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The impact of drying on the structure and photosynthesis of boreal peatland vegetation

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Academic Dissertation

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ABSTRACT

Boreal peatlands harbour large stores of carbon as peat below their surfaces. Climate change is expected to cause drying in northern peatlands, which will in turn impact the carbon balance of these ecosystems that is maintained by high water tables and the hydrologically sensitive plants growing there. This study aims to quantify how vegetation will be structured (I) and photosynthesize (II, III) in a future climate as emulated by long-term water level drawdown (WLD). To do this, changes in the vegetation and its photosynthesis after WLD are linked, and the response of *Sphagnum* mosses to periodic drought is investigated.

Field measurements were done at a long-term WLD field experiment that contained a rich (mesotrophic) fen, a poor (oligotrophic) fen and a bog (ombrotrophic) site. Measurements included vegetation surveys from existing permanent sample plots and leaf-level carbon dioxide exchange measurements. For an experiment in controlled conditions peatland surface cores from this field experiment were transported to a greenhouse where the photosynthesis of lawn Sphagna during and after an experimental periodic drought was measured.

The field study revealed that the response of peatland vegetation to WLD depend on peatland type. The species composition in the rich fen was the most impacted by WLD, while the bog vegetation demonstrated stability. Similarly, large increases in photosynthesis occurred following WLD on the vascular plant-covered rich fen, while changes were negligible on the *Sphagnum*-carpeted bog. The vegetation on the two fens shifted from an open sedge-, or sedge and *Sphagnum*-dominated ecosystem, to a tree-dominated ecosystem. Canopy development following WLD further accelerated vegetation changes by shading and sheltering the understorey vegetation. Vascular plants were the most likely to increase productivity from WLD as they are best suited to utilize the nutrients made available by peat mineralization, while *Sphagnum* moss photosynthesis was impacted little. The greenhouse study revealed that lawn *Sphagnum* mosses exposed to long-term WLD were more vulnerable to drought compared to those from wet sites. Large capitula typical to fen *Sphagnum* species appeared to be beneficial for surviving periodic drought.

This work demonstrated that climate change as emulated by long-term WLD will have a large impact on the vegetation composition of northern peatlands and increase photosynthetic function of these ecosystems, fens in particular. To better predict climate feedbacks from these changes, carbon dynamics including peatland vegetation dynamics should be updated in global process models. Future research to better understand the tipping point of different peatland types after WLD in different climatic regions will help us to predict changes in these diverse and globally important systems.

Keywords: plant species composition, *Sphagnum*, global change ecology, carbon fixation, periodic drought, water level drawdown

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Joensuu, January 2024
Nicola Kokkonen

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on data presented in the following articles, referred to by the Roman numerals I-III. The articles I and II are reprinted with the kind permission of the publisher or with rights retained as author. Article III is a submitted version of the manuscript.

I. Kokkonen, N.A., Laine, A.M., Laine, J., Vasander, H., Kurki, K., Gong, J., and Tuittila, E.-S. (2019) Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. Journal of Vegetation Science. 30 (6), 1206-1216. https://doi.org/10.1111/jvs.12794

II. Kokkonen, N. A., Laine, A.M., Männistö, E., Mehtätalo, L., Korrensalo, A., and Tuittila, E.-S. (2022) Two mechanisms drive changes in boreal peatland photosynthesis following long-term water level drawdown: species turnover and altered photosynthetic capacity. Ecosystems. 25 (7), 1601-1618. https://doi.org/10.1007/s10021-021-00736-3

III. Kokkonen, N.A., Laine, A.M., Korrensalo, A., Nijp, J., Limpens, J., Mehtätalo, L., Männistö, E., and Tuittila, E.-S. (2024) A deepened water table increases the vulnerability of peat mosses to periodic drought. Submitted manuscript.

The above publications have been included at the end of this thesis with their copyright holders' permission.

AUTHOR'S CONTRIBUTION

Nicola Kokkonen is fully responsible for the summary of this doctoral thesis.

I. N Kokkonen was the main author of this article and also participated in data collection (2016 only), data analysis, and critical revision of the manuscript. Other authors contributed in part to all stages.

II. N Kokkonen was the main author of this article. She was also primarily responsible for conducting photosynthesis measurements and vegetation cover data (2016 only). N. Kokkonen was fully responsible for upscaling analyses and participated in other analyses, but non-linear mixed effects models were primarily developed by L. Mehtätalo. All other authors contributed to the planning, writing and critical development of this article.

III. N Kokkonen was the main author of this article. She also participated in planning the study, data collection, analyses, and critical revision. Non-linear mixed-effects models were primarily developed by L. Mehtätalo, and all other authors contributed in part to all stages of the study.

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ABBREVIATIONS

CO_2	carbon dioxide
P_{max}	maximum photosynthesis
PPFD	photon flux density
R	dark respiration
WLD	water level drawdown
WT	water table

1. INTRODUCTION

1.1 Feedbacks between peatlands, climate, and carbon storage

Boreal peatlands are under pressure as their water tables (WT) are expected to deepen (Gong et al., 2012; Helbig et al., 2020; Roulet et al., 1992) and growing season droughts are expected to increase in frequency and severity (Donat et al., 2016; IPCC, 2023; Rinne et al., 2020) due to increased evapotranspiration and extreme precipitation patterns associated with climate change. Peatland drainage for agriculture, forestry, and biofuel uses adds additional pressure on these valuable ecosystems and turns them from carbon sinks to carbon sources (Frolking et al., 2011). Northern peatlands have accumulated carbon in the form of peat over the Holocene period. In these ecosystems, the anaerobic conditions present below high water tables, cool temperatures, and acidifying Sphagna slow the rate of decomposition to be lower than the rate of photosynthesis (Clymo, 1984; Rydin et al., 2006). However, projected climatic patterns are expected to destabilize the massive carbon stores (Zhang et al., 2022) – up to 1/3 of global terrestrial carbon or over 1000 GT (Amesbury et al., 2019; Ratcliffe et al., 2021; Yu et al., 2011) – in northern peatlands primarily by increasing decomposition (Straková et al., 2012). However, the impact of long-term drying and seasonal droughts on carbon uptake, i.e., photosynthesis, is little studied across the range of peatland types. By studying this key process, we can better understand if and how the carbon storage of peatlands will shift as the delicate balance between photosynthesis and decomposition changes under the force of a warming climate.

1.2 WLD as a proxy for the long-term impact of climate change on peatlands

The impact of rising global temperatures is predicted to be greatest at high latitudes (IPCC, 2023) and deeper WTs in peatlands are expected despite increased precipitation in northern latitudes (Helbig et al., 2020). Peatland vegetation is largely defined by ecohydrology, namely water table depth and water quality (Rydin & Jeglum, 2013), meaning a lower WT will change the peatland plant community composition and photosynthesis. The warming itself, however, has very little impact on peatland vegetation without a combined drying also occurring (Laine et al., 2018; Mäkiranta et al., 2018; McPartland et al., 2019). As such, water level drawdown (WLD) – a moderate experimental drainage of a peatland – is a good proxy for the impact of climate change on peatland plants. It has been used globally to study changes in peatland vegetation and gas fluxes (Ballantyne et al., 2014; Granath et al., 2009; Jaatinen et al., 2007; Laine et al., 2009; Macrae et al., 2013; Mäkiranta et al., 2018; Munir et al., 2014; Peltoniemi et al., 2015; Riutta et al., 2007; Straková et al., 2012; Weltzin et al., 2000; Whittington & Price, 2006).

