Biogeochemistry **16**: 151—166, 1992

Nitrogen mineralization in heathland ecosystems dominated by different plant species

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Received 18 June, 1991; accepted 4 March 1992

Key words: heathland, N mineralization, nitrification

Abstract. Net N mineralization rates were measured in heathlands still dominated by ericaceous dwarf shrubs (*Calluna vulgaris* or *Erica tetralix*) and in heathlands that have become dominated by grasses (*Molinia caerulea* or *Deschampsia flexuosa*). Net N mineralization was measured *in situ* by sequential soil incubations during the year. In the wet area (gravimetric soil moisture content 74—130%), the net N mineralization rates were 4.4 g N m^{-2} yr^{-1} in the *Erica* soil and 7.8 g N m^{-2} yr^{-1} in the *Molinia* soil. The net nitrification rate was negligibly slow in either soil. In the dry area (gravimetric soil moisture content 7—38%), net N mineralization rates were 6.2 g N m^{-2} yr^{-1} in the *Calluna* soil, 10.9 g N m^{-2} yr^{-1} in the *Molinia* soil and 12.6 g N m^{-2} yr^{-1} in the *Deschampsia* soil. The *Calluna* soil was consistently drier throughout the year, which may partly explain its slower mineralization rate. Net nitrification was 0.3 g N m^{-2} yr^{-1} in the *Calluna* soil, 3.6 g N m^{-2} yr^{-1} in the *Molinia* soil and 5.4 g N m^{-2} yr^{-1} in the *Deschampsia* soil. The net nitrification rate increased proportionally with the net N mineralization rate suggesting ammonium availability may control nitrification rates in these soils. In the dry area, the faster net N mineralization rates in sites dominated by grasses than in the site dominated by *Calluna* may be explained by the greater amounts of organic N in the soil of sites dominated by grasses. In both areas, however, the net amount of N mineralized per gram total soil N was greater in sites dominated by *Molinia* or *Deschampsia* than in sites dominated by *Calluna* or *Erica*. This suggests that in heathlands invaded by grasses the quality of the soil organic matter may be increased resulting in more rapid rates of soil N cycling.

Introduction

Plant species lose different amounts of nitrogen (N) annually from the senescence and loss of aboveground plant parts and roots. Moreover, the organic chemical composition of plant debris varies widely among species. Both of these factors result in different rates of decomposition and net N release from plant debris (Aber et al. 1990; Berendse et al. 1989; Lousier

& Parkinson 1976). As a consequence, a shift in plant species composition may change the rate at which N is mineralized from soil organic matter (Berendse 1990; Nadelhoffer et al. 1991, Wedin & Tilman 1990).

In The Netherlands, plant communities dominated by ericaceous dwarf shrubs such as *Calluna vulgaris* (L.) Hull or *Erica tetralix* L. develop on nutrient-poor, sandy soils. At the start of primary succession the main supply of N to plants occurs through atmospheric deposition and nitrogen fixation. This N becomes incorporated into plant debris, and there is a net accumulation of soil organic matter and organic N. The N supply to plants via the process of mineralization increases concurrently (Berendse 1990). In many dry heathland areas *Calluna vulgaris* has been replaced by perennial grasses like *Molinia caerulea* (L.) Moench or *Deschampsia flexuosa* (L.) Trin. In wet heathland areas *Erica tetralix* has often been replaced by *Molinia caerulea.*

A comparative study of the N cycle was conducted in five communities, each dominated by a different plant species. The ericaceous dwarf shrubs appeared to have a low rate of litter production and to lose small amounts of N relative to the amount of N contained in their live biomass (Aerts 1989; Aerts et al. 1989; Aerts & Berendse 1989). Apparently, this enables them to survive under nutrient-poor conditions. With increasing N supply, *Molinia* is able to expand rapidly because of its high potential growth rate (Aerts 1990; Berendse & Elberse, 1989). *Molinia* dies off aboveground at the end of the growing season, but before abscission, much of the N is retranslocated from the senescing tissues (Aerts 1990; Berendse et al. 1987). Compared with *Calluna* and *Erica*, however, *Molinia* loses more N through litter production relative to the average amount of nitrogen in the plant (Aerts 1990; Berendse & Elberse, 1989).

