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Response of fungal and actinobacterial communities to water-level drawdown in boreal peatland sites

Krista Peltoniemi [a,*], Hannu Fritze [a], Raija Laiho [b]

[a] Finnish Forest Research Institute, Vantaa Research Unit, P.O. Box 18, FI-01301 Vantaa, Finland
[b] Department of Forest Ecology, P.O. Box 27, University of Helsinki, FI-00014 Helsinki, Finland

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ABSTRACT

We used PCR-DGGE fingerprinting and direct sequencing to analyse the response of fungal and actinobacterial communities to changing hydrological conditions at 3 different sites in a boreal peatland complex in Finland. The experimental design involved a short-term (3 years; STD) and a long-term (43 years; LTD) water-level drawdown. Correspondence analyses of DGGE bands revealed differences in the communities between natural sites representing the nutrient-rich mesotrophic fen, the nutrient-poorer oligotrophic fen, and the nutrient-poor ombrotrophic bog. Still, most fungi and actinobacteria found in the pristine peatland seemed robust to the environmental variables. Both fungal and actinobacterial diversity was higher in the fens than in the bog. Fungal diversity increased significantly after STD whereas actinobacterial diversity did not respond to hydrology. Both fungal and actinobacterial communities became more similar between peatland types after LTD, which was not apparent after STD. Most sequences clustered equally between the two main fungal phyla Ascomycota and Basidiomycota. Sequencing revealed that basidiomycetes may respond more (either positively or negatively) to hydrological changes than ascomycetes. Overall, our results suggest that fungal responses to water-level drawdown depend on peatland type. Actinobacteria seem to be less sensitive to hydrological changes, although the response of some may similarly depend on peatland type.

1. Introduction

Peatlands represent the most important store of terrestrial carbon (C). Despite their importance in the global C cycle, microbial communities in peatlands are still poorly understood. Mapping the diversity of the different microbial groups in peatlands has just begun and the microbes involved in methane cycling, i.e., methanotrophic bacteria (e.g., Dedysh et al., 1998; Morris et al., 2002; Jaatinen et al., 2005; Raghoebarsing et al., 2005) and methanogenic archaea (e.g., Galand et al., 2002; Basiliko et al., 2003; Sizova et al., 2003), have been studied the most extensively. Bacterial diversity of peatlands has been explored with molecular methods in, e.g., *Sphagnum* bogs of New England (Morales et al., 2006), two drained fens in Slovenia (Kraigher et al., 2006), and a *Sphagnum* bog in western Siberia (Dedysh et al., 2006). The molecular studies have broadened our general view of the distribution of microbes in peatlands.

The response of microbial communities to a persistent decrease in the water-level is important to document, since this is the ultimate outcome in peatlands following drainage or climate warming. Comparative analysis of various peatland sites in the UK showed that even a short-term drought can change the microbial community and that any changes are dependent on peatland type and the microbial group (Kim et al., 2008). Peatlands sequester organic matter into the anoxic layer, but most of the C flux takes place in the often relatively thin oxic layers above the water level. Lowering the water level of a northern boreal fen is accompanied with coincided with an increased CO_2 flux from peat to the atmosphere (Jaatinen et al., 2008). In oxic conditions, fungi are considered to be the principal decomposers (e.g., Thormann, 2006a, b), although actinobacteria may contribute significantly to the decomposition of organic matter since they are mainly strict aerobes (Goodfellow and Williams, 1983) that can degrade polymers such as lignin, cellulose, pectin, and chitin as well as humic materials (McCarthy, 1987; Pankratov et al., 2006). In Russian peatlands, 30% of sequenced clones were most similar to actinobacteria (Dedysh et al., 2006) and certain members of this group have been found to play a leading role in cellulose degradation (Pankratov et al., 2006).

Here, we study the fungal and actinobacterial communities of a boreal peatland complex with polymerase chain reaction-denaturing gradient gel electrophoresis (PCR-DGGE) fingerprinting. We amplified 18S and 16S ribosomal DNA (rDNA) to study how the communities: (i) differ among pristine sites with different

* Corresponding author. Tel.: +358 10 211 2594; fax: +358 10 211 2206.
E-mail address: krista.peltoniemi@metla.fi (K. Peltoniemi).

