

Effects of water table position and plant functional group on plant community, aboveground production, and peat properties in a peatland mesocosm experiment (PEATcosm)

Lynette R. Potvin · Evan S. Kane ·
Rodney A. Chimner · Randall K. Kolka ·
Erik A. Lilleskov

Received: 15 August 2014 / Accepted: 9 October 2014 / Published online: 18 October 2014
© Springer Science+Business Media B.V. (outside the USA) 2014

Abstract

Aims Our objective was to assess the impacts of water table position and plant functional type on peat structure, plant community composition and aboveground plant production.

Methods We initiated a full factorial experiment with 2 water table (WT) treatments (high and low) and 3 plant functional groups (PFG: sedge, Ericaceae, sedge and Ericaceae- unmanipulated) in twenty-four 1 m³ intact

peatland mesocosms. We measured vegetation cover, aboveground plant production, and peat subsidence to analyze interactive PFG and WT effects.

Results *Sphagnum rubellum* cover increased under high WT, while *Polytrichum* cover increased with low WT and in sedge only PFGs. *Sphagnum* production was greatest with high WT, while vascular plant production was greater in low WT treatments. There was an interactive WT x PFG effect on Ericaceae production. Lowered WT resulted in significant peat surface change and increased subsidence. There were significant PFG and WT effects on net peat accumulation, with the lowest rates of accumulation, high and low WT, in sedge only PFGs.

Conclusions The shift in water balance leading to lowered water table position predicted with changing climate could impact plant community composition and production, and would likely result in the subsidence of peat.

Responsible Editor: Eric J.W. Visser.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-014-2301-8) contains supplementary material, which is available to authorized users.

L. R. Potvin (✉) · E. S. Kane · E. A. Lilleskov
USDA Forest Service Northern Research Station,
Houghton, MI 49931, USA
e-mail: lrpotvin@fs.fed.us

E. S. Kane
e-mail: eskane@mtu.edu

E. A. Lilleskov
e-mail: elilleskov@fs.fed.us

E. S. Kane · R. A. Chimner
School of Forest Resources and Environmental Science,
Michigan Technological University,
Houghton, MI 49931, USA

R. A. Chimner
e-mail: rchimner@mtu.edu

R. K. Kolka
USDA Forest Service Northern Research Station,
Grand Rapids, MN 55744, USA
e-mail: rkolka@fs.fed.us

Keywords Peatland · Plant functional group · Water table · *Sphagnum* · Ericaceae · Sedge

Introduction

Globally, peatland ecosystems store large amounts of soil carbon (C) while occupying only 3–5 % of the entire land surface (Dahl and Zoltai 1997). Northern peatlands are estimated to hold 473–621 Gt of organic C (Yu et al. 2010), which could be at risk of oxidation in future climate conditions. Current trends and climate models predict that climate change could result in

decreased water availability in the summers (Thomson et al. 2005). Increased variability in precipitation patterns are also expected, with more occurrences of extreme rain events and summer drought (Tsonis et al. 1996; Easterling et al. 2000; Kunkel et al. 2003; Groisman et al. 2005). These changes in water availability could lead to shifts in water tables, including large mid-summer declines in water table height (Roulet et al. 1992; Hilbert et al. 2000). Lowered water tables resulting from drainage have been found to cause a shift in peatlands from net carbon sinks to net carbon sources (Trettin et al. 2006). Decreased water availability and lowered water tables could initiate significant changes in carbon balances (including methane) directly by accelerating peat oxidation and altering net primary production, and indirectly by modifying plant community composition (Weltzin et al. 2000; Strack and Waddington 2007; Chivers et al. 2009; Zona et al. 2009; Munir et al. 2014).

A changing climate could alter the absolute or relative abundance of plant functional groups (PFG) within northern peatlands, with potential feedbacks to carbon cycling (Bridgman et al. 1995; White et al. 2008). In this paper we aim to understand the plant community and peat structural response to water table position and changing PFGs. Because plant community is one of the primary drivers of C cycling in these peatlands, an understanding of how the changes in PFG affects ecosystem carbon cycling is essential (Chapin et al. 1996). Bogs are oligotrophic and are rain-fed, nutrient poor, acidic and dominated by three major understory PFGs: *Sphagnum* mosses, ericaceous shrubs, and sedges. Many bogs also have a sparse canopy of trees, in North America, typically *Picea mariana* (Mill.) Britton, Sterns & Poggenb, that can be considered a fourth PFG. Within a bog, small variations in microtopography can have significant influences on the water availability for vegetation (Vitt 2006). Hummocks (relatively elevated and dry), lawns (intermediate) and hollows (wet depressions) are the primary microtopographic features in peatlands and support different plant groups due to distance to water table. Water table manipulation experiments in bog ecosystems have documented contrasting results, with some studies indicating that water table drawdown will likely favor shrubs over graminoids in bog ecosystems (Weltzin et al. 2000, 2003; Riutta et al. 2007), and other studies indicating an increase in sedge abundance, at least in the absence of Ericaceae (Strack et al. 2006b). Given the large differences in physiology

among the different plant functional groups there are *a priori* reasons to expect them to differ in their response to changing hydrology (Chapin et al. 1996). Ericaceous shrubs are shallowly rooted and rely on ericoid mycorrhizal fungi to access nutrients. These shrubs lack root mechanisms to survive in flooded bog conditions and are frequently found on lawn and hummock features, and thus are predicted to increase in dominance and productivity with drier future conditions. However, if water table decline is excessive, drought stress could suppress growth of Ericaceae. In contrast, sedges have special root adaptations (aerenchyma) which permit the active transport of oxygen into roots, allowing them to survive in waterlogged conditions, leading to much deeper rooting zones (Armstrong et al. 1991).

To date, consensus in manipulation experiments suggests an increase in depth of the oxic layer increases shrub net primary production (NPP) while decreasing moss NPP (Laiho et al. 2003; Weltzin et al. 2003; Strack et al. 2006b). *Sphagnum* mosses are a primary driver of peat accumulation due to relatively slow decay and high annual rates of production (Johnson and Damman 1991). *Sphagnum* mosses are ectohydric, meaning they rely on external transport of water via capillarity, and are sensitive to periods of water stress (Proctor 2000; Glime 2007). Extended periods of drought affect *Sphagnum* species differently, depending on the species physiology, microtopographical position and location relative to water table (Hayward and Clymo 1982). This combination of factors indicates that drier conditions could promote a change in the composition of *Sphagnum* mosses. A decline in *Sphagnum* moss productivity is also expected if water tables are drawn down enough so that the capillary fringe does not reach the surface for extended periods (Gerdol et al. 1996). Increased growth of sedges and/or shrubs could also increase the shading of mosses further reducing *Sphagnum* moss production (Limpens et al. 2008), but may also protect mosses from desiccation by extending the boundary layer (Farrick and Price 2009).

Extended and severe summer drought can modify the peat structure, which will feed back to the plant community composition and potentially facilitate additional water stress. As soil moisture and water availability decrease, the peat compresses leading to decreased pore space and an increased bulk density (peat subsidence) (Price and Schlotzhauer 1999). The surface of peat commonly oscillates seasonally (known as ‘bog breathing’) and can rebound after a drought or a larger than normal snowpack (Fritz et al. 2008). However under a

prolonged decrease in water tables the effects of peat subsidence become less reversible (Price and Schlotzhauer 1999). Under extended periods of drought, the decreased pore space can limit capillary rise and unsaturated hydraulic conductivity, which further exacerbates low water availability, and may make it increasingly difficult for plants, particularly *Sphagnum* mosses, to access water. Conversely, in the event of large precipitation events, the increased bulk density of the subsided peat can retain more water and sustain surface moisture for longer time periods than peat with lower bulk density (Price 2003).

We established a water table (WT) and plant functional group (PFG) manipulation mesocosm experiment in Houghton MI USA (Peatland Experiment At The Houghton Mesocosm Facility, hereafter referred to as PEATcosm) to explore the roles of WT position and PFGs on bog ecosystem functioning, and to understand interactions and feedbacks of WT and PFG on carbon cycling, microbial communities, porewater chemistry, and NPP. The primary goal of this paper is to explore plant community dynamics within the ongoing mesocosm experiment, specifically looking at the effects of WT and PFGs on aboveground plant production and composition and the structure of peat. Our main objectives are to 1) assess the response of moss and vascular plant growth to drought in differing PFG assemblages; 2) measure the plant community response to WT and PFG manipulations; and 3) investigate how altered WT and PFGs affect the rate of peat subsidence. We hypothesized that 1) lower water tables would have a positive impact on shrub, sedge (in the absence of ericaceous shrubs) and *Polytrichum* moss growth and percent cover, but a negative impact on *Sphagnum* growth and cover; 2) removal of Ericaceae would have a positive impact on *Sphagnum* production and cover, but a negative impact on hummock *Sphagnum* species; and 3) lowered water tables will result in greater oxidation and subsidence of peat, especially within sedge treatments which will lack physical support for *Sphagnum* provided by Ericaceae.

Methods

Peat harvest

We extracted intact monoliths of peat from an extensive oligotrophic peatland in Meadowlands, MN USA

(N47.07278°, W92.73167°) in May 2010. The peatland vegetation at the harvest site was dominated by the sedge *Carex oligosperma* Michx.; ericaceous shrubs *Chamaedaphne calyculata* (L.) Moench., *Kalmia polifolia* Wangenh., and *Vaccinium oxycoccos* L.; and the mosses *Sphagnum rubellum* Wilson, *S. magellanicum* Brid., *S. fuscum* (Schimp.) Klinggr and *Polytrichum strictum* Brid. Also present were *P. commune* Hedw., *Eriophorum vaginatum* L., *Andromeda polifolia* L. var. *glaucophylla* (Link) DC., *Rhododendron groenlandicum* (Oeder) Kron and Judd, and *Drosera rotundifolia* L.