1.3 Role of hydrology in peatland variation

Peatlands are a diverse group of ecosystems that are unified by high WTs but have distinct ecohydrological patterns that are likely to have unique reactions to climatic change. Minerotrophic peatlands (fens) receive water as lateral flow from surrounding upland soils, which contain dissolved minerals (Rydin & Jeglum, 2013). Within fens, peatlands are defined by their nutrient availability ranging from rich (eutrophic and mesotrophic) to poor (oligotrophic) (Rydin & Jeglum, 2013). Ombrotrophic peatlands (bogs) on the other hand, have surfaces above the impact enriched lateral flow and groundwater making them nutrient-poor habitats (Rydin & Jeglum, 2013). Precipitation plays an important role in surface moisture conditions in bogs (Nijp et al., 2014), but can make surfaces vulnerable to periodic droughts (Rydin & Jeglum, 2013). As a consequence of differing hydrology between fens and bogs, vegetation composition also differs between these two peatland types. Bogs have extensive *Sphagnum* moss cover across all microtopography with dwarf shrubs on hummocks, sedges and forbs are more dominant in fens. Poor fens are intermediate to bogs and rich fens; while the dense *Sphagnum* cover in the bottom layer poor fens resembles bogs, the field layer features large sedge species similarly to rich fens (Zhang et al., 2021). Studies focusing on one peatland type cannot account for differences in hydrology and vegetation between peatland types; these differences likely result in distinctive reactions to climate change ranging from stability to accelerating change (Antala et al., 2022; Laine et al., 2009; Miller et al., 2015; Munir et al., 2014; Strack et al., 2006; Weltzin et al., 2003). In my thesis, I use a range of peatland types to improve our understanding of climate change across a diverse peatland ecosystems characteristic to the Holarctic region.

1.4 Peatland microtopography

Within each peatland type, microtopography – on a scale of centimeters (Graham et al., 2020) – is a driving force behind the variation in plant community composition (Rydin & Jeglum, 2013; Sjörs, 1948). Different habitats are formed by peat accumulation (Hájek, 2009; Rydin et al., 2006) and defined by position relative to the WT (Graham et al., 2020; Rydin & Jeglum, 2013; Sjörs, 1948). Each microform type is associated with unique plant communities that have specialized growth forms and strategies (Andrus, 1986; Sjörs, 1948) to enable them to be productive in these limiting environments. Hummocks are the highest microform and are characterized by a dense *Sphagnum* carpet and ericaceous dwarf shrubs in both fens and bogs (Sjörs, 1948). Lawns, on the other hand, differ between fens and bogs. In bogs, lawns are dominated by Sphagna and host a diversity of *Sphagnum* species (Rydin & Jeglum, 2013; Sjörs, 1948). Fen lawns are characterized by sedges and other vascular species, below which a loose carpet of Sphagna and brown mosses grow (Rydin & Jeglum, 2013). Hollows, or flarks in fens, are the lowest vegetated microtopographical position and are often at or below the water table – an inundated habitat that requires specific adaptations for vascular plants and where Sphagna and brown mosses form very loose carpet cover or individuals (Rydin & Jeglum, 2013; Sjörs, 1948). Further distinctions in microtopography (such as mud bottoms, low lawns, and high lawns) are often made, but differences are more subtle and often not defined by WT depth alone (Rydin & Jeglum, 2013).

Microform communities differ not only in plant species composition, but also in their gas exchange (Bubier et al., 2003; Korrensalo et al., 2018, 2020), and likely their reaction to climate change as well (Strack et al., 2006). By understanding the impact of drying at a microform-level, our insights are valuable to peatlands with different variations of microform patterning, i.e., drier or wetter peatlands than those included in this work (Graham et al., 2020).

1.5 The role of *Sphagnum* mosses in peatlands

Sphagna are ecosystem engineers in peatlands where they often form much of the surface vegetation and are capable of altering their environment (Andrus, 1986; Rydin et al., 2006; Rydin & Jeglum, 2013). Lacking root systems, *Sphagnum* mosses are particularly sensitive to the hydrology of their surroundings and occupy very specific WT positions making them vulnerable to WT changes (Gunnarsson, 2005; Murray et al., 1989; Sytiuk et al., 2020). Sphagna play a key role in the buildup of peat particularly in bogs, but also to some extent in fens (Clymo & Hayward, 1982; Rydin et al., 2006; Rydin & Jeglum, 2013). *Sphagnum* litter is not easily decomposed and the mosses themselves increase the acidity of their environment resulting in a further slowing of decomposition processes (Clymo, 1984; Laiho, 2006; Rydin et al., 2006; Straková et al., 2012). Thus, the accumulation of peat increases.

The photosynthesis of non-vascular *Sphagnum* mosses is tied to their water content: too wet and gas diffusion on leaf surfaces is blocked, too dry and cells lose turgor and photosynthesis slows down (Gerdol et al., 1996; Hájek & Vicherová, 2014; Schipperges & Rydin, 1998; Tuittila et al., 2004). To maintain water availability without a vascular system, Sphagna rely on adaptations such as hyaline cells to store water in leaves, long fascicles, and curved leaves to create extracellular pore spaces, and formation of dense carpets to avoid desiccation when WTs are deep or precipitation is infrequent (Bengtsson et al., 2020; Rydin & Jeglum, 2013; Sytiuk et al., 2020). Due to the importance of Sphagna as ecosystem engineers in peatlands, their role in peat accumulation, and their sensitivity to hydrological changes, it is essential to understand the impact of climate change on *Sphagnum* communities.

Sphagnum mosses have relatively high intraspecific trait variability allowing species to adapt to different moisture conditions (Bengtsson et al., 2020; Laine et al., 2021; Sytiuk et al., 2020). However, the habitat range (i.e., height above the WT) of most Sphagna is relatively narrow and species can be grouped into functional types depending on their microform habitat (Andrus, 1986; Bengtsson et al., 2016; Korrensalo et al., 2016; Väliranta et al., 2007). Hummock Sphagna have adapted to avoid drought under dry conditions by forming dense carpets promoting capillary rise and they are therefore likely to be resilient to a new, drier, hydrological regime induced by climate change (Bengtsson et al., 2016; Hájek & Vicherová, 2014; Rydin, 1995; Schipperges & Rydin, 1998). On the other hand, hollow vegetation avoids drought by growing close to pools and water sources, which often remain moist even in summer droughts, thereby protecting hollow-inhabiting vegetation from the most extreme drought stresses (Hájek & Vicherová, 2014). Lawn Sphagna, however, lack both these desiccation-avoidance strategies and are of particular interest as this makes them sensitive to hydrological changes (Bengtsson et al., 2016; Hájek & Vicherová, 2014; Rydin et al., 2006). In this case, Sphagna have the ability to acclimate to drier conditions and withstand periodic drought either by increasing water-retaining structural traits (Bengtsson et al., 2020; Gong et al., 2020; Jassey & Signarbieux, 2019; Laine et al., 2021) or changing chemical processes following hardening (Gerdol et al., 1996; Hájek & Vicherová, 2014; Murray et al., 1989; Titus et al., 1983). To understand *Sphagnum* moss photosynthesis and community turnover during predicted future climate extremes, we must assess the extent that acclimation to drying occurs in mosses.

