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## Mosses and the struggle for light in a nitrogen-polluted world

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**Abstract** The impact of reduced light conditions as an indirect effect of nitrogen (N) deposition was determined on three mosses in a montane ecosystem, where sedge and grass cover increase due to N enrichment. Additionally, in the greenhouse we established the importance of low light to moss growth as an indirect N deposition effect relative to the direct toxic effects of N. The amount of light reaching the moss layer was strongly and negatively related to graminoid abundance. Mosses showed differing sensitivities to reduced light in the field. *Racomitrium lanuginosum* biomass was found to be highest under high-light conditions, *Polytrichum alpinum* at intermediate light levels, whilst that of *Dicranum fuscescens* was unrelated to light availability. Moreover, *Racomitrium* biomass decreased with increasing amounts of graminoid litter, whereas the other species were little affected. All three mosses responded differently to the combination of elevated N (20 vs 10 kg N ha<sup>-1</sup> year<sup>-1</sup>) and reduced light (60 and 80% reduction) in the greenhouse. *Racomitrium* growth was strongly influenced by both light reduction and elevated N, in combination reducing shoot biomass up to 76%. There was a tendency for *Dicranum* growth to be modestly reduced by elevated N when shaded, causing up to 19% growth reduction. *Polytrichum* growth was not influenced by elevated N but was reduced up to 40% by shading. We conclude that competition for light, induced by vascular plants, can strongly influence moss performance even in unproductive low biomass ecosystems. The effects of reduced light arising from N pollution can be as important to mosses as direct toxicity from N deposition. Yet, different sensitivities of mosses to both toxic and shading effects of elevated N prevent generalisation and can lead to competitive species replacement within moss communities. This study

demonstrates the importance of understanding moss-vascular plant interactions to allow interpretation and prediction of ecosystem responses to anthropogenic drivers such as atmospheric N deposition or climate change.

**Keywords** Competition · Light · Montane · Mosses · Nitrogen enrichment

### Introduction

Mosses and vascular plants co-occur in a wide range of habitats across the world, yet our understanding of their interactions remains limited. This lack of mechanistic understanding hinders our ability to interpret and predict the responses of mosses to anthropogenic drivers such as climate change (Press et al. 1998) and nitrogen (N) deposition (Vitousek et al. 1997; Aerts and Bobbink 1999). In this paper we investigate whether such drivers are directly detrimental to mosses, or if their impact is mediated through effects on vascular plants. Developing our understanding of these interactions is critical given the major role played by mosses in many of the world's biomes (Zimov et al. 1995; O'Neill 2000; DeLuca et al. 2002; Van der Wal and Brooker 2004).

The response of vascular plants and mosses to environmental drivers may be very different. For example, an increase in N availability may assist vascular plants in overcoming nutrient limitation (Tilman 1988), but mosses are rarely limited by nutrients (Bergamini and Peintinger 2002). Their minimal nutritional requirements are readily fulfilled by the direct uptake of dissolved nutrients from the atmosphere over the whole shoot and leaf surface, a feature which appears to make mosses very sensitive to the direct impacts of N deposition (Lee 1998; Proctor 2000). The combination of low nutrient requirements and limited overlap in resource acquisition niche means that the ability of vascular plants to influence mosses by constraining nutrient uptake is limited.

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However, mosses are potentially vulnerable to competition for light as they are generally smaller than vascular plants. Several studies have indeed established negative relationships between moss abundance and vascular plant biomass (Virtanen et al. 2000; Bergamini et al. 2001) suggesting that, despite their generally low values for light compensation (Proctor 2000), light can become a limiting resource for mosses growing beneath a dense cover of vascular plants. Field experimental studies commonly demonstrate that the increase of vascular plant biomass with nitrogen addition causes a reduction in light penetration to the lower strata of the vegetation (Tilman 1988; Huisman et al. 1999a; Van der Wal et al. 2000). Such studies have led to the prediction that, whereas growth of vascular plants in communities along productivity gradients can be co-limited by light and nitrogen (Belcher et al. 1995), growth of mosses is limited by light availability alone (Kull et al. 1995).

Atmospheric N deposition has modified ecosystems throughout the world (Jefferies and Maron 1997; Vitousek et al. 1997). An increase in vascular plant productivity due to atmospheric N deposition may therefore increase canopy closure in a whole range of habitats where vascular plants were N-limited, restraining plants of short stature such as mosses. Thus, N deposition studies provide us with an opportunity to investigate competition for light between vascular plants and mosses, whilst scaling its relative importance to the direct toxic effects of excess N (Bergamini and Pauli 2001; Bergamini and Peintinger 2002; Van der Wal et al. 2003). Although these direct toxic effects of atmospheric N deposition on mosses might need little verification (Woodin and Lee 1987; Morecroft et al. 1994; Carroll et al. 2000; Gordon et al. 2001; Pearce et al. 2003), indirect effects such as reduced light availability have received only limited attention.

