

Effects of nitrogen deposition on growth and survival of montane *Racomitrium lanuginosum* heath

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Abstract

Montane heaths dominated by the moss *Racomitrium lanuginosum* are in decline, for which increased atmospheric nitrogen (N) deposition may be partially responsible. To test this, field plots in northeast Scotland were treated with either low or high (10 or 40 kg N ha⁻¹ year⁻¹) doses of nitrogen (as NO₃⁻ or NH₄⁺) for 2 years. Although *Racomitrium* tissue N increased after treatment, with greater response for low than high N application, activity of the enzyme nitrate reductase and *Racomitrium* growth were severely inhibited by increasing N addition. *Racomitrium* cover declined following N addition and graminoid cover increased, also with greatest effect at high doses. Of all measurements, only nitrate reductase showed a distinction between NO₃⁻ and NH₄⁺ application. The results demonstrate the detrimental effects of even low increases in nitrogen deposition on the moss heath, suggesting that loss of *Racomitrium* and its replacement by graminoids is strongly linked to increased levels of anthropogenic N pollution. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Atmospheric nitrogen deposition; *Racomitrium lanuginosum*; *Carex bigelowii*; Bryophyte growth; Nitrate reductase

1. Introduction

Montane heath dominated by the moss *Racomitrium lanuginosum* (Hedw.) Brid. is found on mountain summits with relatively high latitude and level of oceanicity, but is a threatened community in Britain (Thompson and Brown, 1992; Ratcliffe and Thompson, 1998). Today, only Scotland still harbours extensive *Racomitrium* heath (Ratcliffe and Thompson, 1998), but past evidence suggests that the distribution of the heath was once more extensive, covering summits in northern England and Wales which are now dominated by grass communities (Thompson et al., 1987; Bunce et al., 1999). Although the species *Racomitrium* is found throughout the world (Hill et al., 1992), occurrence of well developed *Racomitrium* heath outside Britain is limited in temperate regions, and largely restricted to montane fellfield areas in the arctic and sub-arctic zones, for instance Iceland, the Faroes and western Norway (Thompson and Baddeley, 1991; Jónsdóttir et al., 1995; Virtanen et al., 1997b).

There are a number of factors proposed responsible for the decline of *Racomitrium* heath, including pollution and changes in land use such as heavy grazing pressure. Increasing rates of nitrogen (N) deposition as a result of anthropogenic emissions may be one of the main factors involved in the deterioration and loss of *Racomitrium* heath in recent decades (Thompson et al., 1987; Lee et al., 1988; Thompson and Baddeley, 1991). However, no manipulative experiments have conclusively demonstrated cause and effect. On the contrary, experimental results from a field study in Iceland indicated no reduction in growth of *Racomitrium* when exposed to very low levels of additional N (4 kg N ha⁻¹ year⁻¹) over 3 years, despite the fact that the additional N was absorbed by the moss (Jónsdóttir et al., 1995).

Like many mosses *Racomitrium* is ectohydric, as it has no root system, and intercepts and absorbs all the solutes needed for growth from water droplets in the surrounding atmosphere. This makes the species particularly sensitive to changes in N deposition. *Racomitrium* tissue N content has indeed been correlated with atmospheric N deposition levels (Baddeley et al., 1994; Pitcairn et al., 1995), and a short-term increase of tissue N was recorded in response to pulses of either NO₃⁻ or

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NH_4^+ (Soares and Pearson, 1997). Montane vegetation is likely to be exposed to higher atmospheric deposition than surrounding lowland sites due to increased precipitation with altitude, and the presence of long periods of orographic cloud cover causing occult deposition, which typically has two to five times the pollutant concentrations of rain (Grace and Unsworth, 1988). High N concentrations can disrupt metabolic processes, such as pH regulation and N assimilation by nitrate reductase, inducing phytotoxic effects on bryophytes. *Racomitrium* has been shown to be particularly sensitive to such high addition of either NO_3^- or NH_4^+ solutions (Greven, 1992; Soares and Pearson, 1997).

