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The impact of long-term water level draw-down on microbial biomass: A comparative study from two peatland sites with different nutrient status

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ABSTRACT

We examined the effects of long-term (51 years) drainage on peat microbial communities using phospholipid fatty acid (PLFA) analysis. We analysed the peat profiles of natural and adjacent drained fen and bog sites. Viable microbes (i.e. microbial PLFA) were present in relatively large amounts even in the deepest peat layers of both peatland sites, a finding that warrants further investigation. Microbial biomass was generally higher in the fen than in the bog. Microbial community structure (indexed from PLFA) differed between the fen and bog sites and among depths. Although we did not exclude other factors, the effect of drainage on the total microbial biomass and community structure was not limited to the surface layers, but extended to the deepest layers of the fen and bog. Long-term drainage increased the total microbial PLFA biomass in the surface, subsurface and bottom layers of the fen, but decreased it in the surface and bottom layers of the bog site. Drainage also increased the characteristic FAs of Gram-positive and Gram-negative bacteria in the surface and subsurface layers of the fen, and decreased them in the bottom layers of the bog site. The characteristic fungal FA was only reduced in the surface layers of the bog site by drainage. Thus, by affecting the microbial community beyond the surface layers, long-term peatland water-level draw-down can alter the microbial contribution to deeper peat organic matter stabilization. This suggests that long-term drainage may have a more significant climate change effect than revealed by the surface layer analyses alone.

1. Introduction

Peatlands are crucial global carbon (C) stores [1,2], containing about 15–30% of all terrestrial organic C (OC); equivalent to 455 Gt (10^{15} g) C [1]. Microbes are key actors (as catalysts) in all peat biogeochemical processes, controlling the peat OC accumulation and decomposition [3]. They also contribute to the peat C exchange via respiration and, upon cell death, necromass addition to the peat soil organic matter (SOM), via the microbial carbon pump (MCP [4]). Different microbial groups, with complementary enzymatic activities and different responses to environmental variables, interact in the peat *C*-cycling processes [5]. For example, the Gram–negative and Gram–positive bacteria are mainly associated with the mineralization steps involving labile and more recalcitrant C materials, respectively [6], and the exo-enzymatic capabilities of fungi make them important in the decomposition of macromolecules and recalcitrant C materials [7,8]. Changes in climate factors, such as hydrology, affect microbial community biomass and activity, both spatially and temporarily [9,10].

Models predict a warmer global climate (average temperature increases of about 4 °C) up to the year 2100 [11] and, under these scenarios, increased evapotranspiration due to increased temperatures would lead to a lower water table (WT) in peatlands [12]. Persistent draw-down of the peatland WT affects the niches of peatland microbes by increasing the thickness of the aerated surface layer [10]. The impacts of changed hydrology on the microbial community depends on the peatland type, intensity of change and

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the extent of change in space and time [9,13–15]. While changes in microbial niches may lead to increased diversity in the short-term, repeated replacement of specialist by generalist microbes may lead to loss of diversity in the long-run [14]. Changes in plant species cover following water level draw-down also modifies the influence of temperature and water content on peat microbial activities [16]. Studies have suggested that drainage could increase or decrease total microbial biomass or the biomass of some microbial groups, depending on the peatland type and depth [9,13]. Jaatinen et al. [13] showed that fungi and actinobacteria suffer from drainage in a nutrient-rich fen, but that in a drained bog, while fungi either suffer or benefit, actinobacteria abundance remains the same or increases. Fungi and bacteria generally benefit (undergo biomass increase) from persistent drainage of wet mesotrophic fen sites, though actinobacteria suffer or show only minor responses [9,15]. Changes in peat C accumulation and decomposition activities following drainage have also been related to changes in the structure of below-ground microbial communities [5,16]. Altered microbial diversity, due to drainage-induced changes in the quality and quantity of OC inputs, coupled with better oxygen availability, could increase the rate of soil OC (SOC) cycling; this leads to changes in the balance of peat-atmosphere C exchange [5,10,17].

Phospholipid-derived fatty acids (PLFA) are reliable quantitative biomarkers of viable microbes, since they are short-lived and readily metabolized upon cell death. Microbial biomasses, community structure and community responses to changing peat hydrology at different sites, have been studied with PLFAs [9,13,18]. Differences in microbial community structures between peatlands and the effects of treatments (e.g drainage) have also been analysed in several studies based on PLFAs alone [13,18–21], and their results are similar to those obtained using other molecular methods [22].

To our knowledge, previous studies on the effects of drainage on microbial communities (like those mentioned above), focused on the upper layers of peatlands (e.g. Refs. [13,22]). However, drainage-induced increases in oxygenation coupled with temperature changes in the surface layers could prompt dissolved OC (DOC) release to deeper depths via the “enzymatic latch” process [23]. This increase in the flow and lability of DOC [24], coupled with deeper deposition of labile root exudates by roots of vascular plants [25–27], could modify the biomass of microbial communities and their composition in deeper peatland layers. Recent molecular evidence [17] and higher bulk peat stable C isotope ($\delta^{13}C$) values, indicating peat degradation in the bottom of drained peat, supports this view [17,28].