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vegetation and nutrient levels and (ii) change following water-level drawdown. The sites covered the common peatland types in boreal Eurasia: two minerotrophic fens and an ombrotrophic bog exhibiting microtopographical variation as hummock, lawn level and hollow surfaces, and included a control (contemporary water-level regime) as well as two levels of hydrological manipulation. Results from our earlier work (Jaatinen et al., 2007) showed how both fungal and actinobacterial phospholipid fatty acids (PLFAs) biomarkers responded to water-level drawdown, and fungal PLFAs were positively correlated with potential CO_2 production in these sites, thus supporting our experimental rationale.

2. Materials and methods

2.1. Site description and sampling

Sampling was conducted at Lakkasuo peatland complex in central Finland (61°48′ N, 24°19′ E, ca. 150 m above sea level) on May 18, 2004. A detailed description of Lakkasuo and the study sites can be found elsewhere (Laine et al., 2004; Jaatinen et al., 2007). The study sites represented three different nutrient levels along a fen-bog gradient, each with a characteristic vegetation type: two minerotrophic fens; mesotrophic (ME; a relatively nutrient-rich "intermediate fen") and oligotrophic (OL, "poor fen"), and an ombrotrophic bog (OM; nutrient-poor) (hereafter referred to as nutrient levels; see Table 1 for surface peat nutrient concentrations and pH). Minerotrophic sites received ground water and nutrient inputs from the surrounding catchment whereas the ombrotrophic site was "fed" by precipitation and dry deposition only.

Each site (see abbreviations in Table 1) included a pristine control plot (P), a plot with short-term water-level drawdown (STD), and a plot with long-term water-level drawdown (LTD), all of which had uniform vegetation and soil properties before disturbance. The P and STD plots at the OM site included dry hummock (Hu), intermediate lawn (La) and wet hollow (Ho) microforms. The LTD plots were drained by ditching for forestry in 1961 and the STD plots were ditch drained in 2000/2001 to simulate a predicted effect of climate change (Laine et al., 2004). The average water-level drawdown induced in the STD plots was about 10 cm during the growing season of 2003 in all sites, which is close to the estimate for the impact of climate change on water levels in northern peatlands (Roulet et al., 1992). In the LTD plots, the average water levels were about 15 (bog)–30 (fen) cm deeper than in the corresponding pristine sites. Together, these plots formed a successional gradient from a wet pristine peatland towards a dry peatland forest (Laiho et al., 2003). Water levels at the time of sampling are given in Table 1. The upper limit of the anaerobic layer is usually 5–15 cm closer to the surface than water level (Lähde, 1969, 1971).

The vegetation in the pristine ME site was characterized by sedges (*Carex rostrata* Stokes, *Carex lasiocarpa* Ehrh.), some herbaceous species (e.g., *Potentilla palustris* Scop. and *Menyanthes trifoliata* L.) and mosses (e.g., *Sphagnum fallax* (Klinggr.) Klinggr.,

Table 1
Average water-levels, peat element concentrations and pH (6 mL fresh peat in water; 1:3; vol:vol) with standard errors (SE) for each plot at the time of sampling (May 2004).

