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Desiccation and product accumulation constrain heterotrophic anaerobic respiration in peats of an ombrotrophic temperate bog

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ABSTRACT

To gain insight into the effects of drying and rewetting events on anaerobic respiration in ombrotrophic peat soils, we investigated bacterial sulfate (SO_4) reduction and methane (CH_4) production in anaerobic incubations of intact peat microcores from 30 to 40 cm depth of Mer Bleue bog, Ontario/Canada. Concentrations of dissolved SO_4, carbon dioxide (CO_2), CH_4, acetate, and hydrogen (H_2) were recorded and net turnover rates calculated from regression. Gross rates of bacterial sulfate reduction were determined by $^{35}SO_4$ tracer incubation. After incubation, the peat was dried and rewetted, with saturated peat serving as control. CO_2 production was initially rapid (up to <360 nmol cm^{-3} d^{-1}) and slowed towards an endpoint of 2–3 mmol l^{-1}, which was only partly related to thresholds of Gibbs free energies of the involved processes. Acetate rapidly accumulated to levels of 600–800 μmol l^{-1} and remained constant thereafter. CH_4 production (0–2.8 nmol cm^{-3} d^{-1}) was small and delayed, even after SO_4 was depleted, by about 30–40 d. Hydrogenotrophic methanogenesis was endergonic and the process thus likely followed an acetotrophic pathway. Drying and rewetting replenished the SO_4 pool, enhanced SO_4 reduction rates and suppressed methanogenesis. The overall contribution of net SO_4 reduction and methanogenesis to the CO_2 production rate was small (0.5–22%) and only enhanced in replicates subjected to drying (35–62%). The major fraction of respiration in the incubated peat cores thus followed yet unidentified pathways.

1. Introduction

Peatlands store between 250 and 450 Gt of carbon (C) (Gorham, 1991; Turunen et al., 2002) and generally only slowly exchange carbon dioxide (CO_2) with the atmosphere due to low productivity and slow decomposition in cold, waterlogged, and anaerobic soils. Peatland soils are also sources of methane (CH_4), contributing about 4–10% to the atmospheric CH_4 burden (Fung et al., 1991). Peatlands are further mostly located in regions that are anticipated to undergo a significant climate change over the next decades, including more intense and frequent drought (Moore et al., 1998). How anaerobic respiration could be affected by more frequent and intense drying and rewetting and changes in the composition of soil solution is thus a question of interest.

It has been suggested that drying–rewetting events affect anaerobic respiration rates and the distribution between pathways of anaerobic respiration over time, in particular the rates of fermentation, SO_4 reduction, and methanogenesis. Terminal respiration and fermentation processes, which produce intermediates such as acetate, CO_2, and hydrogen (H_2) may then decouple (Shannon and White, 1996; van Hulzen et al., 1999), and the relative importance of methanogenic pathways shift (Avery et al., 2003). Elevated rates of anaerobic mineralization have also been described as a consequence of rewetting (Aerts and Ludwig, 1997; Blodau and Moore, 2003a).

Following drying–rewetting, the distribution between SO_4 reduction and methanogenesis can further be modified, with possible ramifications regarding methane emissions. Methanogenesis and bacterial SO_4 reduction contribute in variable portions to anaerobic respiration in ombrotrophic peats (Vile et al., 2003b), even when SO_4 pools in peat pore water are small (10–300 μmol l^{-1}) (Nedwell and Watson, 1995; Wieder et al., 1990). A periodic recycling of reduced sulfur back to oxidized forms, driven by penetration of oxygen into the peat during dry periods (Bayley et al., 1986), could thus fuel additional SO_4 reduction and continue to the suppression of methanogenesis after rewetting. Indeed it has been observed that methanogenesis lags behind oxygen depletion following water saturation (Kettunen et al., 1999; Öquist and Sundh, 1998). An inhibition of methanogenic enzyme systems as well as the desiccation of cells during a preceding dry period may contribute to this effect

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(Fetzer et al., 1993). Anaerobic respiration may finally be lowered by accumulation of CO_2 and CH_4, which is then restored by degassing during drought periods. Dissolved CO_2 concentrations above about 4–8 mmol l^{-1} are rare (e.g. Blodau et al., 2004). This fact is potentially related to slowing decomposition when Gibbs free energies of methanogenesis and fermentation diminish with end-product accumulation (Beer and Blodau, 2007).

In this contribution we investigated the process dynamics of anaerobic respiration in peat samples from an ombrotrophic peat bog during a drying and rewetting cycle in a controlled laboratory experiment. In particular we sought information about (I) the main pathways of CO_2 production, (II) the response of CO_2 and CH_4 production rates over time to the drying and rewetting events, and (III) the occurrence of product inhibition, for example by accumulation of CO_2. Process rates were quantified from concentration change over time in incubation experiments and by application of a ^{35}S-sulfate radiotracer, and dried and rewetted samples compared to anaerobic controls (Fig. 1).

2. Site, materials and methods

2.1. Sampling site

Mer Bleue is an open, slightly domed, and ombrotrophic peat bog 15 km east of Ottawa, Ontario, Canada, and dominated by mosses (e.g. *Sphagnum capillifolium*, *Sphagnum angustifolium*, *Sphagnum magellanicum* and *Polytrichum strictum*) and ericaceous shrubs (e.g. *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Kalmia angustifolia* and *Vaccinium myrtilloides*). Mer Bleue has been extensively investigated before (e.g. Moore et al., 2002). For our study, we selected a homogeneous area of about 100 m^2 in an ombrotrophic part (Fig. 1A) and sampled peat cores from adjacent hollows.

