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Short Communication

Species-specific effects of plants colonising cutover peatlands on patterns of carbon source utilisation by soil microorganisms

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Abstract

Root exudates and litter are the main sources of inputs of labile carbon into the microbial pool in successional ecosystems. Here we studied whether typical pioneer species (*Eriophorum vaginatum*, *Eriophorum angustifolium* and *Calluna vulgaris*) alter the functional response of the microbial community of a previously cutover peatland. Peat was sampled at three depths (0–5, 20–25 and 40–45 cm) from beneath these species and from bare soil areas. MicroResp analysis using ecologically relevant, radiolabelled, carbon sources showed significant separation in community level physiological profiles (CLPP) of soil microorganisms according to peat depth. This effect was also reflected in microbial biomass carbon, which also decreased with increasing depth. Furthermore, distinct differences in CLPP were observed between the three plant species and the bare soil in the absence of an effect on microbial biomass carbon or total soil carbon. The plant species effects were driven by differential utilisation of xylose, glutamic acid, lysine and phenylethylamine. The data suggest that 'new' carbon inputs from plants colonising abandoned cutover peatland may support communities of microorganisms that have functionally distinct roles in carbon turnover.

Keywords: Community level physiological profiling (CLPP); Plant succession; Microbial community structure; Peat

Peatlands have a worldwide coverage of 353.4 Mha (Moore, 2002) and contain approximately 455 Pg carbon, about a third of the global capital (Gorham, 1991). There are currently considerable pressures on peatlands that threaten their role as carbon reserves, the most significant arising from their commercial exploitation to supply the horticultural and sylvicultural industry. In the EU alone, it has been estimated that 38% of the total of peatlands have been severely affected by commercial harvesting (Raeymaekers, 2000). The result of large-scale harvesting is the exposure of previously anaerobic ancient deposits of peat to aerobic conditions and this stimulates microbial activity and contributes to further carbon losses. In the short-term, the net loss of carbon is further exacerbated in recently cutover peatlands because in the absence of plants there are no new carbon inputs from photosynthesis (Waddington et al., 2002).

The mineralisation of carbon in soil is undertaken by heterotrophic microorganisms and so the potential role of cutover peatlands to act as carbon sources can only be properly determined if we have an understanding of the size and activity of associated microbial communities and the factors that regulate them. It is likely that plant invasion of bare peat will have a significant impact on microbial communities because plants provide a pathway through which labile carbon is allocated belowground. The main mechanisms of labile carbon inputs are from rhizodeposition (Toal et al., 2000) and allocation of carbon to mycorrhizal fungi that associate with many plant species (Johnson et al., 2002). Evidence from drained peatlands suggests that between 50% and 70% of net soil respiration is driven by the turnover of recent plant assimilate (Komulainen et al., 1999).

The effects of coloniser plant communities on soil microorganisms can be rapid and plant species-specific. Soil microbial community structure was found to differ markedly beneath a range of plant species that had

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colonised previously glaciated terrain for 12–15 years (Bardgett and Walker, 2004). Similar species-specific effects on microbial community structure (Loranger-Merciris et al., 2006; Grayston et al., 1998) and biomass (Johnson et al., 2003) have also been shown for established upland grassland communities. One likely mechanism though which plant species may select for certain groups of rhizosphere microbes is by exudation of carbon compounds that differ in both quality and quantity, as reflected for example, by distinct patterns of carbon utilisation in Biolog® microplates (Grayston et al., 1998). In fungal dominated peatland soil, the Biolog system is likely to have limited applicability because it primarily targets fast growing bacteria that can be readily extracted. To overcome this limitation, whole soil carbon utilisation approaches have been developed (Degens and Harris, 1997), the latest more sensitive methods using ^{14}C-labelled carbon sources in microplates (MicroResp^{TM}, Campbell et al., 2003). The community level physiological profiles (CLPP) obtained from MicroResp are used here as a measure of functional diversity of the whole microbial community. The identity and concentration of the carbon compounds used in the present study were selected on the basis of those typically produced as root exudates (Campbell et al., 1997) and that represent phenolic compounds and monosaccharide markers of peatland vegetation (Bourdon et al., 2000). For example, *Eriophorum vaginatum* has been found to produce exudates comprising citric and malic acid, fructose, galactose and glucose (Saarnio et al., 2004), all of which are used in the MicroResp plates. In vegetated cutover peatland, distinctive patterns of carbon utilisation profiles from whole soils were observed at different depths and approximately 70% of the variation was explained by degree of decomposition of the peat as characterised by the ratio of polysaccharide to carboxylate in FTIR spectra (Artz et al., 2006). However, the effects of specific coloniser plant species on patterns of carbon utilisation and microbial biomass in these systems are unknown. This information is important for subsequent management of cutover peatlands to maximise their potential to act as carbon sinks rather than carbon sources. In this paper, we test the hypothesis that different plant species that have recently colonised cutover peatland support functionally distinct microbial communities. We used MicroResp^{TM} whole soil community level physiological profiling to test the functional response of the microbial communities in terms of the utilisation of ecologically relevant carbon sources in bare soil and from the rhizosphere of peat colonised by *Calluna vulgaris* L. (Hull), *E. vaginatum* L. and *Eriophorum angustifolium* L.

