (Eq. 1). However, species differences in h, the rate constant of the labile pool, were much larger than those observed for k, the overall rate constant from Eq. 1. The labile rate constant ranged from 0.044 $week^{-1}$ for *Schizachyrium* to 0.262 $week^{-1}$ for *Agrostis*. N_1 ranged from 1.9% of soil total N (i.e., 19 mg N g^{-1} N) for *Agrostis* to 3.1% for *Schizachyrium*.

Correlation of field and laboratory measurements

When in situ N mineralization estimates (Wedin and Tilman 1990) and weekly mineralization rates from the laboratory incubations were compared on a plot by plot basis ($n=15$), the correlation was significant ($P<0.01$) on the first sampling date ($r=+0.661$) and decreased sharply after that, becoming negative by d66, the third sampling date (Fig. 2). Correlations between field mineralization and cumulative mineralization in the laboratory also decreased after the first sampling period, and were not significant by d66 (Fig. 2). The correlation on a plot by plot basis between annual in situ mineralization and cumulative laboratory mineralization after one year was +0.047.

Among our estimates of the pool sizes and turnover rates of potentially mineralizable N, the only significant correlate of annual in situ N mineralization was h, the rate constant for the labile fraction of potentially mineralizable N (correlations based on species means, $n=5$, Table 4). Soil C:N ratio, the only bulk soil measure which species affected significantly within four growing seasons, was positively correlated with N_0 and negatively correlated with k (Table 4). Soil C:N ratio was also

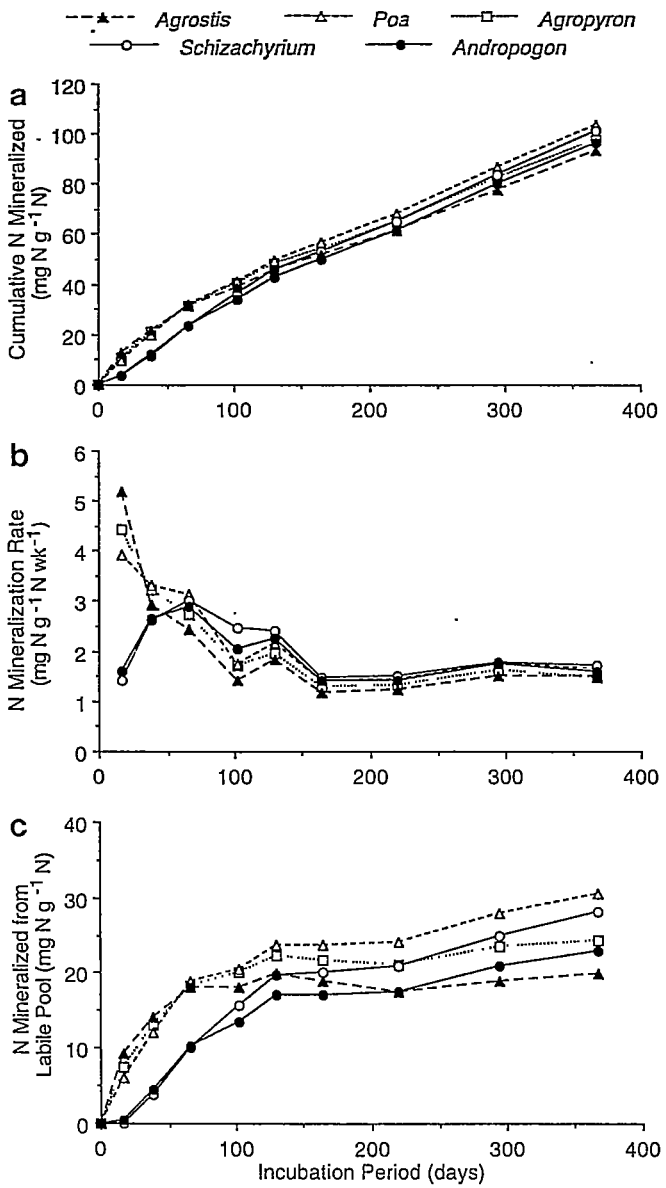

Fig. 1a–c. Net N mineralization over 367 d in laboratory incubations of soils from monocultures of five grass species: a cumulative N mineralization (per g soil N); b weekly N mineralization rates; c cumulative N mineralization from the hypothesized labile pool of soil N. See text for details

negatively correlated with the initial mineralization rate in the laboratory incubations.

