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Contribution of plant photosynthate to soil respiration and dissolved organic carbon in a naturally recolonising cutover peatland

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ABSTRACT

The aim of this study was to investigate how three vascular plant species (*Calluna vulgaris*, *Eriophorum angustifolium* and *Eriophorum vaginatum*) colonising an abandoned cutover peatland affect fluxes of recent photosynthate to dissolved organic carbon (DOC), soil and plant respiration and shoot biomass. We used *in situ* $^{13}CO_2$ pulse labelling to trace carbon (C) throughout a 65 day pulse chase period. Between 16 and 35% of the pulse of ^{13}C remained in shoot biomass after 65 days with significant differences between *C. vulgaris* and *E. angustifolium* ($P = 0.009$) and between *C. vulgaris* and *E. vaginatum* ($P = 0.04$). A maximum of 29% was detected in DOC beneath labelled plants and losses of ^{13}C from peat respiration never exceeded 0.16% of the original pulse, showing that little newly fixed C was allocated to this pool. There were no significant differences between the different plant species with respect to ^{13}C recovered from DOC or via peat respiration. More C was lost via shoot respiration; although amounts varied between the three plant species, with 4.94–27.33% of the ^{13}C pulse respired by the end of the experiment. Significant differences in ^{13}C recovered from shoot respiration were found between *C. vulgaris* and *E. angustifolium* ($P = 0.001$) and between *E. angustifolium* and *E. vaginatum* ($P = 0.032$). Analysis of $\delta^{13}C$ of microbial biomass indicated that recently assimilated C was allocated to this pool within 1 day of pulse labelling but there were no significant differences in the ^{13}C enrichment of the microbial biomass associated with the different plant species. The data suggest that peat respiration represents a small flux of recent assimilate compared to other fluxes and pools and that different vascular plant species show considerable variation in the quantities and dynamics of C allocated to DOC.

1. Introduction

It has been estimated that northern hemisphere peatlands may contain as much as 455 Pg of C (Gorham, 1991), approximately a third of the global C held in soils. In the EU, it is estimated that 38% of the total area of peatlands have been severely affected by commercial harvesting (Raeymaekers, 2000) and in the UK only 6% of lowland raised bogs remain undamaged. In Scotland, raised mires are estimated to have covered 28 000 ha in 1900 but only approximately 2500 ha now remain, following extensive drainage, harvesting and afforestation (JNCC, 1999). Modern methods of peat cutting require extensive drainage after which layers of peat are progressively removed. At the end of harvesting, many sites are abandoned with no active restoration programme, which can result in many peatlands becoming net sources of C to the atmosphere (Waddington et al., 2002). Restoring peatlands by raising water levels and seeding with appropriate species is slow and expensive. Considerable work has investigated the most appropriate methods for reinstating *Sphagnum* spp. on post-harvested sites (Campbell and Rochefort, 2003) but it is not always possible to raise water levels sufficiently to create appropriate conditions for recolonisation of *Sphagnum* spp. In such situations, it is important to consider whether any particular combination of vascular plants might minimise losses of C from these sites and should thus be encouraged to grow on abandoned sites.

Even without an active restoration programme, cutover peatlands are colonised within a few years of abandonment. In northern Europe, the plants most commonly associated with early colonisation of bare peatlands are acidophilic species such as *Eriophorum vaginatum* L., *Eriophorum angustifolium* Roth and *Calluna vulgaris* (L) Hull (a monotypic genus and hereafter referred to as *Calluna*). These species differ markedly in their ecology. *E. vaginatum* is a long-lived, deep-rooted, tussock-forming, rhizomatous perennial that appears to thrive on drying bogs; individual tussocks can persist for over 100 years (Wein, 1973). *E. angustifolium* has an extensive sympodial system of unbranched rhizomes and like *E. vaginatum* does not form mycorrhizal associations. It has a preference for wetter areas and forms dense patches comprising many

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individual shoots. *Calluna* is a common dwarf shrub species that produces extensive mats of fine "hair" roots which are heavily colonised by ericoid mycorrhizal fungi (Read, 1991).

Colonisation of cutover peatland by plants is likely to have significant impacts on C turnover as plants provide inputs of newly fixed, labile C (Bardgett, 2005) into a substrate that largely comprises recalcitrant C and is resistant to microbial degradation (Jorgensen and Richter, 1992). These inputs of labile C could 'prime' microbial communities thus allowing them to breakdown older, recalcitrant C compounds (Kuzyakov, 2002) and increases efflux of CO_2 to the atmosphere. Alternatively, if significant quantities of newly fixed C enter and below-ground C pools through rhizodeposition and remain there, or are bound to peat fractions, this could be important in shifting abandoned peatlands from C sources to C sinks. It is, therefore, important to determine how recent assimilate from plants colonising cutover peatlands contribute to the major pools and fluxes of C and whether different species affect this in different ways.

