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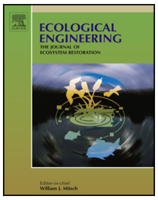

Sphagnum farming in a eutrophic world: The importance of optimal nutrient stoichiometry

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ABSTRACT

Large areas of peatlands have worldwide been drained to facilitate agriculture, which has adverse effects on the environment and the global climate. Agriculture on rewetted peatlands (paludiculture) provides a sustainable alternative to drainage-based agriculture. One form of paludiculture is the cultivation of *Sphagnum* moss, which can be used as a raw material for horticultural growing media. Under natural conditions, most *Sphagnum* mosses eligible for paludiculture typically predominate only in nutrient-poor wetland habitats. It is unknown, however, how the prevailing high nutrient levels in rewetted agricultural peatlands interfere with optimal *Sphagnum* production.

We therefore studied the effect of enriched nutrient conditions remaining even after top soil removal and further caused by external supply of nutrient-rich irrigation water and (generally) high inputs of atmospheric nitrogen (N) to habitat biogeochemistry, biomass production and nutrient stoichiometry of introduced *Sphagnum palustre* and *S. papillosum* in a rewetted peatland, which was formerly in intensive agricultural use.

Airborne N was responsible for the major supply of N. Phosphorus (P) and potassium (K) were mainly supplied by irrigation water. The prevailing high nutrient levels (P and K) are a result of nutrient-rich irrigation water from the surroundings. Peat porewater (10 cm below peatmoss surface) CO_2 concentrations were high, bicarbonate concentrations low, and the pH was around 4.2.

Provided that moisture supply is sufficient and dominance of fast-growing, larger graminoids suppressed (in order to avoid outshading of *Sphagnum* mosses), strikingly very high biomass yields of 6.7 and 6.5 t DW ha^{-1} yr^{-1} (*S. palustre* and *S. papillosum* [including *S. fallax* biomass], respectively) were obtained despite high N supply and biomass N concentrations. Despite high P and K supply and uptake, N:P and N:K ratios in the *Sphagnum* capitula were still low. *Sphagnum* mosses achieved high nutrient sequestration rates of 34 kg N, 17 kg K and 4 kg P ha^{-1} yr^{-1} from May 2013 to May 2014, which shows that the site acted as an active nutrient sink. Nutrient management still needs further improvement to reduce the competitive advantage of fast growing peatmoss species (cf. *S. fallax*) at the expense of slower growing but preferred peatmosses as horticultural substrate (*S. palustre* and *S. papillosum*) to optimize the quality of biomass yields.

In conclusion, Sphagnum farming is well able to thrive under high N input provided that there is a simultaneous high input of P and K from irrigation water, which facilitates high production rates. Due to the lack of suitable, nutrient poor sites, it seems to be useful to remove the topsoil (mainly P removal) prior to start growing *Sphagnum* mosses. In addition, bicarbonate concentrations have to stay sufficientlylow to ensure a low pH, CO_2 supply from the peat soil should be sufficiently high to prevent C limitation, and graminoids should be mown regularly.

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1. Introduction

Worldwide, large areas of peatlands have been drained to facilitate agriculture, forestry and peat extraction (Grootjans et al., 2006; Zedler and Kercher, 2005). These activities destroy the biodiversity, carbon storage capacity and hydrological regulation function of fens and bogs (Hassan et al., 2005; Lamers et al., 2015; Verhagen et al., 2009; Verhoeven and Setter, 2010). Large-scale drainage of peatlands globally results in carbon dioxide (CO_2) and nitrous oxide (N_2O) emissions of more than 2 Gt CO_2-eq yr^{-1} (Joosten and Couwenberg, 2009). Apart from increased CO_2 and N_2O emissions, continuation of peatland drainage to sustain agricultural activities leads to severe land subsidence, deterioration of surface and groundwater quality and higher flood risk (Dawson et al., 2010; Lamers et al., 2015; Schothorst, 1977; Verhoeven and Setter, 2010). Currently, agricultural yields on drained peatlands are decreasing and it is becoming more difficult to cover the ever-increasing drainage costs, emphasizing the urgent need for alternative land use for these agriculturally-used peatlands (Joosten and Clarke 2002; Kowatch 2007; Wichtmann and Joosten, 2007).

A solution to these problems would be paludiculture. Paludiculture (from Latin “palus” = “mire, swamp”) is agriculture on wet or rewetted peatlands, with cultivation of wetland species such as *Phragmites australis, Typha* spp. or *Sphagnum* moss spp., in a way that preserves the peat body (Joosten et al., 2012). The benefits of paludiculture as opposed to conventional drainage-based land use on peat soils are considerable (cf. Joosten et al., 2012). The high water table associated with paludiculture stops peat oxidation and land subsidence, because less peat is aerated, which results in much lower peat decomposition rates (Dawson et al., 2010; Renger et al., 2002). Nutrient discharge into groundwater and surface water is reduced due to lower mineralization rates. Furthermore, ecosystem services including water purification and water retention in peatlands are restored (Joosten et al., 2012).

