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Impact of *Phalaris arundinacea* cultivation on microbial community of a cutover peatland

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Organic peat soils have been extensively drained and used for agricultural, horticultural and energy purposes. The management practices of organic soils accelerate decomposition processes resulting generally in loss of carbon. Microbes are the key players in soil carbon cycling. We studied the effects of cultivation of a perennial bioenergy plant (reed canary grass, *Phalaris arundinacea*) on microbial biomass carbon, microbial respiration and microbial communities in an old, previously uncultivated peat soil. The cultivation increased the amount of microbial biomass carbon and microbial respiration in peat mostly in the uppermost 5 cm layer where the impacts of roots and litter are most pronounced. As shown by phospholipid fatty acid (PLFA) analysis, the abundance of fungi and gram-negative bacteria increased with cultivation, while the abundance of gram-positive bacteria decreased. The implications of these changes on carbon cycling and carbon storage in peat under reed canary grass are discussed.

Introduction

Peatlands are a substantial carbon storage containing 30% of the global C pool (Gorham 1991). These soils are abundant in the northern regions where they are extensively used for agricultural, horticultural and energy purposes. The management of peat soils generally requires drainage which together with agricultural practices such as tilling, fertization and liming accelerates decomposition processes causing loss of carbon (Paustian *et al*. 2000). Peat extraction for energy purposes or horticulture is a special land-use option where after drainage of the site peat deposits are gradually removed starting from peat surface layers. It is not possible to utilize all of the peat deposits, and when the peat extraction ceases, the cutaway peatlands still comprise a remarkable amount of bare peat which decomposes and releases carbon dioxide (CO_2) to the atmosphere (Alm *et al*. 2007). The remaining peat is very old, up to about 10 000 years. When considering the atmospheric CO_2 load, an important question is how decomposable this old peat

is, and how various after-use options, e.g. agricultural practices, affect the decomposition rate.

Microbes play an essential role in the soil carbon cycle. Temperature and moisture, together with the availability of oxygen and substrates, are the main controlling factors of microbial activities. Agricultural practices change the soil physico-chemical conditions. Below- and above-ground litter input and root exudates from plants further alter the growth environment of soil microbes by increasing availability of organic substrates.

The role of various microbial groups differs in the soil carbon cycle. Gram-negative bacteria are usually associated with the initial steps of fresh carbon turnover whereas gram-positive bacteria are more capable of using recalcitrant carbon sources (Waldrop and Firestone 2004, Kramer and Gleixner 2006). Fungi can quickly incorporate fresh carbon into their biomass but they also are able to decompose recalcitrant carbon compounds (Denef *et al*. 2007). Changes in the composition of microbial communities can thus alter the overall microbial functioning of soils. It has been suggested that the composition of the microbial community has an impact on the carbon sequestration potential of the soil (Bailey *et al*. 2002, Allison *et al*. 2005). Fungal biomass is not as susceptible to decomposition as bacterial biomass because of a more complex chemical composition. Furthermore, fungi assimilate and store carbon more efficiently than bacteria do. However, Bailey *et al*. (2002) concluded that it is unclear whether fungi actually enhance carbon sequestration or whether a soil type capable to carbon sequestration, e.g. no-till systems, also favours fungal growth.

The cutaway peat extraction sites in Finland are increasingly used to produce biomass for energy purposes (Information Service of Agricultural Statistics in Finland 2007). Reed canary grass (RCG; *Phalaris arundinacea*) has proven to be an excellent plant for biomass production on cutaway peatlands. This perennial C3 plant is well adjusted to northern conditions with short growing periods and low temperatures (Lewandowski *et al*. 2003). RCG produces large amount of biomass not only above- but also belowground (Kätterer and Andrén 1999). In this study, we investigated whether the cultivation of RCG at a cutaway site with a peat age of 7000 years alters the activity and community structure of heterotrophic microbes. Our hypothesis was that the microbial activity and microbial biomass would increase due to cultivation. Additionally, we hypothesized that the relative abundance of gram-negative bacteria would increase. This site offers an excellent opportunity to assess the effects of cultivation of plants, which have an extensive capacity for litter production, on soil microbes that are adapted to use recalcitrant peat compounds in old peat. The study is the first step in our research programme to link the below-ground processes to the overall carbon dynamics of old cutaway peatland sites cultivated with RCG.

