

Contributions of algae to GPP and DOC production in an Alaskan fen: effects of historical water table manipulations on ecosystem responses to a natural flood

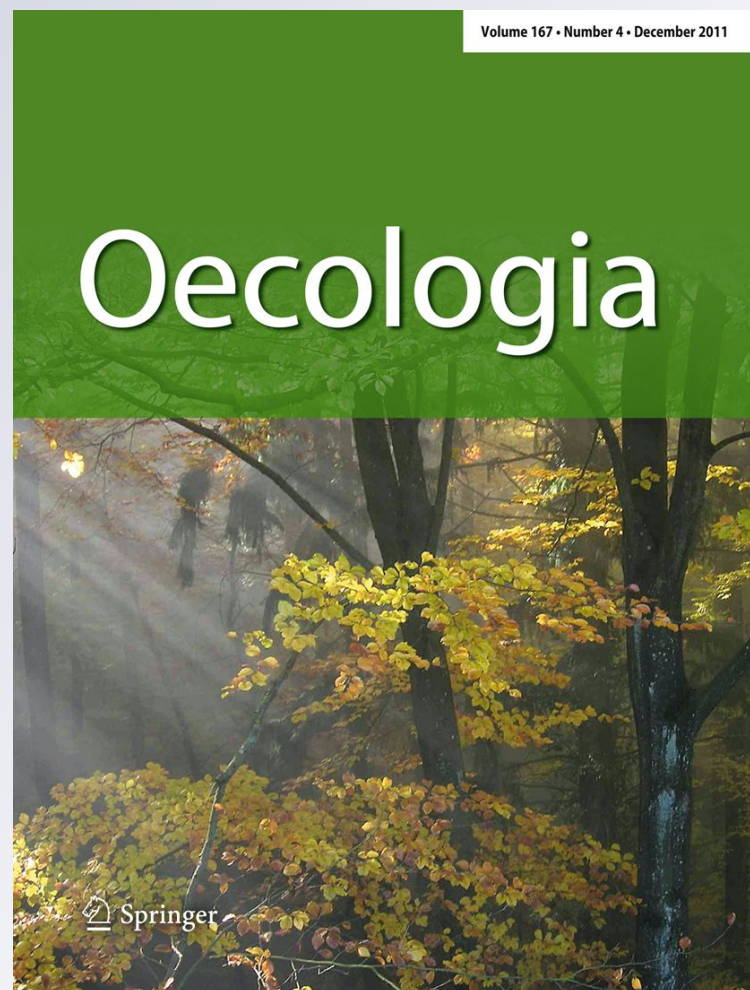
Kevin H. Wyatt, Merritt R. Turetsky, Allison R. Rober, Danilo Girollo, Evan S. Kane & R. Jan Stevenson

Oecologia

ISSN 0029-8549

Oecologia

DOI 10.1007/s00442-011-2233-4



Your article is protected by copyright and all rights are held exclusively by Springer-Verlag. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Contributions of algae to GPP and DOC production in an Alaskan fen: effects of historical water table manipulations on ecosystem responses to a natural flood

Kevin H. Wyatt · Merritt R. Turetsky ·
Allison R. Rober · Danilo Giroldo · Evan S. Kane ·
R. Jan Stevenson

Received: 25 June 2011 / Accepted: 9 December 2011
© Springer-Verlag 2011

Abstract The role of algae in the metabolism of northern peatlands is largely unknown, as is how algae will respond to the rapid climate change being experienced in this region. In this study, we examined patterns in algal productivity, nutrients, and dissolved organic carbon (DOC) during an uncharacteristically wet summer in an Alaskan rich fen. Our sampling was conducted in three large-scale experimental plots where water table position had been manipulated (including both drying and wetting plots and a control) for the previous 4 years. This study allowed us to explore how much ecosystem memory of the antecedent water table manipulations governed algal responses to natural flooding. Despite no differences in water table position between the manipulated plots at the time of sampling, algal primary productivity was consistently

higher in the lowered water table plot compared to the control or raised water table plots. In all plots, algal productivity peaked immediately following seasonal maxima in nutrient concentrations. We found a positive relationship between algal productivity and water-column DOC concentrations ($r^2 = 0.85$, $P < 0.001$). Using these data, we estimate that algae released approximately 19% of fixed carbon into the water column. Algal exudates were extremely labile in biodegradability assays, decreasing by more than 55% within the first 24 h of incubation. We suggest that algae can be an important component of the photosynthetic community in boreal peatlands and may become increasingly important for energy flow in a more variable climate with more intense droughts and flooding.

