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ARTICLE

Response of plant community structure and primary productivity to experimental drought and flooding in an Alaskan fen[1]

Amber C. Churchill, Merritt R. Turetsky, A. David McGuire, and Teresa N. Hollingsworth

Abstract: Northern peatlands represent a long-term net sink for atmospheric CO_2, but these ecosystems can shift from net carbon (C) sinks to sources based on changing climate and environmental conditions. In particular, changes in water availability associated with climate control peatland vegetation and carbon uptake processes. We examined the influence of changing hydrology on plant species abundance and ecosystem primary production in an Alaskan fen by manipulating the water table in field treatments to mimic either sustained flooding (raised water table) or drought (lowered water table) conditions for 6 years. We found that water table treatments altered plant species abundance by increasing sedge and grass cover in the raised water table treatment and reducing moss cover while increasing vascular green area in the lowered water table treatment. Gross primary productivity was lower in the lowered treatment than in the other plots, although there were no differences in total biomass or vascular net primary productivity among the treatments. Overall, our results indicate that vegetation abundance was more sensitive to variation in water table than total biomass and vascular biomass accrual. Finally, in our experimental peatland, drought had stronger consequences for change in vegetation abundance and ecosystem function than sustained flooding.

Key words: primary productivity, peatland, hydrologic manipulation, drying, flooding.

Résumé : À long terme les tourbières nordiques constituent un puits net pour le CO_2 atmosphérique mais ces écosystèmes peuvent passer d'un puits à une source nette de carbone (C) à cause du changement climatique et des conditions environnementales. Plus particulièrement, les modifications de la disponibilité en eau associées à l'effet du climat influencent la végétation des tourbières et les processus d'absorption de C. Nous avons étudié l'influence de la modification du régime hydrique sur l'abondance des espèces végétales et la production primaire de l'écosystème dans une tourbière basse en Alaska. Le régime hydrique a été modifié en manipulant la nappe phréatique avec des traitements sur le terrain visant à reproduire les conditions d'une inondation (élévation de la nappe phréatique) ou d'une sécheresse (abaissement de la nappe phréatique) qui ont persisté pendant 6 ans. Nous avons observé que les modifications de la nappe phréatique ont influencé l'abondance des espèces végétales : la couverture de carex et de graminées a augmenté alors que la couverture de mousses a diminué où la nappe phréatique avait été élevée tandis que la superficie occupée par les plantes vasculaires a augmenté où la nappe phréatique avait été abaissée. La production primaire brute était plus faible où la nappe phréatique avait été abaissée que dans les autres parcelles mais il n'y avait pas de différences entre les traitements quant à la biomasse totale ou la productivité primaire nette des plantes vasculaires. Globalement, nos résultats indiquent que l'abondance de la végétation est plus sensible à la variation de la nappe phréatique que la biomasse totale et l'accroissement de la biomasse des plantes vasculaires. Finalement, dans notre tourbière expérimentale la sécheresse a davantage contribué à modifier l'abondance de la végétation et la fonction de l'écosystème que l'inondation persistante. [Traduit par la Rédaction]

Mots-clés : productivité primaire, tourbière, manipulation hydrologique, sécheresse, inondation.

Introduction

Carbon (C) sequestration in the biosphere plays a substantial role in offsetting increases of atmospheric C from anthropogenic sources (Esser et al. 2011). Despite a small global land area, northern peatlands are important long-term C sinks that have produced a net cooling effect on global climate for the past 8000 to 11 000 years (Tarnocai et al. 2009; Yu et al. 2003; Frolking and Roulet 2007). In total, peatlands are estimated to store 280 Pg of C in the northern circumpolar permafrost zone, or approximately 10% of total terrestrial C (Schuur et al. 2008; Yu 2012). Most of this C is stored as accumulated peat, which develops due to an imbalance between plant primary production and ecosystem carbon losses from decomposition, leaching, and combustion (Gorham 1991). Annual C fixation rates in individual peatlands are largely controlled by environmental conditions, thus it is not uncommon for individual peatlands to oscillate between C sinks to sources

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from one year to the next depending on relative fluxes of primary production and heterotrophic respiration (Moore et al. 2002; Bubier 2003; Ward et al. 2009).

Relative water availability is typically one of the main environmental controls on peatland C accumulation (Blodau 2002). In high-latitude ecosystems, climate change is altering water availability through increased evapotranspiration and permafrost thaw. Water availability directs numerous vegetation processes responsible for C uptake by serving as one of the primary environmental gradients influencing plant community composition and function and by controlling decomposition through regulation of microbial activity (Blodau 2002; Limpens et al. 2008). In particular, alterations in water availability, whether through drought or flooding, mediate C cycling processes across temporal scales, from instantaneous flux rates of C uptake (gross primary production) and annual plant productivity (net primary productivity) to successional changes in biomass and plant species abundance that can occur over decades to centuries (Weltzin et al. 2000; Riutta et al. 2007; Strack and Waddington 2007; Chivers et al. 2009).

Previous results from descriptive and experimental studies in peatlands indicate that gross primary production (GPP) and net primary production (NPP) are often reduced by plant water stress that occurs with reduced water availability (Alm et al. 1997; Lafleur et al. 1997; Chivers et al. 2009; but see Muhr et al. 2011). Studies examining multidecadal drainage have documented shifts in the plant community from one dominated by hydrophilic mosses toward one dominated by drought-tolerant vascular species (Bubier et al. 1999; Laine et al. 1995; Murphy et al. 2009; Riutta et al. 2007; Strack et al. 2006). When decreases in moss cover and productivity occur simultaneously with increases in tree and shrub biomass and productivity, the result may be no change in net plant biomass and productivity, which likely contributes to the resilience of peatland C accumulation to environmental change at community scales (Weltzin et al. 2000; Baird et al. 2012). In other studies, increases in the productivity of trees and shrubs in drained peatlands have led to increased rates of peat accumulation, thereby increasing the C sink potential of peatlands (Laine et al. 1996). These different responses of peatland vegetation to drainage highlight the need for further long-term studies of how plant composition and productivity in peatlands respond to drought.