In the present study we aim to determine the importance of reduced light conditions as an indirect effect of N deposition on mosses. Our study system is a moss-dominated montane heath where sedges and grasses increase in abundance under conditions of enhanced N deposition (Pearce and Van der Wal 2002; Van der Wal et al. 2003). We tested the hypothesis that resultant low light levels contribute to the decline of montane heath dominated by the moss *Racomitrium lanuginosum* and trigger its replacement by other mosses, putting at risk a habitat of great conservation value (Thompson and Brown 1992; Bunce et al. 1999). Under controlled conditions, we determined the relative importance of N addition and low light availability to the performance of three moss species commonly co-occurring in montane habitats across Europe.

## Materials and methods

### Study system

The study was conducted on Glas Maol, an unproductive and exposed mountain summit plateau (1,068 m

a.s.l.) in the Grampian Mountains, near Braemar, NE Scotland (56°53'N, 3°22'W). The habitat is classified as *Carex bigelowii*–*R. lanuginosum* montane heath (Rowdwell 1992), a community found on mountain summits at relatively high latitude and oceanicity. Within the UK, only Scotland currently harbours extensive *Racomitrium* heath, but past evidence suggests an extensive distribution in northern England and Wales, although the sites here are now dominated by grass communities (Eddy et al. 1969; Thompson and Baddeley 1991; Bunce et al. 1999). The plateau of Glas Maol is largely dominated by the sedge *C. bigelowii* (Torrey ex. Schweinitz) occurring at a wide range of densities, either interspersed or with the mosses *R. lanuginosum*, *Dicranum fuscescens* and *Polytrichum alpinum* underneath. Other widespread cryptogams include *Pleurozium schreberi*, *Ptilidium* spp. and *Cladonia* spp.. Grass species *Deschampsia flexuosa*, *Festuca vivipara*, *F. ovina* and *Agrostis capillaris* are scattered and gradually replace *C. bigelowii* with decreasing altitude. Forbs, of which *Galium saxatile* and *Vaccinium myrtillus* are the most widespread, are only locally abundant. The plateau is subject to modest cryoturbation over winter, has a cool oceanic climate and receives relatively high levels of precipitation, both as rainfall and occult deposition. N deposition levels, corrected for altitudinal occult deposition, are estimated as 12–18 kg N ha<sup>-1</sup> year<sup>-1</sup> (Pearce and Van der Wal 2002; Pearce et al. 2003), which is towards the lower end of the recorded British range.

### Study species

*Racomitrium lanuginosum* (Hedw.) Brid. (hereafter referred to as *Racomitrium*) is a relatively tall (up to 10 cm in the study system) pleurocarpous moss with a very wide bipolar distribution, becoming montane further towards the equator. Within the UK it is a common species occurring largely in unproductive sites, particularly over rock, from near sea level to mountain summits where it can form extensive mats and occur as *Racomitrium* heath. The long hairs at the leaf tip (hence the common name woolly-hair moss) of this ectohydric and highly desiccation-tolerant species facilitate interception of rain droplets and occult deposition.

*Dicranum fuscescens* Sm. (hereafter referred to as *Dicranum*) is an acrocarpous moss with a circumboreal distribution occurring in a wide range of habitats, from sheltered woodland on logs and trees to exposed mountain sites. Here it forms turfs which are shallower and generally more compact than those formed by *Racomitrium*. *Dicranum* is predominantly ectohydric, but it lacks specialised morphological structures that assist in capturing and retaining water.

*Polytrichum alpinum* Hedw. (hereafter referred to as *Polytrichum*) is a tall acrocarpous moss with a very wide bipolar arctic–alpine distribution, found on upland heaths and moorland but most commonly in montane habitats. It forms very loose distinct tufts. The species is

endohydric, having well differentiated internal water conducting tissues. A protective cuticle is present. Part of the water and nutrient transport takes place via rhizoids, which also anchor the moss to the substrate. Information drawn from Smith (1978), Hill et al. (1992) and Shaw and Goffinet (2000).

#### Field observational study: moss abundance in relation to light availability and graminoid litter

To determine the effects of graminoid cover on light availability and the abundance of mosses, 60 plots were selected across the plateau of Glas Maol in late August 2002. To ensure full coverage of the plateau (350×450 m), six regularly spaced plots (10×10 cm) were placed along each of ten transects. Actual sampling locations of the 60 plots were determined by pacing out the required distance between two plots and subsequently throwing a thin metal frame over the shoulder. Reselection of plots took place on few occasions, and only when the frame landed on ground with >10% rock. Live and dead graminoid cover for each plot was estimated visually by a consensus between two observers. Light levels were recorded by measuring photon flux density with a fibre optic probe with PAR sensor filtering (Skye SKP 210S) directly above (1× per plot) and below (4×) the graminoid canopy, on top of the moss layer. Light extinction was calculated as the percentage of full light that did not reach the moss layer. Measurements were taken between 1100 and 1500 hours under relatively stable light conditions with photon flux density above the graminoid canopy averaging  $44.5 \pm 2.2$  (SE)  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Light quality (red to far-red ratio) has not been considered in this study. Subsequent to cover and light recordings, the full 10×10 cm section of the sward was harvested and sorted in the lab. The decomposing layer underneath the mosses was removed, and remaining moss tissue and graminoid litter and standing dead material above the moss layer was weighed after drying plant samples to stable weight at 60°C. *Racomitrium*, *Dicranum* and *Polytrichum* were the only abundant mosses in the samples, although small amounts of liverworts and *P. schreberi* were also found.

