

REPORT

Interplay between nitrogen deposition and grazing causes habitat degradation

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Abstract

Increased atmospheric nitrogen (N) deposition has been held responsible for the large-scale invasion of graminoids (grasses, sedges and rushes) in a wide range of habitats from forests to upland heaths, causing dramatic changes in plant species composition. Concurrently with an increase in N deposition over the last century, livestock grazing has intensified in many parts of the world following policy reform, leading to large-scale degradation of natural and seminatural ecosystems. On the basis of a series of experiments conducted in a Scottish montane ecosystem, we discovered that grazing and N deposition do not operate independently, and the interplay between them is leading to the replacement of valuable moss-dominated habitat by grasses and sedges. Our study indicates that in setting 'critical loads' of N, widely used to minimize habitat degradation, it is necessary to account for substantial amplification of N-deposition effects by grazing.

Keywords

Competition for light, critical loads, habitat degradation, herbivore attraction, montane ecosystems, moss–sedge interactions, nitrogen deposition, positive feedback loop, *Racomitrium* heath, sheep grazing.

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INTRODUCTION

Atmospheric nitrogen (N) deposition is a widely acknowledged key driver of environmental change, affecting ecosystems throughout the world (Bobbink *et al.* 1998; Matson *et al.* 1999). However, our understanding of the full extent of N-deposition impacts on terrestrial ecosystems is still in its infancy, because interactions between N deposition and other environmental drivers of change, including grazing, are poorly understood (Jefferies & Maron 1997; Asner *et al.* 2001; Strengbom *et al.* 2002). Concurrently with an increase in N deposition over the last century, livestock grazing has intensified in many parts of the world following policy reform, leading to large-scale degradation of natural and seminatural ecosystems (Kashulina *et al.* 1997; Adler & Morales 1999; Sansom 1999; Shi & Li 1999; Manzano *et al.* 2000). Moss- or lichen-dominated arctic and montane ecosystems, covering >20% of the earth's land surface (Longton 1988), are perhaps at greatest risk, being particularly sensitive to both increased levels of N deposition (Press *et al.* 1986; Gordon *et al.* 2001; Jones *et al.* 2002; Pearce & Van der Wal 2002) and grazing (Krahulec *et al.* 2001; Olofsson *et al.* 2001; Van der Wal *et al.* 2001a). Here

we demonstrate, for the first time, that these two key drivers of environmental change do not operate independently, and that the interplay between them causes the degradation of moss-dominated montane ecosystems. Increased atmospheric N deposition has been held responsible for the large-scale invasion of graminoids (grasses, sedges and rushes) in a wide range of habitats from forests to upland heaths, causing dramatic changes in plant species composition (Bobbink *et al.* 1998; Lee 1998). We report on a similar phenomenon of graminoids gradually replacing mosses in Scottish montane ecosystems under combined pressure of increased atmospheric N pollution and sheep grazing.

MATERIALS AND METHODS

Field site

Field experiments were performed at around 1000 m asl on Glas Maol summit (56°53'N, 3°22'W) in eastern Scotland. The vegetation is moss–sedge (*Racomitrium lanuginosum*–*Carex bigelowii*) montane heath with grasses *Festuca ovina*, *F. vivipara*, *Deschampsia flexuosa* and *Agrostis capillaris*. The site

has a cool oceanic climate and is grazed by sheep from June to September. Total N deposition is estimated at $12 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Pearce & Van der Wal 2002).

Nitrogen addition experiment

To determine the sensitivity of *Racomitrium* heath to anthropogenic N deposition, an N-addition experiment was conducted during the four growing seasons of 1998–2001. Two forms of N solution, KNO_3 and NH_4Cl , were applied to separate $0.6 \text{ m} \times 0.6 \text{ m}$ plots each of which was randomly assigned to one of five treatments: low NH_4^+ or NO_3^- ($10 \text{ kg N ha}^{-1} \text{ year}^{-1}$), high NH_4^+ or NO_3^- ($40 \text{ kg N ha}^{-1} \text{ year}^{-1}$) and distilled water control. There were 10 replicate blocks, each containing one plot per treatment (Pearce & Van der Wal 2002). To ease presentation and because atmospheric N deposition includes both ions, we pooled the NH_4^+ and NO_3^- treatments and present data for control, low N and high N. Pin-frame vegetation recordings were taken at the beginning (June 1998) and end (August 2001) of the experiment. *Racomitrium* or graminoid cover did not initially differ between the designated treatments ($0.15 < P < 0.61$).