Material and methods

Research site and soil sampling

The research site, Linnansuo peatland complex, is situated in eastern Finland (62°30´N, 30°30´E; 110 m a.s.l.). It is an ombrotrophic *Sphagnum fuscum* bog. The peatland in its pristine state is described in detail by Tolonen (1967). In 1976, a major part of the the peatland was drained and peat extraction was initiated in 1978. In 2001, 15 ha were left out of the peat extraction and cultivated with RCG (variety Palaton). The age of the leftover surface peat layers is approximately 7000 years (Tolonen 1967). The initial cultivation procedures included liming (fine-crushed dolomitic limestone 7800 kg ha^{-1}), fertilization (350 kg ha^{-1} N:P:K 17:4:13, nitrogen as ammonium nitrate), tilling and deepening of drainage ditches. Since then, fertilization is carried out yearly in spring and liming every 4–5 years. The crop has been harvested every spring starting from the third year of sowing the RCG. In some parts of the peatland complex peat extraction has continued. These areas have a similar history as the currently cultivated cutaway areas. Therefore, a still actively extracted site, called here "bare peat", adjacent to the cultivated site was chosen to serve as a control to the RCG site. More information on the research site, cultiva-

tion practices and a map of the site is available in Shurpali *et al*. (2008).

Soil sampling was done on four occasions in 2004. Samples taken on 29 June and 17 August were used for respiration measurements and microbial biomass carbon was determined from samples taken on 13 July and 14 September. The samples taken on 14 September were also used for PLFA analyses. Each time we took 3–4 replicate soil cores within 10-m distance (peat profile of 0–15 cm) from both RCG and bare peat areas. The sampling was done with a soil corer (diameter 7 cm). The soil cores were divided into subsamples of 0–5 cm, 5–10 cm and 10–15 cm and the replicate samples from the plots were pooled. Three replicates were then taken from this pooled sample for each layer. PLFA analyses were done in two replicates from the pooled samples for each layer.

Soil physico-chemical analyses

Prior to the analyses, roots were removed and samples were manually homogenized. Manual homogenization instead of sieving was done because of the fibrous structure of the peat. Dry weight was determined by drying the soils at +65 °C for 24 hours. Water holding capacity (WHC) was determined by placing soil samples onto moist filter papers and pouring water on them until the soil was water-saturated. The WHC was calculated by recording the weight of the soil samples before and after water saturation.

Soil pH was determined from the samples taken in August from a soil-water suspension (1:3 vol/vol) with a pH meter (WTW pH340). In connection to another study, additional soil samplings were made to determine bulk density and C and N contents (4–9 replicates). Soil profiles with known volume were weighted before and after drying (+65 °C) to determine bulk density. Total carbon and nitrogen contents of soil without roots were determined using a C/N analyzer (Elementar Variomax C/N) at the Geological Survey of Finland. At the RCG site, the soil sampling for the C and N analyses was done from layers of 0–10 and 10–20 cm and in bare peat area from the 0–15 cm layer.

Respiration

A basal soil respiration rate was measured as carbon dioxide (CO_2) evolution during one-week incubation at +15 °C. Field moist soil (18 g) was weighted into 600 ml flasks (three replicates) and the soil moisture was adjusted to 60% WHC. The flasks were sealed for incubation with rubber septa and screw caps and 100 ml overpressure of air was added to avoid underpressure resulting from gas sampling. Gas samples were taken with polypropylene syringes equipped with three-way stopcocks at the beginning of the incubation, six hours after the start of the incubation and thereafter daily during the total incubation period of 7 days. CO_2 concentrations were analyzed with a gas chromatograph (GC, HP 5890 Series II) equipped with a thermal conductivity detector (TCD) (Nykänen *et al*. 1995).