#### Field experimental study: *Racomitrium* performance under reduced light levels

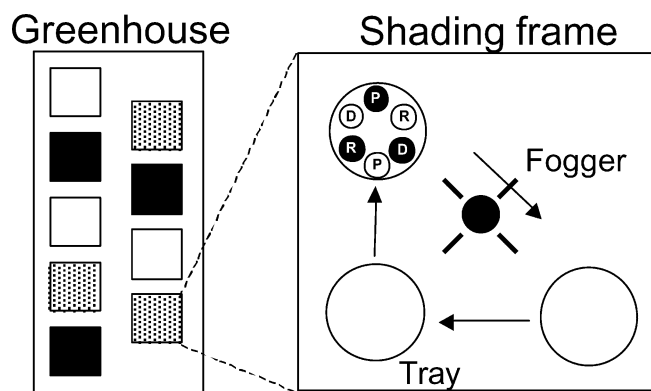
A shading experiment was established on the summit of Glas Maol in spring 2001 to investigate the effect that reduced levels of light has on *Racomitrium* performance in the field. Locations within the moss heath that were dominated by an open *Racomitrium* mat with no vascular plant canopy cover, were identified and plots chosen at random within these locations. Light availability was manipulated by placing semi-spherical plastic shading frames (25 cm diameter ×14 cm height) over 20-cm diameter plots of *Racomitrium*. A gap of 5 cm be-

tween the bottom edge of the frame and the top of the vegetation enabled air circulation. The frames were arranged in blocks of four treatments; three light reduction treatments consisting of either a single, double or triple layer of shading cloth covering the frame, and an uncovered frame as a control. There were six replicate blocks spread out across the plateau. Light reduction was estimated by taking three photon flux density readings above and inside each frame with light extinction calculated as the difference between the two averages. Measurements were made for each frame over four visits and under different weather and light conditions. Light reductions for the four treatments were calculated as 16% for control cages and 53, 71, and 81% for the increasing shading layers respectively.

We have no evidence suggesting that the shading material influenced hydration status of the moss, as no differences in shoot water content (mean of eight random shoots per plot, six sampling rounds) were observed among treatments ( $F_{3,16} = 0.17$ ,  $P > 0.9$ ). The cages were out in the field between the beginning of June and end of August in both 2001 and 2002. At the end of August 2002, the depth of the *Racomitrium* mat was estimated as the average of ten moss depth measurements taken for each plot.

#### Greenhouse experimental study: moss performance under reduced light and elevated N

A greenhouse experiment was carried out during winter 2001/2002 to scale the importance of reduced light availability relative to direct toxic N deposition effects for three moss species. To manipulate light available to the mosses nine shading frames were erected on benches inside the greenhouse, representing three replicate sets of three light treatments: full light, 60% light reduction and 80% light reduction (Fig. 1). Underneath each frame



**Fig. 1** Lay-out of the greenhouse experiment (left-hand panel) showing the distribution of the replicate shading frames at a given day for the treatments full light (white), 60% light reduction (grey) and 80% light reduction (black). Underneath each shading frame (right-hand panel) were three trays, each with two full sets of mosses (*R. lanuginosum*, *D. fuscescens*, *P. alpinum*) of which one set received the equivalent of  $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$  (white) whilst the other set received  $20 \text{ kg N ha}^{-1} \text{ year}^{-1}$  (black)

were placed three replicate trays, each containing two sets of three pots with either *R. lanuginosum*, *D. fuscescens* or *P. alpinum*; the first set receiving low N additions, and the second set subjected to elevated N additions. N addition treatments were applied as  $\text{KNO}_3$  at rates equivalent to either  $10 \text{ kg ha}^{-1} \text{ year}^{-1}$  to represent background deposition in the field, or  $20 \text{ kg ha}^{-1} \text{ year}^{-1}$  representing an elevated N deposition level also applied in the long-term field experiment. Solutions were sprayed once a week as a fine mist using a hand-held sprayer at concentrations of either 4.28 mM (background level) or 8.56 mM (elevated level). The total number of individual pots with moss equalled 3 species  $\times$  2 N levels  $\times$  3 replicate trays  $\times$  3 light treatments  $\times$  3 replicates per light level = 162.