A temporary road was constructed using swamp matting to facilitate heavy equipment entering the site. Areas with low microtopographic variation (lawns) were selected to harvest. We removed the monoliths intact using a custom designed steel peat cutter (Online Resource 1) and transferred into mesocosm bins. There was no evidence of peat compaction or disturbance to aboveground vegetation during the transfer. Within 2 days of the harvest, the 24 mesocosm bins containing peat monoliths were transported to the USDA Forest Service Mesocosm Facility in Houghton MI.

At the time of harvest we also extracted one 10 cm³ block of peat at each of the following five depths (0–10, 10–20, 20–30, 50–60, and 70–80 cm) from one of the faces remaining after the monolith was removed, for all 24 monoliths. These blocks were processed for bulk density measurements and carbon (C), nitrogen (N), $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ analysis at the Michigan Tech Forest Productivity Lab, Houghton MI (Costech Elemental Combustion System 4010 connected to a Thermo Finnigan ConFloIII Interface and Deltaplus Continuous Flow-Stable Isotope Ratio Mass Spectrometer). $\Delta^{14}\text{C}$ values were also measured at all five depths for a subset of samples (5 of the 24 peat harvest sites distributed across the sampling area). Ground peat was prepped for ¹⁴C in the Carbon, Water and Soils Lab (Houghton MI) using the methods of Vogel et al. (1984) and measured at the Van de Graaff FN accelerator mass spectrometer (AMS) at the Center for AMS at Lawrence Livermore National Laboratory (Berkeley, CA).

Mesocosm

Site and facility description

The Mesocosm facility is located at the USDA Forest Service Northern Research Station, Forestry Sciences

Laboratory in Houghton, Michigan USA (N 47.11469°, W 88.54787°). Air temperatures range from an average low of -13°C in January to an average high of 24°C in July, with an average growing season of 132 days. Mean annual precipitation totals 870 mm, with approximately 50 % of the total precipitation inputs falling as snow (Stottlemeyer and Toczydowski 1991) [NOAA National Climatic Data Center, 30 year means at Houghton County Airport, MI]. The Mesocosm Facility was constructed in 2009 and contains a climate controlled tunnel with belowground access to the 24 mesocosm bins (Online Resource 2). The $\sim 1\text{ m}^3$ mesocosm bins have an open top exposed to ambient conditions, three sides and a bottom which are Teflon coated (DuPont Teflon PFA 532–13032, DuPont, Delaware) stainless steel and a glass window on the fourth side for observation of root dynamics, sealed with organism-safe silicone (NuFlex 333 Aquarium Sealant, NUCO Inc., Ontario). The upper edge and sides of the mesocosm bins are insulated to minimize lateral thermal gradients, while the bottom is uninsulated to facilitate a vertical temperature gradient from surface to base.

Systems control and datalogging

We use National Instruments (NI) LabVIEW software for systems control, monitoring and data logging in the mesocosms; this software is programmed with an alarm system to notify personnel of potential system problems. Temperature, water level, and dissolved oxygen are logged every 10 min to a NI Controller (CompactRIO 9074) linked to monitoring software (LabVIEW, Austin, TX). Vertical and horizontal temperature profiles are measured using two probes in each bin, one at the center and another 10 cm from the edge. Each temperature probe has thermistors at five depths (5, 10, 20, 40 and 80 cm below peat surface). Water level is monitored using submersible vented pressure transducers (Grainger 2HMC7) deployed in PVC well pipe, with weekly manual checks to ensure sensor accuracy and permit manual correction as needed. Each pressure transducer is linked via LabVIEW to a proportional valve (Asco Posiflow Valve). This valve is used to regulate and collect outflow water when water tables are at levels high enough to initiate flow. Dissolved oxygen is measured using In-Situ RDO Pro optical sensors (In-Situ Corporation, Ft. Collins, CO), deployed in the pressure transducer wells. Logged data is continually checked for errors and calibrations were carried

out prior to deployment of sensors. Outdoor conditions are monitored with a Campbell Scientific datalogger (CR1000) which collects hourly temperature (107-L), photon flux density (LI-COR Quantum Sensor LI190SB-L), wind speed and direction (2D Windsonic-4 L), precipitation (Met One rain/snow gage 385-L) and humidity (Vaisala temperature and relative humidity probe HMP50-L).

Experimental design

In June 2011 we initiated a full factorial experiment with 2 water table (WT) \times 3 PFG treatments with 4 blocks in a randomized complete block design (total = 24 experimental units). We used a 45 year record of WT data (Sebestyen et al. 2011) from the USDA Forest Service Marcell Experimental Forest, located approximately 60 km north of the Meadowlands harvest site, to inform our WT treatments. The target WT seasonal profiles are based on 1) low variability, average WT years (hereafter referred to as ‘high’) and 2) high variability, low WT years (‘low’). The WT treatments are maintained using a combination of artificial rainwater additions, rain-out shelters and regulated outflow. The rain-out shelters were constructed of clear corrugated fiberglass and positioned to allow airflow while selectively preventing rainfall into the bin according to prescription. The shelters are removed immediately following precipitation events. The artificial rainwater was formulated using rainwater chemistry averaged over five years from a nearby National Atmospheric Deposition Program site (pH range of 4.8 to 5.3; Chassell MI, site MI99). Water is drained only during spring melt or large precipitation events when water levels risk overtopping bins. Outflow is taken from the approximate location of the acrotelm-catotelm boundary, and hence the zone of highest hydraulic conductivity in *Sphagnum* peatlands (Holden and Burt 2003). When water tables fall below the level of the outflow port, water tables are regulated naturally by the balance between evapotranspiration and precipitation. Depth of water table beneath peat surface is measured using pressure transducers combined with mean peat elevation measurements and reported as means by day.

PFG treatments were initiated in June 2011 as follows: 1) all Ericaceae removed (“sedge” or “S” treatment), 2) all sedge removed (“Ericaceae” or “E” treatment), and 3) no vegetation removed (“unmanipulated” or “U” treatment). PFG manipulations were carried out

by gently removing stem and roots (if roots could be extracted without surface damage), or clipping at the base of the stem (when roots of sedges and Ericaceae were not easily removed) to minimize disturbance to mosses. Treatments were maintained with weekly clipping of new growth of the excluded species. In establishing the PFG treatment we removed $144 \pm 5 \text{ g m}^{-2}$ (mean \pm SE) of aboveground Ericaceae biomass from the sedge only treatments, with *C. calyculata* comprising $42 \pm 12 \%$, *K. polifolia* at $31 \pm 11 \%$, and *V. oxycoccus* at $25 \pm 8 \%$ of the total mass removed. *R. groenlandicum* and *A. polifolia* accounted for $\sim 2 \%$ of the biomass. Woody stem mass comprised 57.8% of *C. calyculata*, 59.7% of *K. polifolia*, and 41.3% of *V. oxycoccus* total aboveground mass harvested. In the Ericaceae only treatments we removed an average of $24 \pm 6 \text{ g m}^{-2}$ sedge living aboveground biomass. All vegetation removed in the initial clipping was separated by species and root vs. shoot (where roots were present), dried at 55°C , weighed and analyzed for C, N, ^{13}C and ^{15}N at Michigan Tech Forest Productivity Lab, using a Costech Elemental Combustion System 4010 connected to a Thermo Finnigan ConFloIII Interface and Deltaplus Continuous Flow-Stable Isotope Ratio Mass Spectrometer. Throughout the remainder of the paper and in figures the treatments will be referred to as follows: HS (high WT, sedge present); HE (high WT, Ericaceae present); HU (high WT, no PFG manipulation); LS (low WT, sedge present); LE (low WT, Ericaceae present); and LU (low WT, no PFG manipulation).

Sampling methods

We measured shrub, sedge, and moss cover from 2010 to 2013 using the point-intercept method (Bonham and Ahmed 1989; Mitchell et al. 2000), shrub and sedge aboveground biomass using allometric equations derived from destructive harvests (Gray and Schlesinger 1981; Fahey and Knapp 2007), and moss production using the cranked wire method (Clymo 1970). To estimate plant cover using the point-intercept method, a standard sampling frame was constructed to fit over the mesocosm bins, with a movable bar to create an 8×8 grid over the 1 m^2 area. For each bin, the frame was placed in a standard location and leveled. Using laser pointers mounted in the frame we recorded all living and dead species the laser intersected, carefully moving vegetation to capture all canopy layers including bryophytes (Bonham and Ahmed 1989; Buttler

1992). By dividing the total number of laser hits to each species by the number of grid points, percent cover for each species is calculated (total can sum to $>100 \%$ because of multiple vegetation layers). To estimate aboveground biomass we developed allometric equations of the dominant shrub and sedge species by destructive harvesting at the harvest site in MN (Online Resource 3). Briefly, we measured height, basal stem diameter, and branch diameter and separated the plants into leaves, stems, roots, and fruit/flowers for the shrubs *C. calyculata*, *K. polifolia*, *R. groenlandicum* and *A. polifolia* (Weltzin et al. 2000). The material was dried at 55°C to constant mass. While the diameter \times height measurement yielded the highest R^2 for aboveground biomass, basal stem diameter alone was also a strong predictor and was chosen as the most efficient and least intrusive means of sampling (Online Resource 3). Due to the very small vining stems of *V. oxycoccus*, these plants were not readily amenable to diameter-based allometric equations. Instead, percent cover measurements from the plant survey were scaled to aboveground biomass (Hribljan, unpublished) and annual production rates for *V. oxycoccus* were determined using annual change in estimated biomass. For the sedge *C. oligosperma*, we measured the height and dry weight at 55°C of each stem, and developed an equation with stem counts as the predictor (Chapin et al. 2004). *E. vaginatum* biomass was calculated using stem counts and a published mass/shoot equation (Chapin and Shaver 1996). In May and October of 2012 and 2013 we measured the diameter of every *C. calyculata*, *K. polifolia*, *A. polifolia* and *R. groenlandicum* in Ericaceae and unmanipulated treatments. We counted the number of *C. oligosperma* and *E. vaginatum* stems at peak biomass (late summer 2012 and 2013) in the sedge and unmanipulated treatments. From this data aboveground biomass and production were calculated for 2012 and 2013.