Microbial biomass carbon

Microbial biomass was determined by the substrate induced respiration (SIR) method (Anderson and Domsch 1978) at soil moisture of 60% WHC. Prior to the actual experiments a pre-experiment with different glucose concentrations was done to determine the optimum glucose concentration, which was 10 mg ml^{-1} in soil solution. Soil samples of 18 g (three replicates) were incubated in 600 ml flasks (*see* above). After addition of glucose flasks were left open for 30 minutes. Samples for CO_2 analyses were taken 30, 75 and 120 minutes after the flasks were closed. The CO_2 concentrations were analyzed with a gas chromatograph (*see* above). The CO_2 flush obtained during the incubation was transformed to correspond microbial biomass carbon according to Anderson and Domsch (1978).

PLFA analysis

The microbial biomass and community structure were analyzed using a phospholipid fatty acid (PLFA) analysis. Soil samples of 5 g were extracted for lipids. Lipids were then fractionated using silicic acid chromatography to neu-

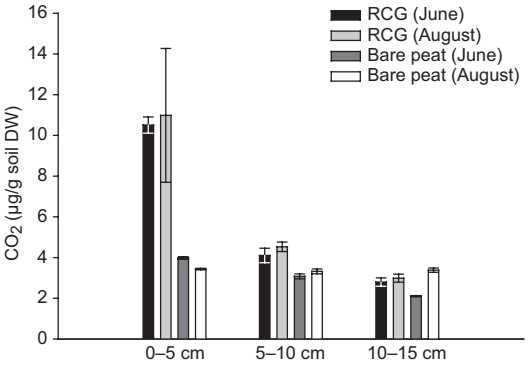

Fig. 1. Respiration rates of soil collected from the 0–5 cm, 5–10 cm and 10–15 cm soil layers of the reed canary grass (RCG) site and bare peat site in June and August 2004. The results are averages of three replicates (± SD).

tral, gluco- and phospholipid fatty acids. There were two replicates of each sample. Phospholipid fatty acids were saponificated, methylated and methyl esters were analyzed using gas chromatography mass spectrometry with total ion monitoring (Keinänen *et al*. 2003, Koponen *et al*. 2006). PLFAs 18:2 and 18:1ω9 were used as biomarkers for fungi and the sum of these was used to calculate the proportion of fungi in the total microbial biomass. PLFAs *i*-13:0, *i*-14:0, *br*-15:1, *i*-15:0, *a*-15:0, *i*-16:0, *br*-17:0, *i*-17:0 and *a*-17:0 were used as biomarkers for gram-positive bacteria and 15:1, 16:1ω9, 16:1ω7c, 16:1ω5, 18:1ω7, *cy*-17:0 and *cy*-19:0 for gram-negative bacteria (Bååth 2003).

Statistical analyses

The differences in basal respiration rates and microbial biomass carbon (SIR) were elucidated by non-parametrical statistical tests because of the limited number of replicates. Soil layers were compared using the Kruskal-Wallis test, the differences between the RCG and bare peat with the Mann-Whitney *U*-test, and sampling times with the Wilcoxon test. Differences in the PLFA profiles were expressed using a principal component analysis (PCA). Calculations were carried out with SPSS 14.0.

Results

Soil physico-chemical characteristics

Soil pH was highest in the uppermost layer of the RCG site (Table 1). In the bare peat pH was on average 4.2 with no differences between layers. Mean carbon content of the bare peat was 56.5%, similar to that of the lower soil layers at the RCG site. The upper peat layers of the RCG site had less carbon (on average 23.9% C) resulting from the mixing of sand from ditches with the surface peat during the site preparation. Bulk density of the RCG peat was higher as compared with that of the bare peat (0.42 *vs*. 0.18 g dry matter cm^{-3}). C/N ratios ranged between 40.0 and 44.6, and were similar in both peat profiles. The bare peat had higher water content and water holding capacity (WHC) (Table 1).

Respiration

Respiration rates in the RCG peat profile were generally significantly higher (Mann-Whitney *U*-test: $p < 0.05$) than those in respective layers of the bare peat profile (Fig. 1). Respiration rate

Table 1. Soil physico-chemical properties.

	RCG			Bare peat		
	0–5 cm	5–10 cm	10–15 cm	0–5 cm	5–10 cm	10–15 cm
pH[1]	6.3	5.0	4.3	4.3	4.2	4.2
Soil water content (%)[2]	54.2 ± 3.2	70.4 ± 4.4	77.0 ± 1.2	72.9 ± 1.6	77.2 ± 0.9	79.0 ± 1.0
WHC	2.0 ± 0.0	3.5 ± 0.1	6.4 ± 0.1	6.1 ± 0.0	7.5 ± 0.2	9.5 ± 0.8

[1] Measured in soil-water suspension.
[2] Calculated as percentage of fresh weight.