Reductions in light availability were provided by either a single or double layer of shade netting on the top and sides of the shading frames (85 $\times$ 85 $\times$ 55 cm height), leaving an unobstructed air gap of 10 cm at the bottom of the sides. Halogen lamps were suspended above each frame to provide uniform irradiance levels and also extend day length, thus maintaining conditions consistent with the montane summer photoperiod. The halogen lamps fully compensated the reduction in light due the greenhouse structure, hence providing the mosses with a light regime that was on a par with outside conditions. To avoid the possibility of differential dehydration among treatments caused by both daylight and supplementary halogen lamps, a transparent spectrum neutral filter (130 Clear; Lee filters, Andover) cutting out < 6% of the incoming irradiance covered each shading frame. To avoid complications due to heterogeneity of environmental conditions within the greenhouse the shading frames and their respective trays with pots of mosses were moved to a random bench position every week. Temperature build-up under the shading frames was prevented by enhancing air circulation with two ventilators placed at bench height at both ends of the greenhouse. Temperature profiles recorded every 30 min over 25 days (HOBO-H8 temperature loggers) demonstrated a close match between the treatments, with identical patterns at the lower temperature range, but slight differences with respect to elevated temperatures. Average temperatures therefore were highest in the full light treatment ( $11.8^\circ\text{C} \pm 4.4 \text{ SD}$ ), followed by the 60% ( $10.9 \pm 4.2^\circ\text{C}$ ) and 80% light reduction treatments ( $10.5 \pm 4.0^\circ\text{C}$ ). We expect that these differences are too small to have influenced our measurements of moss growth (Uchida et al. 2002). For the years 1998–2001 the mean monthly temperature (June–August) on Cairn Gorm (1,245 m, 57°N, 3°W), a nearby mountain top with a similar aspect to Glas Maol, was  $8.25 \pm 0.82^\circ\text{C}$  (Department of Physics, Heriot Watt University, Edinburgh, <http://www.phy.hw.ac.uk/resrev/aws/weather.htm>). Given that Glas Maol summit has an altitude of 1,068 m a.s.l., and that the lapse rate is approximately  $1^\circ\text{C}$  for a 200 m change in altitude, our greenhouse temperature regime approaches the predicted mean summer temperature in the field.

Mosses were collected from large homogeneous patches on Glas Maol and allowed to acclimatise for 1 week before being placed as single species stands in 7 cm high, 4 cm diameter pots. These were half filled with mineral sand on which parts of the collected moss mats were placed at natural density. To prevent low water potentials in *Polytrichum*, the only endohydric moss, shoots of this species were kept wet by partly filling the pots with distilled water. All mosses were kept moist during most of the day by spraying a fine mist of distilled water from overhead foggers (Fig. 1) connected to a pressurised and automated water supply system. Trays underneath each shading frame were moved round one position each day to avoid potential effects of differences in water supply among pots. Ten shoots of the respective species had their lower sections removed to leave 4-cm lengths, and these were bundled together and placed in the centre of each pot at the onset of the experiment. The moss bundles were retrieved after 9 weeks, and tissue in excess of the initial 4 cm was measured, cut off and weighed after drying to stable weight at  $60^\circ\text{C}$ .

#### Field experimental study: N deposition effects on moss cover

An N loading experiment was initiated in 1998, simulating an increase in wet atmospheric deposition in the form of pollution episodes. Two forms of N solution,  $\text{KNO}_3$  and  $\text{NH}_4\text{Cl}$  were applied to 0.6 $\times$ 0.6 m plots as a fine mist using a handheld sprayer. Although the long-term experiment includes treatments representing both low ( $10 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) and high ( $40 \text{ kg ha}^{-1} \text{ year}^{-1}$ ) levels of N deposition, in this study we made use only of the low  $\text{KNO}_3$  treatments and distilled water controls to allow comparison with the  $\text{KNO}_3$  addition treatments in the greenhouse experiment (see Pearce and Van der Wal 2002 and Pearce et al. 2003 for full details of the experimental design, and effects of high N loading). Treatments were applied 3–6 times between July and August of each year (1998–2002). The percentage cover of *Racomitrium*, *Dicranum* and *Polytrichum* was estimated after 5 years of experimental treatment in the first week of September 2002. For this we employed pin-frame recording with 120 hits per plot, documenting both first (canopy) and second (ground layer) intercepts.

#### Statistical analyses

All data were analysed in SAS for windows v8. Regression analyses involved fitting a generalised linear model to the data by maximum likelihood estimation of the parameters through an iterative fitting process (Genmod procedure in SAS). Significance levels were derived from a  $\chi^2$  distribution as the change in  $-2\log$  likelihood of the model after inclusion of a parameter relative to the change in degrees of freedom. Specifically, the relationship between light extinction and graminoid

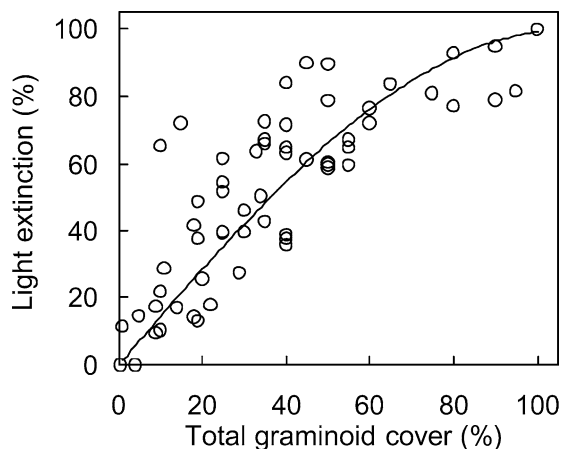
cover was forced through the zero intercept, and assumed normal distribution and employed an identity link function. Analyses of the biomass of different moss species (where present) in relation to either light extinction or graminoid litter employed log-link functions and assumed normal distributions, except for *Polytrichum* vs. graminoid litter. Here, a Poisson distribution was used, as the variance was proportional to the mean. Analyses of the greenhouse, field light manipulation and N-addition field data were carried out using linear mixed models, which included both fixed and random effects (Mixed procedure in SAS). Data were log-transformed where appropriate, and the residual variances were modelled as constant to the mean. In both field experiments, the different blocks of treatment were modelled as a random effect. Both shading frame and replicate tray nested within each shading frame were modelled as random effects in the greenhouse experiment. Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell et al. 1996).