1.6 Vascular plants in peatlands

In contrast to Sphagna that are adapted to avoid dry conditions, vascular plants in peatlands are adapted to survive high WTs and limited nutrients (Rydin & Jeglum, 2013). Conservative growth strategies are widespread among peatland-inhabiting vascular plants; low photosynthesis rates, nutrient recycling, and small growth form are common traits among peatland plants (Grime, 2001; Korrensalo et al., 2016; Rydin & Jeglum, 2013; Small, 1972). Aerenchyma – hollow tubes in the roots and stems of certain vascular plants – transport gases below the WT and allow these plants to grow in otherwise saturated anaerobic conditions (Rydin & Jeglum, 2013). Non-aerenchymatic species are forced to occupy the higher microforms to keep their roots above the water table (Rydin & Jeglum, 2013): a strategy that leaves them prone to desiccation and makes small, waxy, or inrolled leaves beneficial in these exposed conditions (Crawford, 1983; Laine et al., 2021). Compared to bogs where limiting conditions make acid-tolerating ericaceous shrubs are the most common vascular species, fens tend to have higher cover and diversity of vascular plants (Rydin & Jeglum, 2013; Sjörs, 1948; Warner & Asada, 2006). The relatively nutrient-rich groundwaters that flow into fens mean that acquisitive plants can grow here; sedges (*Carex* spp.), deciduous shrubs, and herbs make vascular plant communities in fens diverse (Robroek et al., 2017; Rydin & Jeglum, 2013). Depending on the WT and water chemistry, vascular plants in peatlands can include trees with cover ranging from sparse individuals to a multi-layered canopy (Rydin & Jeglum, 2013). Plants in different peatland types are likely to respond differently to a deepened WT due to diverse species assemblages; some may benefit from drainage and increase growth, while others may suffer from drying and give way to acquisitive species.

1.7 Photosynthesis of peatland vegetation

Peat accumulation in mires occurs because plant material is created faster than it decomposes in these waterlogged ecosystems. However, photosynthesis rates tend to be lower in peatlands than in terrestrial systems due to the restrictive environment for plant growth. Sphagna in particular have lower photosynthesis rates than vascular plants (Korrensalo et al., 2016), but the cover of these mosses is so extensive in peatlands that the overall contribution to total biomass production and to peat is significant - up to an estimated 300Gt dry mass of *Sphagnum* exists in boreal peatlands (Rydin & Jeglum, 2013). Vascular plants have higher photosynthesis rates in fens than in bogs because higher nutrient availability in fens supports species with acquisitive growth strategies (Laine et al., 2021). Overall, photosynthesis is closely tied to the water table (Korrensalo et al., 2020), which varies by peatland type and microtopographical position, and is therefore expected to respond to WLD.

Sphagnum photosynthesis rates tend to decrease with increased distance to the water table (Schipperges & Rydin, 1998), suggesting that WLD may further decrease *Sphagnum* productivity. Hollow-inhabiting Sphagna tend to have the highest photosynthesis rates and are easily decomposable (Bengtsson et al., 2016; Hájek, 2009; Rydin et al., 2006). In hollows, an open surface structure or even floating individuals form the “carpet”; for these mosses, investing biomass production in dense wicking structures is unnecessary when the WT is so close. This contrasts with hummock habitats where conservative growth strategies aimed at outlasting rather than outgrowing competitors dominate (Rydin & Jeglum, 2013). Here, a dense carpet is needed to facilitate the capillary rise of moisture to the surface from lower layers and reduce exposure to drying winds (Rydin & McDonald, 1985). Lawns Sphagna are less predictable; interactions between the WT and other environmental drivers (vascular plant shading in fens, for example) impact moss carpet traits and function (Bengtsson et al., 2020; Kuiper et al., 2014). As lawn habitats are some of the most productive surfaces in a peatland (Korrensalo et al., 2020), their expected sensitivity combined with variable species cover means that potential reactions to WLD and periodic drought are of particular interest.

Current reports of plant community shifts (Laine et al., 2009; Macrae et al., 2013; Mäkiranta et al., 2018; McPartland et al., 2019; Peltoniemi et al., 2015; Strack et al., 2006) and functional changes (Ballantyne et al., 2014; Chivers et al., 2009; Harris et al., 2020; Laine et al., 2009; Munir et al., 2014, 2015; Oechel et al., 1998; Riutta et al., 2007; Strack &

Waddington, 2007) after WLD give highly variable messages depending on peatland type and depth of WLD. Long-term studies of these issues are lacking. As a result, the impact peatland system dynamics will have on the future climate is still poorly understood.

1.8 Objectives and hypotheses

My thesis aims to quantify how vegetation in boreal peatlands will be structured (I) and photosynthesize (II, III) in a future climate as emulated by long-term water level drawdown (WLD; Fig. 1).

I hypothesize that long-term deepened water tables in northern peatlands will:

I. result in compositional and structural changes in the vegetation community. I expect arboreal plants to benefit from drainage while species adapted to high water levels will lose their advantage.

II. increase ecosystem productivity for both the species-level photosynthetic capacity and through species turnover to plants with higher productivity. Peatlands with greater nutrient availability undergo greater productivity increases than nutrient-poor peatlands in response to WLD.

III. diminish the impact of periodic drought suggesting acclimation to drier conditions

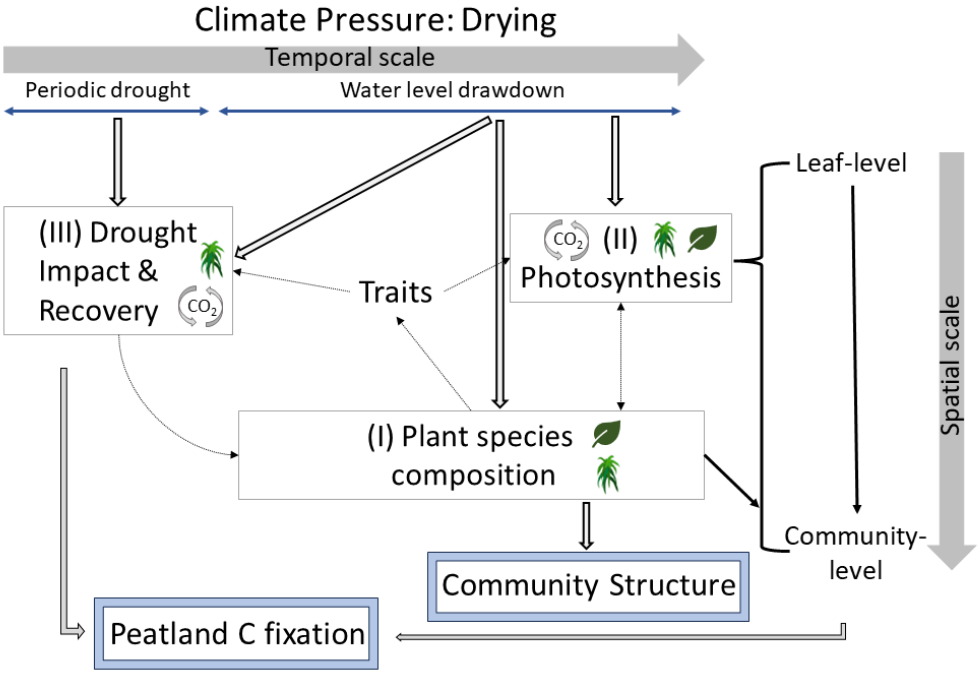

Figure 1. A schematic of the three studies presented in this thesis. The two main objectives (boxed in blue) were to assess the plant community structure (I) and carbon fixation (II, III) of boreal peatlands as impacted by drying associated with climate change at different temporal scales. We studied drying at both a short time scale (periodic drought, 43 days) as well as a long time scale (17-year water level drawdown experiment). Spatial scales spanned from individual leaves through microforms up to ecosystem-level. Both vascular plants (indicated by a leaf) as well as Sphagna (indicated by a moss) were included in the studies. Data included plant community composition and carbon dioxide (CO_2) fluxes (indicated by circulating CO_2 symbol). Thick arrows indicate research questions and their answers, solid arrows indicate information combined in calculations, and dotted lines indicate linked or associated connections and feedbacks.