Keywords Climate change · Decomposition · Drought · Ecosystem memory · Nutrient cycling

Communicated by Robert Hall.

K. H. Wyatt · A. R. Rober · R. J. Stevenson
Department of Zoology, Michigan State University,
East Lansing, MI 48824, USA

Present Address:
K. H. Wyatt (✉)
Department of Biology, Institute for Great Lakes Research,
Central Michigan University, Mt. Pleasant, MI 48859, USA
e-mail: wyatt1kh@cmich.edu

M. R. Turetsky
Department of Integrative Biology, University of Guelph,
Guelph, ON N1G2W1, Canada

D. Giroldo
Instituto de Ciências Biológicas, Universidade Federal do Rio
Grande-FURG, Rio Grande, RS 96201, Brazil

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

Introduction

The influence of warming on carbon (C) cycling in boreal ecosystems is a key issue in global change biology. This influence is particularly acute for boreal peatlands, given the strong interactive controls of thermal and moisture regimes on many processes in these ecosystems (Sulman et al. 2010). Peatlands are important to the global C cycle because they store a large component of the world's soil C stocks (Gorham 1991; Tarnocai et al. 2009) and supply most of the dissolved organic C (DOC) entering boreal lakes and rivers (Urban et al. 1989; Molot and Dillon 1996). In recent years, considerable effort has been made to quantify primary productivity in boreal peatlands and to understand climatic controls on vegetation community structure and productivity (cf. Thormann and Bayley 1997;

Weltzin et al. 2000; Chivers et al. 2009). For the most part, estimates of primary productivity and net ecosystem production in boreal peatlands have been limited to measurements of macrophyte and moss growth (Wieder 2006). However, in temperate wetlands, algal productivity can be substantial, commonly accounting for 50% or more of the total above-ground primary production when water is present at the surface (Goldsborough and Robinson 1996). Thus, studies in boreal peatlands may be underestimating total primary productivity by not including contributions from algal photosynthesis.

Algae are extremely sensitive to desiccation and, therefore, are vulnerable to variations in hydrology. Research examining algal responses to different hydroperiods and water depths has been conducted mainly in marshes occurring in southern boreal regions (Robinson et al. 1997) and the Everglades (i.e., Gottlieb et al. 2005; Thomas et al. 2006). In contrast, little is known about hydrological drivers of algal productivity in northern peatlands. For instance, it is unclear whether algae are restricted to peatlands where the water table is near the peat surface for most of the growing season (i.e., wet fens), or if they can be abundant in peatlands that experience shorter durations of saturation, such as following snowmelt or precipitation.

Northern high latitude regions are experiencing rapid warming, which is likely to alter wetland hydrology in several ways (Hinzman et al. 2005). For example, climate change is widely expected to reduce the extent of permafrost (perennially frozen ground; Woo et al. 1992; Hinzman et al. 2005), which could reduce the wetland area in boreal regions but increase the wetland area in arctic regions (Smith et al. 2005). Across interior Alaska, open water bodies in wetland-rich landscapes have declined in area in recent decades due to increased summer moisture deficits, drainage after permafrost thaw (Hinzman et al. 2005) and/or terrestrialization by wetland vegetation (Roach et al. 2011). However, landscape topography strongly influences Alaskan wetlands, and melt-water runoff from surrounding uplands has resulted in increased flooding in some areas. For example, increased snowmelt in the Alaska Range has resulted in hydrologic upwelling and the expansion of open water in the Tanana Flats region (Osterkamp et al. 2000).

The net effect of altered hydrology on algal primary productivity, particularly in boreal wetlands, is not clear because water table position could affect algal metabolism in opposing directions. For example, increased evapotranspiration associated with warmer temperatures may lead to lower water table positions in northern wetlands and algal desiccation. However, increased microbial decomposition due to thicker active layers, as well as warmer drier soil conditions, may increase nutrient availability (Bridgman et al. 1995) and stimulate algal productivity

(Thomas et al. 2006). Additionally, algal productivity in at least some wetlands could become more pulse-driven with increasing frequency and intensity of drying–rewetting events (Sheffield and Wood 2008).

