The effect of plant species on soil nitrogen mineralization

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Summary

1 To ascertain the influence of different plant species on nitrogen (N) cycling, we performed a long-term garden experiment with six grasses and five dicots with different potential growth rates, that are adapted to habitats with different nutrient supplies. We measured *in situ* N mineralization and nitrification of the soil under monocultures of each species during the fourth year of the experiment.

2 We focused on the effects of the different species on (i) annual net N mineralization; (ii) the seasonal pattern of N mineralization; and (iii) the fraction of the total N mineralization that is nitrified. Our hypothesis was that plant species of nutrient-rich habitats would enhance the N mineralization compared with species of nutrient-poor habitats.

3 The results demonstrate a strong influence of the species on net N mineralization and net nitrification, both of which fluctuated strongly during the year. Overall, species from high fertility habitats increased N mineralization and nitrification more than species from low fertility habitats. About 90% of the mineralized ammonium was oxidized to nitrate. There was no significant difference in this proportion in the plots of species from nutrient-rich, moderate and nutrient-poor habitats.

Key-words: grasses, dicots, monocultures, nitrogen mineralization, nitrification

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Introduction

The species composition, species diversity and primary productivity of terrestrial ecosystems are strongly affected by the rates at which limiting nutrients such as nitrogen (N) are supplied (Chapin 1980; Berendse 1983; Wedin & Tilman 1990; Olff *et al*. 1994). For nitrogen, the supply rate of N depends largely on mineralization, i.e. the microbial-mediated conversion of organic N to inorganic forms (NO_3^- and NH_4^+) that, in turn, is regulated by both abiotic (Swift *et al*. 1979) and biotic factors (e.g. plants, soil animals and microorganisms, Van Breemen 1993).

Earlier studies have shown that the effects of dominant plant species can be as important as abiotic factors in controlling ecosystem fertility (Berendse 1990; Wedin & Tilman 1990; Van Vuuren *et al*. 1992). There is great variation in the amount and decomposability of litter produced by plant species (Aber *et al*. 1990; Berendse *et al*. 1989; Van Vuuren *et al*. 1992). Such differences are likely to have important consequences for soil organic matter dynamics and nutrient mineralization

when plant species composition changes during succession. Various studies have indeed demonstrated the influence of the dead plant material on N mineralization (Olson 1958; Berendse 1990), including species level effects (Wedin & Tilman 1990; Van Vuuren *et al*. 1992; Stelzer & Bowman 1998). However, most of these studies have only compared clearly divergent species (Berendse 1990; Van Vuuren *et al*. 1992; Stelzer & Bowman 1998).

Wedin & Tilman (1990) found that N mineralization was higher when plots contained early rather than late successional grasses. Van Vuuren *et al*. (1992, 1993), however, found that litter from early successional species with low potential growth rates decomposed less easily than that from late successional, faster growing species. They contended that increased decomposability, combined with an increased biomass turnover, resulted in the accelerated increase in N mineralization observed during other studies on succession (cf. Berendse 1998). Interpretation of observational studies may therefore be confounded by the choice of the species.

It is difficult to interpret the results of descriptive field studies on the relationship between species composition and soil nutrient mineralization. Not only does plant species composition affect the release of nutrients, but soil fertility also has a major impact on the plant community composition. We therefore carried out a long-term garden experiment with 14 species (six grass species and eight dicotyledonous species)

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with a range of potential growth rates and adaptations to habitats with different nutrient supplies. The species, which were assigned to high, intermediate or low soil fertility groups on the basis of the nutrient level of their preferred habitat, respectively, were planted in monocultures in garden plots to ensure that the soil conditions were initially identical. The nitrogen mineralization and nitrification was measured in soil samples taken from and incubated in these plots in order to analyse the long-term effects of each species. We focused on the effects of the test species on: (i) annual net N mineralization; (ii) the seasonal pattern of N mineralization; and (iii) the fraction of the total N mineralization that is nitrified. Our hypothesis was that different plant species have different effects on nitrogen mineralization and that plant species of nutrient-rich habitats enhance N mineralization compared with species of nutrient-poor habitats.