2. MATERIALS AND METHODS

2.1 Experimental field site: Lakkasuo

To understand ecosystem changes resulting from drying on different northern peatland types (I, II) and test the impact of long-term deepened WTs on the resistance and resilience of lawn Sphagna to periodic drought (III), a water level drawdown (WLD) experiment was applied on Lakkasuo peatland located in Orivesi, Finland (61°47′N, 24°18′E; Fig. 2). Lakkasuo is an eccentric raised peatland complex composed of different peatland types, which range from minerogenic fens in the extensive lag area in the northern part of the peatland, to an ombrogenic bog in the southern area (i.e., raised bog center).

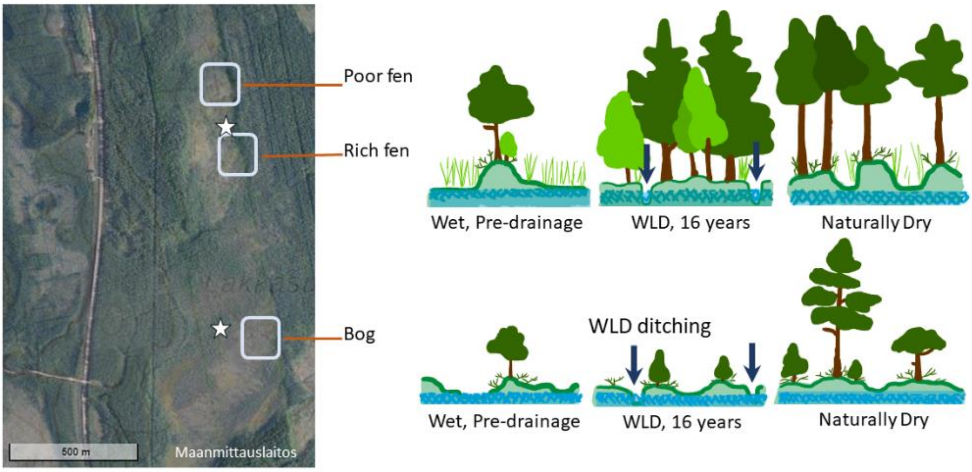

Figure 2. A satellite image of Lakkasuo experimental site and an illustrated cross-section of the three subsites on the bog and rich fen. Proportions shown in the cross section are approximate, but show the general WT, microtopographical variation, and vegetation cover on each subsite within each peatland type. Note that the state of the WLD subsites is represented 16 years after experimental ditching. Prior to experimental ditching, WLD and wet control subsites did not differ. The deep forestry drainage is not illustrated here but can be seen in the satellite image adjacent to (East of) experimental sites. The location of naturally dry subsites where mesocosms samples were taken are indicated by stars.

In the Lakkasuo WLD experiment three peatland types were included: a rich fen (mesotrophic), a poor fen (oligotrophic), and a bog (ombrotrophic) (Fig. 2). Each of these sites was divided into three adjacent subsites where treatments were applied: an undrained control, an experimental moderate WLD, and a forestry drainage where the WT was decreased ca. 50 cm. The experimental WLD was established in 2000 on the rich fen and bog, while the poor fen WLD was established a year later in 2001. To lower the WT ca. 15 cm, narrow ditches ca. 30 cm in depth were dug into the peat surrounding each WLD subsite using a chainsaw and spades (Fig. 1 in I). The deep forestry drainage was established in 1961 - prior to the beginning of our monitoring - by creating ca. 70 cm deep ditches. WT changes were monitored throughout the growing season in each survey year, i.e., annually from 2000 to 2004, 2009, and 2016. Nutrient analysis of surface peat was done in 2016 for all subsites. NK participated in experimental work from 2016 onwards.

To include a wider range of WT histories in the mesocosm study (III), two additional subsites from Lakkasuo were included: a naturally dry and treed fen and a naturally dry and treed bog (Fig. 2). These additional subsites were proximate to experimental WLD areas and were used as source areas for mesocosm samples.

Within each site prior to WLD, there was no difference in vegetation cover between control and WLD subsites, but the vegetation between the three sites differed (Fig. 2 in I). The rich fen had a high diversity of both vascular plants - particularly sedges (*Carex* spp.) - and bryophyte species including brown mosses and *Sphagnum*. The poor fen was dominated by intermediate lawn surfaces with an extensive cover of a few *Sphagnum* species and scattered sedges. The bog surface was less uniform than the surface of the fens. The bog was characterized by a dominant *Sphagnum* moss carpet across a mosaic of microforms. The distribution of microtopography varied between sites. The rich fen was the only site to contain mesotrophic flarks and lawns. The rich fen also included the same microforms as were found in the poor fen: oligotrophic lawns, minerotrophic high lawns and hummocks. Four microform communities were defined in the bog: hollows, low lawns, high lawns, and hummocks.

2.2 Permanent sample plots and vegetation surveys

To measure changes in the vegetation community over time (I), permanent sample plots were established on all subsites along transects that crossed flarks and hollows with systematic 1.6 m spacing between plots (Fig. 3). A total of 40 permanent sampling plots were located on each control and WLD subsite, while forestry-drained subsites had 20 plots. Visual cover estimates of each plant species from the moss layer and field layer were done in each circular fixed-area (0.07 m^2) plot. Prior to WLD treatments (2000 on the bog and rich fen, 2001 on the poor fen), species cover was estimated on permanent sample plots on all experimental subsites to quantify the starting point of the vegetation community. Measurements were repeated in 2001, 2002, 2003, 2004, 2009 and 2016 on all sites. In 2016 only, the naturally dry and treed rich fen and bog were surveyed using the same method.