Element cycling in the skeletal montane soils that support the heath vegetation is slow due to the short growing season, low temperatures and periods of drought as a result of low soil organic matter content. Increasing inputs of dry and wet deposited nitrogen are therefore likely to substantially increase system productivity (Lee et al., 1988) causing changes in plant species composition. Little is known, however, about the relationships between plant species within the montane heath, particularly *Racomitrium* and graminoids, and the effects N deposition has on species dominance and community composition.

This paper examines the impact of N addition on the performance of *Racomitrium* within montane *Racomitrium lanuginosum*–*Carex bigelowii* heath and its effect on species cover. Plots on the summit of a field site in the relatively unpolluted northeast Scottish highlands were subject to experimentally increased low ($10 \text{ kg ha}^{-1} \text{ year}^{-1}$) and high ($40 \text{ kg ha}^{-1} \text{ year}^{-1}$) N input in both reactive forms ($\text{NO}_3^-/\text{NH}_4^+$) for a period of two summer seasons. The N load was added in a total of seven applications over the two seasons to simulate pollution events. Nitrogen content and growth of *Racomitrium* in response to N addition were determined, nitrate reductase activity measured, and plant species composition of the heath recorded.

2. Methods

2.1. Site description

The study site lies on the exposed summit (1068 m. a.s.l.) of Glas Maol ($56^\circ 53' \text{ N}$, $3^\circ 22' \text{ W}$) in the south eastern part of the Grampian Mountains, Scotland. It falls within the Caenlochan SSSI that supports a number of rare arctic-alpine communities predominantly found within base-rich areas and scree slopes. The *Racomitrium* heath itself provides important breeding habitat for dotterel, a rare bird listed under Annex 1 of the EC Birds Directive (EC Directive 79/409/EEC). The weathered granite substrate is subject to frost heave over winter and shows signs of solifluction. Total N

deposition for the Glas Maol area, corrected for the effects of altitudinal occult deposition, is estimated as approximately $12 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (CLAG, 1997; Sutton, personal communication). This is toward the lower end of the recorded British range: less than $3 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in northern Scotland increasing to $30 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and above in the Pennines, Cumbria. (UKRGAR, 1997). The vegetation consists of *Carex bigelowii*–*Racomitrium lanuginosum* montane heath (National Vegetation Classification U10a, Rodwell, 1992) in which both species are often co-dominant. The moss *Racomitrium* forms extensive mats up to 10 cm thick, and is accompanied by graminoids, in particular *C. bigelowii*, *Festuca ovina*, and *Festuca vivipara*.

The site is grazed predominantly by mountain hares throughout the year and by sheep in the summer months. A number of red deer are also occasionally present, although do not significantly contribute to herbivore numbers on the plateau (Welch and Scott, 2001).

2.2. Fertiliser application

The N loading experiment, simulating an increase in wet atmospheric N deposition in the form of pollution episodes, was carried out in June and July of both 1998 and 1999. Two forms of nitrogen solution, KNO_3 and NH_4Cl , were applied to separate plots at two rates equivalent to a total of $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$ and $40 \text{ kg N ha}^{-1} \text{ year}^{-1}$, representing low and high N deposition levels within Britain (UKRGAR, 1997). Although, actual concentrations applied are possibly at the upper range or may exceed that of natural pollution events at the site. Distilled water was applied alone as a control. The five different treatments (control, low NO_3^- , low NH_4^+ , high NO_3^- , high NH_4^+) were applied to $0.6 \times 0.6 \text{ m}$ plots in 0.5-l amounts as a fine mist by using a knapsack sprayer. Solutions were applied three (1998) or four (1999) times in June and July to give the total dose of 10 kg N ha^{-1} and 40 kg N ha^{-1} required for each year. The experiment was set-up on two sites, ca. 200 m apart, within the same summit vegetation. At each site there were five replicate blocks, each containing one plot for each treatment.