## Results

Field observational study: moss abundance in relation to light availability and graminoid litter

The amount of light the moss layer received in the field was strongly and negatively related to the combined abundance of sedges and grasses (i.e. graminoids;  $\chi^2 = 141.47$ ,  $n = 60$ ,  $P < 0.0001$ ), with substantial light extinction already occurring at 50% graminoid cover (Fig. 2).

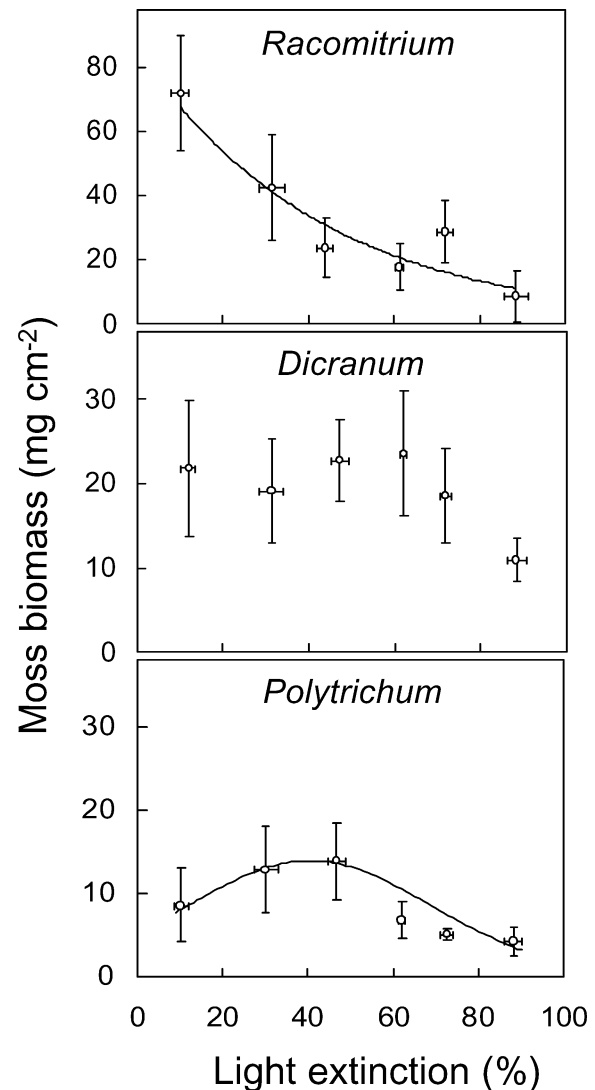
Different relationships between moss abundance and light availability under the vascular plant canopy in the field were found for each of the three moss species studied (Fig. 3). *Racomitrium* biomass was negatively related to light extinction ( $\chi^2 = 12.24$ ,  $n = 39$ ,  $P < 0.001$ ), reaching high biomass only when the moss layer received ample light. For *Dicranum* no significant relationship could be detected between its biomass and the amounts



**Fig. 2** The percentage of light extinguished by the vascular plant canopy measured in a montane heath in relation to the estimated percentage cover of graminoids (live and dead)

of light reaching the moss layer ( $\chi^2 = 1.56$ ,  $n = 57$ ,  $P > 0.2$ ), suggesting a greater tolerance to low light levels than *Racomitrium*. Data on *Polytrichum* biomass indicate greatest local abundance at intermediate levels of light extinction, resulting in a slight unimodal relationship (light extinction:  $\chi^2 = 2.92$ ,  $n = 31$ ,  $P > 0.08$ ; light extinction<sup>2</sup>:  $\chi^2 = 3.91$ ,  $P < 0.05$ ).

Analogous patterns were observed when relating moss abundance on Glas Maol to quantities of graminoid litter present (data not presented). *Racomitrium* biomass was found to rapidly decrease with increasing amounts of graminoid litter ( $\chi^2 = 58.26$ ,  $n = 39$ ,  $P < 0.0001$ ), suggesting a tighter fit with graminoid litter than with light interception. No such dramatic decline with increased graminoid litter was observed for *Dicranum* over the range in which *Racomitrium* showed a response. Although the data across the whole range of litter quantities may suggest a pattern of decreasing *Dicranum* biomass with increasing litter, this trend was



**Fig. 3** The abundance of the mosses *R. lanuginosum* **a**, *D. fuscescens* **b** and *P. alpinum* **c** in a montane heath in relation to the amount of light extinguished by the vascular plant canopy

only marginally significant ( $\chi^2 = 3.23, n = 57, P = 0.07$ ). No significant relationship could be established between graminoid litter and *Polytrichum* biomass ( $\chi^2 = 1.72, n = 31, P > 0.18$ ).

Field experimental study: *Racomitrium* performance under reduced light levels

The shading experiment conducted in the field confirmed the sensitivity of *Racomitrium* to reduced light availability ( $F_{3,15} = 3.93, P < 0.05$ ). After two subsequent summers of treatment, the average depth of the moss layer was shallower in shaded plots ( $48 \pm 4$  mm) compared to the high light controls ( $57 \pm 4$  mm;  $F_{1,15} = 11.63, P < 0.005$ ). However, there was no effect ( $P > 0.7$ ) of increasing layers of shading cloth on depth of the moss layer despite the marked decrease in *Racomitrium* biomass with increasing light extinction seen in the observational study (Fig. 3).