Nitrogen toxicity to moss

To determine effects of N additions on *Racomitrium* growth and physiology, moss shoots were collected from each field plot in early June 2000, cut to 4-cm apical lengths, put into netlon cylinders and replaced into the moss mat within their respective plots. Shoots were retrieved in September 2000 and tissue in excess of the initial 4 cm was measured. N content was determined in apical 2 cm lengths of *Racomitrium* shoots sampled randomly from each plot in August 2000. Plant material was washed and air dried before acid digestion and colorimetric analysis of total N. Nitrate reductase activity was measured on plant material that was acclimatized to a constant light and temperature in the laboratory, and determined 6 h after spraying with 1 mM KNO_3 solution, coincident with peak induction of activity as determined in initial time course assays (Woodin & Lee 1987). Potassium (K^+) membrane leakage was measured on *Racomitrium* shoots sampled from plots in August 2001. Two centimetres of live green apical material was removed, mechanically shaken in distilled water at 300 rpm for 30 min and left to stand for 3 h (in the absence of soluble calcium) before determining K^+ content of the water using a flame photometer.

Effects of shading on moss growth

To determine whether *Racomitrium* would suffer not only from N deposition directly, through toxic effects, but also indirectly, through shading caused by stimulation of

graminoid cover, a greenhouse experiment was carried out during winter 2000/2001. Netlon cylinders containing 10 *Racomitrium* shoots were each placed in the middle of a 6-cm diameter pot filled with a layer of the moss over washed sand. Mass of new growth was determined after 7 weeks. Spray treatments were applied weekly. Half the pots received N (KNO_3) at a rate equivalent to $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$ to represent background deposition in the field. The other half were subject to the equivalent of $20 \text{ kg N ha}^{-1} \text{ year}^{-1}$, mimicking the low N treatment in the field experiment. All pots were irrigated with distilled water every day to prevent desiccation. Pots were arranged in pairs (one 'background N', one 'low N addition'). Daylight was supplemented by halogen lamps and 51 and 79% reduction in irradiance were provided by shade netting placed above individual pairs of plots. A third of 150 random light measurements taken in July 2001 in the field at the top of the moss mat showed light interception by graminoids $\geq 79\%$.

Sheep grazing and graminoid abundance

Habitat use by sheep was established using 15 sets of five dung plots arranged across the summit of Glas Maol. Previous seasons' sheep dung was removed from each $6 \text{ m} \times 6 \text{ m}$ plot in early June 2000 and new pellet groups were counted and removed every 3 weeks until early September 2000 when the sheep moved to lower altitude. Cumulative number of faecal pellet groups was related to graminoid and grass cover, assessed by visual estimation of species cover in the centre $2 \text{ m} \times 2 \text{ m}$ of each dung plot.

Sheep grazing and moss growth

To determine the impact of sheep grazing on *Racomitrium* growth, 10 grazing cages ($1 \text{ m} \times 1 \text{ m}$) were erected in early June 2001, excluding sheep for a single growing season. Moss growth was measured on shoots in four netlon cylinders (10 shoots per cylinder, measurement as above) placed within the moss mat within each cage and associated control plot ($\geq 10 \text{ m}$ apart).

Sheep grazing and vegetation change

Effect of sheep density on *Racomitrium* and graminoid cover was assessed using plots at a range of distances from a snow fence erected in 1986. Monitoring of sheep utilization began in 1990 on 15 transects perpendicular to the fence. On each transect 10 m-long plots were established parallel to the fence at distances of 0–1, 3–5, 13–15, 23–25 and 43–45 m from it. The plots were visited at 3-week intervals from May to October during 1990–96. Dung densities per plot were

converted to stocking rates (sheep ha⁻¹) using a mean deposition rate of 17 dung groups sheep⁻¹ day⁻¹ for an average utilization period of 6 months (Welch & Scott 2000). Vegetation composition was recorded by pin-frame in 1 m × 0.5 m plots at each dung plot in July 1990 and July 1996. Relationships between vegetation composition and sheep grazing pressure are presented graphically (Fig. 3) by grouping the sheep grazing pressure data in nine similar-sized stocking-rate classes for which average *Racomitrium* and grass cover were calculated.