2.3. Shoot nitrogen content

Racomitrium was sampled prior to fertilisation treatment on 12 June 1998, 24 h after the final application on 11 July 1999, and again at the end of the growing season on 11 September 1999. The top 2-cm sections were removed from the shoots, washed gently in a stream of distilled water and air dried. The dried plant material was milled and analysed for total N content using a continuous flow colorimetric autoanalyser (Segmented Flow Autoanalyser, Burkard Scientific, Uxbridge, UK), following wet acid digestion (Allen, 1989). Nitrogen

content was measured as ammonium by a modified Bertholet reaction (Hinds and Lowe, 1980; Rowland 1983). Only the apical 2-cm sections of *Racomitrium* tissue were analysed, as N content has been shown to be constant over this distance from the apex, but declines rapidly further down the stem (Baddeley et al., 1994).

2.4. Nitrate reductase assay

Measurement of nitrate reductase activity provides an indication of nitrate availability in an ecosystem and subsequent plant nitrogen metabolism (Morgan et al., 1992). As such it is regarded as a useful tool in studying the physiological effects on plants of nitrogen pollution. Samples of *Racomitrium* were collected from each plot on 23 August 2000, following N additions in June and July as applied in the previous 2 years. The sampled material was subsequently allowed to acclimatise in a growth chamber under continuous lighting to avoid possible diurnal effects for 72 h prior to the assay, and kept moist with distilled water. Assays were carried out on current year's growth, identified as the top bright green section of the shoot, and three samples of 10 shoots each were used from each plot. All assays were performed *in vivo* following the method used by Woodin and Lee (1987) and enzyme activity was induced using 1 mM KNO₃ solution. Nitrate reductase activity was measured prior to induction and after 6 h, coincident with peak enzyme activity as determined in initial time course assays on *Racomitrium* shoots.

2.5. Shoot growth

Shoot growth (increase in length at the apical bud) of *Racomitrium* was measured on samples collected from each plot which had their lower sections cut off to leave 4-cm lengths, placed into a netlon cylinder and carefully placed back into the moss mat within their respective plots. Ten shoots were placed into each cylinder with two cylinders per plot. The length of the cut shoots was measured again at the end of the growing season and results from the two cylinders were combined to give a mean shoot increase for each plot.

2.6. Vegetation composition

To test for differences in initial plant cover, a pin frame was used recording first intercepts ('hits') over 36 points within each of the selected plots on 12 June 1998, prior to the start of the experiment. Records were made using the following categories; *Racomitrium*, *C. bigelowii*, other graminoid, other bryophyte, lichen, dead vegetative material, bare ground and rock. No significant differences in plant cover between plots designated to the various treatments could be detected ($0.15 < P < 0.61$, Generalised Linear Mixed Model

(GLMM), as described in Section 2.7). At peak biomass in September 1999, vegetation cover was again measured, with first intercepts over 132 pin points recorded in each plot.

2.7. Statistical analyses

All results were analysed using a GLMM Generalised Linear Mixed Model in SAS version 6.12 with 'treatment' and 'site' as fixed effects and 'plot within site' as a random effect. A specific set of contrasts allowed subsequent testing for the effects of N-application (data from treated plots contrasted with data from control plots), dose (high versus low dose) and ion type (NO₃⁻ versus NH₄⁺). Data on plant cover were arcsin $\sqrt{\cdot}$ -transformed to meet assumptions of the statistical models used.

3. Results

3.1. Physiological response

Tissue N content of *Racomitrium* from plots taken before the start of the treatments in 1998 showed no differences between treatment and control plots ($F_{4,32} = 1.9$; $P = 0.13$) or between sites ($F_{1,8} = 2.01$, $P = 0.19$). Samples of *Racomitrium* taken 24 h following the final application of NO₃⁻ and NH₄⁺ solutions in July 1999 had significantly higher N content than control plots ($F_{1,32} = 20.25$, $P < 0.0001$), demonstrating that the additional nitrogen was taken up by the moss (Fig. 1). However, by the end of the growing season (September 1999; Fig. 2a, Table 1), this elevated N content was no longer apparent in the high dose plots and did not differ from N content in control plots ($F_{1, 18} = 0.44$, $P = 0.52$).

