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Direct uptake of soil nitrogen by mosses

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Mosses are one of the most diverse and widespread groups of plants and often form the dominant vegetation in montane, boreal and arctic ecosystems. However, unlike higher plants, mosses lack developed root and vascular systems, which is thought to limit their access to soil nutrients. Here, we test the ability of two physiologically and taxonomically distinct moss species to take up soil- and wet deposition-derived nitrogen (N) in natural intact turfs using stable isotopic techniques (^{15}N). Both species exhibited increased concentrations of shoot ^{15}N when exposed to either soil- or wet deposition-derived ^{15}N, demonstrating conclusively and for the first time, that mosses derive N from the soil. Given the broad physiological and taxonomic differences between these moss species, we suggest soil N uptake may be common among mosses, although further studies are required to test this prediction. Soil N uptake by moss species may allow them to compete for soil N in a wide range of ecosystems. Moreover, since many terrestrial ecosystems are N limited, soil N uptake by mosses may have implications for plant community structure and nutrient cycling. Finally, soil N uptake may place some moss species at greater risk from N pollution than previously appreciated.

Keywords: atmospheric nitrogen deposition; bryophytes; moss; *Polytrichum alpinum*; *Racomitrium lanuginosum*; soil nitrogen uptake

1. INTRODUCTION

Over 10 000 moss species (phylum Bryophyta) have been described, making them the second most diverse group of plants (Buck & Goffinet 2000). Mosses occur in ecosystems from the tropics to high latitudes and generally dominate montane, boreal and arctic plant communities where they can strongly influence nitrogen (N) cycling (DeLuca *et al.* 2002). N is the limiting factor of net primary productivity in many terrestrial ecosystems, particularly in temperate and boreal regions (Vitousek & Howarth 1991). Most plants derive N principally from the soil (Chapin *et al.* 2002). However, unlike higher plants, mosses lack root and developed vascular systems, which is thought to limit their access to soil nutrients and transport to shoots; instead, atmospheric deposition has traditionally been considered their major nutrient source. While it has been suggested that mosses may use soil N (Van Tooren *et al.* 1990), this has not been demonstrated conclusively. We measured soil- and wet deposition-derived N uptake in two coexisting and common, but physiologically and taxonomically distinct, moss species via ^{15}N labelling. *Polytrichum alpinum* (class Polytrichospida) is predominantly endohydric, transporting water up from underlying substrate by means of water-conducting hydroids (Longton 1988; Buck & Goffinet 2000), whereas *Racomitrium lanuginosum* (class Bryopsida) is ectohydric and mostly absorbs water from precipitation (Proctor 1982; Buck & Goffinet 2000). Because moss nutrient acquisition is thought to relate to the pattern of water uptake (Buch 1945, 1947) we hypothesized that *P. alpinum* would take up dissolved N from the underlying substrate, whereas no uptake was predicted for *R. lanuginosum*.

2. MATERIAL AND METHODS

In August 2004, 20 moss turfs ($5\times 5\times 2$ cm deep), 10 dominated by *R. lanuginosum* and 10 by *P. alpinum*, were collected from the summit of Glas Maol, Scotland ($56°53'$ N, $3°22'$ W; 1060 m elevation). The field site lies within the Caenlochan Site of Special Scientific Interest that supports numerous arctic and alpine plant communities. The plant community on the summit is mostly *R. lanuginosum–Carex bigelowii* moss heath (Rodwell 1992), and other common species include *P. alpinum*, *Agrostis capillaris*, *Deschampsia flexuosa*, *Festuca ovina* and *Festuca vivipara*.