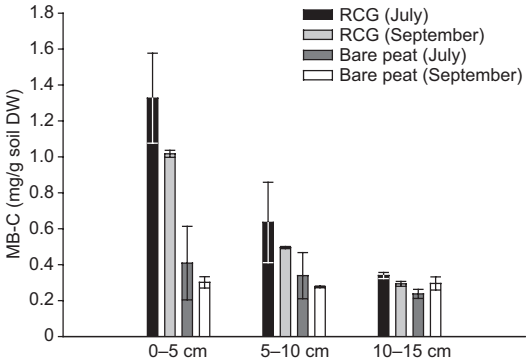

Fig. 2. Microbial biomass carbon (MB-C) in 0–5 cm, 5–10 cm and 10–15 cm soil layers in the reed canary grass (RCG) site and bare peat site in July and September 2004. The results are averages of three replicates (± SD).

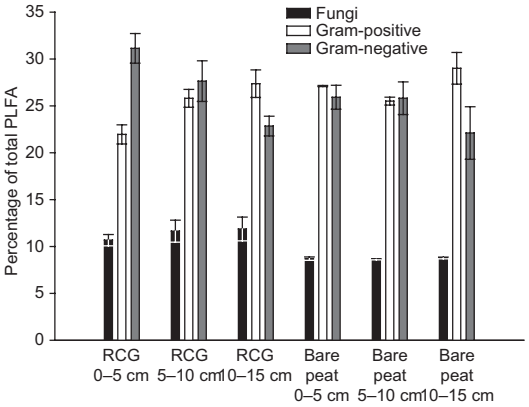

Fig. 3. Percentage of fungi, gram-positive and gram-negative bacteria of the total PLFAs in 0–5 cm, 5–10 cm and 10–15 cm soil layers of reed canary grass (RCG) site and bare peat site. The results are averages of two replicates (± SD).

in the 0–5 cm layer of the RCG site was 10.5 ± 0.4 μg CO_2 DW g^{-1} h^{-1} in June and 11.0 ± 3.3 μg CO_2 DW g^{-1} h^{-1} in August. In this layer, respiration was at least twice that of the other layers of the RCG site (lowest–highest = 2.8–4.8 μg CO_2 DW g^{-1} h^{-1}), and of all layers of the bare peat profile (2.1–4.0 μg CO_2 DW g^{-1} h^{-1}). There were no statistically significant differences (Wilcoxon test) in soil respiration between the two sampling times (June and August).

Microbial biomass carbon

The amount of microbial biomass carbon was higher in the the RCG peat than in the bare peat (Fig. 2). Especially the uppermost layer of RCG peat profile had high amount of microbial-biomass carbon as compared with that in the bare peat. The differences between the peat profiles were statistically significant (Mann-Whitney *U*-test: $p < 0.05$) except for the 10–15 cm layer in the last sampling.

PLFA analysis (microbial communities)

There were differences in the microbial community structures between the sites and various peat layers (Figs. 3–5). In the 0–5 cm layer of the RCG peat profile gram-negative/gram-positive ratio was 1.4, i.e. the abundance of gram-negative bacteria exceeded that of gram-positive bac-

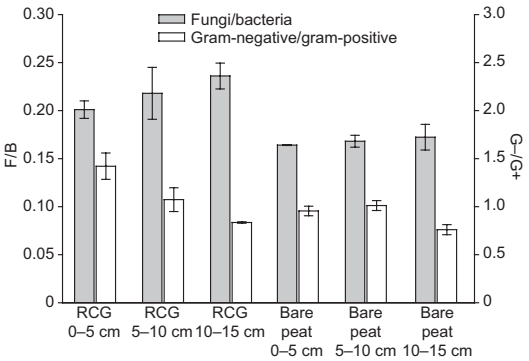

Fig. 4. The ratios of fungi/bacteria (F/B) and gram-negative/gram-positive bacteria (G–/G+) in 0–5 cm, 5–10 cm and 10–15 cm soil layers of reed canary grass (RCG) site and bare peat site. The results are averages of two replicates (± SD).