RESULTS

The treatment of field plots for 4 years with either low or high (10 or 40 kg N ha⁻¹ years⁻¹) doses of N caused significant loss of woolly hair moss *R. lanuginosum* and an increase in graminoid abundance (Table 1a). Whereas this clearly indicates the negative impact of N deposition on moss-dominated ecosystems, we discovered that the radical vegetation changes are the net result of N deposition and grazing interacting through a sequence of mechanisms to trigger the degradation of this sensitive ecosystem. Pathways include direct toxicity of N to the moss, N stimulation of graminoid growth, canopy shading of the moss layer, herbivore attraction to graminoid-rich swards, and consequent trampling damage (Fig. 1).

The *direct toxicity* of N deposition to *Racomitrium* is evident from its physiological and growth responses (Table 1b). Tissue N content of the moss was substantially elevated in plots receiving both low and high doses of N. Also, the inducibility of the enzyme nitrate reductase was greatly diminished, even by low N doses. Nitrate reductase is responsible for nitrate assimilation and is substrate inducible, but inhibited by accumulation of N within the moss tissue (Woodin & Lee 1987). Loss of inducibility thus demonstrates that the moss was most

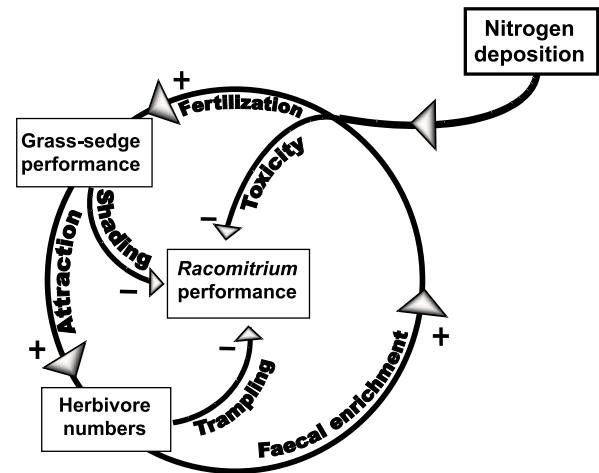


Figure 1 Conceptual model integrating impacts of nitrogen deposition and grazing. This multi-step positive feedback loop shows how atmospheric nitrogen deposition leads to the replacement of the moss *Racomitrium lanuginosum* by sedges and grasses. Nitrogen deposition is directly toxic to the moss and indirectly limits light availability by stimulating graminoids. These in turn attract sheep resulting in greater trampling impact on the moss. Deposition of nutrient-rich faeces enhances graminoid performance and completes this downward spiral of events.

likely N saturated. Moreover, cell membrane integrity was damaged by N addition, indicated by greatly increased potassium leakage in moss subject to both low and high levels of N application. These direct negative effects of increased N deposition on the moss physiology are ultimately reflected in its severely impeded shoot growth (Table 1b).

In contrast, N deposition has a *direct fertilization* effect on graminoid growth (Table 1a), as a result of which the graminoid canopy closes and reduces light availability to the

Table 1 Plant responses to nitrogen addition. (a) The abundance (% cover ± SE) of the moss *Racomitrium lanuginosum* and graminoids (sedges and grasses) in field plots receiving nitrogen additions at either low (10 kg ha⁻¹ year⁻¹) or high (40 kg ha⁻¹ year⁻¹) doses for four growing seasons, and untreated controls. (b) Physiological and growth response (mean ± SE) of *R. lanuginosum* in field plots subject to low and high levels of N addition after 3 years of treatment (K⁺ leakage after 4 years). Sample sizes are 10 replicate untreated plots, 20 low N and 20 high N addition plots

Parameter	Untreated	Low N	High N	F	P
<i>(a) Plant abundance</i>					
<i>Racomitrium</i> cover (percentage cover)	41.4 (1.8) ^a	26.6 (3.0) ^b	15.3 (2.2) ^c	24.21	<0.0001
Graminoid cover (percentage cover)	37.1 (2.5) ^a	49.3 (3.4) ^b	56.4 (3.3) ^c	14.17	<0.0001
<i>(b) Moss physiological and growth response</i>					
Tissue nitrogen conc. (percentage dw)	0.77 (0.02) ^a	0.95 (0.03) ^b	0.99 (0.03) ^b	12.14	<0.0001
Nitrogen reductase activity (μmol NO ₂ mg ⁻¹ dw h ⁻¹)	0.36 (0.04) ^a	0.17 (0.03) ^b	0.08 (0.02) ^c	28.38	<0.0001
K ⁺ leakage (percentage of total K ⁺)*	2.76 (0.47) ^a	6.77 (0.83) ^b	9.02 (0.61) ^c	24.28	<0.0001
Shoot growth (mm)	3.97 (0.42) ^a	2.58 (0.26) ^b	1.02 (0.18) ^c	38.28	<0.0001

*K⁺ measured as ppm g⁻¹ dw.