The expansion of *Deschampsia* in sites previously dominated by *Calluna* has been attributed to a larger nitrogen supply and to the effects of damage by the heather beetle *Lochmaea suturalis* Thomson (Berdowski & Zeilinga, 1987; Brunsting & Heil, 1985). *Calluna* and *Deschampsia* are evengreen species and reduce their losses of nitrogen by efficiently retranslocating nitrogen. The annual nitrogen loss resulting from litter production is smaller for *Deschampsia* than for *Calluna* (Aerts 1990; Aerts unpublished data).

Litter decomposition experiments conducted in the same areas used for this study revealed that shoots and roots of *Molinia* or *Deschampsia* decompose faster than those of *Calluna* or *Erica* (Van Vuuren, unpublished data). Thus, organic N in the soil may be mineralized faster when contained in grass residues than in residues of dwarf shrubs. The present study investigated whether the shift in dominant plant species towards *Molinia* or *Deschampsia* has led to a greater N availability in these

communities by assessing *in situ* net N mineralization rates using a sequential incubation method.

Study areas

The study was conducted in two heathland areas in The Netherlands, the "Uddeler Buurtveld" (52°15′N, 5°47′E) (henceforth referred to as 'the wet area') and the "Edese Heide" (52°02′N, 5°50′E) (henceforth referred to as 'the dry area'). The soils can be classified as a humus-iron podzol at the wet area, and a humus podzol at the dry area (Kubiena 1953). The surface organic horizons of the soils can be distinguished into a loose litter layer (L) and a humus layer (FH). Weather data that were obtained from a station located in Wageningen (51°58′N, 5°40′E) indicate a mean annual precipitation of 740 mm and a mean annual temperature of +9.3 °C (based on the 1980—1989 records).

The wet area has a high soil moisture content throughout the year because water stagnates on the iron pan. Two adjacent sites were selected, one dominated by *Erica tetralix* and the other by *Molinia caerulea*. The *Molinia* site had been dominated by *Erica* in the past and remains of *Erica* stem litter can still be found in the surface organic horizon of the soil.

In the dry area the water table is always several meters below the soil surface. Three sites were selected, dominated by *Calluna vulgaris*, *Molinia caerulea* and *Deschampsia flexuosa*, respectively. The *Molinia* and the *Deschampsia* sites used to be dominated by *Calluna*. *Calluna* stem litter can still be found in the surface organic horizon of the soils. The sites were close together, the most widely separated pair being 600 m apart. In both areas, at each site the dominant plant species made up > 95% of the total aboveground biomass.

Materials and methods

Net N mineralization measurements

Net N mineralization was measured at all sites from 29 February 1988 until 27 February 1989. Soil cores were incubated *in situ* for five periods of 8 weeks and one period of 12 weeks (in winter). At each site a plot of 100—150 m^2 judged to be representative of the vegetation was divided into 10 subplots. At the start of each incubation period, two paired samples of soil (10 to 15 cm apart) were taken in each subplot, using

preweighed polyvinyl chloride tubes (diameter 2.8 cm, length 15 cm, wall thickness 2 mm). The tubes were pushed through the loose litter (L) into the soil to a depth of 10 cm below the boundary between the L and the FH layer. The FH layer of the soil at the wet sites was about 5 cm thick, whereas the FH layer of the soil at the dry sites was about 2 cm thick. The tubes were then removed and their ends capped; the caps were made from low-density polyethlene. One of the tubes (initial sample) was taken to the laboratory. The other tube was returned to its original position in the soil and left there (incubated sample). The incubated soil tube had four 4 mm diameter holes in the part that remained above the soil surface to allow for the passage of air. At the end of each incubation period the incubated samples were also taken to the laboratory and a new pair of samples was taken.

Retrieved tubes were stored for one night at 5 °C. The loose litter was separated from the soil core and discarded. The soil samples were mixed and 20 g field-moist soil was extracted with 50 ml 1 N KCL. The same day the extract was analysed for NH_4^+ and NO_3^- using a Technicon Autoanalyser II system. Soil moisture content was determined after drying field moist soil overnight at 105 °C. The soil moisture content was calculated relative to the amount of dry soil. The bulk density of the 0—10 cm soil layer at each site was calculated from the average amount of dry soil per initial sample, using data from all sampling dates.