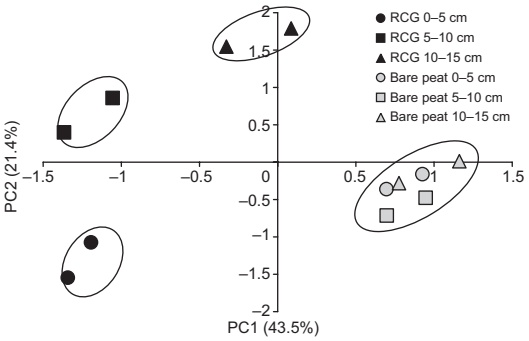

Fig. 5. Score plot of principal component analyses of phospholipid fatty acids (PLFA) from reed canary grass (RCG) site and bare peat site. Percentage of variance expressed is indicated on each axis. Ellipses enclose all soils of bare peat site and the different soil layers of RCG site. PC1 represents the cultivation effect and PC2 differentiates the layers of the RCG site.

teria (Fig. 4). In the 0–5 cm layer of the bare peat profile and 5–10 cm layers of both peat profiles the ratios were approximately 1. In the 10–15 cm layer of both peat profiles the ratio was < 1, i.e. the gram-positive bacteria were more abundant than the gram-negative bacteria.

Fungal biomarkers were more abundant in the reed canary grass peat than in the bare peat. Vertically there were no differences in the bare peat whereas in the RCG peat profile fungal biomarkers were slightly increasing with soil depth. The fungal-to-bacterial biomass ratios (F/B) were 0.19–0.25 and 0.16–0.18 in the RCG peat and in the bare peat, respectively (Fig. 4). PLFA16:1ω5, here classified as gram-negative biomarker along with other monounsaturated straight chain fatty acids, is also often considered as a biomarker for arbuscular mycorrhizal fungi (Olsson *et al*. 1999, Olsson 1999, Allison *et al*. 2005, Rinnan *et al*. 2007). The amount of this biomarker in the total PLFAs was 2.5%–3.1% in the 0–5 cm and 5–10 cm layers, and 1.4%–2.0% in the 10–15 cm layer of the RCG peat profile. In all layers of the bare peat profile the content of 16:1ω5 was similar to that in the deepest layer of the RCG peat profile.

In the principal component analysis (PCA) PC1 accounted for 43.5% of the variation and PC2 for 21.4% (Fig. 5). PC1 represents the cultivation effect as indicated by the negative loading for the 0–5 and 5–10 cm layers of the RCG peat profile and positive loading for all layers of the bare peat. The 10–15 cm layer of the RCG peat profile lies in between those two groups. PC2 differentiates the layers of reed canary grass site (Fig. 5).

Discussion

Soil microorganisms of 7000-year-old drained peat responded markedly to cultivation of perennial plant, reed canary grass, as shown by increase in respiration rates, microbial biomass carbon and shifts in the microbial community structure. The increase in microbial biomass and activity resulted most likely from the increase in the availability of substrates derived from RCG. This conclusion is supported by the results that the changes were highest in the surface peat (0–5 cm) where most of the RCG roots exist. RCG is capable of producing a large amount of biomass out of which a large proportion remains in the soil as stubbles or roots after harvesting (Kätterer and Andrén 1999).

Fresh plant litter from perennial grasses improves the substrate quality of recalcitrant peat (e.g. Hobbie *et al*. 1995). The substrate quality is often reported as the main controller of microbial activity in organic soils (Hogg *et al*. 1992, Brake *et al*. 1999, Waddington *et al*. 2001, Andersen *et al*. 2006). Additionally, the input of fresh substrates can induce increase in the decomposition of the old, more recalcitrant organic matter (priming effect, Kuzyakov *et al*. 2000). It is thus possible that this priming effect occurs in the soil under RCG, particulary, when priming is known to be more abundant in carbon rich soils (Kuzyakov *et al*. 2000). Other factors, i.e. fertilization (Manning *et al*. 2008) and increase in soil pH (Cookson *et al*. 2008), could also have had an impact on the soil microbial activity. Due to the site preparation for cultivation, the RCG soil was better aerated, as indicated by the lower soil water content. There was also mixing of sand with peat which might have accelerated microbial activities. Mineral soil addition improves the fertility of peat soil (Hytönen *et al*. 2008). Microbial biomass and respiration followed generally similar patterns. The better nutrient status and improved environmental conditions may have favoured both microbial activity and associated microbial biomass production.