Some northern peatlands may experience wetter conditions as a result of climate warming, associated with changes in permafrost thaw and altered groundwater flow between upslope ecosystems and floodplains. In general, few studies have examined ecosystem responses to flooding in peatlands. Several water table manipulation studies have documented increases in GPP in response to increased water availability (Chivers et al. 2009; Updegraff et al. 2001). However, individual plant growth forms in peatlands can respond differently to flooding, with increasing abundance and NPP of groups such as graminoids, forbs, and mosses and declines in shrubs (Thormann et al. 1998; Weltzin et al. 2000). These patterns are generally similar to documented changes in the plant community during permafrost thaw and collapse scar formation, where rising water table favours the growth of sedges and moss at the expense of trees and shrubs (Camill 1999).

In 2005, the Alaskan Peatland Experiment (APEX) was initiated to examine the long-term impacts of warming and changing water table on vegetation and C cycling in a moderate rich fen located in interior Alaska. Experimental treatments included a lowered water table position to simulate sustained drought and a raised water table position to simulate sustained flooding. This study addresses two questions related to the responses of primary productivity and plant community composition. (1) How have changes in hydrology influenced plant community composition? (2) What are the effects of hydrologic manipulations on primary productivity? Based on results from the first 2 years of water table manipulation at this site (Chivers et al. 2009), we expected that water stress in the lowered water table treatment (drying) initially would reduce gross primary production compared with the other treatments. However, with succession, we anticipated that changes in species composition favoring woody tissue production at the expense of mosses would stimulate productivity in the lowered water table treatment, and we predicted that we would quantify increasing NPP in the lowered treatment during the period of study. Additionally, our initial findings from this experiment showed greater rates of gross primary productivity in the raised water table treatment, and we expected that this trend would strengthen through time. We also predicted that plant community composition in the raised plot would diverge from the control plot, mainly due to increasing moss abundance.

Materials and methods

Field measurements

Study site

Our research was conducted at the APEX sites adjacent to the Bonanza Creek Experimental Forest, approximately 35 km southwest of Fairbanks, Alaska (64.82°N, 147.87°W). In the Fairbanks region, the 50-year mean annual precipitation is 287 mm, and mean annual temperature (1917–2000) averages –3.1 °C (Hinzman et al. 2006). The APEX site used in this study is a nontreed moderate rich fen (surface water pH 5.2–5.4) with existing shrubs <0.50 m in height. In 2005, we established three water table position manipulation plots (a control plot, a lowered (drought) water table treatment plot, and a raised (flooded) water table treatment plot), each 120 m^2 (30 m × 40 m) in size with more than 20 m between each plot (Chivers et al. 2009). Water table manipulation plots were maintained annually by groundwater pumping from approximately snowmelt until ground freeze-up. On average, the lowered plot water table was 10 cm below the control plot, whereas the raised plot water table was 5 cm above the control plot, although discussions of variation in these levels are examined more thoroughly by both Kane and Wyatt (Turetsky et al. 2008; Chivers et al. 2009; Kane et al. 2010, Wyatt et al. 2012). Despite differences in mean growing season water table position, all three plots experienced short-term fluctuations in water table following rain events, as well as a seasonal drawdown during the summer when the control water table starts above the peat surface and then drops below the peat before peak biomass. During the four growing seasons included in this study, the manipulation plots experienced both natural drought and flooding that briefly nullified the water table manipulations (e.g., in 2009, all plots had water table positions near the vegetation surface for some time).

Due to the lack of replication in water table treatment, the results are specific to the particular locations of each plot, which were installed in conditions representative of the rich fen. Prior to the start of the water table manipulations in 2005, there was no difference in vegetation among plots (Chivers et al. 2009).

We collected climate data (air temperature, relative humidity, and precipitation) continuously using CR10X dataloggers (Campbell Scientific Inc., Logan, Utah) and soil temperature data at each plot (n = 3; 0 cm, 2 cm, 10 cm, and 25 cm below ground surface) using thermisters. We manually measured water table relative to the peat surface using bubble tubes in wells fixed in the peat column, in coordination with sampling dates for gross primary productivity (GPP). We determined active layer depth as the seasonal maximum thaw depth in each water table treatment plot.

Gross and vascular net primary productivity

We measured ecosystem CO$_2$ flux using a clear static chamber and galvanized steel metal collars permanently placed in the peat surface (dimensions of 0.3721 m^2 × 26 cm deep; Chivers et al. 2009). Each water table treatment plot contained three permanent gas flux collars under ambient air and soil temperature

(Chivers et al. 2009). Net ecosystem exchange (NEE) measurements were collected under ambient light conditions. In this paper, negative values for CO_2 fluxes indicate carbon uptake from the atmosphere to the ecosystem, and positive values indicate carbon gains to the atmosphere. Ecosystem respiration (ER) measurements were collected as NEE fluxes under dark conditions, accomplished by covering the chamber with shrouds to block incoming photosynthetic photon flux density (PPFD). Gross primary productivity (GPP) was calculated as the difference in carbon flux rates between NEE and ER, or the flux rate of carbon fixed by photosynthesis during the measurement period (Chapin et al. 2006; Chivers et al. 2009). Carbon dioxide concentrations ($\mu mol \cdot m^{-2} \cdot s^{-1}$) and percent relative humidity were measured using an EGM-4 infrared gas analyser by PP Systems (Amesbury, Massachusetts) with an internal pump for gas circulation. NEE flux measurements were collected under a range of ambient and manipulated (with shrouds) PPFD intensities following the protocol outlined in Chivers et al. (2009), creating a range of GPP flux measurements under varying light conditions for each collar on a sampling day using the same ER flux rate. These data were used to develop relationships between GPP, PPFD intensities, and water table position at the plot scale. However, our estimates of mean GPP at the plot level include only ambient light conditions.

In total, our dataset includes 431 GPP measurements ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$) under ambient light in all plots (106, 155, 54, and 116 in 2007, 2008, 2009, and 2010, respectively) and 761 GPP measurements, including light manipulations (ambient fluxes plus altered light conditions; 241, 189, 149, and 182 in 2007, 2008, 2009, and 2010 respectively; Supplementary Fig. S1[2]). Measurements were collected at each plot every 1–2 weeks from approximately mid-May through mid-September from 2007 through 2010 and were collected between 0900 and 1600 h (Supplementary Table S1[2]).