Net N mineralization is the increase in NH_4-N plus NO_3-N whereas net nitrification is the increase in NO_3-N in the incubated samples relative to their paired initial samples. For each period, this was multiplied by the bulk density of the 0—10 cm soil layer to obtain results in g m^{-2}. The annual net N mineralization and nitrification rates were calculated per subplot by summing the net N mineralization and nitrification rates of the six incubation periods. The standard errors of the annual net N mineralization and nitrification rates were determined from the variation in subplot values.

In November 1988 10 soil samples were taken from each site (one per subplot), using a soil auger with a diameter of 8 cm. The loose litter was separated from the sample in the field, and the sample was truncated at a depth of 10 cm below the boundary between the L and the FH layers. In the laboratory the 0—10 cm soil layer was subdivided into the FH layer and the underlying mineral layer (M). Roots were not removed. The FH and M layers could be distinguished visually by differences in colour and texture. The thickness of both layers was measured. The pH was measured in a 1 : 5 (FH) and a 1 : 2.5 (M) air-dry soil : water suspension. The L, FH and M fractions of each core were dried (105 °C) and ground. The organic matter content was determined as the loss in mass upon ignition (650 °C,

2 h). The total carbon (C) and nitrogen content were determined using a Heraeus CHN-RAPID elemental analyser. For the determination of the total phosphorus (P) content, samples were digested with a mixture of equal amounts of 96% sulphuric acid and 65% nitric acid. The diluted digests were analysed colorimetrically with a Technicon Autoanalyzer II system, using the ammonium molybdate method (Van Schouwenburg and Walinga 1967). The total amounts of organic matter, N, C and P were expressed on a g m^{-2} basis using the bulk densities determined for each soil layer.

Statistical analyses

ANOVA's were performed on the data using the Genstat programme (Genstat 5 Committee, 1988). ANOVA's were done separately for each study area. The data on net N mineralization and net nitrification per incubation period, and the data on soil moisture content in the initial samples were analysed by a nested ANOVA (blocks: subplots: 'treatment factors': incubation period and site). For each site, a one-factor ANOVA was performed per incubation period, to test for differences between the soil moisture contents of the initial and the incubated samples. One-factor ANOVA's were used to test differences in soil properties among sites. When the ANOVA was significant, Tukey's studentized range tests were used to test for significant differences among means.

Results

Wet area

The annual net N mineralization rate was significantly ($p < 0.01$) slower in the *Erica* site (4.4 SE $\pm$ 0.3 g N m^{-2} yr^{-1}) than in the *Molinia* site (7.8 SE $\pm$ 1.0 g N m^{-2} yr^{-1}) (Fig. 1a). At both sites, the net N mineralization rate varied significantly ($p < 0.001$) among the incubation periods. About 60% of the annual net N mineralization occurred during the two incubation periods that included the months May, June and July.

On average 10% of the mineral N in the initial samples of both sites was in the form of nitrate (data not shown). The annual net nitrification rate was zero in the *Erica* site and 0.1 (SE $\pm$ 0.1) g N m^{-2} yr^{-1} in the *Molinia* site.

Throughout the year, the average gravimetric soil moisture content of the initial samples varied between 74—130% in both soils (Fig. 2a). Seasonal changes in the soil moisture content within the sites were signifi-

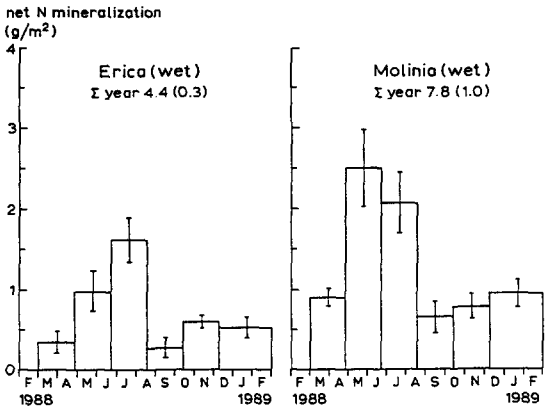

Fig. 1(a) Net nitrogen mineralization (g N/m^2) per incubation period in wet heathlands dominated by *Erica tetralix* or *Molinia caerulea*.