Considerable progress has been made in recent years to trace the fate of plant assimilate using *in situ* isotope pulse labelling methods. For example, field based $^{13}CO_2$ labelling of temperate grassland has demonstrated that plant photosynthate is rapidly allocated below-ground and recycled very rapidly to make a substantial contribution to soil respiration rates (Johnson et al., 2002; Leake et al., 2006). Similar results have been found in laboratory-based experiments using ^{13}C pulse labelling to investigate C fluxes from *Sphagnum* mosses into dissolved organic carbon (DOC) in pore water and amounts retained in plant biomass (Fenner et al., 2004). Pulse labelling of tundra mesocosms with ^{14}C has also determined fluxes of recent assimilate into soil organic matter fractions (Loya et al., 2002), methane emissions (King and Reeburgh 2002; King et al., 2002) and coarse and fine roots (Olsrud and Christensen 2004). However, there have been no field experiments specifically designed to follow the fate of plant assimilate in cutover peatlands, despite their importance as C stores. Here we used ^{13}C pulse labelling on three plant species (*E. vaginatum, E. angustifolium* and *Calluna*) naturally colonising an abandoned cutover peatland to quantify fluxes of newly fixed C through ecologically important C pools. We hypothesised that: (1) newly fixed photosynthate would be rapidly allocated below-ground into DOC and microbial biomass and ultimately respired from the peat surface, and (2) fluxes of C transfers below-ground would differ between the three plant species due to distinct differences in morphology and productivity. Finally, we discuss these results within the framework of the C sequestration potential of abandoned cutover peatlands.

2. Materials and methods

2.1. Site description

The study was carried out at Middlemuir Moss, a former raised mire site in North East Scotland: 57°36′ N, 2°9′ W, altitude 110 m asl. The site has a long history of manual and mechanised peat cutting; it is estimated that a depth of up to 4 m of peat has been removed during mechanised harvesting operations that started in 1961. Peat was harvested in baulks and trenches approximately 100 m wide. Remaining peat depth varies from 2 to 4 m. The remaining peat is highly acidic ($pH \leq 3$) and humified. No restoration has been carried out and the site is unmanaged. The area used for the experiment was dominated by *Calluna*, *E. vaginatum* and *E. angustifolium* with scattered patches of *Sphagnum auriculatum* and extensive areas of bare peat. The experiment used a trench created during harvesting where the water table averaged -9.57 ± 2.3 cm over a nine-month period (January–September). The remaining depth of peat on this part of the site is approximately 4 m with an approximate dry bulk density of 0.15 g cm^{-3}.

2.2. Experimental design

The experimental area was divided into four blocks along the trench approximately 5 m wide. Blocks were between 1 and 10 m apart. Each block contained four experimental plots of approximately 1 m^2 each containing one similarly sized *Calluna*, *E. vaginatum* or *E. angustifolium* plant at its centre or bare peat as a control plot. The experiments used plants that had naturally recolonised the peatland site and which were spatially separated by large areas of bare peat. This approach also eliminated disturbance to root systems that would inevitably have occurred had we attempted transplanting individuals to particular areas of the site. Any other plants growing within the plot were cleared and roots passing in or out of the plot were severed to approximately 30 cm depth. Four days before the start of the experiment, a plastic collar 5 cm deep and 15 cm diameter was inserted next to each experimental plant (or control) for use during CO_2 flux measurements. All other plants were removed from the plots and any plant regrowth removed at each visit.

2.3. In situ $^{13}CO_2$ pulse labelling of plants

Plants were labelled on 17 July 2006, using clear acrylic chambers fitted with a fan. Each plant was exposed to elevated $^{13}CO_2$ by addition of 20% lactic acid to 0.416 g $NaH^{13}CO_3$ (^{13}C at 99 atom%; Sigma, UK). Two blocks were labelled in the morning for 3 h 15 min and two blocks in the afternoon for 3 h 45 min. The cumulative total solar radiation was 58 mol s^{-1} m^{-2} in the morning and 52 mol s^{-1} m^{-2} in the afternoon. Statistical tests on initial ^{13}C biomass uptake showed no differences between the plants labelled in the morning and those labelled in the afternoon. Atmospheric CO_2 concentrations inside the chambers monitored using a portable infrared gas analyser (EGM-4, PP Systems, Hertfordshire, UK). CO_2 concentrations did not fall below ambient at any point during the labelling.

2.4. Sampling

Plant biomass, soil microbial biomass, plant respiration and soil respiration pools (except as stated) were sampled 4 days before the start of the experiment and 1, 2, 4, 8, 16, 32 and 65 days after labelling. All samples were collected in random order at each time point. Each shoot biomass sample comprised four or five leaves or leaf sections (*Eriophorum* spp.) or short shoots (*Calluna*) taken from different areas of the plant directly after labelling had finished and at each sampling point. A bulk peat sample was taken from beneath each plant and from control plots at the end of the experiment. Shoot and peat samples were weighed, oven dried at 105 °C for a minimum of 24 h and ground in a ball mill. After drying, 1 mg of each ground plant biomass sample or bulk peat was weighed into a 4×6 mm tin cup and analysed for total C content and $\delta^{13}C$ by continuous flow isotope ratio mass spectrometry using a Europa Scientific ANCA-NT stable isotope analyser with ANCA-NT Solid/Liquid Preparation Module (Europa Scientific Ltd., Crewe, UK).

Carbon dioxide samples from peat adjacent to labelled plants and from plants were taken using chamber measurements. Carbon dioxide flux from peat was measured using a dark chamber inserted into the collar next to labelled plants with an air-tight rubber seal. Carbon dioxide fluxes were measured for 3–5 min. At the end of the measurement period a gas sample (10 ml) was taken for stable isotope analysis by injection into a pre-evacuated septum-capped exetainer (12 ml capacity, LabCo, UK Ltd.). Carbon dioxide fluxes from plants were also measured using the same approach on days 1–32. Carbon dioxide fluxes (mg C m^{-2} d^{-1}) were calculated by converting CO_2 concentrations to μmoles, using the measured soil temperature and the ideal gas constant. Gas samples were