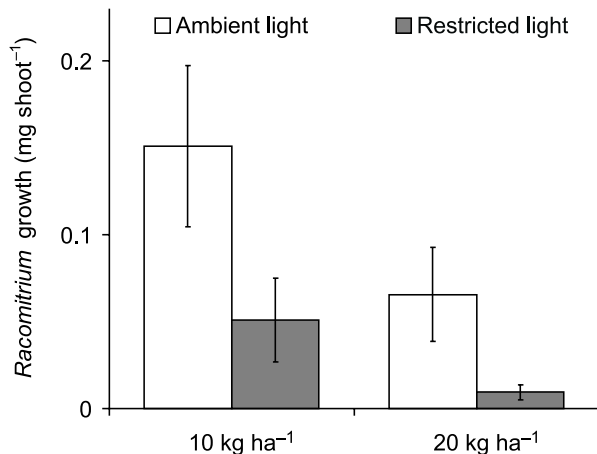


Figure 2 Moss response to light reduction and nitrogen addition. The performance of the moss *Racomitrium lanuginosum* subject to ambient (open bars) and restricted (dark bars) light levels, and low and elevated levels of N deposition. *Racomitrium* shoot growth was significantly reduced by both shading ($F_{1,10} = 8.13$, $P < 0.02$) and fertilization ($F_{1,10} = 6.71$, $P < 0.05$) with the effects being additive rather than multiplicative (shading \times fertilization: $F_{1,10} = 0.38$, $P > 0.5$).

ground layer. Light reaching the moss under graminoid cover is typically reduced by 80–98% from incident irradiance. Such shading reduces *Racomitrium* shoot growth. In a greenhouse experiment a 79% reduction in light availability hampered growth to a similar extent as that of low level N addition (Fig. 2). In combination, shading and N addition reduced moss growth by 90%. Thus N deposition greatly limits the performance of *Racomitrium*, both directly, through toxic effects, and indirectly, through shading caused by stimulation of graminoid cover.

The greater abundance of graminoids, particularly grasses, attracts sheep ($F_{1,13} = 7.09$, $P < 0.02$) which cause direct damage to the moss mat through trampling, leading to a demonstrable reduction in moss growth: *Racomitrium* shoot growth was 40% lower in grazed plots compared with plots from which sheep were excluded during a single growing season ($F_{1,65} = 11.62$, $P < 0.002$).

The ability of sheep at high density to convert moss-dominated vegetation into a graminoid-dominated sward was evidenced through an unintentional experiment. The erection of snow fences, favoured by sheep for shelter, generated a dramatic gradient in sheep grazing pressure away from the snow fence (Welch & Scott 2000). Ten years after the erection of these fences, the distribution of *Racomitrium* was strongly negatively related to sheep grazing pressure ($F_{1,87} = 33.13$, $P < 0.0001$; Fig. 3a). On the contrary, grasses (Fig. 3b) were most abundant where sheep grazing pressure was highest ($F_{1,87} = 74.08$, $P < 0.0001$).