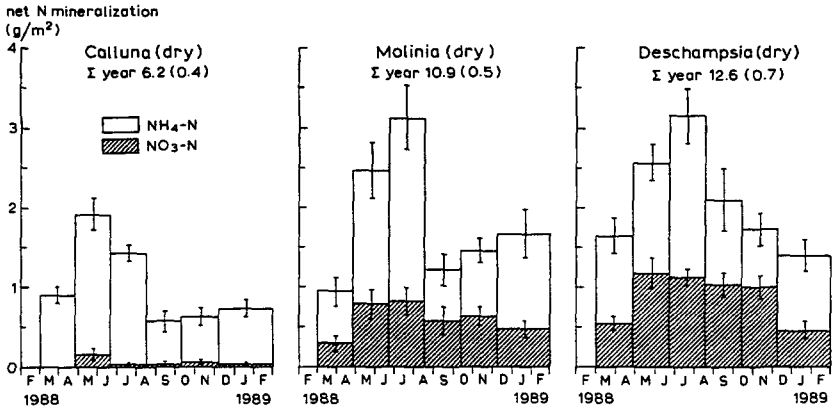

Fig. 1(b) Net nitrogen mineralization and net nitrification (hatched part) (g N/m^2) per incubation period in dry heathlands dominated by *Calluna vulgaris*, *Molinia caerulea* or *Deschampsia flexuosa*.

For each site the mean annual net nitrogen mineralization rate is calculated by summing the amounts of the six incubation periods ($n = 10$, standard error of the mean between parentheses).

cant ($p < 0.05$), but the *Erica* soil and the *Molinia* soil did not differ from each other on the sampling dates. There was no significant difference in soil moisture content between the initial samples and the corresponding incubated samples of the same incubation period ($p \geqslant 0.18$), except for the *Molinia* soil during the fourth incubation period ($p = 0.05$) (cf. Fig. 2a).

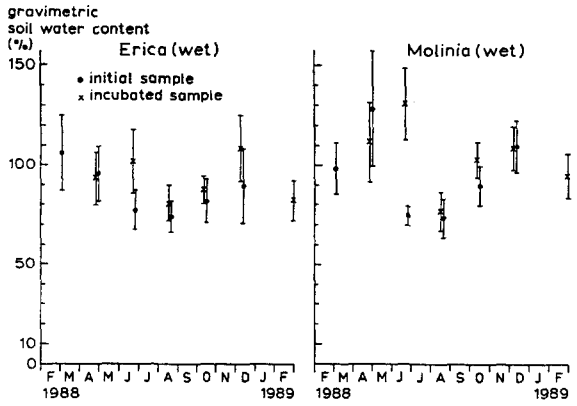

Fig. 2.(a) Gravimetric soil water content (%) of the initial and the incubated soil samples of each incubation period, in wet heathlands dominated by *Erica tetralix* and *Molinia caerulea*.

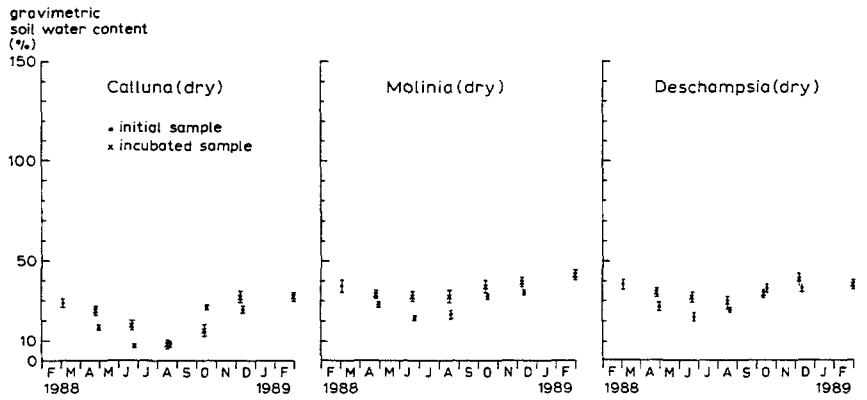

Fig. 2(b) Gravimetric soil water content (%) of the initial and the incubated soil samples of each incubation period, in dry heathlands dominated by *Calluna vulgaris*, *Molinia caerulea* or *Deschampsia flexuosa* ($n = 10$, bars indicate standard errors of the mean).

