



Plant rhizosphere oxidation reduces methane production and emission in rewetted peatlands



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ARTICLE INFO

Keywords:

Peatlands
Suppression of methanogenesis
Restoration
Rhizosphere
Mediated electrochemical reduction and oxidation
Terminal electron acceptors

ABSTRACT

The global loss of peatlands, by drainage or peat extraction, has encouraged measures to restore these ecosystems and their function as carbon sinks. However, there is a potential of high emissions of the potent greenhouse gas CH₄ from restored peatlands. Vascular plants, which often dominate restored sites, play a key role in determining the amount of emitted CH₄: The plants can either fuel methanogenesis by supplying labile carbon or attenuate methanogenesis by transferring oxygen into the rhizosphere. To quantify the net effect of these counteracting processes, we tested in a two-pronged approach CH₄ production, emission, and the underlying processes in (1.) monoliths of three different restored cutover peatlands and in (2.) mesocosms with *Eriophorum vaginatum*, *E. angustifolium* and *Juncus effusus* versus controls with *Sphagnum* and bare peat. Despite waterlogged, and thus persisting anoxic conditions, concentrations of dissolved CH₄ remained close to zero in all tested monoliths. We ascribe this finding to two factors: The poor decomposability of the peat material, as determined in anoxic incubations, and the availability of alternative electron acceptors that sustained anaerobic respiration and competitively suppressed methanogenesis. While inorganic electron acceptor pools were small and rapidly diminished, dissolved organic matter provided constant electron acceptor capacity, indicating that reducible moieties in the organic matter were continuously re-oxidized in the rhizosphere of all tested vascular plant species. This continuous re-oxidation of the dissolved organic matter correlated with plant growth rates ($R^2 = 0.6\text{--}0.8$), suggesting that supply of oxygen through the aerenchyma of plant roots regenerated electron acceptor capacity in the rhizosphere. Vascular plants may have differential effects on the net ecosystem exchange, however, our findings suggest that CH₄ concentrations and emissions may remain low in restored cutover peatlands for months to years. Thus, waterlogging and vascular plant cover of degraded cutover peatlands does not necessarily create hot-spots of CH₄ emissions.

1. Introduction

Peatlands are significant carbon sinks - under waterlogged, anoxic conditions they accumulate incompletely decomposed organic matter (OM) as peat (Clymo, 1984; Dean and Gorham, 1998). Hence, there are currently more than 600 Gt carbon stored in peatlands, equivalent to about one third of the global soil organic carbon (International Peat Society, 2008; Yu et al., 2010). However, peatlands are a substantial biogenic source of the potent greenhouse gas methane (CH₄), and have a large contribution to the total natural and anthropogenic CH₄ emissions (Bridgman et al., 2013). Methane is produced under anoxic conditions after depletion of thermodynamically more favorable terminal electron acceptors (EAs) that are utilized for the oxidation of OM to carbon dioxide (CO₂) (Lovley and Klug, 1983; Conrad, 1999; Blodau,

2011). The typically considered and most abundant inorganic EAs are nitrate (NO₃⁻), ferric iron (Fe³⁺), and sulfate (SO₄²⁻) (Achtlich et al., 1995; Knorr and Blodau, 2009; Keller and Takagi, 2013). In addition to these canonical inorganic EAs, several studies provided evidence for the significance of organic matter (OM) as EA for anaerobic respiration in organic soils (Lovley et al., 1996; Keller and Bridgman, 2007; Klüpfel et al., 2014; Lau et al., 2014). In peatlands drained for agriculture, forestry, and peat extraction methanogenesis is suppressed due to the availability of oxygen (O₂) as potent EA. However, rapid peat oxidation under oxic conditions turns peatlands from carbon sinks into enormous carbon sources (Joosten and Couwenberg, 2001; Succow and Joosten, 2001; Joosten and Clarke, 2002; Waddington and Day, 2007; Lamers et al., 2014). Restoration of peatlands by rewetting is therefore increasingly recognized as a strategy to halt peat oxidation, to reestablish

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<https://doi.org/10.1016/j.soilbio.2018.07.006>