Materials and methods

GARDEN EXPERIMENT

The long-term garden experiment was started in June 1993 when monocultures of 14 species were planted according to a randomized block design with five replicates. Soil was removed from 1×1 m plots to a depth of 50 cm, where the yellow subsoil was present. The sides were lined with 50-cm deep sheeting before refilling with an intermediate fertile sandy soil, with 6.6% organic matter, 2.0 g/kg total N (26.5 NO_3 mg/kg, 6.07 NH_4 mg/kg) and pH of 5.6, that had been sieved to remove old roots. Each block contained two rows with seven plots each. The distance between the rows was 1 m and the distance between adjacent plots in a row was 50 cm. The plots with monocultures of six grass species (*Lolium perenne*, *Arrhenatherum elatius*, *Festuca rubra*, *Anthoxanthum odouratum*, *Festuca ovina* and *Nardus stricta*) and eight dicotyledonous species (*Urtica dioica*, *Rumex obtusifolius*, *Anthriscus sylvestris*, *Centaurea pratensis*, *Achillea millefolium*, *Succisa pratensis*, *Calluna vulgaris* and *Erica tetralix*) were planted using 64 young tillers per plot. Dead plants were replaced by new tillers in August 1993 and each plot was surrounded by 35-cm high shadow gauze from September 1993, to retain plant biomass produced within the plots.

The whole garden experiment was harvested in August 1999. The above ground biomass was clipped and dried at 70 °C to a constant weight.

During the experimental period mean temperature and total precipitation were 4.2 °C and 174 mm during winter (January–March), 12.3 °C and 178 mm during spring (April–June), 16.2 °C and 215 mm during summer (July–September) and 6.3 °C and 230 mm during autumn (October–December) (meteorological data, Wageningen University).

CLASSIFICATION OF THE SPECIES

The species were divided into three groups according to the Clausman N index parameter (Melman *et al.* 1985). This index is a ranking parameter, varying from 1 to 9, that characterizes the relative soil N availability at which the species involved is most frequently found. Species with a Clausman N index higher than 5.5 were classed as species of nutrient-rich habitats (Table 1). Species with an index between 5.5 and 3 (group 2, Table 1) occur in moderately fertile habitats and species with an index below 3 occur in nutrient-poor habitats (group 3, Table 1).

N MINERALIZATION

We measured net N mineralization in the monocultures between 26 March 1996 and 25 March 1997 (i.e. in the fourth year of the experiment). We incubated soil cores *in situ* for four periods of 8 weeks in the period from 26 March until 5 November, one period of 13 weeks from 5 November until 11 February and one period of 6 weeks from 11 February until 25 March.

At the start of each incubation period, paired samples of the top 10 cm of the soil were taken under or near an individual plant in each monoculture, using pre-weighed polyvinyl chloride tubes (internal diameter 2.8 cm, length 15 cm and wall thickness 2 mm) pushed through the loose litter and into the soil. After removal, tubes were closed with low-density polyethene caps and one of each pair of samples (initial sample) was transported to the laboratory in a cooled box and stored overnight at 5 °C. The mineral N was extracted the day after collection. The other tube (incubated sample) was returned to its original position in the soil: four holes of

Table 1 Species used in the garden experiment. The Clausman N index parameters are given in parenthesis

Fertility groups	Grasses	Dicots
Group 1 (> 5.5)	*Lolium perenne* (9.1)	*Rumex obtusifolius* (9.0)
	Arrhenatherum elatius (5.6)	*Urtica dioica* (6.5)
		Anthriscus sylvestris (6.2)
Group 2 (5.5 > × > 3.0)	*Festuca rubra* (3.8)	*Achillea millefolium* (5.1)
	Anthoxanthum odoratum (3.3)	*Centaurea pratensis* (3.2)
Group 3 (< 3)	*Festuca ovina* (2.3)	*Succisa pratensis* (1.1)
	Nardus stricta (1.5)	*Calluna vulgaris* (1.1)
		Erica tetralix (1.1)

4 mm diameter in the part that remained above the soil surface allowed the passage of air but the lids prevented water entering the tube. At the end of the incubation period the incubated samples were removed (as above) and the amount of mineral N accumulated was determined by the method of Berendse (1990).