The cranked wire method was initiated in 2012 as a non-destructive measure of the lineal shoot growth of *Sphagnum*. This method employs stainless steel wires which are set vertically in line with *Sphagnum* shoots to measure the change in distance from the top of the wire to the top of individual *Sphagnum* (Clymo 1970). Fifteen cranked wires per bin were installed in a 10×20 cm grid pattern in June 2012 and measured in October 2012. In 2013 cranked wires were set in June and measured mid-summer and then again in October. To scale to production, we used subcapitulum bulk density which was calculated by

extracting five 2.54 cm diameter cores to a depth of at least 5 cm, from the field harvest site (Dorrepaal et al. 2004). The cores were frozen and then sliced into increments: capitulum 0–0.5 cm and sub-capitulum sections 0.5–2.5 cm. The number of *Sphagnum* stems in each sub-capitulum section was counted to determine shoot density and dried to a constant mass at 60 °C to determine bulk density (0.011 g/cm³). The three species of *Sphagnum* present were grouped for both the cranked wire measurements and bulk density calculations. Annual production was calculated by multiplying the lineal growth of the *Sphagnum* species by the sub-capitulum bulk density values. Production of *P. strictum* was calculated by multiplying the lineal growth rates of *Sphagnum* (Vitt 2007) by the *P. strictum* mass to shoot length ratios from Weltzin et al. (2000). This value was then scaled using percent cover data from the plant surveys. To determine the mass of ericaceous shrub stems buried annually by *Sphagnum* growth, a wood density to stem diameter equation was derived for *K. polifolia* and *C. calyculata*. The basal stem diameter data collected in the fall of 2012 and 2013 was used to estimate the mass of a given buried stem by multiplying the lineal growth of *Sphagnum* for a given bin by the calculated wood density for a given shrub species.

Peat elevation was measured to monitor hummock and hollow growth and subsidence and to accurately gauge WT levels. Using the vegetation sampling frame, we measure the distance at all 64 points from the frame to the sub-capitulum surface of the *Sphagnum* to determine a mean peat elevation, based on the distance of the surface to the base of the bin (hereafter referred to as “peat height”). This measurement was completed once in 2010 and twice per year from 2011 to 2013, at the beginning and the end of the growing season. Peat subsidence was surveyed with two manual elevation sensor rods per bin (Price 2003; Waddington et al. 2010). These sensor rods are wooden dowels with fixed anchors, inserted to a 20 and 40 cm depth, and measured bi-weekly from a fixed frame through the growing season. Change in the distance measured from the fixed frame was used to determine peat subsidence at >40 cm and 20–40 cm. By calculating the change in elevation over the growing season and accounting for peat subsidence, we can estimate how much of the change in elevation is due to *Sphagnum* growth in the top 20 cm.

Statistical analysis

The effects of WT and/or PFG manipulation were analyzed initially using multi-way analysis of variance with WT position (high or low) and PFG group (Ericaceae, sedge and unmanipulated) as the main factors; if significant ($p < 0.05$), the Holm-Sidak test was used for post-hoc multiple comparisons (SigmaPlot 12.5, Systat Software, San Jose, CA). Data were tested for normality using the Shapiro-Wilk W-statistic (Shapiro and Wilk 1965). A portion of the percent cover data by individual species did not meet the assumption of normality or equal variance ($p < 0.05$) and were either arcsine (many zero values) or log₁₀ (proportions greater than one) transformed prior to analysis. 2010, 2013, and change in 2010 to 2013 *P. strictum* cover, 2013 *C. calyculata*, 2013 *V. oxycoccus* and 2010 to 2013 change in *S. fuscum* data were Log₁₀ transformed. 2013 *C. oligosperma* and 2010 to 2013 cover change data for *S. magellanicum* were arcsin square root transformed. Spearman Rank Order was used for correlations with results significant at $p < 0.05$.

Results

Initial peat characterization

Mean bulk density values at time of the field harvest ranged from 0.028 g cm⁻³ at 0–10 cm depth to 0.115 g cm⁻³ at 50–60 cm depth (Table 1). C and N increased with depth, with a slight decrease in N at 70–80 cm below peat surface (Table 1). From 0 to 30 cm the mean ¹⁴C age was modern while our basal depth age (70–80 cm) was 930±21 year BP. There was a ~2% difference in δ¹³C from surface peat to peat at 60–70 cm depth (Table 1), which corresponds to enrichment with continued decomposition; this fractionation factor (Amundson and Baisden 2000) can be compared with other long-term peatland decomposition studies.

Water table and precipitation

Growing season (May to September) precipitation as rain measured 492 mm in 2011, 494 mm in 2012 and 442 mm in 2013. In 2011, to allow mosses to stabilize following PFG manipulations in June 2011 WTs were kept high (data not shown) and the WT treatments were separated by an average of only 5 cm from mid-July

Table 1 Initial peat characteristics from field harvest averaged across 24 harvest sites^a

Depth (cm)	C (%)	N (%)	C:N	Bulk density (g cm ⁻³)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{14}\text{C}$	¹⁴ C Age
0–10	44.4±0.3	0.7±0.03	62.8	0.028±0.002	-28.7±0.5	-6.4±0.1	57.0±00.8	modern
10–20	43.3±0.2	0.7±0.03	61.5	0.031±0.002	-28.0±0.3	-4.5±0.1	99.0±02.4	modern
20–30	43.5±0.2	1.0±0.05	49.5	0.051±0.005	-27.3±0.4	-2.7±0.1	201.4±18.6	modern
50–60	47.8±0.2	1.4±0.04	34.4	0.115±0.003	-26.8±0.3	-1.0±0.1	-57.4±5.8	417.5
70–80	49.3±0.3	1.0±0.02	49.4	0.089±0.003	-26.7±0.3	-2.2±0.1	-116.0±01.0	930.0

The standard errors are given (±SE)

^a $\Delta^{14}\text{C}$ values are averaged across 5 pits distributed throughout the harvest site

through the end of October. In 2012 the WT treatments differed by 10–20 cm from May to September and began to converge at the end of October (Fig. 1). In 2013, the mean low WT was 20–30 cm lower than the high WT from the end of June through September and at peak WT drawdown the mean low WT reached 50 cm below the peat surface and was below 40 cm for 2 months during the summer.

Vegetation cover

Prior to PFG and WT manipulations, the vegetation community composition was relatively uniform (Online Resource 4); however from 2010 to 2013 there was an overall decrease in shrub and sedge cover across all treatments (Table 2). *Vaccinium oxycoccos* cover decreased considerably, but began to recover in low WT treatments in 2013. The biggest reduction in *V. oxycoccos* cover was in the HE treatment, with $28 \pm 6\%$ (mean ± SE) cover in 2013 compared to $75 \pm 8\%$ in 2010; in the LE the *V. oxycoccos* cover decreased from 2010 to 2012 ($76 \pm 24\%$ in 2010 to $41 \pm 6\%$ in 2012) but recovered in 2013 ($61 \pm 20\%$). Overall shrub cover in the HE and HU plots declined from a mean total cover in 2010 of $113 \pm 18\%$ to $70 \pm 1\%$ in 2013, while the total shrub cover in the LE and LU plots declined initially from $125 \pm 8\%$ in 2010 to $88 \pm 6\%$ in 2012; but, driven primarily by *V. oxycoccos*, the shrubs in the low WT treatments recovered to $130 \pm 3\%$ in 2013 (Fig. 2). Total sedge cover also decreased ($37 \pm 4\%$ in 2010 to $17 \pm 3\%$ in 2012) in the sedge and unmanipulated treatments, with the greatest decline detected in the LS treatment (-25.8%) (Fig. 2). Conversely, *Sphagnum* cover across all treatments increased from 2010 to 2013 ($95 \pm 2\%$ in 2010 to $129 \pm 4\%$ in 2013). Under lowered WTs *S. fuscum* cover increased $18 \pm 2\%$, with the largest

increase in the LU treatment. *S. rubellum* cover increased under the high WTs, with a change of $+24 \pm 2\%$ from 2010 to 2012. *Polytrichum* sp. cover increased $40 \pm 17\%$ in the sedge treatments, while decreasing in HE and HU bins.

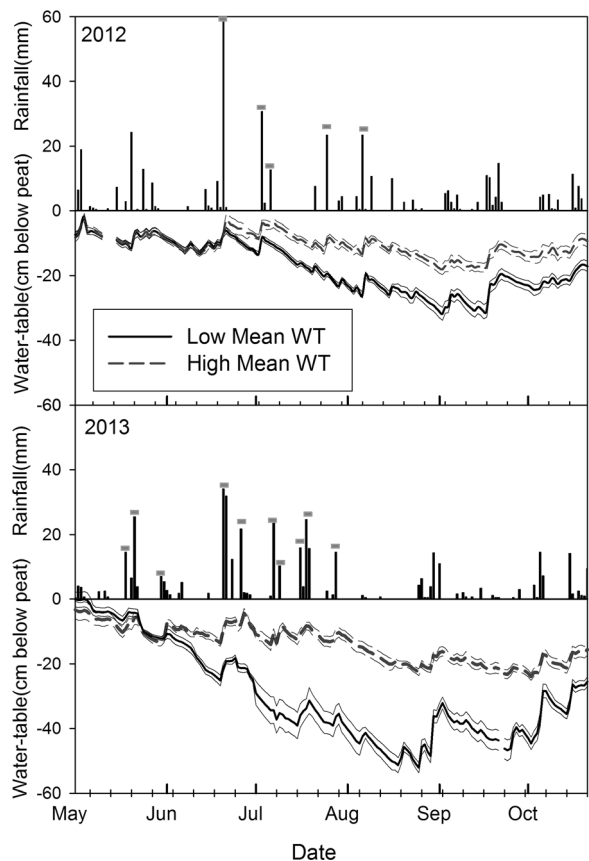


Fig. 1 2012–2013 water table profiles with daily precipitation (thin lines are upper and lower 95 % C.I. for high (dashed) and low (solid) mean WT). Grey bars above precipitation peaks indicate rain events excluded from low WT treatments