The total amount of organic matter was significantly greater ($p = 0.006$) in the *Erica* soil than in the *Molinia* soil (Table 1). However, the total C content was not significantly different between the soils ($p = 0.107$). Both soils contained similar amounts of total nitrogen (about 270 g m^{-2}). The *Erica* soil had significantly ($p < 0.01$) greater C:N ratios in the L and FH layers compared to the *Molinia* soil, but not in the mineral layer ($p = 0.094$). The total amount of P was significantly ($p = 0.020$) smaller in the *Erica* soil than in the *Molinia* soil. In both sites, the amounts of organic matter, C, N and P contained in the L + FH layer

Table 1. Soil properties of the wet heathland area. The mean amount of dry soil, organic matter, total carbon (C), total nitrogen (N), total phosphorus (P), carbon:nitrogen ratio and pH-H_2O in litter (L), humus layer (FH), mineral layer (M) and total (T) to a depth of 10 cm below L layer (n = 10, standard error in parentheses, n.d. = not determined).

	Dry soil ($kg\ m^{-2}$)	Organic matter ($kg\ m^{-2}$)	C ($g\ m^{-2}$)	N ($g\ m^{-2}$)	P ($g\ m^{-2}$)	C:N	pH
ERICA SITE							
L	1.2 (0.1)	1.1 (0.1)	550 (60)	15 (2)	0.3 (0.1)	40 (2)	n.d.
FH	16.9 (0.3)	6.8 (0.8)	4940 (730)	204 (25)	6.3 (0.6)	24 (1)	3.6 (0.1)
M	65.4 (9.1)	2.8 (0.4)	1380 (230)	51 (12)	4.7 (0.7)	31 (4)	4.5 (0.1)
T	83.5 (7.0)	10.7 (0.5)	6870 (560)	269 (20)	11.4 (0.7)	26 (1)	n.d.
MOLINIA SITE							
L	0.8 (0.1)	0.6 (0.1)	300 (30)	13 (1)	0.4 (0.1)	23 (1)	n.d.
FH	14.5 (1.0)	6.0 (0.3)	4310 (300)	205 (14)	8.1 (0.4)	21 (0)	3.5 (0.0)
M	56.2 (5.2)	2.1 (0.3)	1200 (240)	53 (12)	4.9 (0.7)	24 (2)	4.5 (0.1)
T	71.4 (4.5)	8.7 (0.4)	5800 (300)	271 (18)	13.4 (0.4)	22 (1)	n.d.

accounted for 60 to 80% of the total amounts. The average amount of total N in the soil mineralized per year was 16 mg N g^{-1} soil N for the *Erica* site, and 29 mg N g^{-1} soil N for the *Molinia* site (Table 3).

Dry area

The net N mineralization rate was 6.2 (SE ± 0.4) g N m^{-2} yr^{-1} for the *Calluna* site, 10.9 (SE ± 0.5) g N m^{-2} yr^{-1} for the *Molinia* site and 12.6 (SE ± 0.7) g N m^{-2} yr^{-1} for the *Deschampsia* site (Fig. 1b), and all rates were significantly different from each other ($p < 0.05$). The seasonal pattern of net N mineralization was comparable to that in the wet sites: about 50% of the annual mineralization occurred during May, June and July (cf. Figs 1a and 1b).

At the *Calluna* site about 10% of the mineral N in the initial samples was in the form of nitrate (data not shown). At the *Molinia* and *Deschampsia* sites, nitrate made up about 30% of the mineral N in the initial samples. The net nitrification rate differed significantly ($p < 0.05$) among the sites, being 0.3 (SE ± 0.1) g N m^{-2} yr^{-1} in the *Calluna* site, 3.6

(SE ± 0.4) g N m^{-2} yr^{-1} in the *Molinia* site and 5.4 (SE ± 0.5) g N m^{-2} yr^{-1} in the *Deschampsia* site.

Throughout the year, the average gravimetric soil moisture content varied between 7—29% at the *Calluna* site, and between 21—38% at the *Molinia* and *Deschampsia* sites (Fig. 2b). Seasonal changes in the soil moisture content within the sites were significant ($p < 0.001$). The soil of the *Calluna* site was significantly ($p < 0.01$) drier than the soil of the *Molinia* site or of the *Deschampsia* site. In all sites, the soil became significantly ($p < 0.01$) dried during March and April. During August and September a significant ($p < 0.01$) increase in soil moisture content was measured. In 30% of all pairs of samples, the soil moisture contents of the incubated samples had increased significantly ($p < 0.01$) relative to their initial samples (cf. Fig. 2b). This may have been caused by water condensing in the tubes at night.