Greenhouse experimental study: moss performance under reduced light and elevated N

All three moss species responded differently to the combination of elevated N and reduced light imposed on them in the greenhouse experiment (Fig. 4). *Racomitrium* growth was strongly constrained by both N addition ( $F_{1,21} = 6.50, P < 0.02$ ) and shading ( $F_{2,6} = 11.54, P < 0.01$ ). Shading resulted in a 53 and 58% lower shoot growth in the 60 and 80% light reduction treatments, respectively. Shoots receiving full light had 44% lower biomass when receiving elevated N loads. The negative effects of shading and elevated N appeared additive, as the interaction term was not significant ( $F_{2,21} = 1.87, P > 0.17$ ). In combination, shading and elevated N reduced *Racomitrium* growth by 76%.

Shoot growth of *Dicranum* was only marginally influenced by elevated N additions ( $F_{1,24} = 3.55, P = 0.07$ ), with a tendency of only having negative impact when shaded (N  $\times$  shading:  $F_{2,24} = 3.10, P = 0.06$ ). Their combined effect, though not significant, caused a 19% growth reduction. Shading alone did not influence the shoot growth of *Dicranum* ( $F_{2,6} = 0.54, P > 0.6$ ).

Shoot growth of *Polytrichum* was not influenced by elevated N ( $F_{1,26} = 0.11, P > 0.7$ ) but was greatly reduced by shading ( $F_{2,4} = 45.72, P < 0.005$ ), leading to a 14 and 40% growth reduction in the 60 and 80% light reduction treatments respectively. The impact of shading was not dependent on N addition level (N  $\times$  shading:  $F_{2,26} = 0.04, P > 0.9$ ).

Field experimental study: N deposition effects on moss cover

All three moss species responded differently to N additions in the field (Table 1). *Racomitrium* cover was

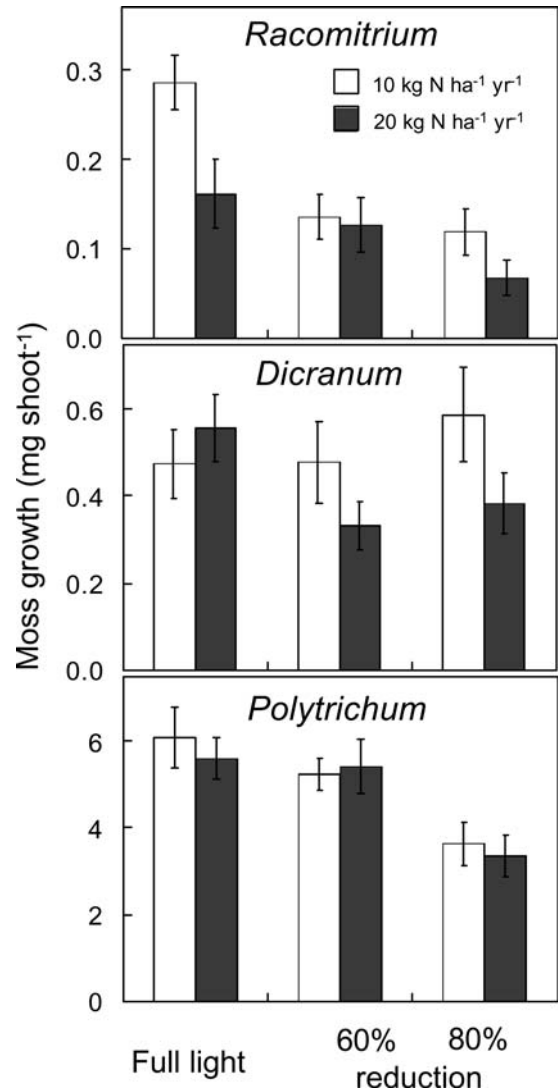


Fig. 4 The performance of the montane mosses *R. lanuginosum* a, *D. fuscescens* b and *P. alpinum* c in a greenhouse experiment in relation to light reduction (three levels) and N loading (two levels—background, and elevated N)

Table 1 The abundance of three montane mosses in field experimental plots subject to background (control) or elevated (10 kg ha⁻¹ year⁻¹) levels of N (added as KNO₃) for 5 years. Significant differences between control and treated plots have a P value in bold

Species	Percentage ground cover		F <sub>1, 9</sub>	P
	Control	10 kg N ha⁻¹ year⁻¹		
<i>R. lanuginosum</i>	71.0 (4.6)	52.3 (6.2)	10.52	<b>0.010</b>
<i>D. fuscescens</i>	8.2 (3.3)	13.8 (3.6)	5.72	<b>0.041</b>
<i>P. alpinum</i>	12.0 (4.0)	16.3 (4.6)	1.82	0.211

found to be 19% lower in plots that received additional N (10 kg N ha⁻¹ year⁻¹) for 5 years. The reverse was found for the less-prevalent *Dicranum*, which had 5% greater cover in N treated plots relative to the untreated controls. Longer-term N additions did not significantly influence the cover of *Polytrichum*.