Before the analysis the loose litter was removed from the soil core and discarded. After removing the roots each sample was homogenized and 20 g of field-moist soil was extracted with 50 mL of 1 mol $KCl\,l^{-1}$. Thereafter the NH_4^+ and the NO_3^- content were determined using a Skalar autoanalyser San^{plus} system. The soil moisture content of each sample was determined by drying the remainder of the field-moist soil overnight at 105 °C. The volumetric soil moisture content was calculated relative to the volumetric amount of dry soil. The bulk soil density of the 0–10 cm soil layer at each site was calculated from the average amount of dry soil per initial sample.

Net N mineralization was calculated as the increase in $N\text{-}NH_4^+$ plus $N\text{-}NO_3^-$, whereas net nitrification was calculated as the increase in $N\text{-}NO_3^-$ in the incubated relative to the paired initial sample. For each period, net N mineralization and net nitrification was multiplied by the bulk density of the 0–10 cm soil layer to obtain results per unit area. Annual net N mineralization and

annual net nitrification was calculated by summing the values for all incubation periods from 26 March 1996– 25 March 1997. Relative nitrification was calculated as the fraction of the annual released inorganic nitrogen that is oxidized to nitrate.

STATISTICS

All data were analysed using analysis of variance (General Linear Model; SPSS 7.0, 1995) with life form (dicot or grass) and fertility group as fixed factors and block as random factor. When variances increased with the means, the data were logarithmically transformed. Tukey's Studentized range tests were used to test for differences among means. The GLM-procedure was used to ascertain whether the three groups to which species had been assigned had different effects on mineralization and nitrification and whether biomass production at the end of the experiment differed between groups.

Results

Nitrogen mineralization (Fig. 1) and nitrification (Fig. 2) per unit area fluctuated strongly during the year. Both were low during autumn and winter (November
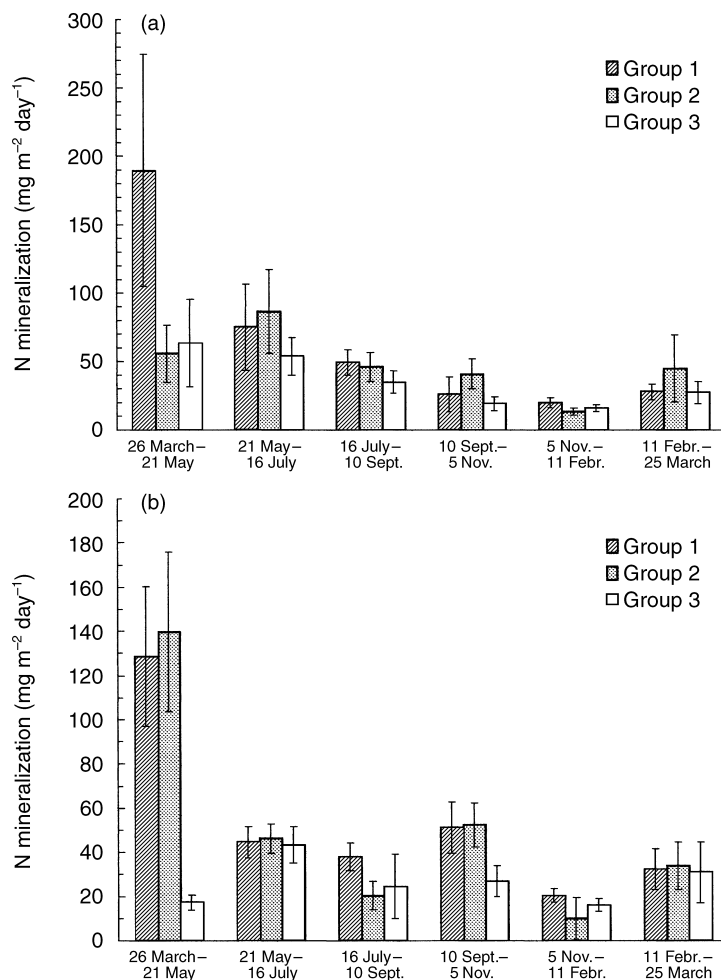