This study examined the effect of long-term drainage on microbial communities in depth profiles from surface to bottom layers of two peatland sites differing in nutrient status. We compared the biomasses and structures of the microbial communities (indexed by total and relative abundance of PLFA, respectively) between the natural and drained sides of fen and bog, representing boreal peatlands of different fertility after 51 years of water level drawdown. We also specifically investigated the effects of drainage on some selected microbial groups. We hypothesised that long-term WT decrease will (1) increase microbial biomass and (2) influence the microbial community structure in the deep anoxic layers. We also hypothesized that (3) there will be higher microbial biomass increase in the fen than in the bog site, due to long-term drainage.

2. Material and methods

2.1. Study sites

The study was conducted at two peatland sites (one fen and one bog) within the Lakkasuo boreal mire complex (61°47′N, 24°18′E, ca.150 m a.s.l.), in the Orivesi area in central Finland. At the nearest weather station to the sites in Juupajoki Hyytiälä (61°85′N, 24°29′E) the mean annual temperature was 3.5 °C and precipitation 711 mm for the period of 1981–2010 [29]. The sampling year was wetter than this long-term mean, with whole year precipitation of 907 mm and an average temperature of 3.2 °C. The mire complex comprises a large variety of typical Finnish mire site types [30]. Part of the Lakkasuo peatland was ditch-drained in 1961 (51 years before sampling) so that there are adjacent natural and drained sides of different fertility along a border ditch (Fig. S1). There were differences in the original fertility, WT and vegetation composition between the natural ombrotrophic cotton grass pine bog with *Sphagnum fuscum* hummocks (bog) and the natural minerotrophic tall sedge fen (fen) sites sampled. Drainage caused marked changes to the hydrology, peat and vegetation properties, carbon dioxide (CO_2) and CH_4 fluxes, especially at the drained fen ([28,30–33]; summarized in Table 1). For example, the six-month average WTs before the sampling date were −8.0 and −34.9 cm for the natural and drained fens, respectively, whereas it was −12.0 and −16.4 cm for the natural and drained bogs, respectively (Fig. 1). CO_2 fluxes increased in both sites whereas CH_4 fluxes ceased in the fen and were reduced by half in the bog after 30–32 years of drainage. Thus, there is strong evidence for significant, long-term changes in peat characteristics and greenhouse gas fluxes. The pH increased from the surface downwards in the natural and drained sides of both sites (Fig. S2). In general, the bog site is more acidic than the fen site and this was confirmed by previously reported pH values (Figs. S2 and S3). Although temperatures vary seasonally, the temperature in deep peat is rather constant (~6–8 °C). The bulk densities (BD) at different depths of the drained and natural sides are the same in the bog site, but different in the fen site (Fig. S2).

2.2. Soil sampling and water table level measurement

2.2.1. Initial soil sampling and water table measurement

In 2012 (November 22nd), three replicate sets of peat samples were collected from random points within each site, located several meters apart along a former boardwalk. Soil was sampled from 4 to −5 depths (0–25 cm, 25–50 cm, 50–100 cm and deepest 25 cm) starting at the surface and extending to the deepest layer above the mineral soil. Using a Russian pattern side-cutting sampler (5 × 50 cm [34,35]), samples were collected in segments along the profile from both the drained and adjacent natural sides. The samples were put into polyethylene bags, mixed and cooled immediately after collection in a box with crushed ice, and later stored at −20 °C until analysis. Part of the samples were oven dried and ground into a fine powder for analysis of their C and N content (Flash EA 1112 elemental analyser, Thermo Finnigan), with a certified birch leaf standard (Elementar Microanalysis, UK) used as a reference. Continuous (3-hourly) WT level measurements were recorded with an automatic WT-HR 64K logger (Fig. 1). The logger values were calibrated by manual measurements.

2.2.2. Additional peat properties measurements

Volumetric samples (from the same depths as the initial samples) were used for pH and temperature measurements, as well as for bulk density determination (Fig. S2). Sampling was done with a similar, but smaller, Russian pattern side-cutting sampler to that described above (5.2 * 50 cm; half cylinder diameter * length) on 14 October, 2015. Sampling and depth measurements were started under a living *Sphagnum* carpet. Samples were transferred from the sampler into plastic bags (Aromata, Lidl Stiftung & Co, Neckarsulm, Germany) and were mixed in the bag before insertion of a pH electrode coupled with a temperature sensor (WTW P3 pH/conductivity with electrode SenTix 41; Weilheim, Germany). Values of