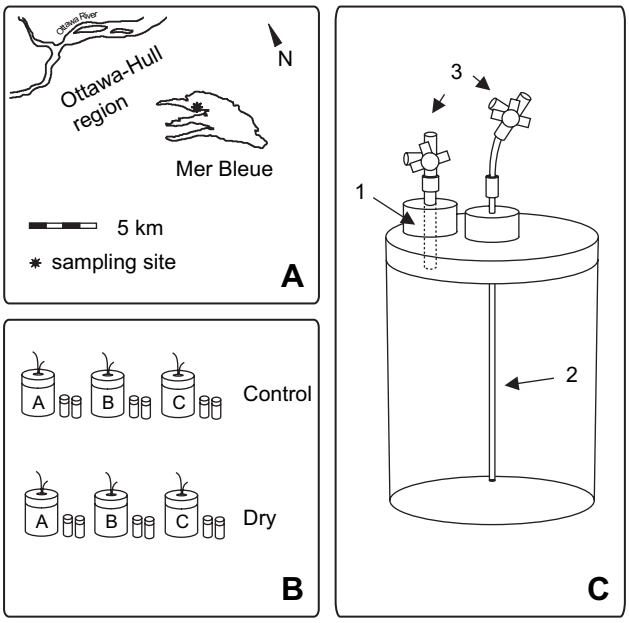

Fig. 1. (A) Sampling site in Mer Bleue peatland, near Ottawa, Ontario/Canada. (B) Design of incubation experiment. Three peat cores (A–C, depth 30–40 cm below surface) were divided into two subcores for incubation containers and four microcores in glass flasks. Sub- and microcores received same treatments: anaerobic incubation during Phase 1 of the experiment, and controlled drainage and headspace flushing [Dry] respective headspace flushing only [Control] before further incubation in Phase 2. Concentration time series were recorded from subcores, sulfate reduction rates by short-term radiotracer incubation at the end of both incubation phases determined on microcores. (C) Sketch of incubation container. (1) Headspace port for gaseous phase sampling and (2) polymer microsuction sampler (0.2 μm filter size) for pore water sampling. All access points are locked with three-way Luer stop cocks (3) to mount a syringe.

2.2. Experimental setup

Air-tight incubation flasks consisted of 440 ml glass containers with tin lid, a headspace port (gas-tight PVC tubing, Legris Inc.), and a microsuction sampler (porous polymer with glass fibre enforcement, 2.5 mm OD, pore size 1 μm, length 8 cm, PVC tubing, ecoTech GmbH) (Fig. 1C). All sampling devices were inserted through borings in the lids lined with butyl rubber stoppers and equipped with a Luer-lock three-way stop cock (polycarbonate) on the outer end, allowing the attachment of syringes. All connections were glued and sealed with liquid silicon rubber, and thoroughly dried before use. In tests with dried liquid rubber no DOC leaching could be detected.

2.3. Peat core sampling and processing

Three peat cores were taken on Sept. 25th, 2005, from peatland hollows with low cover of vascular plants to exclude effects of root respiration and excessive root decay. Visual examination suggested that cores did not contain noticeable quantities of living root biomass. A sharpened PVC tube (20 cm inner diameter, 80 cm length) was placed vertically on top of the peat surface, the peat core perimeter cut with a serrate knife, the tube pushed into the peat, and subsequently dug out covering the bottom with a plastic cap. Compaction of the cores was <10%. The cores were extruded on-site using an upright standing plunger. The sections 30–40 cm below moss surface were cut off, placed into flat cylindrical plastic containers fitting the 10 cm core slices, and flushed with nitrogen (N_2). The containers were sealed with duct tape, stored cool, and transported to the laboratory within 2–3 d, where two cylindrical subcores were extracted from each core, weighed, wrapped into nylon mosquito mesh, placed into the incubation flasks, and inundated with pore water surrogate typical for the site (500 μmol l^{-1} NaCl, 50 μmol l^{-1} Na_2SO_4, 50 μmol l^{-1} NH_4Cl and 60 μmol l^{-1} KCl). Two centimeters of gas headspace were allowed. The flasks were capped and subsequently flushed with pure nitrogen (N_2) three times. For the application of the ^{35}S radiotracer technique, from each subcore two additional microcores of approx. diameter 1 cm and a fresh weight of 12 g were taken, transferred to 20 ml glass crimp vials, treating the samples as described, and leaving a headspace (Fig. 1B). The vials were stoppered and crimped, and flushed with N_2 using two needles. The experiment was carried out in a climate chamber at 15 °C in the dark for the first 88 d (Phase 1).

From day 89 to 95, three replicates were opened and allowed to dry to their initial pore water content at a temperature of 20 °C, recording water loss gravimetrically. Subsequently the cores were re-saturated with pore water surrogate of the composition described above but without Na_2SO_4. This procedure resulted in three subcores without further treatment [Control], and three exposed to controlled drying [Dry]. The headspace of all six incubation containers was flushed with N_2 for 1 min, and the containers were transferred to the climate chamber (15 °C) for 22 d of further incubation (Phase 2). In total, pore water and headspace were sampled on 25 occasions in intervals ranging from 1 to 15 d.

2.4. Pore water analyses

Sulfate, nitrate (NO_3^-) and thiosulfate ($S_2O_3^{2-}$) were analyzed in filtered samples (0.2 μm nylon syringe microfilter) by ion chromatography (Metrohm IC system, Metrosep Anion Dual 3 separation column at 0.8 ml min^{-1} flow rate, conductivity detection after chemical suppression). Volatile fatty acids (VFA) were analyzed by