Fig. 1 Net N mineralization (mg m^{-2} day^{-1}) measured *in situ* in 3-year-old monocultures with grass species (a) and dicot species (b) during different periods of the year. Values are means ± SE.
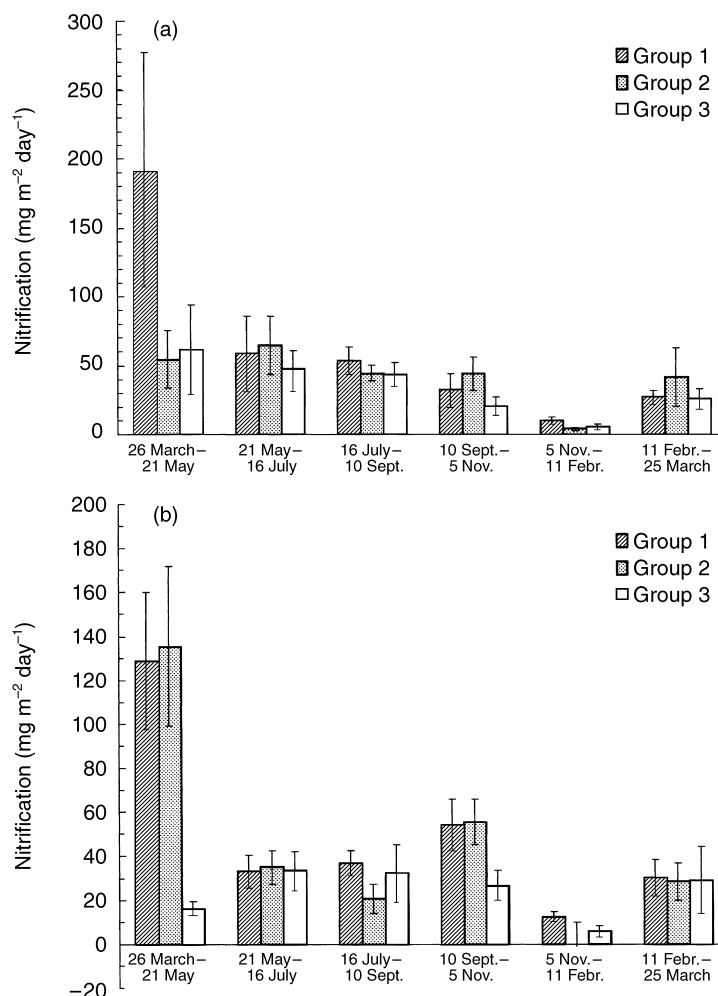
Fig. 2 Net nitrification (mg N-NO$_3$ m^{-2} day^{-1}) measured *in situ* in 3-year-old monocultures with grass species (a) and dicot species (b) during different periods of the year. Values are means ± SE.

Table 2 *F*-values calculated by analysis of variance, using GLM, for annual N mineralization (Nmin), nitrification (N-NO$_3$) and relative nitrification (rel. NO$_3$) from 26 March 1996–25 March 1997 and net living above-ground biomass (g m^{-2}) in August 1999 in plots with grass and dicot species (life form)

Source	d.f.	Nmin	N-NO$_3$	Rel. NO$_3$	Biomass
Life form	1	0.82 NS	1.63 NS	1.92 NS	3.40 NS
Groups	2	9.02***	9.34***	2.36 NS	7.61***
Block	4	2.45 NS	1.58 NS	2.05 NS	0.76 NS
Life form × group	2	0.39 NS	0.51 NS	0.33 NS	1.68 NS
Error	20				

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant.

until March). Only plots with species characteristic of relatively fertile soils showed a sharp peak in March to April: for grasses, species from the nutrient-rich habitat (group 1) gave three times greater values than those from intermediate and nutrient-poor habitats (groups 2 and 3), whereas in the dicot species, values for groups 1 or 2 were up to seven times greater than for group 3.