Table 2 Net difference in percent PFG cover by treatment from 2010 (pre-manipulation) to 2013

	High WT			Low WT		
	Ericaceae	Sedge	Unmanipulated	Ericaceae	Sedge	Unmanipulated
Graminoids						
<i>Carex oligosperma</i>	---a	-15.2	-18.4	---	-37.9	-19.1
<i>Eriophorum vaginatum</i>	---	0.0	1.3	---	15.1	0.0
Shrub						
<i>Andromeda polifolia</i>	0.0	---	0.0	0.0	---	-0.8
<i>Chamaedaphne calyculata</i>	-10.9	---	0.0	9.4	---	15.2
<i>Kalmia polifolia</i>	-1.2	---	-5.5	4.7	---	-3.5
<i>Rhododendron groenlandicum</i>	0.0	---	0.0	1.2	---	0.0
<i>Vaccinium oxycoccos</i>	-46.9	---	-20.3	-15.6	---	-0.4
Moss						
<i>Polytrichum strictum</i>	-13.9	23.0	-20.9	3.0	57.2	4.9
<i>Sphagnum fuscum</i>	16.9	-3.4	3.0	17.0	14.2	21.9
<i>Sphagnum magellanicum</i>	7.9	2.7	6.4	9.6	2.0	-0.1
<i>Sphagnum rubellum</i>	19.1	27.0	24.5	-15.4	-25.7	-8.7

Negative values (in *Italics*) represent a decrease in cover. For absolute cover values see Online Resource 3

^a Three dashes (---) are mesocosms in which all vegetation of the designated plant functional group was removed and was therefore not included in the change analysis from 2010 to 2013

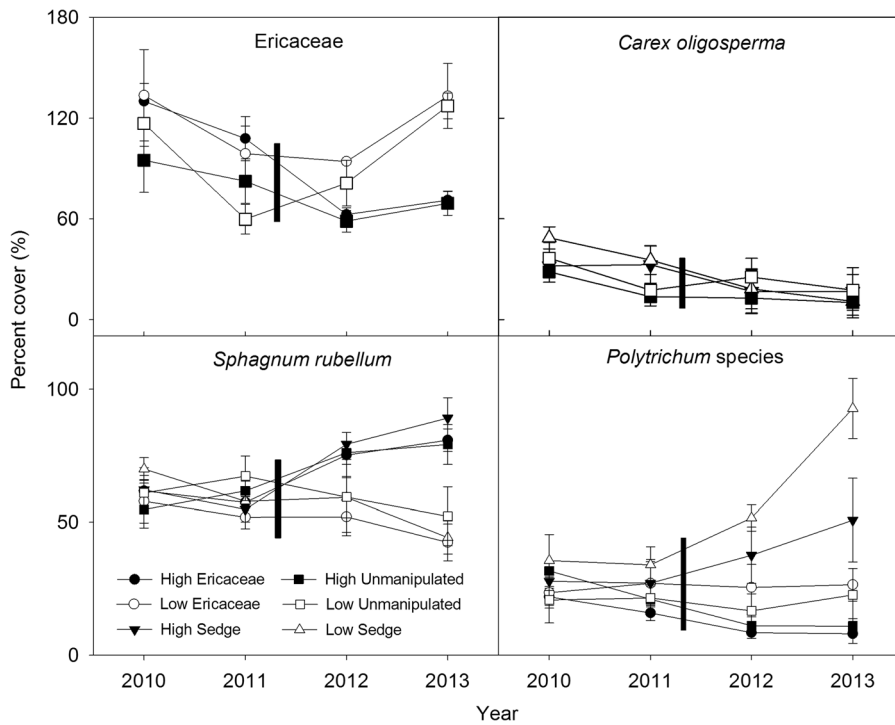


Fig. 2 Vegetation cover from 2010 to 2013 for dominant vegetation types. *Open symbols* indicate low water table treatments. *Solid vertical bar* represents initiation of water table treatments. Means ± SE

By the fall of 2013, there was no detectable WT or PFG effect on *S. fuscum* or *S. magellanicum* cover between treatments (Table 3). There was significantly higher cover of *S. rubellum* ($p<0.001$) in the high WT treatment, and significantly more dead *Sphagnum* in the low WT treatment ($p=0.005$). Total living *Sphagnum* cover in 2013 was significantly greater in high WT treatments ($p<0.001$). Significant water and PFG effects on *P. strictum* were present, with greater cover under low WTs ($p=0.006$) and in sedge only treatments ($p<0.001$). *V. oxycoccus* cover was highest in the lowered WT ($p=0.009$) (Table 3). *K. polifolia* had significantly more cover in low WT treatments in 2013 ($p=0.028$), however this same difference was detected in 2010 ($p=0.006$) prior to the initiation of the WT treatments, and the change from 2010 to 2013 was not significant. In 2013 total ericaceous shrub cover was significantly greater in low WTs ($p>0.001$) but there was no significant cover response to PFGs.

Aboveground biomass and production

Ericaceae-only and unmanipulated mesocosms had greater standing vascular plant biomass than sedge-only mesocosms (Table 4). In 2012 *C. calyculata* accounted for 44–60 % of shrub biomass, with *K. polifolia* comprising 22–34 % and *V. oxycoccus* 10–18 %. In 2013 we saw similar contributions to standing mass, with *C. calyculata* composing 50–65 % of standing shrub mass, *K. polifolia* 20–25 % and *V. oxycoccus* 13–23 %. Calculated aboveground production for *C. calyculata* ranged from 14 to 70 g m⁻² yr⁻¹, *K. polifolia* ranged from no net production to over 20 g m⁻² yr⁻¹, *V. oxycoccus* ranged from no net production to 28 g m⁻² yr⁻¹, and *C. oligosperma* was 0 to over 50 g m⁻² yr⁻¹.

There were no significant treatment effects on the individual Ericaceae species production in 2012 or 2013. However, for Ericaceae in 2013 (*C. calyculata* and *K. polifolia* production was combined), there was a significant WT x PFG interaction ($p=0.011$) (Table 5). Post hoc analysis indicated significantly greater production in the Ericaceae treatment when compared to unmanipulated treatment under low WTs only ($p=0.031$); and within the Ericaceae treatment only, there was significantly more production in the low WT treatment than high WT ($p=0.008$) (Table 5).

The annual contribution of stem mass buried by *Sphagnum* to aboveground standing biomass ranged

Table 3 Two-way ANOVA F and p-values for water table (high or low) and PFG (Ericaceae, sedge, unmanipulated) effects on vegetation cover in 2010 and 2013 and on cover change from 2010 to 2013 (mesocosms with vegetation removed excluded from change analysis and cover comparison for given treatments in 2013)

Year	Factor	Moss		Vascular													
		<i>Polytrichum strictum</i>	<i>Sphagnum fuscum</i>	<i>Sphagnum rubellum</i>	<i>Sphagnum magellanicum</i>	<i>Chamaedaphne calyculata</i>	<i>Kalmia polifolia</i>	<i>Vaccinium oxycoccus</i>	<i>Carex oligosperma</i>	F	P	F	P				
2010	Water	0.79	0.387	1.99	0.175	0.41	0.531	2.00	0.174	0.50	0.496	9.70	0.006	1.80	0.200	4.11	0.058
	Veg	0.98	0.394	0.08	0.919	0.87	0.436	0.48	0.919	0.30	0.296	0.22	0.804	1.11	0.349	1.87	0.182
	Interaction	1.69	0.213	1.02	0.382	0.48	0.627	0.05	0.948	0.96	0.961	2.54	0.107	0.54	0.594	0.17	0.849
2013	Water	9.49	0.006	0.60	0.451	35.32	<0.001	0.85	0.369	2.01	0.181	6.29	0.028	9.74	0.009	0.23	0.639
	Veg	12.84	<0.001	1.45	0.261	0.25	0.780	0.62	0.547	0.00	0.973	1.68	0.220	0.28	0.607	0.01	0.918
	Interaction	0.72	0.502	0.15	0.865	0.72	0.500	0.27	0.765	0.70	0.421	0.06	0.812	0.03	0.877	0.49	0.497
2013–2010 Cover Change	Water	12.74	0.002	1.99	0.177	26.54	<0.001	0.64	0.433	6.96	0.022	0.47	0.505	6.58	0.025	1.03	0.330
	Veg	10.79	<0.001	1.26	0.308	0.33	0.724	0.80	0.464	1.55	0.236	1.21	0.294	4.39	0.058	0.46	0.511
	Interaction	1.49	0.251	0.59	0.565	0.65	0.532	0.19	0.831	0.14	0.713	0.12	0.737	0.32	0.580	0.90	0.362

Values considered significant if $p<0.05$ (bolded in table)

Table 4 Vascular plant aboveground standing biomass (g m^{-2}) and annual production by treatment

	Standing biomass		Production	
	2012	2013	2012	2013
High WT				
Ericaceae	90.4±8.8	99.2±10.0	13.7±5.9	14.7±11.2
Sedge	24.2±5.9	12.6±5.1	24.2±5.9	12.6±5.1
Unmanipulated	98.7±16.6	97.0±4.2	32.4±10.1	44.9±10.1
Low WT				
Ericaceae	107.9±20.4	150.9±28.9	30.1±17.4	57.3±12.9
Sedge	41.1±14.0	15.6±6.3	41.1±14.0	12.0±6.7
Unmanipulated	111.4±3.7	129.2±5.6	40.1±1.9	34.9±7.7

Measurements were made at peak biomass and calculated using allometric equations established in study. Data includes the dominant vascular plants, *Carex oligosperma*, *Eriophorum vaginatum*, *Chamaedaphne calyculata*, *Kalmia polifolia* and *Vaccinium oxycoccos*. The standard errors are given (\pm SE)

by treatment from 14 to 39 % for *C. calyculata* and 11–22 % for *K. polifolia*, with a greater proportion of buried mass in high WT treatments due to higher rates of moss production (Online Resource 5). Although inclusion of this biomass in aboveground or belowground production becomes largely an accounting problem from the perspective of total plant production budgets, from the perspective of tracking net change in aboveground biomass, which is our goal in the present study, it is appropriate to exclude this from aboveground production estimates, so the following production results do not include buried biomass.

