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Peat origin and land use effects on microbial activity, respiration dynamics and exo-enzyme activities in drained peat soils in the Netherlands

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ABSTRACT

This study assessed the risk of decomposition-driven soil subsidence in drained peat soils in the Netherlands, contrasting in peat origin and current land use. In a full factorial design, fen peat and bog peat were sampled from sites in use for nature conservation and for dairy farming, which contrast in history of drainage and fertilisation. In these four peat types, which frequently occur in the Netherlands, the microbial activity and respiration dynamics were studied in samples from superficial oxic peat layers by measuring Substrate Induced Respiration (SIR) and Substrate Induced Growth Response (SIGR). Total and active microbial biomass, microbial growth potential and potential exo-enzyme activities were determined in unamended samples and after nitrogen and/or glucose amendments.

Remarkably, peat origin and land use did not affect basal respiration rates. In contrast, land use affected microbial biomass and potential growth rates as they were quadrupled in dairy meadows compared to nature reserves. This may be attributable to the pulses of organic and inorganic fertiliser that are being supplied in agricultural peatlands. Potential activities of oxidative exo-enzymes (phenol oxidase, POX, and phenol peroxidase, POD), in contrast, depended more on peat type, indicating a difference in peat substrate quality. Basal respiration rates and enzyme activities were not related. Phosphorus enrichment was identified as a potential driver of increased peat decomposition. The activity of the oxidative enzyme phenol oxidase and the concentration of phenolic compounds, which are considered to be the main regulators of peat decomposition according to the enzymic latch theory, were not related to respiration rates. It was concluded that decomposition theories like the enzymic latch theory (attributing a main role in the regulation of decomposition to phenolic compounds and phenol oxidase) were not supported by our research in the drained peat soils in the Netherlands.

1. Introduction

Currently, 450–550 Pg of carbon is in a sequestered state in peat soils worldwide. This is about 70% of the global atmospheric carbon stock (Joosten, 2010). This large carbon stock in peat soils has the potential to be rapidly converted into atmospheric carbon dioxide when environmental or climatological conditions change (Laiho, 2006). Peat soils in the Netherlands have been drained to facilitate agricultural use since centuries. This practice has converted Dutch peat soils from a net sink to a net source of carbon, through an increase in decomposition (Joosten, 2010). In order to anticipate on the resulting soil subsidence (Schothorst, 1977) and its expected future acceleration due to climate change (Keller et al., 2004; Dorrepaal et al., 2009), insight in the characteristics of peat decomposition is important for local and regional governments.

Soil heterotrophic microorganisms involved in the decomposition process produce enzymes that convert complex organic matter into simpler products such as carbon dioxide, water and mineral N molecules, with various intermediary products. These enzymes enter the environment through secretion and lysis and have been called ‘exo-enzymes’ (Sinsabaugh et al., 2009, 2010; Sinsabaugh and Shah, 2011). The factors determining the abundance,

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composition and activity of soil microbial communities include edaphic factors (soil type, moisture content, pH, nutrient availability), land management practices (drainage, fertilisation) and the vegetation composition (Borga et al., 1994; Fenner et al., 2005; Bougon et al., 2009; Eisenhauer et al., 2010).

Most peat in the Netherlands originates from fens and bogs. Fen peat develops in eutrophic conditions and consists of the remains of *Carex* spp., *Phragmites* spp. and/or woody species. On the other hand, bog peat is formed in ombrotrophic conditions and largely consists of *Sphagnum*-derived material. The decomposition of *Sphagnum*-derived organic matter (OM) is generally slower than that of OM formed by *Carex* spp. (Aerts et al., 1999; Scheffer et al., 2001). These differences have been attributed to the lower pH in bog peat compared to fen peat (Bergman et al., 1999) and to differences in chemical composition, which are associated with the botanical composition of the two peat types.

The presence of *Sphagnum*-derived OM restricts decomposition (Verhoeven and Toth, 1995). This effect has been shown to be related to the presence of inhibiting substances like the phenolic compound sphagnum acid (Verhoeven and Toth, 1995; Verhoeven and Liefveld, 1997). These phenolic compounds bind to exo-enzymes such as the hydrolytic enzymes phosphatase and β-glucosidase, which are thereby inactivated (Wetzel, 1992; Verhoeven and Liefveld, 1997; Freeman et al., 2001; Fenner and Freeman, 2011). The enzyme phenol oxidase (POX) catalyses non-specific oxidation reactions, thus stimulating the degradation of the inhibiting phenolic substances. POX is predominantly active in the presence of oxygen. Releasing the oxygen constraint by drainage will lead to increased POX activity, which in turn accelerates the decomposition of soluble phenolic compounds and reduces their inhibitory effect on soil exo-enzymes. This hypothesis is called the 'enzymic latch mechanism' (Freeman et al., 2001). Hence, POX is considered an important regulator of decomposition rates in peat (Freeman et al., 2001, 2004).