The study was undertaken on a cutover peatland at Middlemuir, Scotland (57°36′N, 2°9′W) that was abandoned in 1995. Surface plant cover at the experimental site is still patchy following <15 years of unaided regeneration and the remaining peat is highly humified and of similar degree of decomposition throughout the profile. The most abundant higher plant species on the study area are *C. vulgaris*, *E. vaginatum* and *E. angustifolium* that form distinct monoculture patches. In July 2006, four replicate similar sized and spatially separated patches of each species were identified. *Calluna* plants were in the late building phase (approx 10–15 years), decumbent, but not yet rooting from trailing stems. *Eriophorum* plants were in the building phase with tussocks of <17 cm in diameter for *E. vaginatum* and small clonal patches (<50 cm) of *E. angustifolium*. Soil samples were removed from three depths of old catotelm peat (0–5, 20–25 and 40–45 cm) below each plant and from bare control patches. We have previously shown that this depth range reflects a gradient of carbon quality, notably an increase in lignin and aliphatic-like compounds and a decrease in polysaccharide compounds (Artz et al., 2006). Samples were also removed from 4 patches of bare soil between 3 and 4 m distant from the nearest vegetation. Total C and N were determined on ground oven dried material using a CN analyser (Fisons NA1500 NCS). Soil pH was measured within 24 h on fresh material. Microbial biomass C (Cmic) was determined on sieved (2 mm) peat by fumigation extraction (Vance et al., 1987) using a k_{EC} factor of 0.35 (Sparling et al., 1990). Whole soil CLPP was undertaken using the MicroResp^{TM} assay (Campbell et al., 2003) with modifications for peat soils as described by Artz et al. (2006). The wells of the plates were filled with 300 mg fwt of homogenised peat. Each well received 30 µl of solution containing one of 15 ecologically relevant carbon sources universally labelled with ^{14}C. The plates were incubated for 48 h at 15 °C during which time the amount of ^{14}C released from the wells was trapped in NaOH and counted by liquid scintillation.

Soil properties data were analysed using general linear models in Minitab 14. CLPP data (percent utilisation of each carbon source) were transformed for statistical analyses using the arcsin function. Data were analysed using multivariate analysis of variance (MANOVA), taking into account the nested sampling, to test for the effects of soil horizon and plant species (Genstat 8th edition, VSN International). The residual effects (after excluding depth and species effects as covariates) of soil pH, C:N ratio and microbial biomass carbon (Table 1) were tested using redundancy analyses (RDA) with forward selection of variables after permutation testing (999 repetitions that were restricted for the nested experimental design; Canoco for Windows 4.5, Biometris, Wageningen, The Netherlands). Prior to RDA, the CLPP dataset was analysed using detrended correspondence analysis to confirm that the gradient lengths indicated the suitability of a linear model (RDA) for further analyses.

Soil C content ranged from 51% to 58% and was little affected by plant species (Table 1). However with increasing depth, soil C content significantly increased from 51.8% at 0–5 cm to 54.2% and 56.1% at 20–25 and 40–45 cm, respectively. The reverse trend was seen for Cmic, which decreased significantly from 336 µg C g dwt^{-1} at 0–5 cm to 262 and 252 µg C g dwt^{-1} at 20–25 and 40–45 cm, respectively (Table 1). Whilst these values would