The difference in total amount of soil organic matter was only significant ($p < 0.05$) between the *Calluna* site and the *Molinia* site (Table 2). There were no significant differences among the sites in the total amount of C in the soil. The total amounts of N and P were significantly ($p < 0.05$) smaller in the *Calluna* soil as compared with the *Molinia* and the *Deschampsia* soils. The C:N ratios of the L, FH and M layers differed significantly ($p < 0.001$) among the sites. Except for the L layer, the *Calluna* soil had significantly ($p < 0.01$) greater C:N ratios compared to the *Molinia* or *Deschampsia* soil. In contrast to the wet sites, the LFH layer of the dry sites contained only 20—40% of the total amount of organic matter, C, N and P. The average amount of total N in the soil mineralized per year was 25 mg N g^{-1} soil N for the *Calluna* site, 35 mg N g^{-1} soil N for the *Molinia* site and 36 mg N g^{-1} soil N for the *Deschampsia* site (Table 3).

Discussion

Method of measuring net N mineralization

The *in situ* measurement of net N mineralization by the sequential incubation of soil cores has many advantages compared with laboratory measurements (Binkley & Hart, 1989; Raison et al. 1987). The soil remains relatively undisturbed and the mineralization process occurs under ambient temperatures and, to some degree, ambient moisture conditions. Unlike Adams et al. (1989), we used tubes capped both at the top and the bottom that were not perforated over their entire length. Our

Table 2. Soil properties of the dry heathland area. The mean amount of dry soil, organic matter, total carbon (C), total nitrogen (N), total phosphorus (P), carbon:nitrogen ratio and pH-H_2O in litter (L), humus layer (FH), mineral layer (M) and total (T) to a depth of 10 cm below L layer ($n = 10$, standard error in parentheses, n.d. = not determined).

	Dry soil ($kg\ m^{-2}$)	Organic matter ($kg\ m^{-2}$)	C ($g\ m^{-2}$)	N ($g\ m^{-2}$)	P ($g\ m^{-2}$)	C:N	pH
CALLUNA SITE							
L	0.6 (0.1)	0.5 (0.0)	250 (20)	10 (1)	0.3 (0.0)	25 (1)	n.d.
FH	5.4 (0.5)	3.1 (0.3)	2190 (190)	94 (8)	2.4 (0.2)	23 (0)	3.2 (0.0)
M	113.6 (1.9)	8.5 (0.3)	5260 (200)	147 (5)	9.9 (0.4)	36 (1)	4.0 (0.0)
T	119.6 (1.6)	12.1 (0.3)	7690 (230)	252 (9)	12.7 (0.4)	31 (0)	n.d.
MOLINIA SITE							
L	0.4 (0.1)	0.3 (0.1)	160 (40)	6 (2)	0.2 (0.1)	28 (2)	n.d.
FH	13.5 (0.9)	3.5 (0.2)	2590 (220)	132 (11)	6.0 (0.7)	20 (0)	3.5 (0.0)
M	87.9 (2.7)	6.9 (0.3)	4160 (240)	177 (10)	11.6 (0.6)	24 (1)	4.2 (0.0)
T	101.8 (2.0)	10.7 (0.3)	6920 (270)	315 (15)	17.2 (0.9)	22 (0)	n.d.
DESCHAMPSIA SITE							
L	0.1 (0.0)	0.1 (0.0)	50 (10)	2 (0)	0.1 (0.0)	20 (1)	n.d.
FH	9.1 (0.9)	4.1 (0.3)	2930 (270)	150 (14)	4.3 (0.3)	19 (0)	3.4 (0.0)
M	91.1 (3.1)	7.7 (0.4)	4690 (200)	201 (10)	12.4 (0.5)	23 (0)	3.9 (0.0)
T	100.3 (2.5)	11.9 (0.5)	7660 (410)	354 (20)	16.8 (0.5)	22 (0)	n.d.

method prevents mineral N from being lost by lateral and vertical leaching and prevents the ingrowth of roots. The moisture content in the tubes remains close to the level prevailing at the start of the incubation. This is a limitation of the method, because in the field the moisture content may fluctuate. At the wet sites, however, the data on soil moisture content in the initial samples did not indicate a significant change in soil moisture content in the unconfined soil between consecutive incubation periods. At the dry sites, our method resulted in significant differences in soil moisture content between the soil in the tubes and the unconfined soil during some periods. The error incurred might have been reduced by using shorter periods of containment.