Increased microbial activity could reflect changes in microbial communities. In our study, first of all, the relative amount of fungal biomarkers and consecutively the F/B ratio was higher at the RCG site as compared with that at the bare-peat site. These changes could be induced directly by the introduction of plants or by cultivation practises. During plant succession the F/B ratio usually increases in soils (Bardgett *et al*. 2005) which could be connected with fungi being involved in the degradation of plant litter (Denef *et al*. 2007). In addition, the diversity of the microbial community can increase which leads to a more variable substrate utilization (Bardgett *et al*. 2005). Nitrogen has induced a decrease in fungal biomarkers and an increase in bacterial biomarkers (Innes *et al*. 2004, Bardgett *et al*. 2005, Paterson *et al*. 2006) or an increase

in fungal biomarkers in unimproved (i.e. non-fertilized) sites has been observed (Grayston *et al*. 2004). In our study, the possible inhibitory effects of nitrogen fertilization on fungi might have been surpassed by effects of plants, i.e. by improvements in substrate input and quality (root exudates and litter). The no-till cultivation probably favours the growth of fungi because the soil is not mechanically disturbed. Mycorrhizal fungi might have developed which was indicated by the relative increase of the biomarker 16:1ω5.

Generally the F/B ratios in our study (approximately 0.2) are lower or similar to those determined e.g. by Jaatinen *et al*. (2007) for different surfaces of an ombrotrophic drained peatland (0.4–0.7 in lawn and hummock surfaces; 0.15–0.2 in hollow surfaces). Innes *et al*. (2004) reported similar values (approximately 0.2) on agricultural soil. On natural boreal peatland the F/B ratio is lower, approximately 0.1 (Mörsky *et al*. 2008). It could be that both drainage and cultivation have increased the abundance of fungi in our study site, but that the peat extraction (annual removal of surface peat) at the site before RCG cultivation had originally a negative effect on the growth of fungi.

Our results agree with the concept that gram-negative bacteria (dominant in the uppermost layer of the reed canary grass site) and fungi prefer fresh organic compounds as their substrate but gram-positive bacteria (dominant in the bare peat) are able to use more recalcitrant substrates. Gram-negative bacteria are abundant in the rhizosphere and are known to use plant-derived substrates (Söderberg *et al*. 2004). Kramer and Gleixner (2008) observed a decrease in the amount of gram-negative bacteria along with a decrease in the utilization of recent plant carbon with increasing soil depth. This indicates that the lower soil layers are important when considering carbon sequestration potential in the soil as carbon turnover rate decreases with depth. A similar declining trend in the amount of gram-negative bacteria with depth was observed also in our study.

With shifts in the microbial community composition, the functioning of the soil ecosystems changes. Fungi have an important role in the turnover of soil carbon and nutrients. In the RCG ecosystems, the increased amount of fungi could favour sequestration of carbon derived from reed canary grass since fungi are considered to be more efficient than bacteria in substrate and nutrient utilization (Six *et al*. 2006). Potentially mycorrhizal fungi may have implications for carbon sequestration. The potential to sequester soil carbon is most likely greater in the deeper soil layers with relatively higher fungal biomass, lower abundance of gram-negative bacteria and lower carbon mineralization activity, while the uppermost soil layers showed huge increase in respiration rates and, consequently, potential carbon loss.

Taken together, we found indications that carbon losses may be increased especially from the uppermost peat layers due to accelerated microbial activity associated with the cultivation. On the other hand, some of the carbon derived from plants may be sequestered deeper in peat profile. The higher abundance of fungi in the cultivated area may also increase the carbon sequestartion.

Understanding the functioning of soil microbes is important since they control the carbon flow in soil. This study was the first attempt to elucidate how soil microbial community responds to plant cultivation in this special ecosystem. The observed changes indicate that eventhough the microbial activity increases, the changes in soil microbial community structure might enable carbon sequestration in the soil.

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