Received 21 December 2017; Received in revised form 28 June 2018; Accepted 8 July 2018

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peat forming vegetation, and thereby to re-initiate carbon accumulation (Bonn et al., 2016). Rewetting, however, recreates anoxic conditions under which methanogenesis again becomes a dominant pathway of decomposition. Furthermore, two additional factors have been discussed to create particularly high CH₄ production and emission, both of which coincide in rewetted peatlands: Firstly, altered hydrology, soil properties, and nutrient availability in rewetted peatlands usually favor graminoid dominated vascular vegetation instead of peat-forming *Sphagnum* species (Smolders et al., 2008; Lamers et al., 2014). In comparison to *Sphagnum*, OM of graminoid biomass and root exudates supply labile carbon substrates into an anoxic environment which may fuel methanogenesis (Aerts et al., 1999; Kerdrachoen, 2005). Secondly, transport of CH₄ to the atmosphere is facilitated by aerenchymatic tissues of graminoids rooting in waterlogged environments. Plant-mediated CH₄ transport effectively bypasses zones of CH₄ oxidation (Raghoebarsing et al., 2005; Larmola et al., 2010), and is well documented for the genus *Eriophorum* that can be abundant in restored cutover bogs (Whiting and Chanton, 1992; Frenzel and Rudolph, 1998; Greenup et al., 2000; Bhullar et al., 2013). However, the effect that graminoid vegetation can have on CH₄ production and emission may be ambiguous: On the one hand, venting of CH₄ through the aerenchyma may occur as discussed (Whiting and Chanton, 1992; Schimel, 1995; Shannon et al., 1996; Greenup et al., 2000; Evans, 2004). On the other hand, an aerenchyma provides O₂ to plants rooting in anoxic environments (Vartapetian and Jackson, 1997; Evans, 2004). Molecular O₂ leaking at the root surface may decrease CH₄ concentrations in the rhizosphere by promoting aerobic CH₄ oxidation (Jackson and Armstrong, 1999; Christensen et al., 2003; Evans, 2004) or possibly even suppression of methanogenesis by provision of thermodynamically more favorable EAs (Roden and Wetzel, 1996; Fritz et al., 2011). The extent of rhizosphere oxidation may relate to photosynthesis and total root biomass (Roura-Carol and Freeman, 1999; Dorodnikov et al., 2011; Fritz et al., 2011). In consequence, restored, graminoid dominated peatlands were considered hot-spots of CH₄ emissions (Wilson et al., 2009). For example, exceptionally high CH₄ emissions of 22–51 t CO₂ eqv ha⁻¹ y⁻¹ from graminoid dominated peatlands were reported 30 years after rewetting (Vanselow-Algan et al., 2015). By contrast, other studies found that in the first years after rewetting CH₄ emissions from restored peatlands were lower than from pristine systems (Komulainen et al., 1998; Tuittila et al., 2000). The vegetation, as important factor controlling CH₄ production and transport, can largely vary between sites and may thus explain differences in reported CH₄ emissions (Whiting and Chanton, 1993). Yet, a process-based understanding of the hydrology-vegetation-peat continuum to interpret such emissions remains poorly investigated. To improve the knowledge of potential production, emissions, and dynamics of CH₄ in graminoid dominated, restored peatlands, we conducted two experiments: We determined *ex situ* greenhouse gas (CO₂, CH₄) production, emission and the underlying processes at constant water table levels in intact peat monoliths obtained from three restored cutover bogs (hereafter referred to as (1.) monolith experiment). Thereby, we assessed the effects of graminoids on redox dynamics before and after vascular plant removal. In the second experiment we determined CO₂ and CH₄ production in plant mesocosms and the dynamics of EAs in the rhizosphere of single plant species (*Eriophorum vaginatum*, *E. angustifolium* and *Juncus effusus*) in relation to plant growth, and in comparison to *Sphagnum* and bare peat controls (hereafter referred to as (2.) mesocosm experiment). To characterize redox conditions in the rhizosphere, we considered not only the electron acceptor capacities (EAC) of the canonical, inorganic EAs (EAC_{inorg}), but also of dissolved OM (DOM, EAC_{DOM}) which we quantified by mediated electrochemical reduction (Aeschbacher et al., 2010). Both experiments and the approach to quantify total EAC (EAC_{tot} sum of EAC_{inorg} and EAC_{DOM}), served to assess whether methanogenesis was suppressed by oxidation of the rhizosphere through radial oxygen release from aerenchymatic plant roots, or if methanogenesis was instead fueled by the supply of labile carbon from root

exudates or decaying plant biomass.