To examine plant community structure, we collected aboveground biomass at peak plant biomass (end of July 2009; Supplementary Table S1[2]) in 0.01 m^2 subplots immediately adjacent to gas flux collars for all manipulation plots (n = 3 for each plot), as well as along three transects (three to four samples per transect) every 2–3 m in the undisturbed peatland surrounding the control plot (n = 11). These additional samples were collected to improve estimates of control peatland conditions, while not affecting long-term monitoring areas. We removed all aboveground biomass to the base of living moss in the peat surface layer. All biomass samples were separated into individual vascular plant species, moss growth forms, litter, and woody debris. All living vascular plants were then separated into new growth (leaves and stems) and living tissue associated with previous years (shrubs only) for woody components, following Shaver and Chapin (1991). We calculated aboveground net primary production (ANPP; $g \cdot m^{-2}$) for vascular species by averaging total new growth in samples across treatments. Although this estimate does exclude secondary growth of woody tissue, this component was a small fraction of total ANPP in each sample. Species present within a sample were summed to calculate growth form ANPP (forb, grass, sedge, and shrub). Moss growth forms were included in the aboveground biomass measurement, but not ANPP. Remaining nonliving biomass materials that could be identified to the species level was designated as a standing dead category, whereas remaining unknown dead material was designated as litter (Shaver and Chapin 1991). Moss NPP was not estimated due to fluctuations in the water table during 2009 that prevented the insertion of cranked wires, the traditional method for measuring the vertical growth of sphagnum mosses relative to a wire anchored into the peat surface (Clymo 1970).

We measured belowground NPP (BNPP) using root in-growth bags (diameter, ~6 cm; length, 50 cm). Bags were constructed from nylon netting (1.5 cm opening size) and homogenized root-free surface peat from a local peatland outside the manipulation area (Murphy et al. 2009). We installed in-growth bags in late September 2009 to limit surface disturbance during placement and inserted bags into predrilled holes in the surface peat (4, 2, and 2 in-growth bags at the control, lowered, and raised plots, respectively). Reduced installation of in-growth bags in the lowered and raised plots was necessary to minimize disturbance within the water table manipulation area. Bags were removed in late September 2010 and were measured for exact length and diameter before all new roots were separated from the peat (these were not separated by growth form; Supplementary Table S1[2]). All samples were dried and weighed for determining BNPP ($g \cdot m^{-2}$). Measurements of mean ANPP and BNPP for each treatment were summed to determine total vascular NPP.

We quantified seasonal changes in vascular green area (VGA, expressed as leaf area (m^2)/ground area (m^2)) of dominant species at the plot scale as a feature of the vegetation community structure. Leaf area measurements were conducted every 2 weeks to calculate seasonal changes in photosynthetic surface area. For the first 6 weeks in 2009, leaf area calculations were based on geometric equations for leaf shape approximations (Chivers et al. 2009; Wilson et al. 2007). For the remainder of 2009, we harvested three specimens of dominant vegetation in each treatment plot and measured each specimen for surface area by scanning all leaves with a LI–3000C Portable Leaf Area Meter (LI-COR Biosciences, Lincoln, Nebraska; Supplementary Table S1[2]). In 2010, all leaf area measurements were calculated using the LI-3000C. Stem density for each dominant species per square metre in a plot was measured monthly during the growing season by subsampling gas flux collars (five 7.5 cm × 7.5 cm areas) and averaging density for each collar nested in the plot. We then multiplied leaf area for each species by stem density at 2-week intervals for each plot to calculate the VGA for each species at a given time. Total VGA for a given sampling day was then calculated as the sum of all species present in the gas flux collar.

Plant species composition and abundance

We estimated plant species abundance at each plot using the point frame method for calculating absolute abundance during peak biomass, including moss cover by growth form (Hollingsworth et al. 2010; Jonasson 1988). Point frame samples were 1 m^2, with 20 points per sample, and we used presence of species at each point within the point frame to calculate species abundance. Measurements were recorded in 2007 and 2009, with point frame samples in each water table manipulation overlain on gas flux collars (n = 3; Table S1[2]). Additionally, we visually estimated ground cover for moss growth forms, of a total ground area of 100%, in each gas flux collar once at peak biomass in 2007–2010 (Supplementary Table S1).[2]

For plant composition, we identified vascular plants to species name and nonvascular species to genus (*Sphagnum*) or growth form (brown moss families Amblystegiaceae and Brachytheciaceae: *Drepanocladus aduncus* and *Hamatocaulis vernicosus*; Wieder et al. 2006). Nomenclature followed Hulten (1968), with the exception of sedges (Tande and Lipkin 2003). We classified all plant species by growth form (grass, sedge, deciduous shrubs, herbaceous forbs, brown mosses, and *Sphagnum* spp.) and all nonliving hits from the point frame into debris categories (fine woody debris, leaf litter, and standing dead).

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[2] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0100.

Data analysis

Effects of water table treatment and year on productivity and biomass

Instantaneous GPP measurements under ambient light were analyzed using repeated measures analysis of variance (ANOVA) in Proc Mixed (SAS ver. 9.3, SAS Institute Inc., Cary, North Carolina) and Tukey's post hoc comparison of means (Chivers et al. 2009) to determine how GPP was influenced by water table treatment (control vs. lowered vs. raised plots), study year (2007–2010), and the interaction between treatment and year. Individual flux measurements that were collected at collar 4 during June of 2009 were found to be extreme outliers, likely due to high levels of standing water interacting with the flux chamber fans, and a total of five flux measurements were removed from analysis. Because the water table treatments were not replicated, collars nested within each treatment were used as pseudo replicates. We determined significance using type III errors in the model. We used a similar ANOVA model to examine variation in the PPFD between years using square root transformed data to correct a non-normal distribution (R Development Core Team 2009).

We used an ANOVA model followed by Tukey's post hoc tests to examine the effect of water table treatment on total vascular NPP, ANPP, and BNPP. Aboveground NPP values and aboveground biomass values were log transformed and belowground NPP data were square root transformed to meet assumptions of normality. We used a MANOVA model to examine how plant growth forms contributed to aboveground biomass and NPP in each water table treatment. All analyses of NPP and biomass were performed using the statistical programming language R (ver. 2.9.0, R Development Core Team 2009).