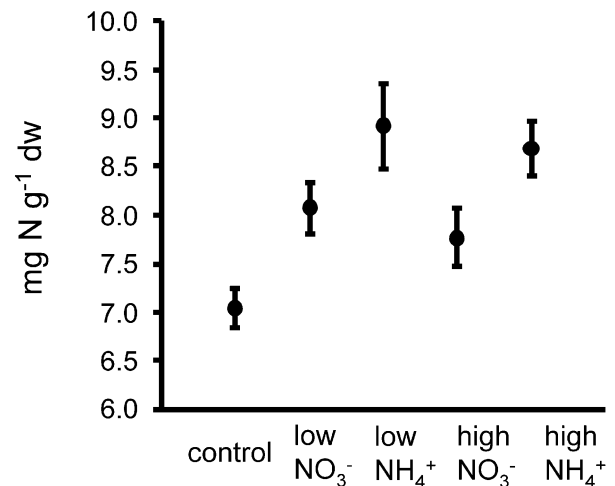


Fig 1. Nitrogen concentration in the uppermost two cm segment of *Racomitrium lanuginosum* shoots measured 24 h after the final N application in July 1999, after two seasons of treatment. (d.w. = dry weight).

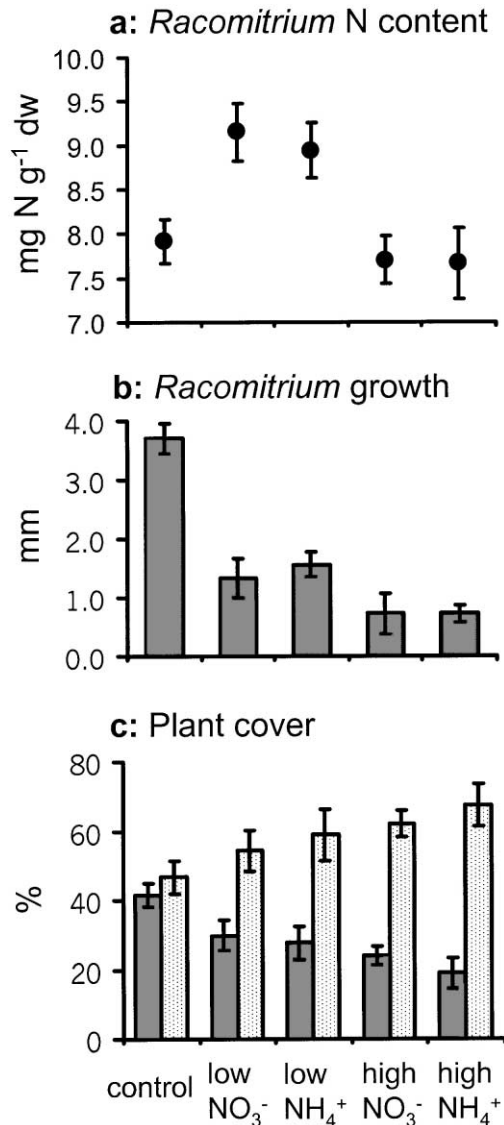


Fig. 2. (a) Nitrogen concentration in the uppermost two cm segment of *Racomitrium lanuginosum* shoots measured in September 1999, after two seasons of treatment; (b) *Racomitrium* shoot growth between May and September 1999; (c) percent cover of *Racomitrium* (■) and graminoids (▨) measured in September 1999. See Table 1 for statistical results.

Table 1

Summary statistics for the effects of nitrogen addition treatment (with distilled water control), concentration (10 or 40 kg N ha⁻¹ year⁻¹) and ion type (NO₃⁻ or NH₄⁺) on *Racomitrium* tissue N, growth and the species composition of *Carex bigelowii*–*Racomitrium lanuginosum* heath in September 1999, after two seasons of treatment

	Effect of		
	Treatment (treated vs. control plots) NDF = 1 DDF = 38	N Dose (Low vs. high) NDF = 1 DDF = 28	Ion type (NO ₃ ⁻ vs. NH ₄ ⁺) NDF = 1 DDF = 28
<i>Racomitrium</i> N content	$F = 1.49$ n.s.	$F = 27.10$ ***	$F = 0.12$ n.s.
<i>Racomitrium</i> shoot growth	$F = 93.32$ ***	$F = 11.20$ **	$F = 0.19$ n.s.
<i>Racomitrium</i> cover	$F = 15.95$ **	$F = 3.79$ n.s.	$F = 0.88$ n.s.
Graminoid cover	$F = 9.69$ **	$F = 3.75$ n.s.	$F = 1.25$ n.s.