## Discussion

### Struggle for light: impact of canopy closure

Competition theory has predominantly been applied to patterns of distribution and change in vascular plants. However, it may need revision before application to interactions between vascular plants and lower plants for two reasons in particular. First, whereas competition for nutrients between vascular plants is largely seen as symmetric (Weiner 1990), this is unlikely to be the case for nutrient competition between vascular plants and cryptogams (mosses and lichens). Both lichens and mosses may constrain vascular plant growth by intercepting and sequestering nutrients from atmospheric deposition (Jónsdóttir et al. 1995; Li and Vitt 1997), or influence soil nutrient availability indirectly by the production of low quality litter (Hobbie 1996) and the maintenance of unfavourably low soil temperature and high moisture conditions (Zimov et al. 1995; Van der Wal and Brooker 2004). Yet, the degree to which vascular plants constrain nutrient uptake in cryptogams may be limited, as the latter group lacks functional roots and thus do not overlap at the site of nutrient capture.

Second, competition theory predicts a qualitative shift from competition for soil resources at low productivity to competition for light at high productivity (Newman 1973; Grubb 1985; Tilman 1988; Huisman et al. 1999a). However, due to their low stature, cryptogams are prone to asymmetric competition for light, and thus may already show reduced growth at relatively low productivity. For instance, experimental studies in a wide range of unproductive Arctic and subarctic ecosystems demonstrated clear negative relationships between abundance of macro-lichens and vascular plants (Cornelissen et al. 2001). Also, competition for light was found to limit the performance of individual moss shoots in colonies of bryophytes under a wide range of densities and humidity conditions (Pedersen et al. 2001).

Our findings indicate that asymmetric competition for light induced by vascular plants can strongly influence the dominance of moss species present in the unproductive montane study system. *R. lanuginosum* develops high biomass swards only under conditions of relatively unrestricted light availability, i.e.  $\leq 25\%$  graminoid cover, implying that any greater vascular plant cover is likely to impinge on the abundance of the moss. The shading experiment conducted in the field confirmed the sensitivity of *Racomitrium* to reduced light levels as the presence of shading cages for only 3 months in two subsequent summers was sufficient to generate a reduction of *Racomitrium* moss layer depth. The fact that increasing layers of shading cloth did not influence moss depth further might be attributed to the short duration of the experiment compared to the permanently established canopy of the natural habitat. The biomass of *P. alpinum* was also constrained by low-light conditions, but appeared less sensitive than *Racomitrium*. In contrast,

biomass accumulation in *D. fuscescens* did not relate to light availability, a finding which connects to its widespread occurrence in relatively low-light environments such as deciduous and spruce forests. That light is a limiting resource in this unproductive environment, where live vascular plant standing crop does not exceed  $100\text{--}200\text{ g m}^{-2}$  (see also Bardgett et al. 2002) may be surprising as this is below the suggested level of  $200\text{--}600\text{ g m}^{-2}$  over which a shift from nutrient to light competition is predicted (Belcher et al. 1995). This may indeed suggest that competition theory developed on interactions between vascular plants may not be directly applicable to cryptogams. Alternatively, the apparent struggle of mosses for light at relatively low site productivity could be related to specific traits of the dominant vascular plant *C. bigelowii*, which produces large quantities of litter of a relatively recalcitrant nature. The observation that *Racomitrium* biomass had a tighter relationship with graminoid litter than with light extinction is in support of this notion. Yet, smothering effects of graminoid litter were not observed in *Dicranum* or *Polytrichum*. The latter species was observed to grow tall enough to avoid being buried under graminoid litter, and incidental *Carex* litter was absorbed by the relatively open *Polytrichum* swards, resulting in greater amounts of litter within the sward than on top. These findings suggest that it is unwise to group all mosses together as a single functional type, i.e. their response to perturbations is more species specific than we perhaps assume.

Changes in graminoid cover will not only influence the light, but also temperature and moisture regimes experienced by mosses growing underneath. Although there may be some beneficial influence of the vascular plant canopy on *Racomitrium* by improving both the moisture and temperature regimes, these effects are evidently outweighed by the negative impact of light reduction. As evidence for this we see that *Racomitrium* growth is reduced at all levels of shading or graminoid cover. There is no evidence of a reduction in the impact of increasing light extinction, which we would expect if facilitative effects were counterbalancing the negative shading impacts. Therefore, for *Racomitrium*, the impact of reduced light levels is clearly far stronger than any possible benefits of an improved moisture or temperature regime beneath a canopy. However, whilst *Dicranum* is unaffected by light extinction, there appears to be an optimum graminoid cover for *Polytrichum* with greatest biomass of this species at around 40% light extinction. Although this relationship may be driven by the beneficial moisture effects of graminoid cover, *Polytrichum* is endohydric and so would be even less responsive to beneficial moisture regime impacts than *Racomitrium* or *Dicranum*. A possible beneficial temperature effect of *Carex* cover cannot be ruled out. However, another mechanism may also be operating, namely competition from *Racomitrium* restricting *Polytrichum* to intermediate light levels where *Racomitrium* becomes competitively inferior. Similarly, the increased

cover of *Dicranum* following N additions in the field may be due to reduced competitive ability of *Racomitrium*. Little is known about the relative competitive ability of mosses, and the factors that control moss dominance hierarchies. These relationships indicate the need for a more detailed consideration of the dynamics of moss communities.