2. Methods

2.1. Monolith experiment

Peat monoliths (40 cm depth, 30 cm diameter, ~28 L peat) were sampled in May of 2014 in two adjacent sites in the Benthullener Moor complex (53°03'40.0" N; 8°05'56.8" E), hereafter referred to as B3 and B7, and in the Veenhuser Königsmoor (53°17'18.1" N; 7°31'06.5" E), hereafter referred to as K3. The sites are located in the North-West German Plain (Lower Saxony, Germany), within a mild atlantic-subatlantic climate with a mean annual temperature of 9.6 °C and mean annual precipitation of 750–800 mm (DWD, 2017). Two monoliths per site were sampled into PVC sewage pipes, avoiding compaction. The monoliths were sealed with a fitted PVC cap to maintain anoxic conditions and to minimize pore water loss. All three peatland sites had originally been nutrient poor ombrotrophic bogs with peat deposits formed mainly from *Sphagnum papillosum* (LINDB.), and with smaller contributions from *Eriophorum vaginatum* (L.). The sites had been extensively drained, and used for agriculture and peat extraction. At the time of sampling, sites have been rewetted 3–7 years ago. The sites were rewetted immediately after industrial peat extraction, resulting in year-round inundation at each site (water table levels +10 cm–40 cm). While the sites differed in peat quality and nutrient status, *Juncus effusus* (L.), and *Sphagnum cuspidatum* (HOFFM.) dominated the vegetation at each site. Coverage by *Juncus effusus* was highest at B7, and lowest in K3. Nevertheless, the sampled monoliths contained a similar-sized tussock of *Juncus effusus* surrounded by *Sphagnum cuspidatum*. Table 1 lists key characteristics of the three sites. For peat characterization, three replicate peat cores were sampled at each site with a Russian peat corer (Eijkkelkamp Soil and Water, Giesbeek, Netherlands), cut in 10 cm increments, transported cooled to the lab and immediately frozen. Similarly, fresh peat from the 0–10 cm, 10–20 cm, and 20–30 cm depth increments was sampled in triplicate cores at each of the three sites for anaerobic incubations (*n* = 27). These incubations served to determine potential *in vitro* decomposition rates of the material present in the monoliths. These fresh peat samples were cooled, transported to the lab in plastic bags to avoid O₂ exposure, and then immediately processed. The monoliths were stored in a climate chamber (Plantmaster, CLF

Table 1
Characterization of sites for monolith sampling.

Site	Benthullener Moor		Königsmoor
	B3	B7	K3
Sampled monoliths (<i>n</i>)	2	2	2
Peat layer thickness (m)	0.5	1	> 1
Humification state ^a VON POST (1924)	H 5–6	H 4–5	H 4
Humification state ^{a,b}	0.91	0.88	0.89
Molar C:N ratio ^a	74	89	50
Molar C:P ratio ^a	895	1195	940
Time since rewetting (yr)	3	7	3
Water table at sampling (cm above surface)	10	30	25
Pore water pH ^c	4.5	4.2	4.3
Dominant vegetation (<i>in situ</i> and in sampled monoliths)	<i>Juncus effusus</i> , <i>Sphagnum cuspidatum</i>	<i>Juncus effusus</i> , <i>Sphagnum cuspidatum</i>	<i>Juncus effusus</i> , <i>Sphagnum cuspidatum</i>

^a Average of the upper 40 cm of three *in situ* sampled replicate peat profiles.

^b Calculated by Fourier-transformed infrared (FTIR) spectra, absorption ratio at wavenumbers of 1620 cm⁻¹ to 1091 cm⁻¹.

^c Average of four depth increments and duplicate monoliths.

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