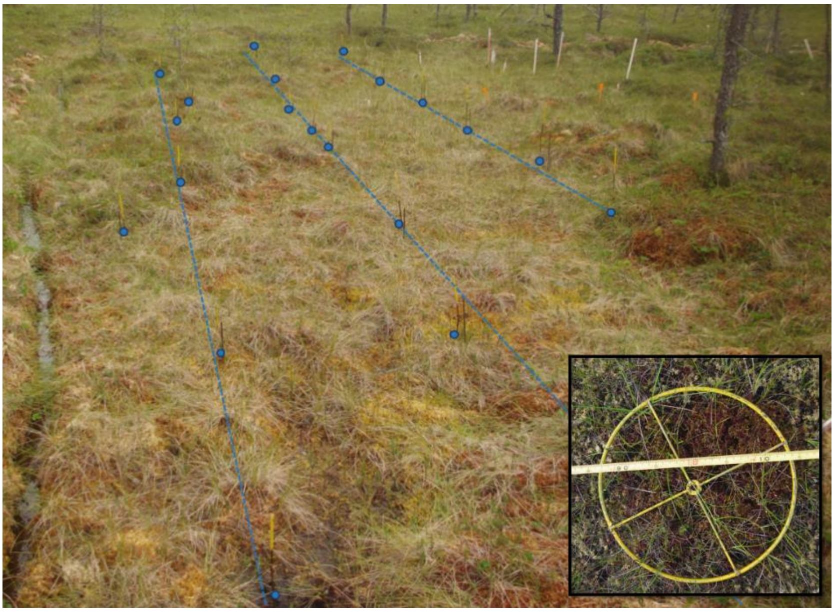

Figure 3. Lakkasuo experimental subsite (WLD bog) in 2017 showing the layout of permanent sample plot center points along transects. Permanent sample plots (inset) were circular with an area of 0.07m^2. All subsites had a similarly designed layout, although the number of transects varied between two and four and the spacing between transects varied by site. Fixed-area plots (inset) were used to estimate species cover and inventory the vegetation at each point. The field markers for each point can be seen in the photo (yellow stakes), but points have been marked in blue for clarity. The experimental WLD drainage ditch can be seen along the left of the photo.

2.3 Photosynthesis sample handling and measurements

To measure photosynthesis as impacted by WLD (II), we selected individual plant samples of the dominant species on control and WLD subsites from each site and measured their CO_2 flux at four light levels. This allowed us to fit a hyperbolic photosynthetic light response curve. Peat surface monoliths approximately 30 cm x 30cm x 20cm (length x width x depth) were removed from peatland subsites to the lab. Samples were collected from the subsites each morning to keep them as fresh as possible and transported to the lab where they were kept moist, and measurements were conducted throughout the remainder of the day. We selected species to measure based on the vegetation composition of each subsite. To obtain an accurate representation of the subsite photosynthesis, we targeted to measure the species which cumulatively accounted for ca. 80% of the vegetation cover on subsite. This target was met on the poor fen and bog (Table 1 in II), but on the rich fen only 68% (WLD) and 78 % (undrained control) of the cumulative vegetation cover was accounted for by species selected for photosynthesis measurements. The photosynthesis measurements were carried out using infrared gas analyzers (Licor LI-6400, Walz GFS-3000) to measure CO_2 concentration change in enclosed cuvettes containing live photosynthetic plant material at four different light levels: 1500, 250, 35 and 0 µmol m^{-2} s^{-1} (Fig. 4). Approximately 10% of the samples we measured were later rejected due to signs of physiological stress related to the sampling.

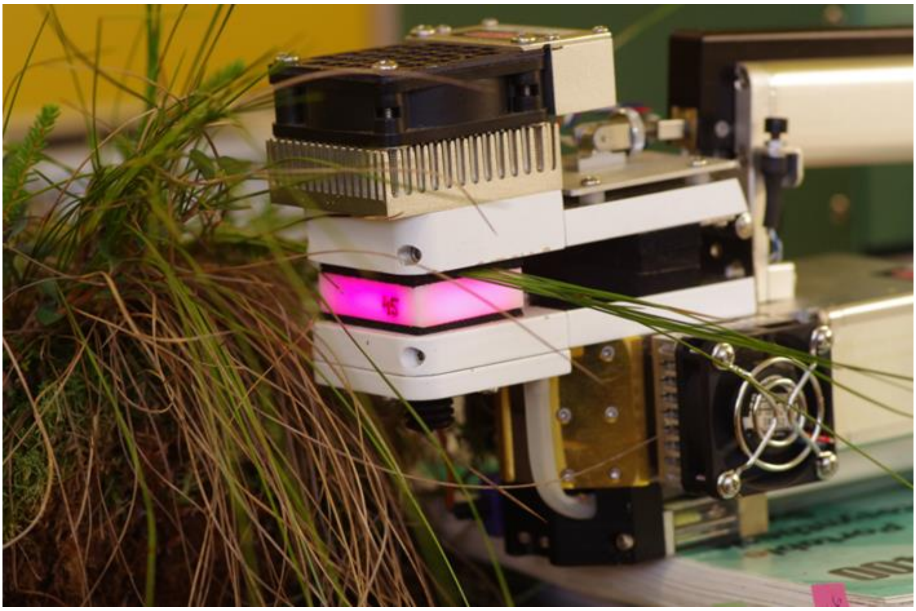

Figure 4. Infrared gas analyzer (Licor LI-6400) measurement head during photosynthesis measurements. The leaf sample (*Eriophorum vaginatum*) is contained in a sealed cuvette of known volume and illuminated at a fixed photon flux density. Temperature, air flow rate, carbon dioxide concentration and relative humidity in the cuvette are controlled during measurements, which lasted around two minutes at a given light level once a stable photosynthesis rate was achieved. Root systems of vascular plants were preserved to the best of our ability during peat monolith removal from the peatland and kept moist throughout the day.

2.4 Periodic drought applied to mesocosms

To quantify the effect of long-term deepened WTs on the response of *Sphagnum* lawn mosses to periodic drought (III), we applied an experimental seasonal drought to *Sphagnum* moss surface cores (mesocosms) and measured the photosynthetic response of mesocosms before, during, and after the drought. As earlier described, mesocosms originated from the rich fen and bog areas in Lakkasuo with three different WT histories: wet pristine, experimental WLD, and dry treed pristine. Two different *Sphagnum* species were selected at each subsite for a total of seven species; we collected a common species from each subsite across a peatland type as well as a species characteristic to each subsite. A 43-day ecohydrological drought representing an extreme summer drought period was implemented in a controlled greenhouse environment by decreasing the WT of the mesocosms from 10 cm to 30 cm below the surface and stopping precipitation treatments. A 43-day drought is seven days longer than the longest recorded drought on record at nearby Hyytiälä research station since 1986 (FMI, 2023). After the drought period, the water table was returned to 10 cm below the surface, precipitation treatments resumed, and mosses were allowed to recover for three weeks.

To measure the photosynthetic light response of the mesocosms, we used a sealed chamber with an internal light source that was adjusted to four different intensities for each measurement, with the fourth measurement in the dark (Fig. 5). Each light level was targeted to be approximately half the photon flux density of the previous level. Light response measurements were completed prior to the drought, at the end of the drought, and weekly during the three-week recovery period. To attain the net photosynthesis rate at each light level, the CO_2 concentration and light intensity inside the chamber was measured every 15 seconds over a 90 s to 180 s period. Selected moss traits (non-destructive) relating to photosynthetic performance and moisture retention were measured alongside net photosynthesis rates, or at the end of the experiment if destructive sampling was required.