We modeled plot average daily VGA using Proc NLIN in SAS ver. 9.3 based on biweekly measurements of gas flux collar total VGA (Chivers et al. 2009; Wilson et al. 2007). This model estimates the maximum amount of VGA for each plot (VGA_{MAX}), as well as the timing of VGA_{MAX} (X_{MAX}). For all analyses, we used a critical value of 0.05 to determine significance. Critical values between 0.05 and 0.1 were interpreted as marginally significant.

To test for significant differences in plant species composition between water table treatments and for any effect of the manipulation through time by comparing years 2007 and 2009, we used a permutation-based nonparametric MANOVA (NPMANOVA) two-way factorial test (Anderson 2001) with Sørensen (Bray–Curtis) distances.

Relationships between environmental variables, vegetation, and GPP

Because variation in light (measured as PPFD), associated with changing vegetation structure as a result of our manipulations, has the potential to alter instantaneous GPP, we examined the nonlinear relationship between light, water table position, and GPP using nonlinear modelling (Proc NLIN, SAS; Chivers et al. 2009). We used estimated parameters from eq. 1 to provide information on biological function across water table treatments (Tuittila et al. 2004):

$$\text{GPP} = P_{\text{MAX(PPFD,WT)}} \cdot \frac{\text{PPFD}}{k + \text{PPFD}} \cdot \exp\left[-0.5 \cdot \frac{(\text{WT} - \text{uP})^2}{\text{tP}^2}\right] \qquad (1)$$

where GPP is the absolute value of measured instantaneous GPP (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$; P_{MAX} values positive), PPFD is the measured photon flux density (PPFD, $\mu mol \cdot m^{-2} \cdot s^{-1}$), WT is the measured water table position (cm), $P_{MAX(PPFD,WT)}$ is the estimated rate of maximum photosynthesis under light-saturated conditions when the water table was at an optimum position for photosynthesis (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$), k is the estimated photon flux density at which GPP was equal to half P_{MAX} ($\mu mol \cdot m^{-2} \cdot s^{-1}$), uP is the estimated optimal water table position for photosynthesis (cm), and tP is the estimated measure of variance in the amplitude of water table position (cm) (Tuittila et al. 2004). Models were run at the treatment level, as convergence was not met using data within individual collars per treatment.

The relationships among VGA_{MAX}, GPP, and moss percent cover were examined to determine potential plant component contributions to GPP (vascular vs. nonvascular) using linear correlation (R Development Core Team 2009). GPP values used for these analyses were values measured within 1 week of X_{MAX} (assumed peak biomass) during 2009 and 2010. Moss cover data was based upon visual moss ground cover data from 2009 and 2010 recorded within 2 weeks of X_{MAX}. We also examined the relationship between visual moss cover and moss cover as determined using the point frame estimate for the summer of 2009 as a means of comparing methods.

Analysis of plant community composition and abundance

We used nonmetric dimensional scaling (NMDS) ordination to visualize species composition across the three plots (PCOrd 5.3, MjM Software Design, Gleneden Beach, Oregon; Hollingsworth et al. 2010). Dimensionality was assessed by comparing stress levels associated with both real (50 runs) and randomized (50 runs) data and selecting the minimum number of axes meeting the criterion of maximum stress and a stability criterion of 0.00001. We applied a weighting-by-ubiquity relativization to data by column (species) from all treatment plots to account for unequal coefficient of variance row totals in the species matrix. We calculated the relative contributions of species to the overall variation and placement of plots in the ordination space using ordination loadings and plots in the ordination space. Pearson correlations between each species, environmental data (water table position, mean growing season soil temperature, and mean annual soil temperature), and the ordination axes were used to examine environmental contributions to compositional gradients across all plots. We also included a coefficient of variance for each environmental variable in the ordination, as variation in environmental variables was likely to have biological implications. Finally, we also ran a series of paired t tests to examine potential changes in abundance of individual species within a single treatment between 2007 and 2009 (R Development Core Team 2009).

All data associated with this study and analyses described above are available through the Bonanza Creek Long Term Ecological Research site, based at the University of Alaska Fairbanks.

Results

Effects of water table manipulations on plant species abundance and community composition

We identified eight vascular plant species in the study site (Supplementary Table S2[2]). Overall, there were significant differences in species composition among water table treatments after 5 years of water table manipulation ($F_{[2,17]} = 6.47$, $p < 0.0002$), with no plot × year interaction ($F_{[2,17]} = 0.96$, $p = 0.48$). All three water table treatments differed from each other specifically in terms of the abundance of species present. The control treatment had the greater brown moss cover and highest forb abundance, producing differences in composition relative to both the lowered ($t = 3.29$, $p = 0.0002$) and raised ($t = 2.13$, $p = 0.0042$) treatments (Table 1). The lowered treatment had the lowest abundance of brown mosses among all three treatments and fewer grasses and sedges relative to the raised treatment ($t = 2.17$, $p = 0.005$). There were also differences in species abundance between study years (Table 1; $F_{[1,17]} = 4.3$, $p = 0.0052$), mostly due to a decline in abundance of both *Potentilla palustris* and brown moss between 2007 and 2009 in all plots. *Potentilla palustris* significantly declined between 2007 and 2009 in both the control and raised treatments (Table 1; $p < 0.05$), whereas the decline in brown moss was not significant.

Three major axes in a NMDS ordination (not visualized in MS) captured 95% of the variance in species composition across water table treatments for data collected in 2009 (final stress of 5.68 and

Table 1. Mean (±1 SE) plant species abundance based on percent cover among water table treatments (control, lowered water table, and raised water table) for 2007 and 2009.