The net N mineralization rate showed a clear seasonal pattern at the sites in both areas. Seasonal fluctuations in the soil moisture content, soil temperatures and/or litter fall may be the factors responsible for this

Table 3. Litter production (g m^{-2} yr^{-1}) and litter nitrogen content (gN m^{-2} yr^{-1}) of *Erica* and *Molinia* sites in the wet area (March 1985—March 1986), and *Calluna, Molinia* and *Deschampsia* sites in the dry area (April 1985—April 1986) (after Aerts & Berendse, 1989; Aerts, 1989; Aerts et al. 1989; Aerts unpublished). Between parentheses: litter nitrogen content, assuming equal percentages of nitrogen retranslocation from roots to those measured for shoots (see discussion).

	Wet area		*Dry area*		
	Erica	*Molinia*	*Calluna*	*Molinia*	*Deschampsia*
Litter production (g m^{-2} yr^{-1})					
shoots	430	980	570	670	250
roots	370	1080	160	1380	180
total	800	2060	730	2050	430
Litter nitrogen (g N m^{-2} yr^{-1})					
shoots	3.2	4.7	6.2	2.9	2.6
roots	5.1 (4.3)	18.4 (6.6)	1.8 (1.6)	19.7 (7.7)	1.7 (0.8)
total	8.3 (7.5)	23.1 (11.3)	8.0 (7.8)	22.8 (10.6)	4.3 (3.4)
Net N mineralization (g N m^{-2} yr^{-1})	4.4	7.8	6.2	10.9	12.6
Net N mineralization (mg N g^{-1} soil N yr^{-1})	16	29	25	35	36

(Kladivko & Keeney 1987; Myers et al. 1982; Nadelhoffer et al. 1991). In the wet area, despite the seasonal fluctuations, the soil moisture content remained high throughout the year (average soil moisture content always $\geqslant 70\%$). This may have inhibited the N mineralization process during all incubation periods. In contrast, in the dry area N mineralization may have been depressed by a shortage of water during the summer months (Fig. 2b). At all sites, the higher soil temperatures are probably the main reason for the faster net N mineralization rates measured during May, June and July.

Differences in annual net N mineralization and nitrification rates

In both areas, the net amount of N mineralized per year varied widely between the sites. As there was only a short distance between the sites within each area, differences in macroclimatic conditions should have been minimal. The soil of the *Calluna* site, however, was consistently drier

throughout the year. This may partly explain why its net N mineralization rate was slower than it was at the *Molinia* or *Deschampsia* sites.

A faster rate of net N mineralization corresponded with a greater amount of total N in the soil in the dry area. In contrast, in the wet area the soils contained equal amounts of total N, but the N mineralization rates differed markedly. In each area, the site dominated by dwarf shrubs (*Calluna, Erica*) contained the largest amount of soil organic matter, but it had the slowest net N mineralization rate. We conclude that the total amounts of soil organic matter or N cannot be used solely to predict net N mineralization rates. Although positive correlations between the amount of soil organic matter or soil N and net N mineralization rates have been found in some studies (e.g., Berendse 1990; Pastor et al. 1987), other authors have reported no relationship between these variables (Nadelhoffer et al. 1983; Pastor et al. 1984). Nadelhoffer et al. (1983) calculated net N mineralization rates per gram soil organic N in 9 forest sites, which ranged from 1.8 to 7.9 mg N g^{-1} soil N. The sites in their study were dominated by different plant species, which probably affected the quality of the soil organic layers and net mineralization rates. In our sites the organic layers present in the *Molinia* and *Deschampsia* soils have been built up by the input of litter from *Calluna* or *Erica* and subsequently by the litter input of the grasses. The lignin concentration in the litter of *Molinia* and *Deschampsia* ranges from 150 to 260 mg g^{-1} organic matter, while litters from *Calluna* and *Erica* contain between 330 and 470 mg lignin g^{-1} organic matter (Van Vuuren, unpublished data). Thus, the quality of the organic layer may have increased by the invasion by grasses resulting in a faster net N mineralization rate per gram soil N (Table 3).