Summed vascular plant production was similar by treatment in 2012, however in 2013 there was a significant PFG effect ($p=0.003$) (Table 5), with greater production in unmanipulated and Ericaceae when

compared to sedge treatments. There was also a significant WT x PFG interaction ($p=0.049$), with production significantly higher in low WT for the Ericaceae treatment ($p=0.003$), but not for sedge or unmanipulated treatments.

In 2012 and 2013 there was a strong WT effect on *Sphagnum* production, with significantly higher growth rates in high WT treatments ($p<0.001$ in 2012 and 2013). No PFG effects on *Sphagnum* production were detected in either year (Table 5). In contrast, there was a significant PFG effect but no WT effect on *Polytrichum* production, which was significantly higher in sedge treatments than Ericaceae or unmanipulated in 2012 and 2013 ($p=0.003$ and $p<0.001$ respectively).

When vascular plant and moss production were combined the high WT treatment had significantly greater

Table 5 Two-way ANOVA F and p-values for water table (high or low) and PFG (Ericaceae, sedge, unmanipulated) effects on aboveground production in 2012 and 2013

Year	Factor	<i>Chamaedaphne calyculata</i> & <i>Kalmia polifolia</i>		<i>Carex oligosperma</i>		All vascular production		<i>Sphagnum spp.</i>		<i>Polytrichum spp.</i>	
		F	p	F	p	F	p	F	p	F	p
2012	Water	1.563	0.237	1.051	0.325	2.899	0.106	20.344	<0.001	0.097	0.760
	Veg	0.003	0.961	2.618	0.132	1.197	0.325	1.182	0.329	7.896	0.003
	Interaction	0.036	0.853	0.566	0.466	0.072	0.931	0.344	0.714	0.626	0.546
2013	Water	2.132	0.170	0.138	0.689	4.348	0.052	40.891	<0.001	0.213	0.650
	Veg	0.195	0.667	0.707	0.417	8.166	0.003	1.679	0.215	10.643	<0.001
	Interaction	9.127	0.011	0.296	0.597	3.583	0.049	1.164	0.335	0.120	0.888

Values considered significant if $p<0.05$ (bolded in table)

aboveground production in 2012 and 2013 ($p=0.003$ and $p<0.001$ respectively). The contribution of vascular plant production to total aboveground net primary production (ANPP) by treatment ranged from 3 % in 2012 with high WT up to 15 % in 2013 with low WT (Fig. 3).

Peat subsidence and net surface change

Peat subsidence below 20 cm was observed across all treatments from 2011 to 2013. Subsidence was greater overall in the shallow depth (20–40 cm) than in the >40 cm depths, but did not differ significantly between treatments over the 3 year period at 20–40 cm (Fig. 4). At depths below 40 cm, subsidence was significantly greater in the low WT treatments ($p<0.001$). When the measured depths were combined, there were significant WT ($p=0.008$) and PFG ($p=0.043$) effects, again with greater subsidence in the low WT treatments (Table 6). Ericaceae only treatments resulted in the greatest subsidence, differing significantly from the unmanipulated treatment ($p=0.040$) but not from sedge only ($p=0.270$)

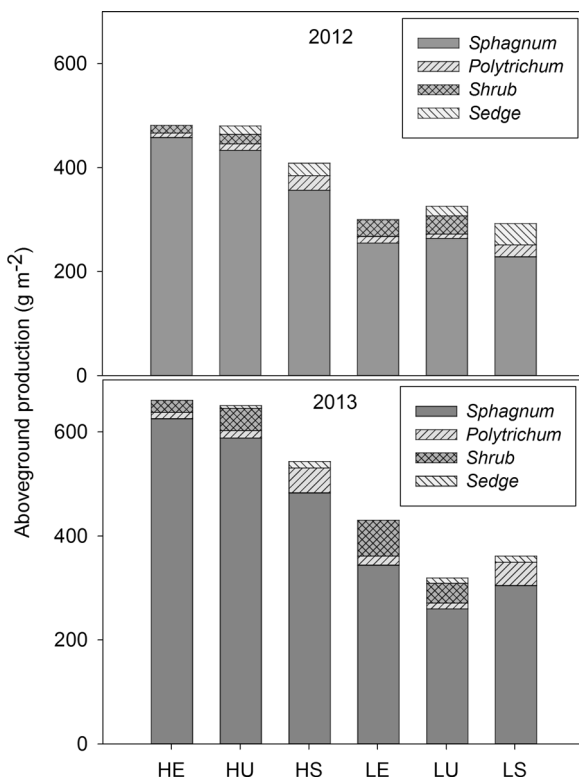


Fig. 3 Aboveground production (g m^{-2}) allocation by treatment for 2012 (top) and 2013 (bottom). Shrubs include *Chamaedaphne calyculata*, *Kalmia polifolia* and *Vaccinium oxycoccos* and sedges include *Carex oligosperma* and *Eriophorum vaginatum*

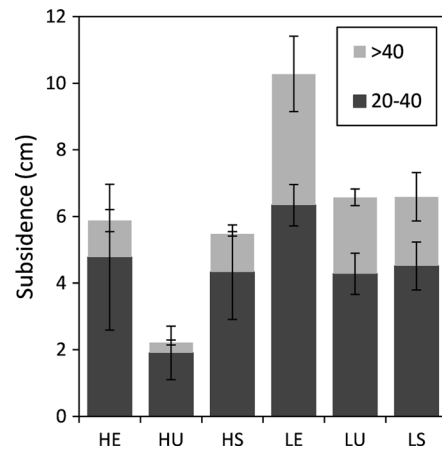


Fig. 4 Shallow (20–40 cm) and deep (>40 cm) peat subsidence from July 2011 to October 2013. Means \pm SE

(Table 6). In 2013 subsidence of peat was in line with the drop in WTs (Fig. 5), with the lowered WT treatments having significantly more peat subsidence ($p<0.001$).

From 2011 until 2013 peat height increased on average 4–13 cm in the high WT treatments and 0–6 cm in the low WT treatments, with the exception of average peat height in LS which decreased over the 3 year period (Fig. 6). The cumulative change in peat height from spring 2011 (pre-PFG or water manipulation) to the fall of 2013 showed significant PFG ($p<0.001$) and WT ($p<0.001$) effects, but no interactive effects. Post-hoc analyses revealed a greater increase in peat height with increased WT height as well as a larger increase in peat height for both Ericaceae and unmanipulated treatments when compared to sedge only ($p<0.001$), but not when compared with each other ($p=0.291$). As expected, changes in peat height during the growing season were positively correlated with lineal growth of *Sphagnum* in 2012 ($r_s=0.55$, $p=0.006$) and 2013 ($r_s=0.78$, $p<0.001$).

There were significant WT and PFG effects, but no significant interactive effects, on 0–20 cm net peat accumulation (change in peat height plus peat subsidence >20 cm) from 2011 to 2013 (Fig. 7). Moss production in 2012 and 2013 was positively correlated with peat accumulation ($r_s=0.59$, $p=0.0026$). The high WT treatments had more net peat accumulation than low WT treatments ($p=0.010$). All treatments had net peat accumulation from 0 to 20 cm, with Ericaceae and unmanipulated having significantly more accumulation than sedge ($p<0.001$ and $p=0.012$ respectively), but no significant difference between Ericaceae and unmanipulated.

Table 6 Two-way ANOVA F and p-values for water table (high or low) and PFG (Ericaceae, sedge, unmanipulated) effects on change in peat surface from 2011 to 2013 and subsidence (>20 cm) and peat accumulation (0–20 cm) from 2012 to 2013

Factor	Peat surface change		Peat subsidence (>20 cm)		Peat accumulation (0–20 cm)	
	F	p	F	p	F	p
Water	76.034	< 0.001	8.994	0.008	8.363	0.010
Veg	26.466	< 0.001	3.765	0.043	10.905	< 0.001
Interaction	2.476	0.112	0.986	0.393	0.385	0.686

Values considered significant if $p < 0.05$ (bolded in table)

Discussion

Vascular plant response

Consistent with our first hypothesis, there was an increase in aboveground ericaceous shrub productivity and abundance with increased depth to water tables in the PEATcosm experiment. Previous studies have supported this shift in vegetation as a result of drier conditions in northern bog and poor fen ecosystems (Weltzin et al. 2000; Laiho et al. 2003; Strack et al. 2006b;

Breeuwer et al. 2009; Straková et al. 2010). The increases we saw in plant cover were attributed primarily to *V. oxycoccos* and *C. calyculata*, which are typically found growing at the dry end of the hydrology gradient in wetlands (Jeglum 1971; Bragazza and Gerdol 1996). The implications of increased shrub presence as depth to water table increases in northern peatlands include alterations of surface temperature due to shading and/or feedbacks to ecosystem C cycling (Limpens et al. 2008; Heijmans et al. 2013). Even with a deeper oxic zone with lower water tables, an increase of ericaceous litter could offset the potentially higher rates of peat decomposition and lead to further creation of environmental