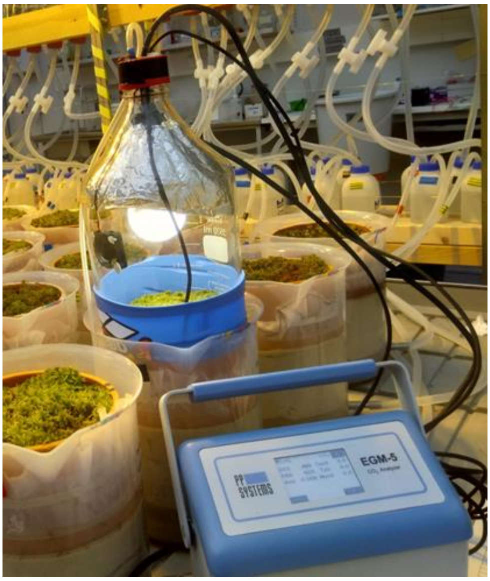

Figure 5. The sealed chamber used for measuring mesocosm net photosynthesis had an internal light source and was connected to an infrared gas analyzer (PP Systems, EGM-5) to monitor the CO_2 concentration in the chamber. Chamber air was constantly circulated, and photosynthetically active radiation was measured at the moss surface. Measurements lasted one and a half to three minutes, after which the chamber was vented.

2.5 Data analyses

Multivariate analyses of vegetation composition

To analyze vegetation community cover (I), we used multivariate analysis techniques. TWINSPAN analyses were used to group plots into similar microform communities based on pre-treatment moss species composition. Ecological gradients were analyzed using detrended correspondence analyses (Ter Braak & Šmilaur, 2012) and principal response curves were used to visualize relative community changes over time. Canoco 5 (Ter Braak & Šmilaur, 2012) and R vegan package (Oksanen et al., 2022) were used for the analyses.

Photosynthesis analyses using non-linear mixed-effects models

To model the photosynthetic response of peatland plants (II, III), nonlinear mixed-effects models (R nlme package) were built based on the hyperbolic photosynthetic light response curve (Eq. 1) Smolander & Lappi, 1985):

$$A_{ijk} = R_{jk} + \frac{Pmax_{jk}*PPFD_{ijk}}{\alpha_{jk}+PPFD_{ijk}} + e_{ijk} \qquad \text{Eq. 1}$$

where, A is the observed net CO_2 exchange at light level i (PPFD, µmol m^{-2} s^{-1}) for species j and sample k. Parameters for dark respiration (R, mg CO_2 m^{-2} d^{-1}), maximum photosynthesis (P_{max} , mg CO_2 m^{-2} d^{-1}), and alpha (initial slope of the curve) were estimated using non-linear mixed-effects models. The residual error (e) was normally distributed with a mean of zero and constant variance.

Models were built in an additive way, i.e., the starting model assumed a random relationship with no predictors, then the most ecologically suitable predictor variables were added individually. We tested for an improved model fit after each variable addition using AIC values. Non-significant variables (*f*-test p >0.05) were not kept in the model unless it was ecologically justified. No further variables were added when the benefit of additional variables was outweighed by high model complexity. For estimating species-level photosynthetic capacity (II), mosses and vascular plants were modeled separately.

To determine the impact of periodic drought on moss photosynthesis (III), we used non-linear mixed-effects models to test the impact of 1) variables resulting from the experimental design and 2) measured moss trait variables on the photosynthetic response (Eq. 1) of mosses in response to and recovery from periodic drought. The first model was based on experimental design variables and tested the impact of origin peatland type, WT history, and their interaction on the P_{max} and R of mosses before, during and after periodic drought. The second model was built using traits variables in an additive way similar to that described above. Model 2 tested which traits are significant in determining the P_{max} and R of mosses, as well as their resistance to and their recovery from periodic drought. Non-significant variables (*f*-test p >0.05) were not kept in the model unless it was ecologically justified. No further variables were added when the benefit of additional variables was outweighed by high model complexity; AIC values were used to select the final model.

Upscaling leaf-level photosynthesis to ecosystem-level

To understand the ecosystem-level impact of WLD on photosynthesis (II), non-linear mixed effects models (described above) were applied using the estimated species biomass from each subsite and light levels from July of 2017 (Fig. 1 in II). To do this upscaling, moss and vascular species biomass on each subsite was estimated and inputted to the models allowing ecosystem-level impact to be estimated. To upscale these models (mosses and vascular plants separately) over time, hourly light levels for July, which is considered the peak growing season, were inputted to the model and summed to calculate daily and monthly photosynthesis on each subsite.

The impact of periodic drought on mesocosm photosynthesis

We calculated the impact of periodic drought on mesocosm maximum photosynthesis (P_{max}) using the concepts of resistance, recovery and resilience as defined by Van Ruijven & Berendse (2010). The P_{max} prior to periodic drought, at the peak of the drought and after three weeks of recovery were used to calculate these values. We used linear mixed-effects models to test the impact of species, WT history, and their interaction on the resistance, recovery, and resilience of P_{max}.

3. RESULTS

3.1 Ecohydrological changes due to WLD

Experimental WLD initially induced a 15 to 20 cm WT drop, but the impact of WLD slowly declined over the duration of the experiment, particularly on the bog and poor fen sites (Fig. 1 in I). However, the WT on WLD subsites remained at least ca. 5 cm deeper than on undrained subsites (Fig. 1 in I). Peat chemistry analyses on each subsite done in 2016 showed that drainage caused a general decreasing trend in pH and carbon to nitrogen ratio (C:N). Patterns in peat chemistry tended to show the rich fen at one end of the range of values and bog at the other, while the poor fen was intermediate. The rich fen had the highest pH, % nitrogen and content of most other minerals, while the bog had the lowest. Similarly, the C:N ratio was lowest on the fen and highest on the bog.

3.2 Impact of WLD on vegetation and microform plant communities

As hypothesized, WLD resulted in vegetation community changes in all peatland types, but the extent and direction of this shift varied by peatland type and WT depth (Fig. 2 in I). Plant species turnover following WLD was highest on the two fens, while vegetation in the nutrient-poor bog was resilient and changed very little following drainage. The rich fen was the most sensitive to a lowered WT; here the vegetation community quickly began to shift away from specialist flark species after WLD (Fig. 2 in I). The poor fen had a more moderate response. The forestry drainage from the 1960's led to a similarly forested ecosystem on both fen types (Fig. 2 in I). In the bog, the vegetation response contrasted with the two fens; we observed no significant changes following WLD, but a canopy of Scots pine (*Pinus sylvestris*) developed following forestry drainage with many peatland-associated plants remaining in the understory (Fig. 2 in I). In both fens, tree canopy development following drainage accelerated plant community changes and strengthened the impact of WLD on peatland vegetation (Fig. 4 in I). Overall, there was a decrease in the cover of plant species associated with wet habitats and an increase in the cover of forest species in all drained sites.

Experimental WLD caused vegetation communities on microforms close to or at the WT to change faster than the microforms further above the water table. We found three different rates of change among microforms following WLD: decelerating change, accelerating change, and stability (Fig. 4 in I). Of the eight pre-WLD microform communities determined using TWINSPAN analysis, the wettest fen microforms, flarks and minerotrophic low lawns, changed the fastest following WLD. These wet microforms lost cover of flark-adapted specialists, particularly brown moss species (Fig. 4 in I). Intermediate fen microforms (oligotrophic lawns and high lawns) did not undergo immediate or rapid change, but species turnover increased with time as a tree canopy developed (Fig. 4 in I). Hummocks - the communities located highest above WT - were the most stable, but tree canopy development on the fen resulted in vegetation turnover on these high microforms as well (Fig. 4 in I). With the exception of the wettest hollows, bog microforms did not undergo directional change (Fig. 4 in I).