		Control		Lowered		Raised	
Species	Growth form	2007	2009	2007	2009	2007	2009
Brown moss	Brown moss	75.0±9	70.0±5	3.3±3	1.7±2	60.0±13	31.7±6
Calamagrostis sp.	Grass	0.0±0	0.0±0	3.3±2	0.0±0	8.3±4	11.7±7
Carex atherodes	Sedge	8.3±4	23.3±12	18.3±6	21.7±6	30.0±3	25.0±8
Carex canescens	Sedge	0.0±0	1.7±2	1.7±2	0.0±0	6.7±4	3.3±3
Carex lasiocarpa	Sedge	0.0±0	0.0±0	0.0±0	0.0±0	0.0±0	10.0±6
Equisetum fluuviatile	Forb	6.7±2	15.0±5	10.0±3	5.0±5	5.0±3	3.3±2
Galium trififum	Forb	3.3±3	0.0±0	5.0±3	0.0±0	3.3±3	0.0±0
Potamogeton gramineus	Forb	0.0±0	5.0±3	0.0±0	3.3±3	0.0±0	0.0±0
Potentilla palustris	Shrub	50.0±3*	8.3±2*	21.7±6	11.7±6	21.7±6†	5.0±3†
Sphagnum	Sphagnum	13.3±7	18.3±7	8.3±6	45.0±15	18.3±18	25.0±16

Note: No significant differences in abundance of a species other than *Potentilla palustris* were observed within a treatment between years.

*Significant difference in abundance of *Potentilla palustris* between 2007 and 2009 in the control treatment (p = 0.0063).

†Significant difference in abundance of *Potentilla palustris* between 2007 and 2009 in the raised treatment (p = 0.0377).

a final instability of <0.00001). Axis 1 (15% of variance) was positively correlated with growing season surface temperature (r = 0.5), negatively correlated with *P. palustris* abundance (r = 0.5), and positively correlated with *Carex atherodes* abundance (0.8). Axis 2 (35% of variance) was positively correlated with water table position (r = 0.7), soil temperature at a depth of 25 cm (r = 0.7), air temperature in the growing season (r = 0.7), and *Sphagnum* abundance (r = 0.7). Axis 3 (46% of variance) was positively correlated with the variation of growing season soil temperatures between 2 and 10 cm (r = 0.6) and with brown moss abundance (r = 0.9).

Effects of water table manipulation on primary productivity and biomass

We found that instantaneous GPP (μmol CO_2·m^{-2}·s^{-1}) measured under ambient light varied between water table treatment plots ($F_{[2,6]}$ = 14.36, p = 0.005; Fig. 1) and by year ($F_{[3,18]}$ = 6.41, p = 0.004), with no interaction among these main effects ($F_{[6,18]}$ = 1.33, p = 0.295). Mean GPP was similar in the control and raised treatments (least square means, –3.58 ± 0.18 and –4.09 ± 0.18 μmol·m^{-2}·s^{-1}, respectively; $t_{[6]}$ = 2.00, p = 0.194), whereas the lowered treatment (–2.74 ± 0.16 μmol·m^{-2}·s^{-1}) was significantly different from both the control ($t_{[6]}$ = –3.23, p = 0.041) and raised treatment ($t_{[6]}$ = 5.32, p = 0.004). Averaged across all treatments, the year 2010 was significantly different from 2007 ($t_{[18]}$ = –2.90, p = 0.043), 2008 ($t_{[18]}$ = –3.65, p = 0.009), and 2009 ($t_{[18]}$ = –3.62, p = 0.010), whereas all other interyear comparisons were not significantly different from one another (p > 0.05). The lack of a water table treatment × year interaction demonstrates that although average across-treatment GPP differed among study years, the treatments responded similarly to the differences across the four growing seasons included in this dataset.

Fig. 1. Instantaneous gross primary productivity (GPP) measured under ambient light conditions averaged for each year and water table treatment. Same-letter designations indicate nonsignificant differences among plots (a vs. b) and years (x vs. y). Data include measurements collected biweekly from 2007 to 2010.

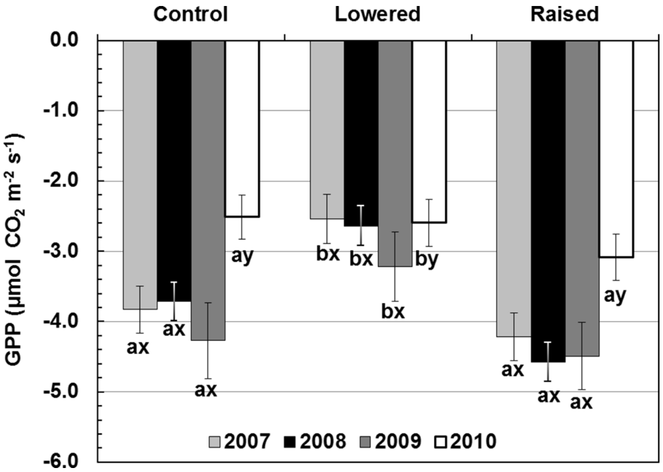


Table 2. Estimated parameters (means ± 1 SE) from the gross primary productivity (GPP) model following eq. 1.

Water table treatment plot	$P_{MAX(PPFD,WT)}$ (μmol CO_2·m^{-2}·s^{-1})	k* (μmol·m^{-2}·s^{-1})	uP (cm)	tP (cm)	R^2†
Control	6.690±0.75	264.4±69.5	15.2±12.7	39.3±11.8	0.79
Lowered	4.309±0.36	268.3±70.5	–4.6±3.4	38.9±26.3	0.81
Raised	6.776±0.48	300.3±70.3	0.7±1.6	21.7±2.6	0.85

Note: $P_{MAX(PPFD,WT)}$, parameter associated with maximum rates of GPP under optimal levels of light and water table; k, the estimated photon flux density at which GPP was equal to half P_{MAX}; uP, the estimated optimal water table position for photosynthesis; tP, the estimated measure of variance in the amplitude of water table position.

*Estimates are provided for each water table treatment using rates of GPP quantified under all light level conditions from data collected from 2007 to 2010.

†All models were significant at p < 0.0001.