The three species groups had different effects on the annual net nitrogen mineralization (Fig. 3a). For both grass and dicot species, values for group 1 (nutrient-rich habitats) were almost double those for the nutrient-poor

group 3. Values for N mineralization in the plots with species of group 2 were intermediate. Statistical analyses indicate that the overall effect is significant (Table 2), though group 2 species were significantly different from group 3 but not from group 1.

Nitrification (Fig. 3b) showed the same pattern as the N mineralization. Group 1 species gave values twice as high as group 3 species and this difference was significant. Overall, for both grasses and dicots, nitrification in the group 2 plots was lower than in the group 1 plots, but this difference was not significant.
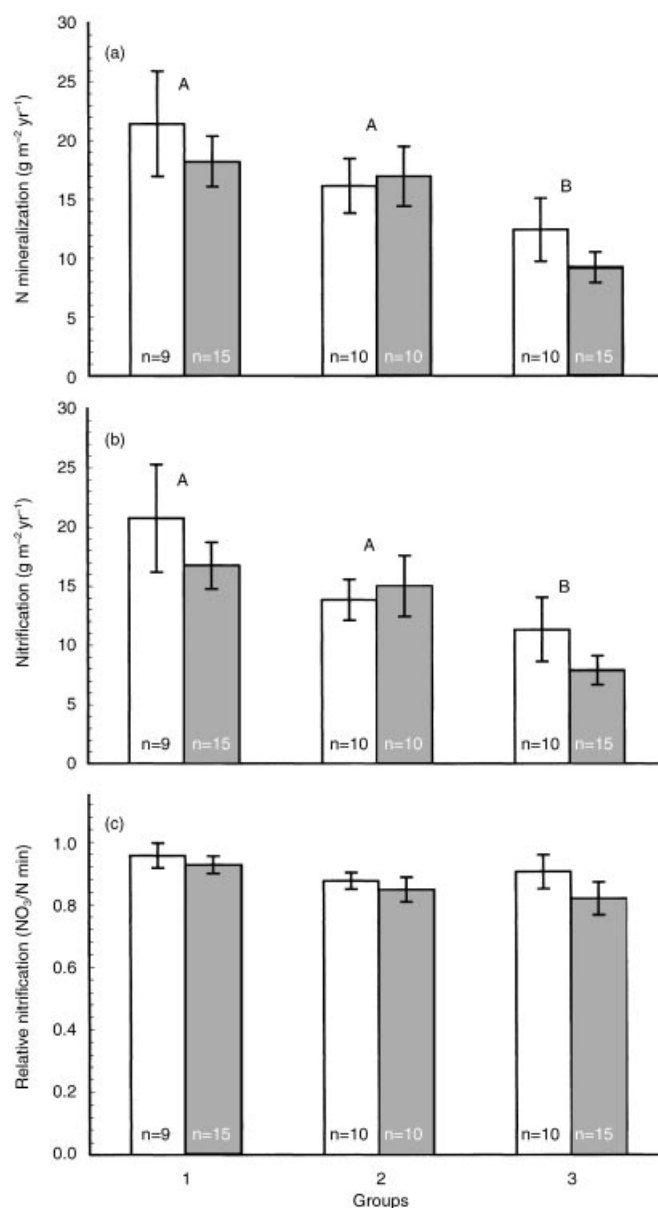
Fig. 3 (a) Annual net N mineralization, (b) annual nitrification and (c) annual relative nitrification measured *in situ* from 26 March 1996–25 March 1997 in 3-year-old monocultures with six grass species (open bars) and eight dicot species (dark bars). Values are means ± SE.