3.3 Impact of WLD on peatland plant photosynthesis

Leaf-level changes in photosynthesis following WLD

Long-term WLD significantly increased the photosynthetic capacity of vascular plant species especially, but also *Sphagnum* moss photosynthesis (Fig. 4 in II). The impact of WLD on vascular plant photosynthesis increased from the bog to the rich fen (Fig. 4 in II). However, Sphagna on the poor fen had the greatest P_{max} increase due to WLD (Fig. 4 in II). On the WLD rich fen, we found the highest vascular plant P_{max} values of all subsites (Fig. 4 in II). Vascular plant P_{max} was greatest for large-leaved species such as downy birch (*Betula pubescens*) and low for those, such as crowberry (*Empetrum nigrum*), with needle-like leaves (Fig. 5 in II). Despite occupying diverse environments, *Sphagnum* species had little variation in P_{max} (Fig. 5 in II). Similarly, there was very little variation in *Sphagnum* respiration rates, although WLD significantly increased vascular plant respiration (Table S-6 in II). WLD caused the initial slope of the photosynthesis response - alpha - of mosses to increase significantly on all peatland types, but only on the rich fen for vascular plants (Fig. 4 in II).

Ecosystem-level changes in photosynthesis following WLD

At the ecosystem-level, WLD increased photosynthesis in all sites; the greatest overall increase (the difference between WLD and control subsites) was in the rich fen (Fig. 7 in II). The ecosystem-level photosynthesis was similar among the control subsites across the different peatland types (Fig. 7 in II). However, the proportion of photosynthesis accounted for by vascular plants varied between peatland types: high nutrient availability benefitted vascular plant productivity (Fig. 7 in II). In the rich fen, vascular plants on the control subsite accounted for a greater proportion of ecosystem-level photosynthesis than in any other control subsites (Fig. 7 in II). This proportion increased further due to WLD (Fig. 7 in II). Similarly to the rich fen, WLD in the poor fen resulted in greatly increased vascular plant photosynthesis, while moss photosynthesis also increased but to a lesser extent (Fig. 7 in II). However, compared to the rich fen, mosses in the poor fen contributed a greater proportion of the overall photosynthesis (Fig. 7 in II). WLD did not cause the estimated total photosynthesis in the bog to change. In the bog, *Sphagnum* mosses accounted for the greatest proportion – roughly half – of ecosystem-level photosynthesis compared to all other sites (Fig. 7 in II).

3.4 Impact of periodic drought on the photosynthesis of lawn mosses

Long-term exposure to deep or deepened water tables increased the physiological stress of bog lawn Sphagna as seen by the low photosynthesis measured on mesocosms originating from these subsites (Table 3 in III).

The mesocosm study showed that *Sphagnum* mosses from lawn surfaces were sensitive to periodic drought; the drought caused a significant drop in maximum photosynthesis for all mesocosms (Fig. 2 & Table 2 in III). In the experimental design model, we found that mesocosms with a WT history of long-term deep WTs (WLD and naturally dry) had a larger drought-induced drop in photosynthesis than mesocosms from naturally wet subsites (Table 2 in III). In the trait-based model, we found that species with large capitula resisted drought significantly better than those with small capitula (Table 3 in III). This trait was found in moss species originating from the fen (*S. divinum* and *S. recurvum* collective), particularly from WLD and dry subsites (Fig 4 in III). Overall, samples with higher N content and photosynthetic area had the highest P_{max} rates (Table 4 in III).

The recovery of *Sphagnum* photosynthesis following periodic drought was significant and occurred at a constant rate for all mesocosms after re-wetting (Fig. 2 & Table 2 in III). However, we found no differences in recovery rates between mesocosms from different peatland types or WT histories. During the three-week recovery period following rewetting, P_{max} did not return to pre-drought levels for any mesocosm, meaning that recovery was incomplete (Fig. 2A in III).

When the resistance, recovery, and resilience of *Sphagnum* P_{max} were separately addressed, we found significant differences between species (Fig. 3 in III). The most resistant species was *Sphagnum divinum* (Fig. 3A in III) with large capitula. Resilience, i.e., how close P_{max} returned to pre-drought levels (Fig. 3C in III), was highest in Sphagna that were either most resistant to drought (*S. divinum*, Fig. 3A in III) or recovered best from drought (*S. recurvum* coll.; Fig. 3B in III). Lawn mosses from bog subsites, particularly *S. rubellum* and *S. tenellum,* had the smallest capitula and also had some of the lowest resistance to drought (Fig. 4 in III).

4. DISCUSSION

This long-term study showed that the greatest changes in vegetation and photosynthesis following WLD occurred in nutrient-rich fens while bogs appeared to be more resistant to change. The combined effects of altered hydrology and nutrient availability drove the vegetation changes we observed in Lakkasuo (I, II). We found that the greatest change in the vegetation community occurred in the rich fen, followed by the poor fen, while the bog was resistant to change (I). Immediately following WLD, vegetation composition changed rapidly on the wettest microforms making these the most sensitive to WLD (I). As with community composition, we found that the greatest change in photosynthesis after WLD occurred on the rich fen, while the bog was stable (II). In contrast to fens, bogs did not undergo large changes in vascular community cover and did not undergo community-level changes in photosynthesis (II). While studies I and II support *Sphagnum* mosses as stabilizing components of the vegetation community after WLD, study III found that lawn mosses were sensitive to desiccation during periodic droughts and WLD exacerbated the negative effects of drought.

4.1 Drying-induced changes in the vegetation community

Immediately following WLD, the response of the vegetation communities depends on its proximity to the WT. Peatland habitats at or close to the original WT dry out quickly and the unique plants adapted to these semi-submerged conditions become desiccated and are lost (Strack et al., 2006). Drainage causes surface-dwelling mosses to lose their connection to sustaining groundwaters and the cover of species with better moisture-retaining traits increases. In contrast, we found that dry microforms (hummocks) in both fens and bogs demonstrated stability soon after WLD (I). In hummocks, *Sphagnum* functional traits support moisture conservation. This includes dense carpet formation - in both capitula and fascicles – which strengthens and increases the capillary transport of water to the moss capitula allowing them to photosynthesize and persist after WLD (Bengtsson et al., 2016; Hájek, 2009; Laine et al., 2021; Rydin & Jeglum, 2013; Schipperges & Rydin, 1998). This pattern agrees with earlier observations of vegetation change immediately following WLD (Riutta et al., 2007; Strack et al., 2006).

Despite very little species replacement on bogs, climate-induced drying will likely change the overall distribution of microform communities by shifting it away from hollows and toward hummock communities. In these *Sphagnum*-dominated ecosystems, the main growth-limiting factor is a nutrient deficit, which is not lessened by WLD as there are few nutrients available in bog peat to be released by mineralization (Rydin & Jeglum, 2013). Instead, only conservative species that can withstand these nutrient limitations occupy bogs (Rydin & Jeglum, 2013); these specialized species persist after WLD while limiting conditions prevent new species from invading bog habitats. Additionally, the overall impact of WLD on bog surface moisture can be softened by an effect known as “bog breathing” where the bog's surface drops with the WT (Morton & Heinemeyer, 2019).