Relationships between instantaneous GPP and PPFD showed that our measurements captured GPP across a wide range of ambient light (Supplementary Fig. S1[2]) and allowed us to estimate biologically relevant parameters associated with eq. 1. There was no effect of year on differences in PPFD ($F_{[1,415]}$ = 0.579, p = 0.447), and therefore year-to-year variation in light is not likely to have influenced annual differences in GPP. The PPFD measurements were collected above the tallest vegetation in all three plots, and thus differences in light (PPFD) due to changing vegetation structure across our treatments is also unlikely. Using eq. 1, we found that the lowered water table plot had a smaller P_{MAX} (μmol CO_2·m^{-2}·s^{-1}) than the raised and control treatments (Table 2). Estimates of k (the photon flux density at which GPP was equal to half P_{MAX}) have a trend of being largest in the raised plot and smallest in the control plot (Table 2); however, they did not vary among treatments due, in part, to large error terms. The optimal water table position (uP) for GPP was higher (wetter) in the control plot than in the two manipulation plots. Finally, the small estimate for our amplitude in water table parameter (tP) in raised treatment suggests that GPP occurred over a more narrow window of water table positions in this treatment relative to the other plots.

There were no differences in total vascular NPP (control, 381 ± 60 g·m^{-2}; lowered water table, 533 ± 245 g·m^{-2}; raised water table,

Fig. 2. Results associated with an aboveground biomass harvest in 2009 with (A) net primary productivity (NPP) of the aboveground vascular layer by growth form at the water table treatment plots, including forbs, grasses, sedges, and deciduous shrubs (D. Shrub) and (B) total aboveground biomass of growth form categories, including brown mosses, grass, forbs, sedges, deciduous shrub (D. Shrub), standing dead (StdDead), and *Sphagnum* mosses. Error bars shown are ±SE for total NPP.

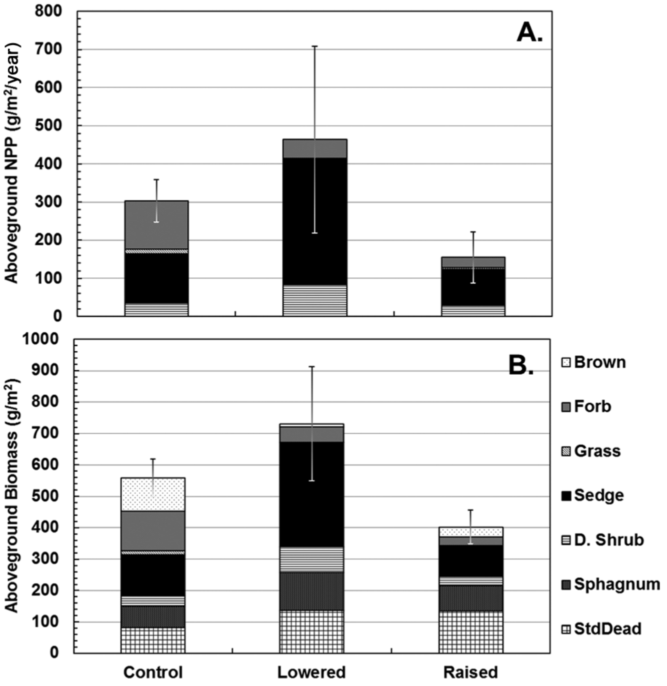
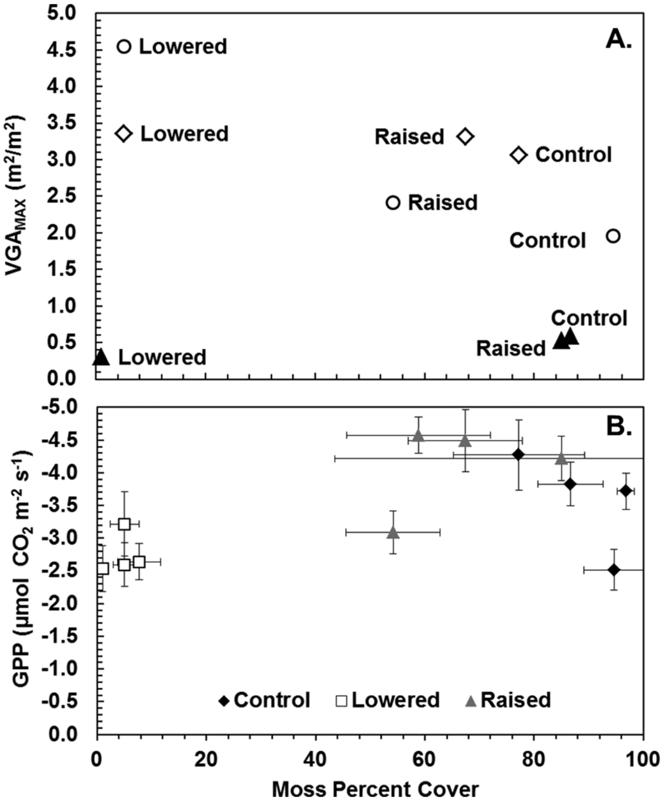


Table 3. Parameters from a vascular green area (VGA) model in 2009 and 2010 following Wilson et al. (2007).

		Water table treatment plot		
Parameter	Year	Control	Lowered	Raised
VGA_{MAX}	2009	3.07±0.48	3.36±0.38	3.32±0.63
	2010	1.96±0.25	4.55±0.55	2.42±0.50
X_{MAX}	2009	178.1±12.3	186.1±5.05	170.4±54.7
	2010	201.6±8.5	203.2±4.08	215.8±15.9
b	2009	35.86±19.1	32.34±9.6	55.59±84.5
	2010	48.72±17.7	−31.13±5.55	41.35±21.3

Note: Data are presented as means ± 1 SE. VGA_{MAX}, the maximum amount of VGA produced in the plot; X_{MAX}, the day of year that the VGA_{MAX} occurred; b, parameter relating to the shape of the curve.

Fig. 3. (A) Relationship between VGA_{MAX} and visual percent ground cover of moss from 2009 (diamonds) and 2010 (circles) across water table treatments (adjusted $R^2 = 0.47$). Measurements reported in Chivers et al. (2009) are shown in solid triangles for comparison. (B) Relationship between mean moss percent cover and GPP from 2007 to 2010 across water table treatments (adjusted $R^2 = 0.24$).