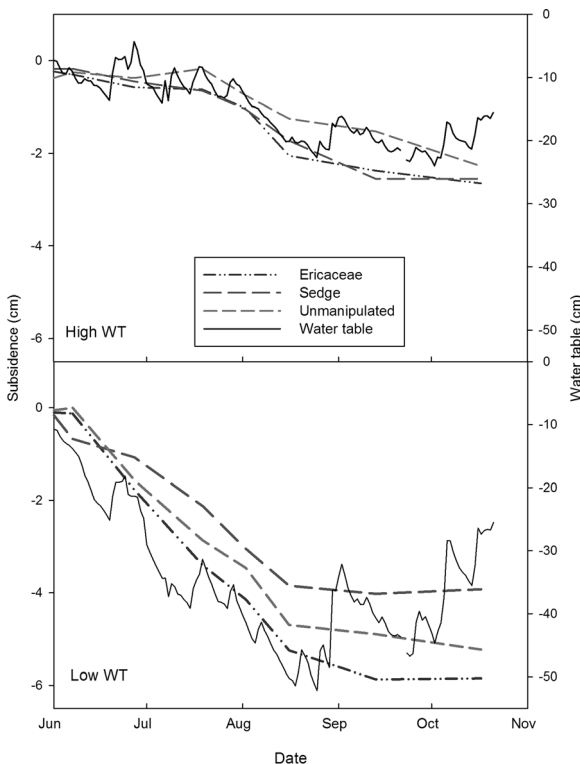


Fig. 5 Subsidence (20–40 cm and >40 cm combined) and mean water table (solid line) through 2013 growing season for High (top) and Low (bottom) WT treatments

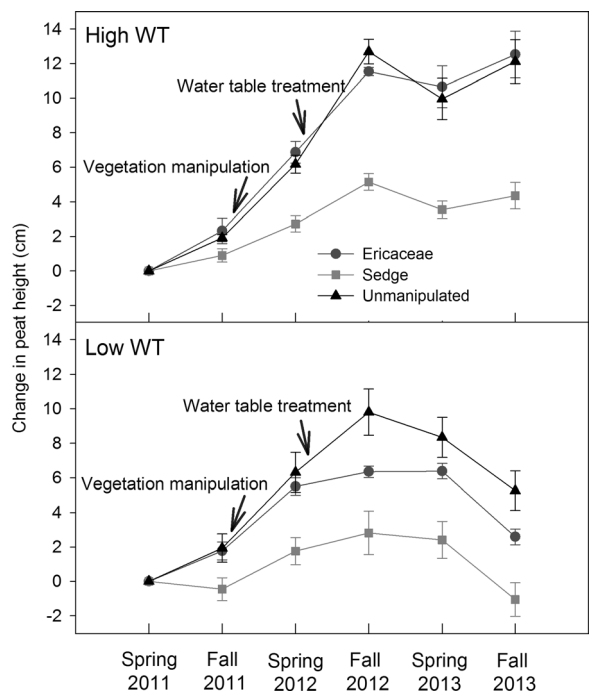


Fig. 6 Change in peat height 2011–2013. PFG manipulation and full WT treatment indicated with arrows. Means by PFG and water table treatment \pm SE

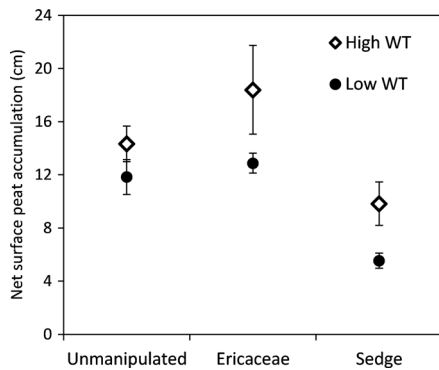


Fig. 7 Net surface peat (0–20 cm) accumulation 2011–2013. This is calculated from the change in peat height plus subsidence below 20 cm. Low WT treatments are open diamonds. High WT treatments are closed circles. Means \pm SE

conditions preferable to shrub growth. In addition, larger and more productive shrubs could cause more shading for understory plants and limit bryophyte production (Berendse et al. 2001).

Interestingly, the significant WT \times PFG interactions for Ericaceae growth and vascular plant production indicated that the positive response of shrubs to lower water tables was stronger in the absence of sedges. Whether this represents a release from competition or some other mechanism is unclear. We found no studies testing for sedge-Ericaceae competition in bogs. Further study of these interactions is warranted, given the potential importance of these interactions for predicting peatland vegetation dynamics.

In our first hypothesis we also expected an increase in sedge cover and production under lower WTs, but instead we found sedges were negatively affected by all treatments, with decreasing cover from experiment initiation through 2013. In contrast, Strack et al. (2006b) reported an increase in *C. oligosperma* in drained lawns over a 2 year period. However, temporal variation in sedge cover, regardless of hydrology, has been demonstrated in a number of studies (Laine et al. 1995; Thormann and Bayley 1997; Weltzin et al. 2000, 2003; Bragazza 2006). Sedge abundance in the Minnesota bog mesocosm study (Weltzin et al. 2003) initially increased with lowered water tables, but after 4 years the cover dropped considerably. The year-to-year variability detected in sedges could be due to sensitivity to water table fluctuations (Visser et al. 2000), increased competition from shrubs under lowered water tables and/or bryophytes under high water tables, sensitivity to changes caused by our experiment, or temperatures outside of

the species range. While Houghton is within, but toward the warmer end of, the range of mean annual temperatures reported for *C. oligosperma* populations in one study (Gignac et al. 2004), the native range of this species extends much further south (Indiana, Illinois) than our site (USDA-NRCS 2014). Multiple minor stressors combined with competition could be sufficient to reduce sedge growth in our study system. Annual rates of aboveground sedge production in wetlands vary widely, but annual production rates in northern, oligotrophic peatlands have been reported under $15 \text{ g m}^{-2} \text{ year}^{-1}$ (Solander 1983; Weltzin et al. 2000; Chapin et al. 2004), and are similar to the production we have measured in the PEATcosm (Table 4).

Basal stem diameter was used as our predictor in allometric equations for standing biomass. Thus, there are likely underestimates of aboveground production of ericaceous shrubs under high WT due to a stem burial effect, where the basal stem diameter measured in the spring gets buried by *Sphagnum* and the diameters measured in high WT in the fall are measured slightly higher on the stem than in low WT. In an ericaceous shrub dominated *Sphagnum* mire, Wallén et al. (1988) estimated that annually 3 to 20 % of standing mass was buried, assuming a lineal moss growth rate of 2 mm/year. In our system we measured lineal growth rates of *Sphagnum* to be 3–6 cm/year in high WT and 1.5–4 cm/year in low WT. These high rates of lineal growth result in a significant stem burial effect. In fact when we calculated the amount of aboveground biomass buried (*C. calyculata* and *K. polifolia* combined) based on lineal *Sphagnum* growth and wood density (conservatively assuming a cylinder rather than a taper) we estimated 20–27 % of standing biomass was buried in high WT treatments and 13–16 % buried under low WT. This shift from aboveground to belowground biomass can be highly variable by species and environmental conditions. Murphy et al. (2009) studied the shifting biomass allocation dynamics in relation to depth to water table and found that as the depth to WT increases, the amount of biomass produced both below- and aboveground increases. While our aboveground production estimates increase substantially if buried stem estimates are factored in (Online Resource 5), particularly in high WT, the plant cover data aligned with our production estimates as calculated (excluding stem burial effects), with both showing significantly higher Ericaceae cover and aboveground production under low WT treatments.

Bryophyte response

As predicted in our first hypothesis, *Sphagnum* moss production increased with increasing water table levels. *Sphagnum* mosses are highly sensitive to changes in water content and both very high and low water conditions can result in decreases in photosynthesis and production (Schipperges and Rydin 1998). In cases of extreme and prolonged drought *Sphagnum* is susceptible to irreversible desiccation (Schipperges and Rydin 1998). *Sphagnum* production was positively correlated with higher water tables in a Minnesota peatland mesocosm experiment (Weltzin et al. 2000). And while overall production of *Sphagnum* is important, the species response can also be highly variable. Generally, hummock species have been found to be most resilient to drought (Hayward and Clymo 1982; Robroek et al. 2007b). Drought avoidance strategies in hummock species of *Sphagnum* mosses include increased stem bulk density and more efficient capillary transport (Grosvernier et al. 1997; Robroek et al. 2007b). Along the microtopography gradient *S. rubellum* typically occupies areas with higher moisture content and *S. fuscum* is found on drier hummocks (Robroek et al. 2007a; Kotiaho et al. 2013). In the PEATcosm, *S. rubellum* increased in cover in the high WT, and there was a trend towards increasing *S. fuscum* cover with low WT treatments, however in 2013 high rates of *Sphagnum* mortality in these low WT mesocosms muted the species response. *S. magellanicum* has been shown to be highly sensitive to drought conditions and has greater moisture requirements than *S. rubellum* and *S. fuscum* (Wallén et al. 1988; Robroek et al. 2007a, b), but no significant drought effects on *S. magellanicum* cover were detected in our study.

We hypothesized increased *Sphagnum* production and cover with ericaceous shrub removal due to greater light availability; however no PFG effect was found. In some peatland restoration studies increased survival and production of *Sphagnum* mosses is associated with greater shrub cover because of shading and wind interception, which reduces evaporative loss at the peat surface (McNeil and Waddington 2003; Farrick and Price 2009). We also expected to see a decline in hummock *Sphagnum* species cover when Ericaceae were removed due to a loss of hummock structural support by shrub roots, but there were no significant effects on *Sphagnum* species attributed to PFG treatments. This is likely due to our selection of systems with relatively

small changes in microtopography at the onset of the experiment.

In low WT treatments where rates of *Sphagnum* mortality were high and in sedge only bins, *Polytrichum* increased in cover as we hypothesized. *Polytrichum* is much better adapted than *Sphagnum* to prolonged periods of drought and disturbance and has been used as a transitional species for restoring cutover, drained or burned peatlands (Benscoter 2006; Groeneveld et al. 2007). As an early successional species, *Polytrichum* thrives in open canopy conditions, and is able to photosynthesize at high levels, even in water stressed conditions that would otherwise inhibit the growth of other mosses (Callaghan et al. 1978).