Table 3 Net living above-ground biomass (g m^{-2}) in monocultures with grass and dicot species in August 1999. Values are means ± SE. Different letters indicate significant differences between the means ($P < 0.05$)

Group	Growth form		
	Grasses	Dicots	Means
1	171.1 ± 42.6	269.1 ± 58.4	228.2 ± 39.0[b]
2	217.7 ± 53.8	526.2 ± 155.7	371.9 ± 88.2[b]
3	379.4 ± 88.3	1677.1 ± 291.3	1205.2 ± 230.1[a]
Means	248.4 ± 38.0	864.4 ± 157.5	

There were no significant differences between the three groups in the fraction of mineralized N that was converted into nitrate (Table 2). On average 0.91 and 0.87 g N-NO$_3$ were nitrified per g N mineral-

ized in plots with grass and dicot species, respectively (Fig. 3c).

At the end of the experiment, the living above-ground biomass did not differ significantly between plots with grass and dicot species ($P = 0.07$, Tables 2 and 3). The amount of biomass in plots with species of group 3 was, however, significantly higher than in plots with species of group 1 and 2.

Discussion

The differences between the three species groups in the net N mineralization and nitrification rates during the fourth year of the experiment, despite initially identical soils, clearly show that plant species can affect soil N mineralization rates. Higher N mineralization rates in the plots with high fertility species were associated with lower mean living biomass in August 1999. From earlier

studies we know that both biomass production and its turnover rate is much greater for high fertility species (Grime 1994; Berendse *et al.* 1998). We therefore attribute the lower amount of living biomass of the high and moderate fertility species at the end of the experiment to these higher turnover rates. The dead leaves supply large quantities of litter for decomposition resulting in an increased N mineralization rate.

There was a strong seasonality within patterns of soil N mineralization. Such patterns of N mineralization and nitrification can be largely attributed to seasonal variation in temperature and soil moisture content (Swift *et al.* 1979; Sierra 1997), with a low rate during winter (November until March) reflecting low temperature and high soil moisture content. The rise in temperature during spring (March until May) should increase microbial activity and enable more inorganic N to be released (Sierra 1997), although this pattern was only observed in plots with dicot species of groups 1 and 2 and grasses of group 1. The N mineralization and nitrification rates of the dicots of groups 1 and 2 were also higher than group 3 in autumn (September until November), with the species of group 1, characteristic of fertile soils, having high values for both production and turnover of biomass (Berendse *et al.* 1998). Late summer senescence of leaves of these species supplies large quantities of litter for decomposition in autumn, whereas most grasses remain green until the winter. It therefore seems likely that the timing of senescence of the plant biomass and the amount of litter produced were responsible for the higher net mineralization of the high and moderate fertility dicots during autumn and spring and for high fertility grass species during spring.

Almost all the mineralized nitrogen was oxidized to NO_3^- for all three groups of both dicots and grasses. The N mineralization rate in monocultures with species from high fertility habitats was 18 g N m^{-2} year^{-1} for dicots and 21 g N m^{-2} year^{-1} for grasses, compared with 9 g N m^{-2} year^{-1} and 12 g N m^{-2} year^{-1}, respectively, for low fertility species. Differences of the same order of magnitude were reported in N mineralization in early 'nutrient-rich' (17.6 g N m^{-2} year^{-1}) and late 'nutrient-poor' (6.1 g N m^{-2} year^{-1}) fields during reversed grassland succession (Olff *et al.* 1994).

Other authors have reported that changes in N supply have important effects on species replacement (Chapin 1980; Berendse 1983; Wedin & Tilman 1990; Olff *et al.* 1994). We found evidence that species replacement during succession might also have major effects on the N cycle. The species from fertile habitats caused an increase in N mineralization, whereas species from much less fertile habitats had a relatively negative effect on the N release from the soil. The differences in N mineralization and nitrification in our experiment were not simply a function of the net plant biomass production but are probably also due to differences in biomass turnover rate (Berendse *et al.* 1987; Aerts *et al.* 1992; Schläpfer & Ryser 1996) and litter decomposability (Berendse *et al.* 1989; Van Vuuren *et al.* 1993; Cornelissen 1996). We postulate that high fertility species can accelerate and low fertility species can slow down the N cycle and that such species-specific feed-backs could affect the rate of change in species composition during succession. More knowledge about the below-ground carbon and nutrient flows from plant to the soil is needed to obtain a deeper insight into the effects of different plant species on nutrient mineralization.

Acknowledgements

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