217 ± 74 g·m^{-2}), BNPP ($F_{[2,9]} = 0.21$, $p = 0.813$; control, 77.6 ± 23 g·m^{-2}; lowered water table, 69.5 ± 7 g·m^{-2}; raised water table, 61.9 ± 31 g·m^{-2}), ANPP ($F_{[2,17]} = 1.348$, $p = 0.286$; control, 303 ± 56 g·m^{-2}; lowered water table, 464 ± 245 g·m^{-2}; raised water table, 155 ± 68 g·m^{-2}), or ANPP of individual vascular plant growth forms among the treatments (MANOVA Pillai test; $F_{[8,30]} = 1.11$, $p = 0.387$; Fig. 2A). Additionally, there were no significant differences between water table treatments in total aboveground biomass (control, 559 ± 60 g·m^{-2}; lowered water table, 731 ± 181 g·m^{-2}; raised water table, 402 ± 54 g·m^{-2}; $F_{[2,17]} = 2.7$, $p = 0.09$) or the contribution of individual plant growth forms to total biomass (MANOVA Pillai test; $F_{[22,16]} = 0.89$, $p = 0.591$; Fig. 2B).

Maximum VGA (VGA_{MAX}, m^2·m^{-2}) varied among the water table treatments and between study years (2009 vs. 2010) (Table 3). Averaged across years, VGA_{MAX} was greater in the lowered water table treatment than in the other water table treatments. Although VGA_{MAX} declined between 2009 and 2010 at the control and raised water table plots, VGA_{MAX} increased between 2009 and 2010 in the lowered plot. The date associated with VGA_{MAX} (X_{MAX}) shifted to later dates between 2009 and 2010 by as much as 30 days, likely in association with changes in ambient water availability across the fen. There was no effect of water table treatment on X_{MAX}.

There was no relationship between VGA_{MAX} and GPP across treatments and years for fluxes collected on dates nearest to X_{MAX} within each plot ($F_{[1,4]} = 0.002$, $p = 0.97$). There was a marginally significant negative relationship between VGA_{MAX} and moss percent cover across treatments ($F_{[1,4]} = 5.433$, $p = 0.08$, $R^2 = 0.47$; Fig. 3A). The lowered water table plot had greater VGA_{MAX} but smaller cover of mosses than the other treatments. Additionally, there was a marginally significant negative relationship between GPP and moss percent cover ($F_{[1,10]} = 4.461$, $p = 0.06$, $R^2 = 0.24$; Fig. 3B) using visual estimates of moss cover in late July and GPP values that coincide with those sampling dates. However, individual plot responses to interannual variation in water table conditions (particularly in 2009 and 2010) prevented meaningful analysis of individual treatment relationships. Due to the timing of flooding and seasonal water table draw-down, there was no clear relationship between visual estimates of moss cover and moss cover as measured using point frame abundance (Supplementary Fig. S2).[2]

Discussion

Effects of water table manipulations on species abundance and biomass

Studies conducted over relatively short time intervals (seasons to years) have focused on changes in the productivity of the existing species pool in response to environmental changes (Thormann et al. 1998). However, studies of multidecadal drainage of peatlands have documented dramatic changes in community structure from moss-dominated communities towards more woody terrestrial communities (Laine et al. 1995; Murphy et al. 2009). The increased abundance of drought-tolerant vascular species in wetlands can also lead to a decrease in vegetation diversity at the landscape level (gamma diversity), despite little overall change in species richness within individual peatlands (alpha diversity), as aquatic and lawn species are replaced by shrubs and trees (Laine et al. 1995). In short, aquatic obligate species are lost from the landscape as wet areas are populated with drought-tolerant species. These community shifts are directly the result of changing environmental conditions, although changes in the species pool and landscape richness can be limited by dispersal and competition.

Four years after establishing our water table manipulations, we saw evidence of shifts in species abundance and overall community composition. Changes in species presence included the loss of some hydrophilic sedges in the lowered water table plot relative to the control and raised treatments. This likely occurred as the drier lowered water table plot lost aquatic obligates without the introduction of new species (Supplementary Table S2[2]). Other changes in composition were primarily associated with shifts in abundance, including reductions in *P. palustris* for both the control and raised plots between 2007 and 2009, higher *P. palustris* abundance in the lowered plot, and lower moss percent cover in the lowered treatment than in the other treatments. These changes are accounted to sustained manipulation of the water table position in the different treatment plots, associated with succession. Even after six summers of sustained dry conditions in our lowered water table plot, the establishment of drought-tolerant species was limited, suggesting that dispersal or competition could be constraining the establishment of species more tolerant of drier soil conditions. Studies examining changes in species composition associated with long-term drought in Finnish peatlands showed that oligotrophic species of Sphagna were reduced and eventually replaced by more mesic forest mosses on a time scale of 5–20 years following peatland drainage (Laine et al. 1995). These findings suggest that our manipulation is following predicted changes in drought-tolerant species vs. aquatic species through time. However, given that our treatments were conducted in experimental plots and that the entire peatland is not drained, the area between treatments may serve as a "mesic barrier" in preventing the dispersal and competitive success of upland species in the lowered plot.

There is less information in the literature regarding the effects of flooding on peatland vegetation. Ten years after flooding of a boreal peatland in the Experimental Lakes Area of Ontario, there was a slight increase in species richness of forbs (and graminoids) and a shift toward greater moss productivity (Asada et al. 2005). In our experiment, sustained flooding increased the number of graminoid species and altered community composition by increasing the abundance of grasses (8% and 12% vs. 0% in the control plot) and sedges (37% and 38% in the raised plot vs. to 8% and 25% in the control), while decreasing the abundance of forbs (8% and 3%) relative to the control plot (10% and 3%).

Effects of water table manipulations on primary productivity

Few studies have followed the trajectory of ecosystem GPP in response to prolonged manipulation of the water table position in peatlands. Likewise, few studies have examined whether ecosystem responses to water table manipulation are consistent with interannual variation in water availability. This study explored whether water table manipulations maintained over six growing seasons influenced vegetation structure and primary productivity in a boreal fen. Our measurement period included years with both high (2008) and low (2009) levels of precipitation that affected all three water table treatments. This allowed us to examine the effect of our water table manipulations under naturally dry and wet years.