** $P = < 0.01$.

*** $P = < 0.0001$.

However, the nitrogen content of *Racomitrium* from low dose plots was still significantly higher than the controls ($F_{1,18} = 20.06$, $P < 0.001$). Tissue N content in *Racomitrium* from plots which had received the low dose contained an average of 9.0 ± 0.1 mg g⁻¹ dry weight, 1.3 mg more than in moss from plots receiving the high dose or distilled water control.

A significant difference in *Racomitrium* tissue N content according to ion type was evident 24 h following the final application of NO₃⁻ and NH₄⁺ solutions, with an average of 0.9 mg g⁻¹ dry weight more in plots receiving reduced rather than oxidised forms ($F_{1,28} = 10.51$, $P < 0.01$). However, there was no effect of the type of ion applied on tissue N content by the end of the growing season (Table 1).

Induction of nitrate reductase activity was significantly decreased in *Racomitrium* from all treated plots compared to the controls ($F_{1,32} = 45.27$, $P < 0.0001$; Fig 3). Nitrate reductase activity in *Racomitrium* from plots receiving the low N dose was 53% less than in the controls, but with no difference between ion type. At the high doses, nitrate reductase activity was even further reduced. Material from plots which had received N

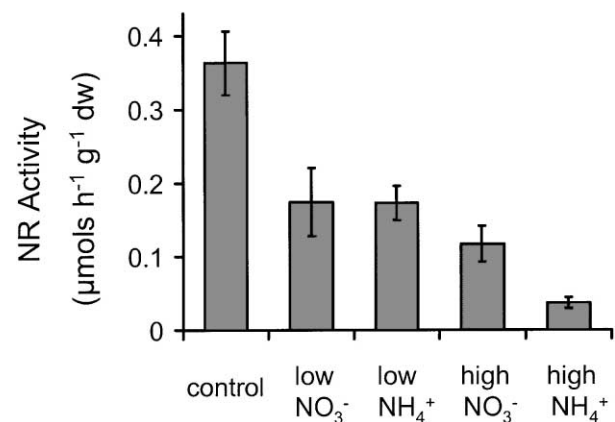


Fig 3. Induced nitrate reductase activity (NRA; $\mu\text{mol NO}_2^- \text{h}^{-1} \text{g}^{-1}$ dry weight) in current year's growth of *Racomitrium lanuginosum* shoots collected in August 2000, after three seasons of N treatment. Material was induced with 1 mM nitrate and NRA measured after 6 h.

addition in the form of NH_4^+ showed an even greater reduction than that of NO_3^- , to only 11% that of the controls.

3.2. Growth response

Shoot growth measured in the second year of treatment (1999) showed a dramatic negative response to N addition (Fig. 2b; Table 1). Growth in control plots was $3.7 \text{ mm} \pm 0.27$ (S.E.) mm, and in treated plots this was reduced by at least 58%. Nitrogen concentration had a significant effect on growth, as that measured in low dose plots was 1.5 ± 0.2 mm compared to only 0.7 ± 0.2 mm in high dose plots. Again, there was no effect of ion type on shoot growth (Table 1).

3.3. Vegetation composition

In the second year of treatment the N additions had a significant effect on vegetation composition within the plots (Fig. 2c; Table 1). *Racomitrium* cover was on average 40% lower in plots receiving N additions compared to those treated with distilled water. High N doses tended to have a greater adverse effect on *Racomitrium* cover than low doses (48% versus 31%), but this was only marginally significant ($P=0.06$; Table 1). Other bryophytes generally reached only low cover percentages and, as a combined species group, appeared not to be affected by N treatment ($F_{4,32}=1.58$ $P=0.20$). The N treatments had a significant effect on cover of graminoids (*C. bigelowii* and grasses) within the vegetation (Fig. 2c; Table 1). Plots receiving nitrogen had an average of 61% graminoid cover compared to control plots with only 47%. There was a trend ($P=0.06$; Table 1) towards greater graminoid cover occurring in high dose plots (65%) rather than low dose plots (57%), but ion type had no significant effect.

