



Five years of simulated atmospheric nitrogen deposition have only subtle effects on the fate of newly synthesized carbon in *Calluna vulgaris* and *Eriophorum vaginatum*

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ABSTRACT

To understand the implications of atmospheric nitrogen deposition on carbon turnover in peatlands, we conducted a ¹³C pulse labeling experiment on *Calluna vulgaris* and *Eriophorum vaginatum* already receiving long-term (5 years) amendments of 56 kg N ha⁻¹ y⁻¹ as ammonium or nitrate. We examined shoot tissue retention, net ecosystem respiration returns of the ¹³C pulse, and soil porewater DOC content under the two species. ¹³C fixation in *Eriophorum* leaves was enhanced with nitrogen addition and doubled with nitrate supply. This newly fixed C appeared to be relocated below-ground faster with nitrogen fertilization as respiration returns were unaffected by N inputs. By contrast, increases in ¹³C fixation were not observed in *Calluna*. Instead, net ecosystem respiration rates over *Calluna* increased with N fertilization. There was no significant label incorporation into DOC, suggesting a conservative strategy of peatland vegetation regarding allocation of C through root exudation. Greater concentrations of total DOC were identified with nitrate addition in *Calluna*. Given the long-term nature of the experiment and the high N inputs, the overall impacts of nitrogen amendments on the fate of recently synthesized C in *Eriophorum* and *Calluna* in this ombrotrophic peatland were surprisingly more moderate than originally hypothesized. This may be due to N being effectively retained within the bryophyte layer, thus limiting, and delaying the onset of, below-ground effects.

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1. Introduction

Reactive nitrogen (N) emissions from anthropogenic sources have increased by 3–5 fold over the last century (Reay et al., 2008) and are predicted to increase further in many regions during the 21st century (Galloway et al., 2004; Lamarque et al., 2005; Dentener et al., 2006; Reay et al., 2008). Most of this reactive N is deposited on terrestrial ecosystems; Lamarque et al. (2005) estimates this figure to equal 70% of total emissions. Nutrient-poor ecosystems such as ombrotrophic peatlands have adapted to low N availability, as they receive no inputs from fertilizer or external sources of N other than from precipitation; this makes them potentially vulnerable to rising levels of atmospheric deposition of

reactive N. Most undisturbed peatlands sequester carbon (Belyea and Malmer, 2004) because carbon dioxide (CO₂) fixation and deposition of dead organic material exceeds the losses through plant and soil respiration (Raich and Tufekcioglu, 2000; Hill et al., 2007). Alterations in the carbon accumulation processes of peatlands, through for example, increased nutrient availability, could result in an increased release of carbon dioxide into the atmosphere, which in turn may increase the greenhouse effect and contribute to climate change. This has been observed in arctic heathlands (e.g. Christensen et al., 1997; Dormann and Woodin, 2002). In boreal and temperate peatlands, N additions have also been linked to changes in mechanisms affecting C sequestration (Gunnarsson et al., 2008), for example, the acceleration of litter decomposition (Aerts et al., 1995; Anderson and Hetherington, 1999; Bragazza et al., 2006), changes in plant productivity (see above and also Gordon et al., 1999; Leith et al., 1999), and higher CO₂ emissions and dissolved organic carbon (DOC) release (Bragazza et al., 2006).

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Most studies suggest that the impacts of short-term or moderate increases in N inputs on N availability and decomposition processes will result in increased plant growth (Fog, 1988; Schlesinger, 2009). However, long-term or excessive addition of N may lead to a reduction in rates of nutrient cycling with possible adverse effects on plant health through acidification and nutrient imbalances (Reuss and Johnson, 1986; Fog, 1988; Bouwman et al., 2002). This has also been detected in peatland ecosystems. For example, four years of N treatment resulted in a dose-related increase in shoot extension, canopy height and shoot N contents in *Calluna vulgaris* in upland heathland, as well as an accumulation of litter with increased N concentrations (Carroll et al., 1999). In contrast, subsequent (5–10) treatment years resulted in no further changes in growth parameters due to N addition but rather to higher winter injury susceptibility, indicating deleterious effects of long-term N additions on these plants (Carroll et al., 1999).

High levels of atmospheric N deposition in peatlands have repeatedly been associated with changes in plant diversity. In many cases, grasses have been observed to flourish to the detriment of ericaceous species (Hartley and Amos, 1999), *Sphagnum* mosses (Malmer, 1990; Limpens and Berendse, 2003; Saarnio et al., 2003; Bubier et al., 2007), and lichens (Carroll et al., 1999). A reduction of the C to N ratio in *Sphagnum* tissue due to N uptake (Limpens and Berendse, 2003; Gerdol et al., 2007) also appears to negatively affect photosynthetic rates and reduces the tissue water content inducing plant necrosis (Van der Heijden et al., 2000). The enhanced decay of *Sphagnum* represents increased N availability for co-existing vascular plants (Heijmans et al., 2002). It has also been documented that enhanced N deposition in the form of reduced N (NH_4^+) has a greater negative effect on plant growth rates than oxidized N (NO_3^-). For example, in *Calluna*, NH_4^+ treatments slowed down plant growth rates (Van den Berg et al., 2008), depressed the concentration of phenolics and condensed tannins in the leaves and retarded mycorrhizal colonization of the roots (Yesmin et al., 1996; Hartley and Amos, 1999; Hofland-Zijlstra and Berendse, 2009), while NO_3^- additions did not show any significant effects (Yesmin et al., 1996; Van den Berg et al., 2008). These studies suggest the potential for differential effects between reduced and oxidized forms of N on key aspects of growth and physiology. As there can be differences in the relative rates of deposition of oxidized (mainly originating from fuel combustion) and reduced N (mainly originating from agricultural sources) (Galloway, 1995), it is important to determine whether the effects of reduced and oxidized forms of N lead to changes in below-ground carbon allocation in ombrotrophic peatlands subjected to differentiated field applications of N form.