Discussion

After four growing seasons, we did not find significant changes in either total soil C or N that corresponded to the divergence in N mineralization rates observed in the field among these five grass species (Wedin and Tilman 1990). Although soil C:N ratios diverged significantly among the five species, these changes were relatively small, ranging from 12.9 to 14.1 (Table 1). Nor did the species significantly affect the total amount of N mineralized (per g soil N) in year-long aerobic laboratory incubations (Table 2). Together, these results suggest that the species had had little effect on the bulk of the soil organic matter in the monocultures after four years.

In contrast there were large and highly significant differences among the five species in their short-term N mineralization dynamics in the laboratory incubations. These differences were significantly correlated with differences in N mineralization observed in the field. The largest difference among species in N mineralization rates (mg N g^{-1} N $week^{-1}$) occurred over the first 17 days of the study. By day 102 of the laboratory incubations, there had been a complete reversal in mineralization rates among species. *Agrostis,* which had the highest mineralization rate in the field and on day 17 in the laboratory, dropped to the lowest rate by day 102. *Schizachyrium* on the other hand, had the lowest mineralization rate in the field and on day 17 in the lab, but had the highest mineralization rate after day 102 in the lab. Schimel (1986) observed a similar pattern in laboratory incubations with cropland and grassland soils. In his study, N mineralization rates for cropland soils were initially high but declined sharply with time, while rates for soils from nearby intact grasslands were initially low but increased by day 30. In our study, the correlation between weekly mineralization rates in the laboratory and annual in situ mineralization was not significant after day 17, and became negative after day 66.

Of all our various estimates of pool sizes and associated rate constants for fractions of potentially mineralizable N based on the laboratory incubations, the best correlate of annual in situ N mineralization was the rate constant for the labile pool of mineralizable N (h in Eq. 3, see Tables 2 and 4). Our estimates for the size of this labile pool (N_l in Eq. 3, Table 2) range from 2% to 3% of total soil N for the five species.

Therefore, our results suggest that species need only affect the dynamics of a small, but highly active, fraction of soil organic matter to have large affects on N turnover. Studies using aerobic incubations have often emphasized differences in N_o rather than differences in k, in other words, the pool size of mineralizable N rather than its dynamics (Stanford and Smith 1972). In doing so, researchers may be underestimating differences in the N dynamics of soils with distinct disturbance, vegetation or management histories (Paul 1984). The consideration of multiple fractions of soil organic matter (e.g., Eq. 3) may help to address this problem. Again, however, we conclude that the activity (i.e. the rate constant) of our hypothesized labile fraction, rather than its size, was our best correlate of N mineralization observed in the field.

The fraction of soil organic matter responsible for short-term N mineralization dynamics in laboratory incubations is poorly defined (Paul 1984; Binkley and Hart 1989). It may contain dead microbial biomass resulting from the air-drying of the soils prior to incubation, root detritus, fine roots, mycorrhizal hyphae disturbed during sampling, and various low molecular weight organics such as root exudates associated with rhizosphere symbionts. Various studies suggest that the C_4 grasses *Schizachyrium* and *Andropogon,* both dominant species in North American tallgrass prairie, create a high poten-

Table 3. Summary of non-linear regression models using equations 1–3 for results from 1yr aerobic laboratory incubations. Cumulative N mineralization results were fitted iteratively with the Gauss-Newton method (SAS 1988). Convergence of parameter estimates on constant values was tested using the Residual Sums of Squares and standard criteria of SAS. "Yes" indicates that convergence criteria were met. R^2 for each model was calculated as: (corrected total sum of squares-residual sum of squares)/(corrected total sum of squares). Parameter estimates and 95% confidence intervals for equations 1 and 3 are in Table 2. See text for discussion of residual plots associated with the various models