4. Discussion

4.1. Physiological and growth response

Racomitrium was shown to be extremely sensitive to even low concentrations of atmospheric N deposition. When subjected to the low dose of only $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$ it responded with a raised tissue N content and severely reduced shoot growth. Higher doses of N caused an even stronger growth reduction. The mechanisms for this are unclear, but the decrease of at least 58% in treated plots relative to controls demonstrates that increases in atmospheric N deposition are likely to have deleterious effects on annual growth. This is in contrast to work by Jónsdóttir et al. (1995) where no significant effect was detected at the much lower loading of $4 \text{ kg N ha}^{-1} \text{ year}^{-1}$. However, studies of stem

growth in other bryophyte species with comparable nutrient acquisition strategies to *Racomitrium* have shown a negative effect of N addition (Chapin and Shaver, 1985; Potter et al., 1995).

As with the effect on shoot growth, *Racomitrium* tissue N concentration responded differently to the two N doses. The significant increase in tissue N of *Racomitrium* sampled 24 h after the final application indicates the moss' capacity to reflect atmospheric supply and immobilise deposited N in its uppermost two cm section. *Racomitrium* growing in an ombrotrophic mire in north Wales, which was exposed to N deposition approximately twice that of the region's $12 \text{ kg N ha}^{-1} \text{ year}^{-1}$ background level, also showed a marked increase in moss tissue concentration (Baddeley et al., 1994). However, although the high N dose in our study was four times more concentrated than the low dose, this was not reflected in the moss tissue. This discrepancy was even more apparent by the end of the growing season, where *Racomitrium* tissue N in low dose plots was significantly greater than that in high dose plots. Low tissue N concentration at the high dose is unlikely to be the result of growth dilution as shoot growth was significantly reduced compared to the other treatments. Instead, the lack of tissue N accumulation may reflect physiological damage caused by the raised N supply. This may take the form of tissue membrane damage, as demonstrated in snowbed bryophytes exposed to acidic meltwater pollutants (Woolgrove and Woodin, 1996), resulting in greater solute loss from *Racomitrium* treated with the high N dose. *Racomitrium* also appears pH sensitive, with high N concentrations interfering with its ability to accumulate added nitrogen, thus reducing uptake efficiency (Soares and Pearson, 1997). Solutions of low pH have been known to similarly harm boreal mosses such as *Hylocomium splendens*, reducing nutrient content, segment length and biomass (Bates, 2000). A similar response in *Racomitrium* may explain the low tissue N content in high dose plots, and the growth reduction in all N treated plots.

The greater uptake of reduced over oxidised forms of N measured 24 h after the final application is probably due to a high cation exchange capacity which is common in mosses (Bates, 2000). Uptake of reduced N is generally regarded as more energy efficient than oxidised. Where both oxidised and reduced forms of N are available, preference for uptake of NH_4^+ has previously been observed in *Racomitrium* (Soares and Pearson, 1997). However, when both ions are at the same rate of supply, NH_4^+ has been shown to cause greater inhibition of the enzyme nitrate reductase in *Sphagnum* species (Woodin and Lee, 1987) and may increase overall acidity of the moss (Pearson and Stewart, 1993). Inhibition of nitrate reductase induction was indeed observed in N treated plots within this study, with repression greatest at the high NH_4^+ dose. The raised

tissue N in *Racomitrium* treated with NH_4^+ compared to NO_3^- , however, was not apparent at the end of the growing season and so does not appear to be a long term effect.