We found that gross primary productivity (GPP), averaged across years, was largest in the raised water table treatment and smallest in the lowered water table treatment. This agrees with Chivers et al. (2009), who found that the lowered treatment switched from serving as a CO_2 sink to a source to the atmosphere in 2006, after 2 years of manipulation at our experimental site. These findings are in contrast to our prediction that vegetation in the lowered water table plot would recover and exhibit greater productivity over time (Ballantyne et al. 2014). Instead, our results suggest that during extended drought, GPP in the lowered treatment remained low, and as a result, the plant community in the lowered treatment is less likely to take up C from the atmosphere, relative to control conditions. Over the same time period, we did not see a significant change in GPP between the raised and control plots, suggesting that prolonged flooding is less likely than drought to influence annual trends of C uptake in this system.

Our GPP modelling allowed us to control for variation in light associated with weather and examine the effects of changing water table position across years and water table treatments on GPP. Trends in P_{MAX} across water table treatments reported in this study agree with those reported by Chivers et al. (2009), as we also found lower P_{MAX} in the lowered treatment than in the control or raised water table treatments. This suggests that the variation in P_{MAX} among treatments that emerged after 2 years of manipulation continued to persist over the longer time period reported in this study. Additionally, our estimates of uP showed that maximum GPP in the raised and control plots occurred when the water table was at or above the peat surface, whereas maximum GPP in the lowered plot occurred when the water was below the peat surface (Table 1). Given that each plot experienced water table levels ranging from flooded conditions, with water tables well above the peat surface, to dried conditions, with water tables more than 20 cm below the peat surface, this trend in uP is not likely to be driven by variation in water table alone. Instead, it seems likely that variation in uP across water table treatments is a result of changing vegetation composition resulting from our manipulations. As such, optimum GPP in the lowered plot occurred under conditions favorable to existing drought-adapted plants in the community, despite no introduction of more xeric species.

Although GPP was sensitive to the water table treatments, ANPP and BNPP did not vary among our plots in this study. Thus, the lower rates of mean GPP at the lowered plot did not translate into reduced biomass accrual. There are a number of possible explanations for this observation, including the potential for differences in the rate of GPP and respiration by plants associated with drought stress. Additionally, we note that our estimates of NPP did not include nonvascular productivity due to the difficulty of measuring productivity across a diversity of moss types and submerged plants during the spring of 2009. Therefore, our estimates of NPP underestimate total vegetation productivity, particularly in the raised and control water table plots that had greater moss cover than the lowered plot. Although few studies report both GPP and NPP for the same peatland area, a large mesocosm study in northern Minnesota also found that increases and decreases in GPP with experimental flooding and drought, respectively, did not translate into changes in NPP (Updegraff et al. 2001). Although a detailed comparison of NPP and GPP was not the emphasis of this study, together these findings lend weight to a disparity between instantaneous photosynthetic responses vs. growth.

Several studies have shown negative relationships between mosses and woody plant productivity with drainage; for example, increasing shrub productivity can occur at the same time as declining *Sphagnum* productivity (Laine et al. 1995; Strack et al. 2006). Although some have interpreted such declines in moss as being driven by canopy closure and light availability (Laine et al. 1995), others have attributed moss reductions to changes in soil moisture and environmental niches, particularly in *Sphagnum* species (Bisbee et al. 2001). Such trade-offs in response to drying may help to stabilize NPP at community scales. Although we did not measure moss NPP, our results suggest a negative relationship between VGA_{MAX} and moss cover associated with the water table manipulation. This result is in contrast to earlier findings from this experiment that reported a positive relationship between VGA_{MAX} and moss cover (Chivers et al. 2009). Although Chivers et al. (2009) found that the lowered treatment had the smallest VGA_{MAX}, here we found that VGA_{MAX} was greatest in the lowered treatment relative to the raised or control treatments. Together, these results indicate increases in vascular cover over time in response to sustained drier conditions. Across all plots, we note that the previous estimates of VGA_{MAX} were lower than the values reported here, which could be due to interannual variation (for example, VGA_{MAX} values reported by Chivers et al. (2009) likely were influenced by dry conditions across all treatments in 2006 and 2007). Despite these differences, it seems clear that VGA has increased over time more so in the lowered water table treatment than in the other plots in response to our manipulation, which is consistent with our predictions. Additionally, our results show that VGA_{MAX} declined between 2009 and 2010 in the control and raised treatment, while increasing in the lowered treatment. Our site experienced a natural drought in 2010 as a consequence of little rainfall during the summer of 2009. These results suggest that this drought reduced VGA in the control and raised treatments and increased VGA in the lowered plot. This may be further evidence of plant succession in response to our experimental manipulations, as vascular vegetation in the experimental drought treatment apparently benefited from a natural drought event. This conclusion is supported by our community analyses showing changes in abundance among treatments. Changes in community composition among treatments showed a higher abundance of *P. palustris* in the lowered plot, and this species contributed an average of 53% (±0.03%) of the total VGA at collection dates nearest X_{MAX}.

In our fen, ecosystem functions such as GPP, VGA, aboveground biomass, and NPP were not significantly affected by sustained flooding. Consequently, the drought manipulation appeared to have a larger effect on C uptake and ecosystem processes than flooding in our boreal fen.

Conclusions and relevance to land management

In general, our results show that experimental manipulation of water table position in a boreal rich fen affected vegetation structure by affecting vascular and nonvascular species composition more so than net productivity or gross C uptake. After six summers of persistent dry conditions in our lowered water table plot, the establishment of drought-tolerant shrubs was limited, suggesting potential limitations to dispersal and invasions by species better able to grow under drier conditions.

Management agencies are devoting increasing time and resources to modeling C fluxes as a tool to understand and improve sustainable forest management practices. Carbon models serve as the basis for some national C accounting frameworks (Kurz et al. 2009). Recently, Bona et al. (2013) determined that forest C stocks could not be simulated accurately without information on both vascular and nonvascular biomass and productivity. Although such efforts in boreal regions have focused on forests, attempts to examine landscape to regional carbon exchange and storage will need to consider peatlands, given that these ecosystems are a dominant land cover type in most northern settings. Peatland responses to climate warming will likely include both drying (as a function of drought and increased evapotranspiration) and flooding (as a function of permafrost thaw), both of which are examined in this study. The results from this study suggest that drying induces a greater impact on ecosystem composition and GPP in our rich fen system than flooding. Prior to dispersal and invasion by more drought-tolerant species, these changes will initially include reductions in species diversity and primary productivity.

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