Plot	WL (cm)	Layer	N	P	K	Ca	pH
P ME	0	L1	2.11 (0.21)	851 (74)	1021 (190)	5910 (804)	5.9 (0.18)
		L2	2.38 (0.02)	814 (17)	786 (64)	6410 (703)	5.7 (0.24)
		L4	2.61 (0.15)	558 (43)	96 (2)	6277 (433)	5.3 (0.02)
STD ME	−15	L1	2.08 (0.15)	933 (39)	1015 (90)	8317 (1230)	5.4 (0.22)
		L2	2.93 (0.10)	1110 (68)	620 (71)	5797 (282)	5.5 (0.13)
		L4	2.40 (0.03)	553 (23)	89 (14)	6370 (297)	5.0 (0.06)
LTD ME	−15	L1	1.52 (0.11)	704 (68)	851 (208)	3177 (352)	3.8 (0.06)
		L2	2.04 (0.34)	766 (116)	322 (17)	3247 (1012)	3.8 (0.13)
		L4	2.52 (0.21)	540 (40)	40 (3)	5127 (767)	4.5 (0.01)
P OL	−11	L1	1.23 (0.03)	338 (24)	958 (139)	5407 (122)	4.6 (0.05)
		L2	1.56 (0.12)	474 (36)	314 (37)	4423 (405)	4.6 (0.08)
		L4	2.54 (0.19)	806 (76)	57 (14)	3813 (128)	4.8 (0.01)
STD OL	−30	L1	1.36 (0.12)	401 (32)	1156 (214)	6830 (1203)	4.9 (0.30)
		L2	1.93 (0.11)	781 (46)	401 (47)	5237 (997)	4.9 (0.25)
		L4	2.54 (0.05)	806 (14)	50 (10)	3830 (101)	4.9 (0.05)
LTD OL	−30	L1	2.21 (0.20)	1330 (119)	734 (196)	3720 (465)	3.9 (0.07)
		L2	2.97 (0.04)	1243 (38)	189 (42)	2473 (238)	4.2 (0.12)
		L4	2.42 (0.05)	762 (19)	30 (0)	3183 (74)	4.6 (0.09)
P OM Hu	−22	L1	0.92 (0.07)	236 (27)	2017 (286)	1500 (32)	4.0 (0.09)
		L2	0.84 (0.08)	213 (18)	830 (215)	1327 (41)	3.8 (0.03)
		L4	1.10 (0.05)	276 (23)	161 (11)	1263 (43)	3.6 (0.03)
STD OM Hu	−24	L1	0.92 (0.01)	278 (41)	1305 (192)	1593 (149)	4.0 (0.14)
		L2	0.96 (0.01)	248 (27)	795 (59)	1247 (15)	3.6 (0.04)
		L4	1.18 (0.03)	280 (28)	222 (27)	1323 (98)	3.6 (0.02)
P OM La	−6	L1	0.87 (0.03)	170 (27)	1917 (406)	1180 (59)	4.4 (0.08)
		L2	0.93 (0.11)	200 (19)	609 (88)	1203 (58)	3.9 (0.08)
		L4	1.08 (0.07)	223 (13)	94 (10)	981 (80)	3.7 (0.06)
STD OM La	−15	L1	1.09 (0.13)	286 (35)	1152 (254)	1180 (49)	3.8 (0.09)
		L2	1.11 (0.09)	278 (55)	464 (28)	1233 (110)	3.7 (0.01)
		L4	1.18 (0.02)	240 (19)	101 (25)	998 (119)	3.8 (0.07)
P OM Ho	−3	L1	0.83 (0.03)	189 (16)	659 (318)	798 (18)	4.0 (0.11)
		L2	1.05 (0.06)	190 (28)	205 (68)	731 (8)	4.0 (0.04)
		L4	1.27 (0.04)	183 (12)	81 (14)	622 (55)	3.9 (0.06)
STD OM Ho	−10	L1	1.09 (0.12)	297 (32)	601 (82)	1023 (9)	4.0 (0.04)
		L2	1.20 (0.10)	246 (49)	216 (64)	825 (10)	4.1 (0.06)
		L4	1.36 (0.12)	228 (33)	57 (3)	721 (129)	3.9 (0.12)
LTD OM	−15	L1	1.48 (0.06)	814 (58)	791 (66)	2923 (156)	3.7 (0.15)
		L2	1.02 (0.05)	461 (38)	393 (59)	2197 (202)	3.6 (0.02)
		L4	1.13 (0.05)	260 (12)	52 (4)	1147 (208)	3.6 (0.01)

P, pristine; STD, short-term drainage; LTD, long-term drainage; ME, mesotrophic; OL, oligotrophic; OM, ombrotrophic; Hu, hummock; La, Lawn; Ho, hollow; WL, water-level. L1, 0–5 cm; L2, 5–10 cm; L4, 20–30 cm.
Nitrogen concentration was measured with a LECO CHN-1000 analyzer, the other element concentrations with an ICP emission spectrometer after dry ashing.