The strong reduction in nitrate inducibility in even the low dose plots suggests that the moss is already saturated with available N. *Racomitrium* heath naturally has a low nutrient status, therefore any N additions would be expected to either not affect or increase nitrate reductase inducibility within the *Racomitrium*. However, the reduction in inducibility observed within treated *Racomitrium*, together with reduction in its shoot growth and percentage cover, indicate that the heath system must already be N loaded. Therefore, the 'critical load' of the moss, defined as the estimate of exposure to N deposition below which changes in ecosystem structure and function are limited (Hornung et al., 1995), was exceeded by additions of only $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$.

A well-developed moss mat can absorb atmospherically deposited N, limiting its availability to surrounding vascular plants for several years (Jónsdóttir et al., 1995). However, reduced efficiency of N uptake at higher pollution concentrations may cause more immediate leaching into the surrounding substrate (Lee et al., 1987). The thickness of the moss mat may also be reduced as a result of N pollution decreasing *Racomitrium* growth, with consequences for the microclimate it provides for other species in the community (Carlsson and Callaghan, 1991). The decreased tissue N in *Racomitrium* at higher deposition doses, together with the potential reduction in biomass accumulation as a result of disrupted growth, suggests that the moss is no longer acting as a nitrogen sink. An increase in available N is therefore a likely result of enhanced pollution scenarios, in the otherwise nutrient deficient skeletal montane soil.

4.2. Vegetation cover

After two seasons of N addition a change in species cover between treated and untreated plots was already apparent, with graminoids significantly increasing at the expense of *Racomitrium*. This suggests that graminoids have utilised the excess nitrogen under conditions that appear supra optimal for the bryophyte. It may also reflect the decreased growth of *Racomitrium* with increasing N supply. This change in cover within the community has implications for interspecific competition. As graminoid cover increases, so too will effects of light competition associated with canopy closure. In layered vegetation, the loss of bryophyte abundance has been connected with an increase in biomass of vascular plants that respond to additional nutrients (Lee and Caporn, 1998; Press et al., 1998; Carroll et al., 1999). A similar increase in graminoids has been shown by Jonasson et al., (1992; 1999) in sub-arctic tundra to cause a reduction in cover of second stratum species which, similar to montane

heath, is mainly comprised of bryophytes. Therefore, as well as direct toxic effects, added N may also have an indirect effect on *Racomitrium* cover due to greater N availability in the substrate, benefiting expansion of faster growing graminoids, and potentially limiting *Racomitrium* through light competition.

A change in species cover within the heath community is likely to have further consequences for nutrient cycling. As stems of moss with elevated N levels eventually decompose, an even greater supply of nitrogen may then become available to higher plants (Aerts, 1999), further favouring graminoids. It is possible that a greater presence of graminoids in the vegetation will make it more attractive to herbivores, chiefly deer, mountain hare and sheep, thereby adding associated grazing damage and fertilisation through dung and urine (Haynes and Williams, 1993). Sheep grazing on Glas Maol was held responsible for localised loss of bryophytes, for instance along snow fences (Welch, 1996) where grazing pressure was greatest. The detrimental effects of N deposition may enhance this vegetation change, resulting in a synergistic effect between N deposition and grazing, the two factors originally proposed responsible for *Racomitrium* decline (Thompson and Baddeley, 1991).

This study supports the hypothesis that N deposition is a key factor contributing to the decline and loss of *Racomitrium* heath throughout Britain. Even small increases in nitrogen affect *Racomitrium* growth and cover, as well as resulting in the spread of graminoids within the vegetation. It is unclear, however, whether the loss of *Racomitrium* is due largely to indirect effects of N deposition via graminoid expansion, and reduced light availability, or the direct effects of N deposition disrupting moss growth. The concentration of N addition will also influence nutrient cycling within the heath. At low N doses, moss tissue N concentration increases, eventually providing micro-organisms with an N-enriched substrate, whilst higher rates of deposition reduce *Racomitrium*'s ability to act as an N sink, potentially releasing greater amounts of available N more immediately into the substrate. Thus, there is also a need to understand the effects of N addition on the complex of vegetation and soil processes, as well as to determine the relative importance of grazers, in causing the decline of *Racomitrium* heath. Since *Racomitrium* has been shown to be extremely sensitive to the level of atmospheric N, the trend for increasing N deposition is a major cause for concern for the condition and survival of montane moss heath.

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