In *Sphagnum* dominated wetlands, moss production can comprise anywhere from 30 % (Weishampel et al. 2009) to 70–90 % of total ANPP (Chapin et al. 2004), with production highly dependent on position of water table (Clymo 1973; Hayward and Clymo 1983; Wallén et al. 1988; Schipperges and Rydin 1998; Weltzin et al. 2001). For instance, when moss accounted for only 30 % of production it was during a severe summer drought (Weishampel et al. 2009). In all PEATcosm treatments the contribution of *Sphagnum* to total ANPP was at least 80 % and was as high as 97 % in the HE treatment. In line with other water table manipulation studies (Weltzin et al. 2001; Robroek et al. 2007b; Breeuwer et al. 2009), high WT had a significant positive effect on *Sphagnum* production in 2012 and 2013. In summary, although there was an opposing effect seen with higher shrub production in low WT treatments, the mosses dominated total ANPP and overrode any impacts of the shifting vegetation dynamics on above-ground plant production. However, changing vascular plant communities are likely to have other significant effects, e.g. on microbial metabolic processes within the peat that affect ecosystem carbon balance and trace gas flux.

Peat structural response

Our low WT treatment resulted in high rates of both shallow (20–40 cm) and deep (greater than 40 cm) peat subsidence over the course of the experiment. In our third hypothesis we expected the sedge only treatments would have the highest rates of subsidence, due the loss of the ericaceous roots in the top 30 cm. Surprisingly, our highest rate of peat subsidence (>40 cm) was measured in the LE treatments. High decomposition rates of

sedge roots were measured in this experiment (unpublished data) and have been reported in the literature (Thormann et al. 2001; Strakova et al. 2012). Sedges might also affect the gas (CO_2 and CH_4) bubble content of the peat, which can be an important factor in peat surface deformation (Comas et al. 2005; Strack et al. 2006a). Although sedges are generally hypothesized to reduce gas content of peat via creation of diffusive flux pathways through aerenchyma (e.g., Green and Baird (2012)), our understanding of these dynamics is incomplete, and it is possible that under certain conditions sedge-mediated stimulation of oxidation could lead to a change in gas content. Thus it is possible the removal of sedge and the subsequent death of sedge roots had more of an effect on peat structure than predicted, contributing to more deep peat subsidence in LE than expected. However, when moss production and surface change were factored in (Fig. 7) there was significantly more subsidence (less peat accumulation) in sedge treatments in the shallow depth (0–20 cm). The 0–20 cm subsidence observed primarily in the sedge treatments is likely due to the removal of the ericaceous roots in this zone which decreased the physical support for the *Sphagnum* mosses. It is important to consider that long term changes in PFG and the associated litter of the PFGs will also affect the rate of decomposition, and will feedback into peat subsidence. Woody shrub and moss litter decompose more slowly than sedge litter, with hummock *Sphagnum* mosses (ie *Sphagnum fuscum*) decomposing more slowly than hollow species (Cornelissen 1996; Straková et al. 2010). In some peatlands where low water table position results in an altered PFG, the chemical quality of litter inputs could offset or slow decomposition, limiting peat subsidence. Ongoing decomposition experiments and analysis of plant litter chemistry within PEATcosm will provide further insight into PFGs and their role in peat subsidence.

There was a strong response in peat subsidence to our WT treatments, with significantly greater subsidence as depth to WT increased. Peat subsidence is common in drained peatlands (Rothwell et al. 1996; Minkinen and Laine 1998; Price and Schlotzhauer 1999; Waddington et al. 2010) and has long-term implications, including increased bulk density and decreased hydraulic conductivity (Price 2003; Whittington and Price 2006). This denser peat could make it more difficult for *Sphagnum* moss to access water during severe droughts due to lower hydraulic conductivity and thus restricted

capillary flow (Price and Schlotzhauer 1999). However, the increased bulk density could also allow for more saturated peat with higher osmotic potential following rain events leading to an increase in soil moisture availability for periods of time and less drying at the peat surface (Silins and Rothwell 1998). In our experiment, long periods of drought coupled with peat subsidence have resulted in lower rates of moss production and increased rates of *Sphagnum* mortality, which suggests strong hydrologic controls over bryophyte cover and production, with subsidence alone not being sufficient to maintain moisture levels for moss proliferation when water tables are significantly reduced.

Conclusions

Our experimental design allowed us to tease apart the independent and interactive effects of WT and PFG composition on aspects of peatland ecology. Both WT and PFG contributed to plant community dynamics, productivity and peat structure, with the importance of these factors and their interaction varying depending on response variables. Water table had the strongest impact on cover of *Sphagnum* and Ericaceae, whereas *Polytrichum* cover was strongly influenced by both WT and PFG. Although WT controlled *Sphagnum* production and hence total ANPP, the experiment revealed Ericaceae production was controlled by interactions between WT and PFG, suggesting that Ericaceae respond more positively to lowered water table in the absence of sedges. In the case of peat subsidence and accumulation, both water table and plant functional group had strong impacts on different aspects, without detectable interactions. Thus both factors have a likely role in structuring the dynamics of peatland vegetation and topography. These observations inform the next phase of research in this system focused on the microbial and plant roles in peatland carbon balance and trace gas production.

Acknowledgments This work was supported primarily by the USDA Forest Service Northern Research Station Climate Change Program and the National Science Foundation (DEB-1146149). The authors would like to thank Todd Ontl and L. Jamie Lamit, as well as two anonymous reviewers, for their helpful comments and suggestions. This work would not have been possible without the help of countless student technicians, including Kayla Griffith, Eryn Grupido and Jesse Barta.

References

- Amundson R, Baisden WT (2000) Stable isotope tracers and mathematical models in soil organic matter studies. In: Sala OF, Jackson RB, Mooney HA, Howarth RW (eds) *Methods in ecosystem science*. Springer, New York, pp 117–134
- Armstrong W, Justin SHFW, Beckett PM, Lythe S (1991) Root adaptation to soil waterlogging. *Aquat Bot* 39:57–73
- Benscoter BW (2006) Post-fire bryophyte establishment in a continental bog. *J Veg Sci* 17:647–652
- Berendse F, Van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H (2001) Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in Sphagnum bogs. *Glob Chang Biol* 7:591–598
- Bonham CD, Ahmed J (1989) Measurements for terrestrial vegetation
- Bragazza L (2006) A decade of plant species changes on a mire in the Italian Alps: vegetation-controlled or climate-driven mechanisms? *Clim Chang* 77:415–429
- Bragazza L, Gerdol R (1996) Response surfaces of plant species along water-table depth and pH gradients in a poor mire on the southern Alps (Italy). *Ann Bot Fenn* 33:11–20
- Breeuwer A, Robroek BJ, Limpens J, Heijmans MM, Schouten MG, Berendse F (2009) Decreased summer water table depth affects peatland vegetation. *J Basic Appl Ecol* 10:330–339
- Bridgham SD, Johnston CA, Pastor J, Updegraff K (1995) Potential feedbacks of northern wetlands on climate change. *BioScience*: 262–274
- Buttler A (1992) Permanent plot research in wet meadows and cutting experiment. *Vegetatio* 103:113–124
- Callaghan TV, Collins NJ, Callaghan CH (1978) Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. *Strategies of growth and population dynamics of tundra plants* 4. *Oikos*: 73–88
- Chapin FS, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77:822–840
- Chapin FS, Bret-Harte MS, Hobbie SE, Zhong H (1996) Plant functional types as predictors of transient responses of arctic vegetation to global change. *J Veg Sci* 7:347–358
- Chapin CT, Bridgham SD, Pastor J (2004) pH and nutrient effects on above-ground net primary production in a Minnesota, USA bog and fen. *Wetlands* 24:186–201
- Chivers MR, Turetsky MR, Waddington JM, Harden JW, McGuire AD (2009) Effects of experimental water table and temperature manipulations on ecosystem CO₂ fluxes in an Alaskan rich fen. *Ecosystems* 12:1329–1342
- Clymo RS (1970) The growth of Sphagnum: methods of measurement. *J Ecol* 58(1):13–49
- Clymo RS (1973) The growth of Sphagnum: some effects of environment. *J Ecol* 61(3):849–869
- Comas X, Slater L, Reeve A (2005) Spatial variability in biogenic gas accumulations in peat soils is revealed by ground penetrating radar (GPR). *Geophys Res Lett* 32:L08401
- Comelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. *J Ecol* 84(4):573–582
- Dahl TE, Zoltai SC (1997) Forested northern wetlands of North America. In: Trettin CC, Jurgensen MF, Grigal DF, Gale MR, Jeglum JK (eds) *Northern forested wetlands: ecology and management*. CRC Press, New York, pp 3–18
- Dorrepaal E, Aerts R, Cornelissen JH, Callaghan TV, Van Logtestijn RS (2004) Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure and production in a sub-arctic bog. *Glob Chang Biol* 10:93–104
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074
- Fahey TJ, Knapp AK (2007) Principles and standards for measuring primary production. Oxford University Press, USA
- Farrick KK, Price JS (2009) Ericaceous shrubs on abandoned block-cut peatlands: implications for soil water availability and Sphagnum restoration. *Ecology* 2:530–540
- Fritz C, Campbell DI, Schipper LA (2008) Oscillating peat surface levels in a restiad peatland, New Zealand—magnitude and spatiotemporal variability. *Hydrological Process* 22:3264–3274
- Gerdol R, Bonora A, Gualandri R, Pancaldi S (1996) CO₂ exchange, photosynthetic pigment composition, and cell ultrastructure of Sphagnum mosses during dehydration and subsequent rehydration. *Can J Bot* 74:726–734
- Gignac LD, Gauthier R, Rochefort L, Bubier J (2004) Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada. *Can J Bot* 82(9):1292–1313
- Glime JM (2007) *Bryophyte Ecology*, vol 1. Physiological ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists
- Gray JT, Schlesinger WH (1981) Biomass, production, and litterfall in the coastal sage scrub of southern California. *American Journal of Botany*: 24–33
- Green SM, Baird AJ (2012) A mesocosm study of the role of the sedge *Eriophorum angustifolium* in the efflux of methane—including that due to episodic ebullition—from peatlands. *Plant Soil* 351:207–218
- Groeneveld EV, Masse A, Rochefort L (2007) *Polytrichum strictum* as a nurse-plant in peatland restoration. *Restor Ecol* 15:709–719
- Groisman PY, Knight RW, Easterling DR, Karl TR, Hegerl GC, Razuvayev VN (2005) Trends in intense precipitation in the climate record. *J Clim* 18:1326–1350
- Grosvernier P, Matthey Y, Buttler A (1997) Growth potential of three *Sphagnum* species in relation to water table level and peat properties with implications for their restoration in cut-over bogs. *J Appl Ecol* 34(2):471–483
- Hayward PM, Clymo RS (1982) Profiles of water-content and pore-size in sphagnum and peat, and their relation to peat bog ecology. *Proc R Soc Lond Ser B Biol Sci* 215:299–325
- Hayward PM, Clymo RS (1983) The growth of Sphagnum: experiments on, and simulation of, some effects of light flux and water-table depth. *J Ecol* 71(3):845–863
- Heijmans MM, Knaap YA, Holmgren M, Limpens J (2013) Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Glob Chang Biol* 19:2240–2250
- Hilbert DW, Roulet N, Moore T (2000) Modelling and analysis of peatlands as dynamical systems. *J Ecol* 88:230–242
- Holden J, Burt TP (2003) Hydrological studies on blanket peat: the significance of the acrotelm-catotelm model. *J Ecol* 91:86–102