The turfs were transported to Lancaster University and kept in a growth chamber maintained at 15 °C with 16/8 h light/dark cycles. The turfs were placed in open, but tightly fitting, plastic bags to minimize soil drying and were sprayed with water as necessary. The turfs were covered with a well-ventilated clear plastic chamber to minimize evaporation while maintaining the air supply. Prior to labelling with ^{15}N, a subsample of moss shoot, cut 1 cm above the soil surface, was taken from each turf for analysis of ^{15}N natural abundance. The experiment had a fully factorial block design with five replicates. Half the turfs for each species received 188 µg $^{15}NO_3:{}^{15}NH_4$ (1 : 1) in 3.6 ml deionized water sprayed onto their shoots, while the other half received the same amount of ^{15}N and water injected directly into the soil. In July 2004, NO_3 accounted for 41.4±2.6% (mean±s.e., $n=35$) of the total soil inorganic N pool at the study site (E. Ayres, R. van der Wal & R. D. Bardgett 2004, unpublished work); thus our 1:1 supply of $NO_3:NH_4$ was close to field conditions. Injections were done laterally at a depth of 1 cm using a needle with four outlets so that the ^{15}N was dispersed within the soil of each turf. Soil bulk density at the field site was 0.35 ± 0.05 g cm^{-3} (mean±s.e., $n=5$); thus, the quantity of ^{15}N added was equal to 10.76 µg g^{-1} dry soil; inorganic N concentrations in the top 5 cm soil near the collection site were 13.25 ± 2.31 µg g^{-1} dry soil (mean±s.e., $n=5$). In addition, 3.6 ml deionized water was injected into the soil of the ‘sprayed’ turfs, similarly, 3.6 ml water was sprayed onto the ‘injected’ turfs. Great care was taken to avoid ^{15}N contamination between samples and within various parts of individual samples. For instance, turfs were taken individually to a separate room for spraying and the quantity of water was small enough to prevent dripping onto the soil. Furthermore, injections were done laterally, through the plastic bag, directly into the soil so that the moss shoot never came into contact with the needle.

Seven days after labelling the moss shoots were cut 1 cm above the soil surface. All moss shoots (including the natural abundance subsamples) were rinsed in 0.5 M $CaCl_2$ to remove ^{15}N adhering to their surface (Näsholm *et al.* 2001), prior to rinsing with water, drying (70 °C) and grinding for ^{15}N isotope analysis. ^{15}N concentration was determined using continuous flow ratio mass spectrometry (ThermoFinigan Delta plus Advantage linked to a Flash EA1112 Series elemental analyser). It is possible that our experimental design promoted the transport of ^{15}N from soil to shoots by enhancing rates of evapotranspiration or wicking (i.e. the convection of water to the moss surface by capillary action, driven by evaporation). However, we believe that any effect of this on N transfer would be minimal for a number of reasons. First, the turfs were covered with a well-ventilated plastic chamber to limit evaporation. Second, the ^{15}N added to the soil was injected 1 cm below the soil surface, thereby limiting the potential for transport

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via wicking. Third, the turfs were maintained at 15 °C, which is within the range of temperatures that commonly occur on the summit of Glas Maol during summer; mean (±standard deviation) temperature on Glas Maol in July–August 2004 was 10.9 (±6.5) °C.

Data were analysed using SAS for Windows v. 8.1 using generalized linear mixed models with 'experimental block' as the random effect. The models were fitted by the method of residual maximum likelihood. Denominator degrees of freedom were estimated using Satterthwaite's approximation and the residual variances were modelled as constant to the mean using PROC MIXED.

3. RESULTS

Analysis of pooled data for both species indicated that labelling significantly increased shoot ^{15}N concentration relative to natural abundance in the wet deposition ($F_{1,14}=21.59$, $p<0.001$) and soil ($F_{1,14}=4.85$, $p<0.05$) treatment. Neither species, nor the interaction between species and labelling, significantly affected shoot ^{15}N concentration in the soil treatment, demonstrating unequivocally that both moss species absorb soil N and transport it to their above ground tissue. Concentrations of soil-derived excess ^{15}N did not differ between species; however, *R. lanuginosum* absorbed more deposition-derived ^{15}N (species × N source interaction: $F_{1,12}=6.60$, $p<0.05$), and concentrations of excess ^{15}N were greatest in the wet deposition treatment ($F_{1,12}=7.16$, $p<0.001$; figure 1).

The mean (±s.e.) quantity of soil- and wet deposition-derived excess ^{15}N per turf was 7.1 (±6.2) and 77.7 (±11.2) µg in *P. alpinum* and 3.2 (±2.2) and 141.9 (±17.9) µg in *R. lanuginosum* shoots, respectively. Thus, for a given quantity of N, uptake and transport of soil-derived ^{15}N to shoots was 9 and 2% that of wet deposition-derived N for the respective species.