Apart from peat origin, land use is another important factor determining peat decomposition rate. In the Netherlands, there are near-natural peatlands with a high groundwater table and a species-rich vegetation, as well as peatlands in use for agriculture, mainly dairy production, with a highly productive species-poor vegetation of grasses growing in fertilised and drained peat soils. The possible effects of land use on the decomposition process are complex, because land use differences encompass an array of different aspects. Firstly, one could expect that the long history of drainage and occasional ploughing has stimulated POX activity leading to lower concentrations of phenolic compounds remaining. This would facilitate the decomposition process, according to the mentioned enzymic latch theory (Freeman et al., 2001; Fenner and Freeman, 2011). It is possible that this results in peat soils with a high proportion of amorphous and recalcitrant OM, as virtually all labile OM has been decomposed (Berg and Meentemeyer, 2002). Secondly, plant biodiversity is lower in agricultural meadows and fields than in nature reserves. The differences in plant community composition affect soil microorganisms as each plant species has a unique contribution to the functioning of the belowground system through their particular litter quality and root exudates (Eisenhauer et al., 2010). Furthermore, in the Dutch peat meadows, primary production is mostly removed by mowing and/or grazing, so that the material available for decomposition has a large proportion of roots and rhizomes. Lastly, OM decomposition is potentially affected by the large amounts of fertiliser applied in agricultural peatlands. Nitrogen addition stimulates the decomposition of easily degradable OM and hampers the decay of recalcitrant organic compounds, such as lignin and other phenolic compounds, as described in the nitrogen mining theory (Berg and Meentemeyer, 2002; Knorr et al., 2005; Moorhead and Sinsabaugh, 2006; Craine et al., 2007). Consequently, nitrogen addition reduces recalcitrant OM decomposition rates (Craine et al., 2007). This was demonstrated experimentally with cores of *Carex*-derived peat, which showed lower decomposition rates after nitrogen amendment (Aerts and Toet, 1997).

This differential response (stimulating as well as retarding) to nitrogen is also observed in potential activity of hydrolytic and oxidative enzymes (Carreiro et al., 2000). The exo-enzymes cellobiohydrolase (CBH) and β-1,4-glucosidase (BG), both involved in the degradation of easily degradable compounds, have been found to be stimulated after nitrogen addition to peat. At the same time, the activity of POX, which is involved in the degradation of recalcitrant (phenolic) compounds, is reduced after nitrogen addition (Carreiro et al., 2000; Sinsabaugh, 2010).

In this study, the effects of peat origin (fen vs. bog) and land use (agriculture vs. nature) on OM degradation in terms of respiration and exo-enzyme activities of peat soils were studied in a full factorial design. We determined respiration rates and potential enzyme activities upon ammonium and/or glucose addition as sources of nitrogen and energy. Furthermore, total microbial biomass and glucose-responsive microbial biomass were determined. We hypothesised that the bog peat from nature reserves has the lowest respiration rates due to the high concentration of phenolic compounds in living *Sphagnum* spp. and *Sphagnum*-derived peat, despite its fibric character. Furthermore, low respiration rates in drained fen hemic peat in agricultural land use were expected, because it was thought that the facilitation of decomposition by drainage of agriculturally used peat has resulted in amorphous peat with a higher recalcitrance of the remaining OM in comparison to the OM in nature reserves. The peat in agricultural use is, therefore, expected to show low decomposition rates in general, which are even further reduced after nitrogen amendment.

2. Material and methods

2.1. Study sites

In this study, the distinction is made between peat that originates from minerotrophic fens, consisting of the remains of *Carex* spp., *Phragmites* spp. and/or wood, and peat formed in ombrotrophic bogs, with a large proportion of *Sphagnum*-derived material. These are two major classes that can currently still be detected in drained peat meadow soils in the Netherlands. Table 1 presents the major characteristics of the common peat soils in the Netherlands. Both these peat types were collected in agriculturally used meadows as well as in nature reserves (Table), resulting in a full factorial design with four peat types. We will refer to these peat types as fen peat or bog peat under agricultural or natural land use. The agricultural sites have a monocultural vegetation of *Lolium perenne*, which is grazed by dairy cattle and mown for hay production. Fertilisation with manure, and occasionally artificial fertilizers, takes place 4–5 times a year through injection into the soil (ca. 150 kg N ha^{-1} yr^{-1} and 30 kg P ha^{-1} yr^{-1}). The sites with hemic fen peat were located in the peat meadows of Zuid-Holland and Utrecht and encompassed a *L. perenne* meadow in agricultural use near Zegveld as well as a mesotrophic hay meadow with a Calthion palustre vegetation type (Zuidhoff et al., 1996) which had never been fertilised in a nature reserve near Nieuwkoop. At the time of sampling, the agricultural meadow and the hay meadow had ditch water levels of 55 and 20 cm below soil surface, respectively. The agricultural meadow with oligotrophic *Sphagnum*-derived hemic peat was located in the province of Friesland and had a *L. perenne* monoculture. Here, the water table was approximately 30 cm below soil surface. The natural *Sphagnum* fibric bog peat was located in the nature reserve Fochteloërveen. This site had a water