	Agrostis scabra	*Agropyron repens*	*Poa pratensis*	*Schiz. scoparium*	*Andro. gerardi*
Equation 1:					
Convergence	yes	yes	yes	yes	yes
R^2	0.92	0.96	0.89	0.97	0.98
Equation 2:					
Convergence	no	yes	no	no	yes
R^2	0.93	0.94	0.90	0.97	0.94
Equation 3:					
Convergence	yes	yes	yes	yes	yes
R^2	0.95	0.98	0.90	0.98	0.98

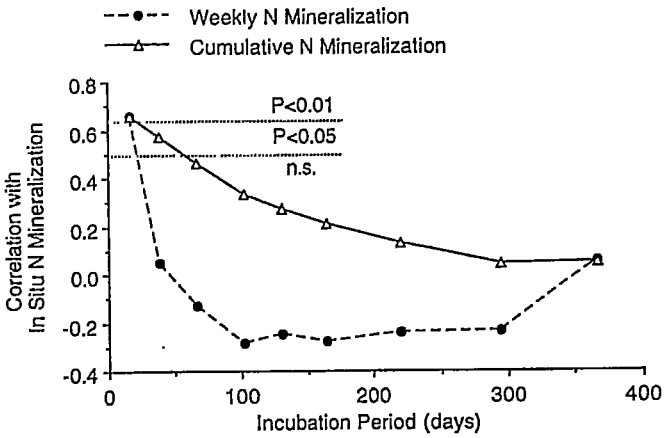

Fig. 2. Correlation coefficients between two laboratory measures of N mineralization (cumulative relative N mineralization, mg N g^{-1} N, and weekly N mineralization, mg N g^{-1} N $week^{-1}$) and estimates of annual in situ N mineralization (see Table 2). Correlations were done on a plot by plot basis for each sampling period using the 15 plots in which both field and laboratory measures were made. Correlation coefficients greater than 0.62 are significant at $P<0.01$ and those greater than 0.49 at $P<0.05$

Table 4. Correlations between species means for various laboratory measures of N mineralization and either in situ N mineralization (Table 2) or the C:N ratio of soils used in the laboratory incubations (Table 1). Correlations marked* are significant at $P \leq 0.05$ for $N=5$

Mineralization parameter	In situ Net N Min	1989 Soil C:N Ratio
Relative N Min. after 367d	−0.656	+0.221
Initial N Min. Rate	+0.792	−0.947*
N_0	−0.753	+0.948*
k	+0.761	−0.932*
N_1	−0.775	+0.593
h	+0.960*	−0.789
1989 Soil C:N	−0.711	

tial for N immobilization in litter and soil organic matter because of their high rates of belowground carbon allocation and their low litter quality (Pastor et al. 1987; Wedin and Tilman 1990; Ojima et al. 1990; Seastedt et al. 1991). In contrast, *Agrostis*, which has a ten-fold smaller root mass and much higher litter quality (root C:N ratios of 25–30) than either *Schizachyrium* and *Andropogon*, presumably has little or no N immobilization during root decomposition (Wedin and Tilman 1990). Johnson et al. (1992) also found large differences in both the size and the species composition of the mycorrhizal community among monocultures of these five grass species. Thus, under field conditions, both the quality and quantity of organic matter entering the labile fraction of soil organic matter appear to differ sharply among these species. However, in the absence of fresh organic matter contributions to the soil and under optimal conditions, as in our laboratory incubations, these differences in the dynamics of the labile fraction disappear quickly.