In this study we focus on the paludiculture crop *Sphagnum* (peatmoss) as a renewable source of raw material for horticultural growing media, which provides a sustainable alternative to unsustainably extracted *Sphagnum* peat. In pristine bogs and poor fens, *Sphagnum*, a genus of bryophytes, is very common and is often the dominant vegetation and peat forming species (Clymo et al., 1984). Like vascular plants, *Sphagnum* productivity is related to pH, water and nutrient availability. However, *Sphagnum* differs by its adaptation to oligotrophic, acidic and wet environments (Clymo, 1964). As a genuine ecosystem engineer, it keeps its environment oligotrophic by efficient nutrient sequestration and very low mineralization rates, and acidic by proton exchange and the production of organic acids. *Sphagnum* strongly limits nutrient mineralization by its low decomposability and the acidic anaerobic environment created (Aerts et al., 1992; Clymo 1963, 1964; Halsey et al., 2000; Lamers et al., 1999; Limpens et al., 2004; Scheffer et al., 2001). *Sphagnum* mosses do not have roots and take up nutrients efficiently via their leaves and stem (Fritz et al., 2014).

Low nutrient concentrations, however, also limit primary production of *Sphagnum*, like it does for any other plant species. In general, the limiting nutrient in pristine bogs appears to be nitrogen (N) (Bragazza et al., 2005, 2004; Lamers et al., 2000), or a combination of N and phosphorus (P) (Fritz et al., 2012). Increases in N supply by increased anthropogenic N deposition from the atmosphere can at first be sequestered by *Sphagnum* species and used for increased growth (Chiwa et al., 2016; Lamers et al., 2000). N concentrations in the *Sphagnum* capitula may reflect the N-availability from rain and surface water supply (Novak et al., 2015) and from N_2 fixation (Lamers et al., 2000). Depending on whether N is limiting biomass production, N concentrations may be increased by higher N availability (luxury consumption, i.e. when other factors are limiting growth), or remain more or less similar (if N is limiting or co-limiting). By rapidly sequestering N, *Sphagnum* acts as a nutrient filter, decreasing nutrient (pore)water concentrations in the rhizosphere of vascular plants (Chiwa et al., 2016; Fritz et al., 2014; Lamers et al., 2000).

However, when N input becomes too high, P will become limiting for *Sphagnum* growth and excess N cannot be allocated to increased growth (Bragazza et al., 2004; Limpens et al., 2011). This may result in internal ammonium (NH_4^+) detoxification evident as N-rich amino acid accumulation and even NH_4^+ poisoning (Bragazza et al., 2012, 2006; Breeuwer et al., 2009; Limpens and Berendse, 2003). Currently, it is debated whether a balanced nutrient stoichiometry can alleviate negative effects of N and if *Sphagnum* can consequently sustain its growth rate under high but balanced nutrient loadings (Bragazza et al., 2004; Jirousek et al., 2011; Limpens et al., 2011).

In this study the peatmoss species *Sphagnum palustre* L., *S. papillosum* Lindb. and *S. fallax* Klinggr. were used (taxonomy follows Michaelis, 2011) as they are common and widespread species with different ecological demands. While the first two species belong to the section Sphagnum, *S. fallax* is included in the section Cuspidata (Daniels and Eddy, 1985; Michaelis, 2011). Natural habitats for these species are described after Daniels and Eddy (1985) and Frahm and Frey (2003).

S. palustre grows in mesotrophic to eutrophic peatland habitats like in wet fen woodlands, and under more open situations in ditches, along streams and at lake margins. It forms loose carpets or tussocks, is shade tolerant and absent from calcareous and strongly acid locations. *S. papillosum* is mainly found in oligotrophic, but also mesotrophic open acid peatlands. It grows at low hummocks to extensive carpets and lawns and is less tolerant of base-rich conditions than *S. palustre*. *S. fallax* occurs in oligotrophic to mesotrophic, but also minerotrophic peatlands in open to shaded habitats. It forms wide lawns and is tolerant of a fairly wide range of hydrological and chemical conditions.

Here we present a study on *Sphagnum* cultivated in a managed paludiculture field site on a rewetted former agricultural peatland. The goal of this *Sphagnum* biomass production is to provide a sustainable alternative to the ongoing extraction of non-renewable white peat (slightly humified *Sphagnum* peat) that is presently being used as a raw material for horticultural growing media (Emmel, 2008; Gaudig et al., 2014; Gaudig and Joosten, 2002; Reinikainen et al., 2012; Wichmann et al., 2014). We hypothesized that (1) the high N supply at this location limits *Sphagnum* biomass production, (2) *Sphagnum* species differ in their response to nutrient availability and stoichiometry, and (3) *Sphagnum* production rates, and N and P accumulation rates in the peatmoss biomass are dependent on site management.

2. Materials and methods

2.1. Study site

The study site is a former bog, situated near Rastede, North-Western Germany (N 53°26′32,4; E 08°26′84,3), with a peat layer of around 2–2.5 m depth that has been drained and used as intensively fertilized agricultural grassland since the 1950s. In March 2011, the 4 ha study field (which is still surrounded by agricultural grasslands on peat soil) was established (Gaudig et al., 2014). The upper 30–50 cm of degraded peat was removed to expose the underlying hardly decomposed and nutrient poor *Sphagnum* peat (98% organic matter content), which has a high water holding capacity and hydrological conductivity. This resulted in an area with maximum height differences of 9.8 cm.

Two *Sphagnum* species were introduced: *S. palustre* and *S. papillosum*. *S. palustre* or *S. papillosum* donor material consisted of 16% or <1% *S. fallax* (based on volume), respectively. Peatmoss fragments