Net nitrification seemed to be absent or to occur at a slow rate in the soils from the wet area. In the dry area, an appreciable amount of nitrate was produced in the incubated soil tubes from the sites dominated by grasses, but only a small amount of nitrate was produced in the soil from the *Calluna* site. The rate of nitrification has been related to various factors, such as: soil pH, availability of ammonium, soil moisture content, and the occurrence of particular plant species that could inhibit nitrifying microorganisms by the production of allelochemicals (Killham 1990). In Dutch heathland soils, chemoautotrophic bacteria capable of oxidizing ammonium under acid conditions occur commonly (De Boer et al. 1990; Troelstra et al. 1990). However, in the wet sites the development of a population of nitrifying bacteria was probably limited by a low oxygen supply. This is supported by the findings of De Boer et al. (1990), who found no net nitrification when they incubated suspensions of FH material from the same wet soils, kept at pH 4 by adding 1% ammonia (NH_3).

Denitrification is a potential loss of mineral N from the incubated soil. However, we assume that the loss of N by this process was small because of the low nitrate availability.

In the dry area, the net nitrification rate increased proportionally with the net N mineralization rate suggesting ammonium availability may control net nitrification in these soils. But we cannot explain the relatively low net nitrification rate in the *Calluna* soil. The *Calluna* soil may have contained more phenolic substances than the *Molinia* or *Deschampsia* soils (Jalal & Read, 1983), but there is still controversy whether or not phenolics inhibit nitrification (Kuiters 1990; McCarty et al. 1991). Denitrification was probably lacking or insignificant at the moisture levels in these soils (Paul & Clark, 1989).

Species effects on N cycling

At all sites the measurements of litter inputs to the soil and their lignin and N contents revealed clear differences among the plant species (Table 3). The data on litter production were obtained from the same plots (*Molinia* (dry area), and *Deschampsia*), or in plots adjacent to the ones used for this study (*Molinia* (wet area), *Calluna*, and *Erica*). *Molinia* produced 2.6 times more above- and belowground litter than the amount produced by *Erica* at the wet site, and 2.8 times more than *Calluna* at the dry site. The litter mass of *Deschampsia* was only 0.6 times the amount produced by *Calluna*. The relative differences between the species in their total N losses from litter production were similar to the relative differences in their litter production (Table 3); however, these data were based on the assumption that N is not retranslocated from dying roots (Aerts 1990). Field measurements of the percentage of N retranslocated from dying aboveground parts revealed that the average percentage was 16% for *Erica*, 12% for *Calluna*, 61 to 64% for *Molinia*, and 54% for *Deschampsia* (Aerts 1990; Aerts unpublished data). It seems unlikely that a plant species will develop an efficient mechanism of N resorption from senescing aboveground parts and not from belowground parts; however, we have not proven this by field measurements. We recalculated the N losses, using the same percentages of N retranslocation for roots as measured for shoots (Table 3). Clearly, compared with *Calluna* or *Erica*, the N loss from the plant via litter production is much greater for *Molinia* but smaller for *Deschampsia*, regardless of which estimate of the total N loss was used.

Comparing *Molinia* sites with *Erica* or *Calluna* sites, the combined effect of the greater N loss through litter production of *Molinia* and the

faster decomposition rate of its litter (Van Vuuren, unpublished data) may explain the faster net N mineralization rates in the *Molinia* soils. The species effect on the N availability is supported by the results from the wet area. The *Molinia* and *Erica* sites contained equal amounts of soil organic N, but the average amount of N that was mineralized was 29 mg N g^{-1} soil N in the *Molinia* soil and only 16 mg N g^{-1} soil N in the *Erica* soil (Table 3).

In the dry area, the N loss through litter production by *Deschampsia* is only half the amount lost by *Calluna*. Still the decomposition rate of *Deschampsia* litter is much faster than that of *Calluna* litter (Van Vuuren, unpublished data), which may explain the relatively high net N mineralization rate in the *Deschampsia* site. However, *Molinia* and *Deschampsia* sites both contained much more soil organic N than the *Calluna* site. Thus the sites dominated by the grasses were probably older successional stages (Berendse 1990). More soil organic N could have accumulated, resulting in faster net N mineralization rates. Nevertheless, the average amount of N that was mineralized per gram soil N was greater at the *Molinia* and *Deschampsia* sites than at the *Calluna* site (35 and 36 mg N g^{-1} soil N compared with 25 mg N g^{-1} soil N; Table 3). This suggests that the shift in plant species composition towards a dominance by *Molinia* or *Deschampsia* led to an increase in the quality of the soil organic matter, resulting in more rapid rates of N cycling.

Acknowledgements

The research was supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO). We thank M. J. A. Werger, P. J. M. van der Aart and two anonymous reviewers for their valuable comments on an earlier draft of this manuscript.

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