4. DISCUSSION

We assessed the ability of two physiologically and taxonomically distinct moss species to take up soil- and wet deposition-derived ^{15}N in natural intact turfs. Our study provides the first conclusive evidence that mosses can access soil N and transport it to their shoots. The ability to transport soil N above ground is of particular importance, since shoots typically have greater N demands due to incorporation within photosynthetic enzymes. Soil N availability in this ecosystem appears to be greater than N deposition rates during the growing season (Pearce *et al.* 2003; Morecroft *et al.* 1992). Based on annual estimates of N deposition on Glas Maol, daily rates of N deposition average 4.7–5.5 mg m^{-2} (Pearce *et al.* 2003). Whereas, mean soil N mineralization rates were 5.0–37.5 mg m^{-2} d^{-1} in 0–5 cm soil on two nearby mountaintops between May and October (Morecroft *et al.* 1992). Thus, although both moss species derived more N from wet deposition in our study, the apparent greater availability of soil N in this ecosystem suggests soils are a potentially important source of moss N. Moreover, data from field plots located near the moss turf collection site indicate that mosses are the dominant vegetation type in this ecosystem, accounting for *ca* 40% of above ground biomass; more than any other vegetation type (grasses, herbs, shrubs or lichens; E. Ayres, R. van der Wal & R. D. Bardgett 2004, unpublished work). Therefore, mosses may be significant competitors for soil N in this ecosystem, with potential consequences for plant community structure and nutrient cycling.

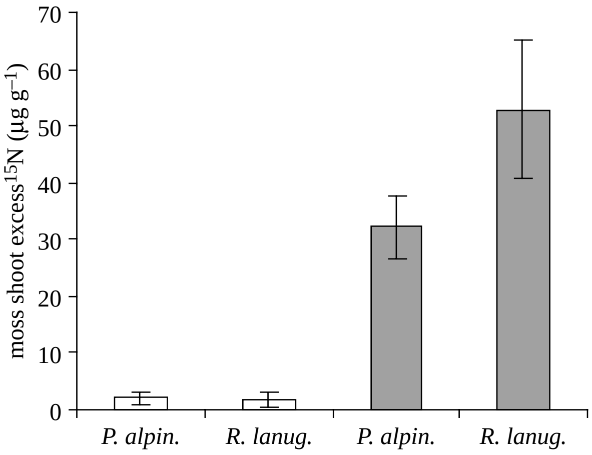

Figure 1. Shoot excess ^{15}N concentration in two moss species, *P. alpinum* (*P. alpin*) and *R. lanuginosum* (*R. lanug*), exposed to dissolved ^{15}N in soil (white bars) or wet deposition (grey bars). In both the soil and wet deposition treatment 188 µg $^{15}NO_3:{}^{15}NH_4$ (1 : 1) was added in 3.6 ml deionized water. Bars represent means ± s.e. ($n=5$).

Since both moss species had the capacity to take up N from the soil, despite their physiological and taxonomic differences, uptake of soil N may be common among mosses. Further studies are required to test this prediction; however, if soil N uptake is common among mosses then their widespread distribution and the fact that they form the dominant vegetation in many montane, boreal and arctic ecosystems, suggests mosses may be important competitors for soil N.

The uptake of soil N by mosses may also have consequences for their ability to tolerate N pollution. Many ecosystems are experiencing increased atmospheric N deposition as a result of anthropogenic activities (Vitousek *et al.* 1997). Mosses are often sensitive to N pollution (Pearce *et al.* 2003; Paulissen *et al.* 2005; Van der Wal *et al.* 2005), and the ability of mosses to take up soil N may indicate their capacity to tolerate N-pollution is lower than currently appreciated. However, moss responses to long-term fertilization often vary between species (e.g. O'Toole & Synnott 1971; Potter *et al.* 1995; Robinson *et al.* 1998; Nilsson *et al.* 2002), thus the potentially negative impacts of soil N uptake by mosses may be species specific.

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