The sensitivity of the fen vegetation communities to drying is linked to both their nutrient status and the role of vascular plants in minerotrophic peatlands. In fens, the primary growth-limiting factor is a high water table, which is removed by WLD (Armstrong et al., 1991). As the surface dries, the aerated peat layer thickens (Whittington & Price, 2006) making the ecosystem more suitable for species adapted to deep water tables and terrestrial environments; vascular plant species with root systems to support them are better able to survive deep WTs than peatland-adapted bryophytes. WLD increases peat decomposition rates – due to a deepened aerobic layer – which leads to an increase in mineralization making more nutrients available (Straková et al., 2012). Vascular plants rooted in this newly aerated layer are the first to benefit from the nutrients released by mineralization, while rootless mosses are unable to readily access these new resources. After WLD, *Sphagnum* species with traits that benefit capitula moisture retention – including large capitula and convex leaves – are favoured (Bengtsson et al., 2016; Laine et al., 2021).

In contrast to *Sphagnum* mosses, vascular plant cover, particularly generalist or acquisitive species, expanded following WLD, which caused further feedbacks to plant photosynthesis. The first vascular plants to flourish after WLD on fens were shrubs, such as *Betula nana*, which existed prior to WLD but expanded into the newfound growing space and quickly spread through vegetative means. Trees and other vascular plants that rely on seeds to regenerate occupied the site more slowly. WLD strengthens acquisitive plant traits, including P_{max} and plant height, on nutrient-rich sites such the rich fen, while little change occurs in nutrient-limited bogs (Laine et al., 2021). The result is a fundamental change in the ecosystem structure of rich fens following WLD from open peatland vegetation to a canopy of vascular plants dominated by dryland species (Köster et al., 2023). The initial stability after WLD of dry-adapted hummock communities disappears as the new sheltering environment drives secondary changes in ground vegetation (Köster et al., 2023). Under a canopy, where light becomes limited and evaporation decreases (Minkkinen et al., 1999; Straková et al., 2012), the functional traits and photosynthetic response of plants adjusts to the new environment (Hájek et al., 2009; Kangas et al., 2014; Laine et al., 2021). Future research focusing on canopy development after WLD would give key insights as to whether this is a tipping point in peatlands from a wetland to a forest ecosystem.

4.2 Carbon-fixation following WLD links to changes in the vascular plant community

Two main drivers exist behind the observed increase in photosynthesis on the rich fen after WLD: species turnover and altered photosynthetic capacity, particularly in vascular plants. Vascular plants have both higher photosynthesis rates and a wider range of maximum photosynthesis than Sphagna have (Korrensalo et al., 2020). An increase in vascular plant cover combined with the ingrowth of more productive species following WLD in fens has a strong effect on increasing community-level photosynthesis and related evapotranspiration. Increased evapotranspiration further reinforces the WLD resulting in a state of positive feedback. The more nutrients that are available in an ecosystem, such as rich fens, means that less WLD is required to cause major ecosystem changes. The question arises: at what WLD depth does this occur in different peatlands? Further research is required to better understand the fate of diverse peatland systems and their role in our future climate.

In bogs where the vascular plant cover is sparse and does not readily respond to WLD, *Sphagnum* moss dominance is key to the photosynthetic stability of these ecosystems. *Sphagnum* species turnover in bogs from hollow-adapted species to hummock-adapted species has little overall impact on community-level photosynthesis as we found the range in photosynthesis rates among Sphagna is low. However, Korrensalo et al. (2020) found that hummocks had lower net ecosystem exchange than lawn surfaces meaning that a shift in microform distribution towards hummocks decreases the carbon sequestration potential of bogs.

The question remains: what will the overall balance of net ecosystem exchange for different peatland types be in the future climate – is the increased photosynthesis on fens enough to compensate for increased belowground respiration after WLD (Laiho, 2006; Riutta et al., 2007; Straková et al., 2012)? Is the inherent stability of bog vegetation a strength that allows bogs to continue their valuable function as a carbon sink despite increases in heterotrophic respiration? Ecosystem-level studies accounting for combined belowground and aboveground (including tree canopy) processes on different peatland types are needed to better understand how CO_2 fluxes change following WLD.

4.3 Impact of long-term drying on the acclimation of Sphagna to periodic drought

WLD or a deep WT history had a negative impact on the photosynthesis of lawn Sphagna during periodic drought by stressing the mosses and making them less resistant to drought, suggesting that no acclimation had occurred as a result of WLD. Lawn mosses originating from fens were less impacted owing to the dominant species having large capitula (Laine et al., 2021). Bog-originating mosses in lawns are stressed by WLD, which makes them more vulnerable to periodic drought; these species lack both large capitula and a dense carpet structure (Laine et al., 2021). Despite high intraspecific trait variation (Laine et al., 2021), species replacement towards a community with more suitable moisture-retaining traits, as we also observed in study I in the rich fen, is more probable than species acclimation to drier conditions.

This study focused on the Sphagna from lawn habitats meaning that the ecosystem-level impact of periodic drought will likely differ owing to microform diversity. Despite fens having lawn Sphagna that are moderately resilient to drought, the limited microform variation and good nutrient availability on fens means that they are vulnerable to WT change and may easily reach a sudden tipping point where they shift to a new stable state (Scheffer et al., 2012) due to long-term drying as we and others have observed (Laine et al., 2019; Miller et al., 2015; Strack et al., 2006). The sensitivity of lawn Sphagna from bogs can be moderated by the diversity of microform habitats in bogs. As drying occurs in bogs, in combination with periodic drought, suffering lawn Sphagna will be replaced by hummock species with denser form and capillary action to maintain moisture allowing them to survive drought (Hájek, 2009).

4.4 Implications of drying peatlands

Under the pressures of a warming climate, we found that even minor changes in WT can result in directional shifts in peatland vegetation composition and photosynthesis. Increases in productivity resulting from long-term drying may outweigh the increases in decomposition immediately following the initiation of WLD (Laiho, 2006; Straková et al., 2012), but secondary changes caused by vegetation turnover could interact with this balance. Plant community changes could occur even faster than originally anticipated because the stress of long-term drying makes mosses even more vulnerable to periodic drought that are expected to be more frequent (Donat et al. 2016).

As shown in this study, interactions between peatland type and WLD depth will make ecosystem responses variable; fen vegetation photosynthesis and composition are clearly more reactive to changes in WT than bogs. In nutrient-rich ecosystems such as fens, a tipping point is easily reached where open peatlands become forested resulting in a positive feedback that maintains and enforces WLD-initiated changes; here, productivity increases with growing vascular plant cover and photosynthesis rates. Vascular plants hold a key role in this positive feedback as a shift from an open to closed-canopy system forces further above- (i.e., sheltering) and belowground (i.e., hydrology, root litter, and microbial community) changes. In fens, a loss of peatland plant diversity occurs as specialist flark species give way to invading upland species. Bogs, on the other hand, will likely be more stable carbon sinks (Korrensalo et al., 2020) where drying results in a shift in internal microform variations towards drier microforms. To increase our understanding of complex climatic changes beyond initial drying, it is essential to integrate different fen and bog reactions to drying, including canopy development, into climate system models (Loisel et al., 2021; Zhang et al., 2022).

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