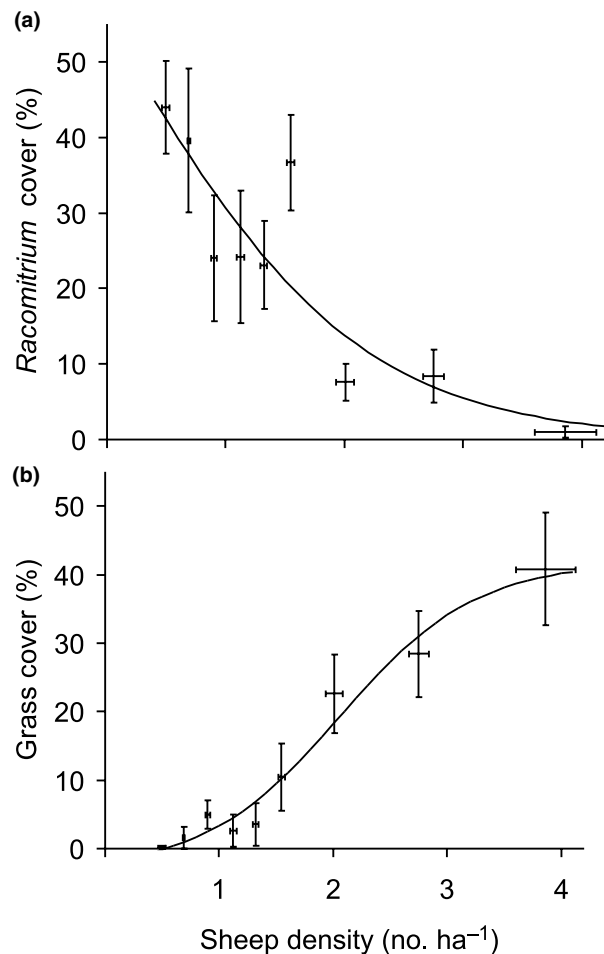


Figure 3 Impact of sheep on plant abundance. The abundance (% cover \pm SE) of the moss *Racomitrium lanuginosum* (a) and grasses (b) in relation to local sheep grazing pressure (sheep density \pm SE). Plant cover estimates were taken 10 years after the establishment of snow fencing which greatly influenced the spatial distribution of sheep.

Analysis of vegetation change between 1990 and 1996 confirmed that sheep grazing had been instrumental in reducing *Racomitrium* cover and allowing graminoids, in general, and grasses, in particular, to expand. A significant negative relationship was established between sheep grazing pressure and change in *Racomitrium* cover ($F_{1,87} = 28.8$, $P < 0.0001$) indicating greatest reduction where sheep grazing pressure was high. Yet, positive relationships were determined between sheep grazing pressure and changes in total graminoid ($F_{1,87} = 6.23$, $P < 0.02$), or grass cover ($F_{1,87} = 91.98$, $P < 0.0001$). The pattern of graminoid invasion may be self-perpetuating, as swards with greatest graminoid cover attract the most sheep grazing and so receive the greatest inputs of nutrient-rich faeces, which may further facilitate graminoids whilst suppressing *Racomitrium*.

DISCUSSION

We have demonstrated that atmospheric N deposition initiates a multistep feedback loop, in which toxicity to moss, graminoid fertilization, shading of moss and attraction of herbivores together lead to the replacement of moss-dominated vegetation by grasses and sedges. The operation of this feedback loop is the likely cause of the dramatic decline of moss-dominated montane communities in the UK over the last 50 years, putting at risk a habitat of great conservation value (Thompson & Brown 1992; Bunce *et al.* 1999) with associated rare and internationally protected bird species such as the dotterel (*Charadrius morinellus* – Galbraith *et al.* 1993). We predict that the conceptual framework provided, in which the effects of N deposition enable grazing impact, is applicable to a wide range of ecosystems, including lowland (Aerts & Bobbink 1999; Jones *et al.* 2002) and upland heath (Alonso *et al.* 2001), mountain ranges (Shi & Li 1999; Krahulec *et al.* 2001), boreal forests (Nams *et al.* 1996; Turkington *et al.* 2002), subarctic heath (Press *et al.* 1998) and arctic tundra (Gordon *et al.* 2001; Olofsson *et al.* 2001; Van der Wal *et al.* 2001b).

A general pattern is emerging, which suggests that N deposition has greatest impact on terrestrial vegetation through amplification of the direct enrichment effects by additional factors such as grazing (this study) or disease (Aerts & Bobbink 1999; Strengbom *et al.* 2002). Dramatic conversion of vegetation, such as we have witnessed on montane heath, is likely to have strong and cascading impacts on ecosystems, influencing biodiversity (Adler & Morales 1999; Aerts & Bobbink 1999), soil biological and physico-chemical properties (Jefferies & Maron 1997; Sansom 1999), and carbon sequestration (Oechel *et al.* 1993, 2000; Wilsey *et al.* 2002).

Our study also indicates that the generally accepted 'critical loads' of N, widely used to advise pollutant emission reduction policy with a view to minimizing habitat degradation throughout Europe (Cowling *et al.* 2001), may require revision to take into account substantial amplification of N-deposition effects by grazing. The concurrent increase, over the past half-century, in atmospheric N deposition and livestock grazing in a wide range of natural or seminatural systems which were previously subjected to only low levels of exploitation has undoubtedly caused widespread ecological degradation. Our conceptual framework of interacting mechanisms of damage provides understanding with which to underpin both sensitive land management and appropriate pollution control.

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