To understand the implications of atmospheric N deposition on carbon turnover in peatlands, we conducted a ^{13}C pulse labeling study within a long-term N addition experiment on two peatland vascular plant species, *C. vulgaris* and *Eriophorum vaginatum*, representing the two major and functionally different vascular plant groups of those systems, to quantify fluxes of newly fixed C from plant shoots to different ecologically important pools. *Calluna* is a slow-growing and robust ericaceous shrub that forms ericoid mycorrhizas and is able to tolerate a wide range of stress conditions (Woodin et al., 1992; Whitehead et al., 1997), whereas *Eriophorum* is a fast-growing and tussock-forming non-mycorrhizal sedge (Gebauer et al., 1995; Tolvanen et al., 2004). We examined shoot tissue C retention, soil pore water DOC content, and respiration rates from plant and soil. We hypothesized that: (1) N addition would alter the uptake and subsequent fluxes of C, manifesting itself by higher net respiration rates and faster allocation of C to below-ground pools; (2) the effects of N addition would be dependent on the N species added; and (3) N effects would be manifested below-ground by higher ^{13}C allocation to exudates and hence soil pore water DOC.

2. Materials and methods

2.1. Site and treatment description

The study was carried out at Whim Moss Experimental Site, an ombrotrophic bog near Edinburgh, Scotland, at 280 m above sea level. The site is a transition between a lowland raised ombrotrophic bog and an upland blanket mire (*C. vulgaris*–*E. vaginatum* blanket mire, NVC M19a, Rodwell, 1991), and the peat layer is at least 3 m in depth. No management has been employed during the past 60 years, apart from fencing erected in April 2007 to minimize rabbit grazing. Background N deposition is relatively low (between 8 and 11 kg N ha⁻¹ y⁻¹). The average mean annual temperature at the site is 10.7 °C and average annual rainfall is 900 mm. The vegetation is spatially heterogeneous but well represented in a repeating mosaic across the entire site (Sheppard et al., 2004). Wet N treatments have been applied since May 2002 using N additions to locally collected rainwater. The treatments are applied at wind speeds of less than 5 m s⁻¹ through a network of fully automated tubes and sprinklers. The ammonium (NH_4^+) treatment is applied as NH_4Cl , the nitrate (NO_3^-) treatment is applied as NaNO_3 ; the treatments are added at rates of 0, 8, 24, and 56 kg N ha⁻¹ y⁻¹. Only the 56 kg N ha⁻¹ y⁻¹ plots were used in this experiment. Each treatment plot is represented by a circular area of 13 m² and is randomly replicated four times across the site (Sheppard et al., 2004). Rainfall events are logged using a tipping bucket (Sheppard et al., 2004) and various meteorological parameters are measured and logged using a Campbell instruments CR23X micrologger (Leith et al., 2004).

2.2. ^{13}C pulse-chase labeling experiment

A pulse-chase experiment was carried out on the four control plots (no N treatment) and the high NO_3^- -N ($n = 4$) and NH_4^- -N ($n = 4$) treatment plots (56 kg N ha⁻¹ y⁻¹) using individuals of the two focal plant species at each plot. Individual plants were chosen carefully to be of similar above-ground biomass within each species. Immediately before labeling, samples of shoot material from each plant as well as soil and water samples were taken (T0, see sampling details below). Each individual plant was covered with a clear plastic bag (10 l), which was secured tightly at the base of the plant to minimize label leakage. A series of tubes was used to connect each plant system to a gas cylinder containing compressed air containing 99 atom% ^{13}C CO₂ at 350 ppm. The experiment was conducted on a sunny, cloud-free, mid-summer day (26 June 2007) to allow maximum photosynthetic activity. Background air was flushed out of the system and replaced with ^{13}C -CO₂ enriched air until the bags were fully inflated. The gas in the bag was replaced every 30 min. This process was repeated 10 times, so that each plant was in contact with a highly ^{13}C enriched atmosphere starting at ~ atmospheric CO₂ concentrations, for a total of 5 h during daylight hours. Preliminary measurements within these head-spaces confirmed that the frequency of replacement resulted in CO₂ concentrations not falling below 130 ppm at the end of a 30 min incubation period. Subsequent sampling was carried out immediately after labeling (T1, 5 h) and on six further occasions over the following three weeks: 27 June (T2, 1 d), 28 June (T3, 2 d), 29 June (T4, 3 d), 4 July (T5, 8 d), 12 July (T6, 16 d), and 18 July 2007 (T7, 22 d). Plots were sampled in random order at each time point, and water table height determined. At the end of the labeling experiment (T7), all plants were destructively harvested, partitioned into above-ground and below-ground biomass, and stored at –18 °C for further analyses.

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