The plant-soil systems we studied in our experimental monocultures had clearly not equilibrated after four growing seasons. Long-term (10–100 year) simulations of soil organic matter dynamics for these monocultures predict that total soil C, total soil N, and soil C: N ratio will diverge among these species as a consequence of species differences in the quality and quantity of litter inputs (unpublished simulations using the CENTURY model, D. Wedin and W. Parton, see Parton et al. 1988 for model details). These simulations also suggest that the divergence in N mineralization observed among these species in the field (Wedin and Tilman 1990) was not a short-term transient effect. If, however, species need only affect a relatively small, labile pool of soil organic matter to have large effects on N cycling, than the feedbacks between vegetation dynamics and soil nutrients may be much stronger and more dynamic than the observation of long-term species effects on soil organic matter development might suggest. Studies in tallgrass prairie have shown that disturbances such as fire (Ojima et al. 1990; Seastedt et al. 1991) or grazing (Holland and Detling

1990: Holland et al. 1992) that affect the N use and carbon allocation patterns of *Schizachyrium* and *Andropogon* can lead to relatively rapid shifts in N mineralization (i.e. less than 1 year). If soil nutrient dynamics can rapidly track shifts in the species composition of vegetation, or even the physiological status of dominant species, than the possibility exists for strong positive or negative feedbacks in the plant-soil system (DeAngelis 1992). Such non-linearities can have important consequences for ecosystem dynamics and stability.

Acknowledgements. We thank G. Abegglen, F. Berendse, A. ElHaddi, D. Tilman, and anonymous reviewers for suggestions and assistance. This study was supported by the National Science Foundation (BSR–8811884) and the University of Minnesota.

References

Binkley D, Hart SC (1989) The components of nitrogen availability assessments in forest soils. Adv Soil Sci 10:57–112

Berendse F (1990) Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J Ecol 78:413–427

Bonde TA, Rosswall T (1987) Seasonal variation of potentially mineralizable nitrogen in four cropping systems. Soil Sci Soc Am J 51:1508–1514

Deans JR, Molina JAE, Clapp CE (1986) Models for predicting potentially mineralizable nitrogen and decomposition rate constants. Soil Sci Am J 50:323–326

Cohen Y, Pastor J (1991) The response of a forest model to serial correlations of global warming. Ecology 72:1161–1165

DeAngelis DL (1992) Dynamics of Nutrient Cycling and Food Webs. Chapman and Hall, London

Hobbie. SE (1992) Effects of plant species on nutrient cycling. Trends Ecol Evol 7:336–339

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049

Holland EA, Parton WJ, Detling JK, Coppock DL (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am Nat 142:685–706

Jenny H (1941) Factors of Soil Formation. McGraw-Hill, New York

Nadelhoffer KJ (1990) Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. Soil Sci Soc Am J 54:411–415

Ojima DS, Parton WJ, Schimel DS, Owensby CE (1990) Simulated impacts of annual burning on prairie ecosystems. In: Collins SL, Wallace LL (eds) Fire in North American Tallgrass Prairie. U. of Oklahoma Press, Norman, OK, USA, pp 118–132

Parton WJ, Stewart JWB, Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5:109–131

Pastor J, Post WM (1986) Influence of climate, soil moisture, and succession on forest carbon and N cycles. Biogeochemistry 2:3–27

Pastor J, Stillwell MA, Tilman D (1987) Little bluestem litter dynamics in Minnesota old fields. Oecologia 72:327–330

Paul EA (1984) Dynamics of organic matter in soils. Plant Soil 76:275–285

SAS (1988) SAS/STAT User's Guide, Release 6.03. SAS Institute Inc., Cary, N.C.

Schimel DS (1986) Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2:345–357

Seastedt TR, Briggs JM, Gibson DJ (1991) Controls of nitrogen limitation in tallgrass prairie. Oecologia 87:72–79

Stanford G, Smith SJ (1972) Nitrogen mineralization potentials of soils. Soil Sci Soc Am J 36:465–472

Tilman D (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton

Tilman D, Wedin D (1991a) Oscillations and chaos in the dynamics of a perennial grass. Nature 353:653–655

Tilman D, Wedin D (1991b) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology 72:685–700

Wedin DA, Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84:433–441

Wedin D, Tilman D (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecol Monogr 63:199–229

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804