Light competition is a conceptually complex subject and predicting the outcome of competition for light remains a major challenge (Tilman 1990). Based on phytoplankton experiments, Huisman et al. (1999b) predict that the species with the lowest critical light intensity should competitively displace all other species. Yet, in more recent work the same authors reach the conclusion that the outcome of multispecies competition involving light as a limiting resource can be fundamentally unpredictable (Huisman and Weissing 2001). A critical issue in terrestrial ecosystems is the strong spatial and temporal heterogeneity of light, which allow plants of short stature to proliferate in transient gaps or use the opportunity to grow early in the year before canopy closure. We conclude that vascular plants may be able to reduce light availability in unproductive ecosystems to levels low enough to strongly influence the performance of individual moss species, potentially influencing competitive replacement among mosses.

Although montane heath characteristically supports up to 50% graminoid cover (McVean and Ratcliffe 1962) with *Racomitrium* and higher plants often co-dominant, only 2 years of N addition to *Racomitrium* heath were sufficient to alter community composition, causing graminoids to reach 70% cover compared to only 40% in control plots (Pearce and Van der Wal 2002). Such an elevated cover of graminoids from N deposition is predicted to cause over 80% light extinction (Fig. 2), which corresponded with minimal *Racomitrium* biomass in the field (Fig. 3). This clearly demonstrates the threat of low light availability for lower plants under increased canopy cover from N enrichment. Analysis of temporal change in the abundance of mosses in unproductive environments subject to continued atmospheric deposition of N could provide a fruitful route to further develop our understanding of interactions between vascular plants and mosses.

#### Struggle for existence: coping with reduced light and elevated N loading

Vascular plants in general, and graminoids in particular are very successful at capturing additional N of anthropogenic origin (Jefferies and Maron 1997; Zogg et al. 2000; Dormann and Woodin 2002). It therefore has been frequently suggested that poor performance of mosses under conditions of elevated N is due to light interception by an expanding vascular plant canopy (Dirkse and Martakis 1992; Mäkipää 1998; Virtanen et al. 2000; Bergamini and Pauli 2001), in

addition to the direct toxic effects of N. Yet, there are only a few studies in which the relative importance of these direct and indirect N deposition effects has been established, and the findings are widely divergent.

Manipulation of both N deposition and light in a greenhouse study demonstrated that both factors had equally strong impacts on the performance of *R. lanuginosum* (Van der Wal et al. 2003). Short-term field experiments in a Swiss calcareous wet meadow determined a strong morphological branching response of the moss *Calliergonella cuspidata* to light but not N supply (Bergamini and Peintinger 2002), but these differences in branching did not translate to changes in overall shoot biomass. A third experiment, again conducted in the greenhouse, failed to find any significant response in *D. majus* to either increased N supply (3.8–42.3 kg ha<sup>-1</sup> year<sup>-1</sup>) or shading, but showed a tendency for reduced performance at high irradiance levels (Bakken 1995). The wide range of responses of mosses to the combined effects of reduced light and elevated N may reflect species-specific responses, but could also have resulted from differences in experimental design.

In this study we have demonstrated that, whilst keeping experimental conditions tightly controlled, the full range of responses to light reduction and elevated N reported in the literature can be detected in different moss species. We found that *Racomitrium* performance was under strong influence of both light reduction and N addition, in combination reducing shoot biomass up to 76%. No response to either factor was observed in *Dicranum*, whereas *Polytrichum* was insensitive to elevated N but strongly responsive to low light levels, reducing its performance up to 40%. Differential sensitivity among mosses to the direct, toxic effects of elevated N is likely to be related to their specific ability to intercept precipitation of different forms, and to maintain positive water status allowing photosynthesis and net carbon gain. Greater tolerance to N pollution of *Polytrichum* is in line with earlier findings for related species (reviewed in Bates 2000) and may be due to the fact that members of this family all have a protective cuticle and an internal water transport system. The lack of a water-proof cuticle in ectohydric species, such as *Racomitrium* and *Dicranum*, allows a moist surface for deposition of nitrogenous and other potentially toxic compounds and free access to the cells (Bates 2000). The high surface area of *Racomitrium* in particular, renders the species highly efficient at trapping rainfall and especially occult moisture. The importance of the latter source of precipitation increases with latitude, and can be several times as much as the volumes of rainfall. Concentrations of nitrogenous compounds, however, are also substantially higher in occult deposition than in rainfall (Fowler et al. 1988; Pearce et al. 2003). Therefore, effective interception of occult deposition, which may have provided montane mosses with a selective advantage in the past, may now have become disadvantageous and trigger competitive replacement, favouring those species that minimise pollutant loading.

We conclude that competition for light, induced by vascular plants, can strongly influence moss performance already in unproductive, low biomass ecosystems. The effects of reduced light arising from N pollution can be as important to mosses as direct toxic N-deposition effects. Yet, differential sensitivity to both toxic and shading effects of elevated N prevent generalisation, and can lead to species replacement within moss communities subject to N deposition.

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