- Jeglum JK (1971) Plant indicators of pH and water level in peatlands at Candle Lake, Saskatchewan. *Can J Bot* 49: 1661–1676
- Johnson LC, Damman AW (1991) Species-controlled Sphagnum decay on a south Swedish raised bog. *Oikos* 61(2):234–242
- Kotiaho M, Fritze H, Merilä P, Tuomivirta T, Väiliranta M, Korhola A, Karofeld E, Tuittila E-S (2013) Actinobacteria community structure in the peat profile of boreal bogs follows a variation in the microtopographical gradient similar to vegetation. *Plant Soil* 369:103–114
- Kunkel KE, Easterling DR, Redmond K, Hubbard K (2003) Temporal variations of extreme precipitation events in the United States: 1895–2000. *Geophys Res Lett* 30:1900
- Laiho R, Vasander H, Penttilä T, Laine J (2003) Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. *Glob Biogeochem Cycles* 17(2):1053
- Laine J, Vasander H, Laiho R (1995) Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *J Appl Ecol* 32:785–802
- Limpens J, Berendse F, Blodau C, Canadell JG, Freeman C, Holden J, Roulet NT, Rydin H, Schaepman-Strub G (2008) Peatlands and the carbon cycle: from local processes to global implications—a synthesis. *Biogeosci Discuss* 5:1475–1491
- McNeil P, Waddington JM (2003) Moisture controls on Sphagnum growth and CO₂ exchange on a cutover bog. *J Appl Ecol* 40: 354–367
- Minkinen K, Laine J (1998) Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. *Can J For Res* 28:1267–1275
- Mitchell EA, Buttler A, Grosvernier PH, Rydin H, Albinsson C, Greenup AL, Heijmans MM, Hoosbeek MR, Saarinen T (2000) Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five Sphagnum-dominated peatlands in Europe. *New Phytol* 145:95–106
- Munir TM, Xu B, Perkins M, Strack M (2014) Responses of carbon dioxide flux and plant biomass to water table drawdown in a treed peatland in northern Alberta: a climate change perspective. *Biogeosciences* 11:807–820
- Murphy MT, McKinley A, Moore TR (2009) Variations in above- and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. *Botany* 87:845–853
- Price JS (2003) Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands. *Water Resour Res* 39:1241
- Price JS, Schlotzhauer SM (1999) Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. *Hydrol Process* 13: 2591–2601
- Proctor MCF (2000) The bryophyte paradox: tolerance of desiccation, evasion of drought. *Plant Ecol* 151:41–49
- Riutta T, Laine J, Tuittila E-S (2007) Sensitivity of CO₂ exchange of fen ecosystem components to water level variation. *Ecosystems* 10:718–733
- Robroek BJM, Limpens J, Breeuwer A, Crushell PH, Schouten MGC (2007a) Interspecific competition between Sphagnum mosses at different water tables. *Funct Ecol* 21:805–812
- Robroek BJM, Limpens J, Breeuwer A, Schouten MGC (2007b) Effects of water level and temperature on performance of four Sphagnum mosses. *Plant Ecol* 190:97–107
- Rothwell RL, Silins U, Hillman GR (1996) The effects of drainage on substrate water content at several forested Alberta peatlands. *Can J For Res* 26:53–62
- Roulet NT, Moore TR, Bubier J, Lafleur P (1992) Northern fens: methane flux and climatic change. *Tellus Ser B Chem Phys Meteorol* 44:100–105
- Schipperges B, Rydin H (1998) Response of photosynthesis of Sphagnum species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytol* 140: 677–684
- Sebestyen SD, Dorrance C, Olson DM, Verry ES, Kolka RK, Elling AE, Kyllander R (2011) Long-term monitoring sites and trends at the Marcell experimental forest. In: Kolka RK, Sebestyen SD, Verry ES, Brooks KN (eds) *Peatland biogeochemistry and watershed hydrology at the Marcell experimental forest*. CRC Press, Boca Raton, pp 15–71
- Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). *Biometrika* 52:591–611
- Silins U, Rothwell RL (1998) Forest peatland drainage and subsidence affect soil water retention and transport properties in an Alberta peatland. *Soil Sci Soc Am J* 62(4): 1048–1056
- Solander D (1983) Biomass and shoot production of *Carex rostrata* and *Equisetum fluviatile* in unfertilized and fertilized subarctic lakes. *Aquat Bot* 15:349–366
- Stottlemeyer R, Toczydlowski D (1991) Stream chemistry and hydrologic pathways during snowmelt in a small watershed adjacent Lake Superior. *Biogeochemistry* 13(3):177–197
- Strack M, Waddington JM (2007) Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Glob Biogeochem Cycles* 21:GB1007
- Strack M, Kellner E, Waddington JM (2006a) Effect of entrapped gas on peatland surface level fluctuations. *Hydrol Process* 20: 3611–3622
- Strack M, Waddington JM, Rochefort L, Tuittila ES (2006b) Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *J Geophys Res Biogeosci* (2005–2012) 111: 2156–2202
- Straková P, Anttila J, Spetz P, Kitunen V, Tapanila T, Laiho R (2010) Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. *Plant Soil* 335:501–520
- Strakova P, Penttilä T, Laine J, Laiho R (2012) Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Glob Chang Biol* 18:322–335
- Thomson AM, Brown RA, Rosenberg NJ, Izaurralde RC, Benson V (2005) Climate change impacts for the conterminous USA: an integrated assessment. Part 4: water resources. *Climate Change* 69:67–88
- Thormann MN, Bayley SE (1997) Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecol* 131:1–16
- Thormann MN, Bayley SE, Currah RS (2001) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. *Can J Bot* 79:9–22
- Trettin CC, Laiho R, Minkinen K, Laine J (2006) Influence of climate change factors on carbon dynamics in northern forested peatlands. *Can J Soil Sci* 86(Special Issue):269–280

- Tsonis AA, Triantafyllou GN, Georgakakos KP (1996) Hydrological applications of satellite data: 1. Rainfall estimation. *Journal of Geophysical Research: Atmospheres* (1984–2012) 101:26517–26525
- USDA-NRCS (2014) The PLANTS Database. National Plant Data Team
- Visser EJW, Colmer TD, Blom CWPM, Voesenek LACJ (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant Cell Environ* 23:1237–1245
- Vitt DH (2006) Functional characteristics and indicators of boreal peatlands. In: *Boreal peatland ecosystems*, Springer, Berlin Heidelberg, pp 9–24
- Vitt DH (2007) Estimating moss and lichen ground layer net primary production in tundra, peatlands, and forests. In: Fahey TJ, Knapp AK (eds) *Principles and standards for measuring primary production*. Oxford University Press, New York, pp 82–105
- Vogel JS, Southon JR, Nelson DE, Brown TA (1984) Performance of catalytically condensed carbon for use in accelerator mass spectrometry. *Nucl Inst Methods Phys Res B Beam Interact Mater Atoms* 5:289–293
- Waddington JM, Kellner E, Strack M, Price JS (2010) Differential peat deformation, compressibility, and water storage between peatland microforms: implications for ecosystem function and development. *Water Resour Res* 46(7):W07538
- Wallén B, Falkengren-Grerup UT, Malmer N (1988) Biomass, productivity and relative rate of photosynthesis of *Sphagnum* at different water levels on a South Swedish peat bog. *Ecography* 11:70–76
- Weishampel P, Kolka R, King JY (2009) Carbon pools and productivity in a 1-km² heterogeneous forest and peatland mosaic in Minnesota, USA. *For Ecol Manag* 257:747–754
- Weltzin JF, Pastor J, Harth C, Bridgman SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. *Ecology* 81:3464–3478
- Weltzin JF, Harth C, Bridgman SD, Pastor J, Vonderharr M (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia* 128:557–565
- Weltzin JF, Bridgman SD, Pastor J, Chen J, Harth C (2003) Potential effects of warming and drying on peatland plant community composition. *Glob Chang Biol* 9:141–151
- White JR, Shannon RD, Weltzin JF, Pastor J, Bridgman SD (2008) Effects of soil warming and drying on methane cycling in a northern peatland mesocosm study. *J Geophys Res Biogeosci* (2005–2012) 113
- Whittington PN, Price JS (2006) The effects of water table draw-down (as a surrogate for climate change) on the hydrology of a fen peatland, Canada. *Hydrol Process* 20:3589–3600
- Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ (2010) Global peatland dynamics since the last glacial maximum. *Geophys Res Lett* 37:L13402
- Zona D, Oechel WC, Kochendorfer J, Paw UKT, Salyuk AN, Olivas PC, Oberbauer SF, Lipson DA (2009) Methane fluxes during the initiation of a large-scale water table manipulation experiment in the Alaskan Arctic tundra. *Glob Biogeochem Cycles* 23:1–11