While few studies have traced the fate of the algal material in peatlands, it is generally considered more labile for heterotrophic metabolism than that of macrophytes, especially mosses, which produce litter that is resistant to microbial breakdown (Lang et al. 2009; Turetsky et al. 2010). Similar to macrophytes, algae release a portion of their photosynthate directly into the water column as DOC (Mykkestad 1995; Wyatt et al. 2010), some of which is comprised of energy-rich carbohydrates (Giroldo et al. 2007). While studies have demonstrated the importance of algal exudates for heterotrophic metabolism in marine and freshwater systems (Baines and Pace 1991), no information exists on their availability or utilization as an energy source in boreal peatlands.

The overall goals of this study were to explore hydrologic and nutrient controls on algal productivity and exudates. Our sampling occurred during a severe natural flood in an Alaskan rich fen. At this site, water table position had been manipulated in three large-scale experimental plots since 2006, including a lowered treatment (in which the water table position was lowered relative to a control plot) and a raised treatment (in which the water table position was raised relative to a control plot). Because our sampling occurred during one of the wettest years on record, when the water tables at each of the three experimental plots were approximately the same, we were able to examine whether the antecedent lowered and/or raised water table treatments affected algal responses to the natural flood (i.e., we tested for memory of the experimental manipulations). We hypothesized that (1) experimental lowering of the water table followed by rewetting during the natural flood would increase water-column nutrient availability, (2) algal productivity would respond positively to greater nutrient availability, and thus would be higher in the lowered plot relative to the other plots, even after flooding caused similar water table positions in all plots, and (3) greater algal productivity would increase the availability of labile DOC for heterotrophic metabolism in the water column.

Materials and methods

Site description and water-table manipulation

This study was conducted at the Alaska Peatland Experiment (APEX) site, located on the floodplain of the Tanana River near the Bonanza Creek Experimental Forest, situated approximately 35 km southeast of Fairbanks, Alaska (64.82°N, 147.87°W). The area within interior Alaska is

classified as continental boreal, with a mean annual temperature of -3.1°C and mean annual precipitation of 287 mm, 35% of which falls as snow (average between years 1917 and 2000; Hinzman et al. 2006). The region has a relatively short growing season (135 days or less), but with more than 21 h of light per day in June. The APEX site is a rich fen dominated by brown moss, *Sphagnum*, and emergent vascular flora, including *Equisetum*, *Carex*, and *Potentilla*. A detailed description of the plant community at this APEX site is given by Chivers et al. (2009).

The APEX study site had three 120-m² plots, which were a control, and lowered and raised water table treatments. The plots were located approximately 25 m apart and bordered by a raised boardwalk. Prior to water table manipulation in 2005, there were no statistically significant differences in early growing season water table position or plant species composition across these three plots (Turetsky et al. 2008). A series of drainage canals (40 cm wide, 1 m deep) diverted water from the lowered water table plot to a small holding trench downslope. Solar-powered bilge pumps transported water into the raised plot from a surface well at a rate of approximately 10 cm day^{-1} . The chemistry of water additions to the raised plot was similar to ambient pore water, with no statistically significant differences in pH, electrical conductivity, and concentrations of anions, cations, or organic acids (Turetsky et al. 2008). A datalogger communication system maintained natural fluctuations in water table levels in the experimental plots based on fluctuations in the control plot associated with precipitation and seasonal drying trends.

Throughout all 4 years of manipulation, the lowered plot had a consistently lower water table height relative to the surface of the peat than the control plot, and the raised plot has been consistently wetter. The mean (\pm standard error) monthly water table position during the growing season for the control and lowered plots across all 4 years of manipulation was 7.2 ± 3.2 and 10.0 ± 3.8 cm beneath the surface of the peat, respectively, whereas the raised plot had water 0.1 ± 2.2 cm above the peat surface on average. The water table position in the lowered plot was also generally more variable than in the control plot, whereas experimentally raising the water table height in the raised plot reduced fluctuations in water table height within the months of June, July, and August (Fig. 1; Kane et al. 2010).

While water table position was controlled to some degree within the experimental plots, the substantial seasonal variation in water table height that is typical for this ecosystem continued to occur across all treatment plots (Fig. 1). In particular, the end of the summer in 2008 was one of the wettest on record, with over 275 mm of precipitation falling in interior Alaska between the months of May and October (National Atmospheric Deposition

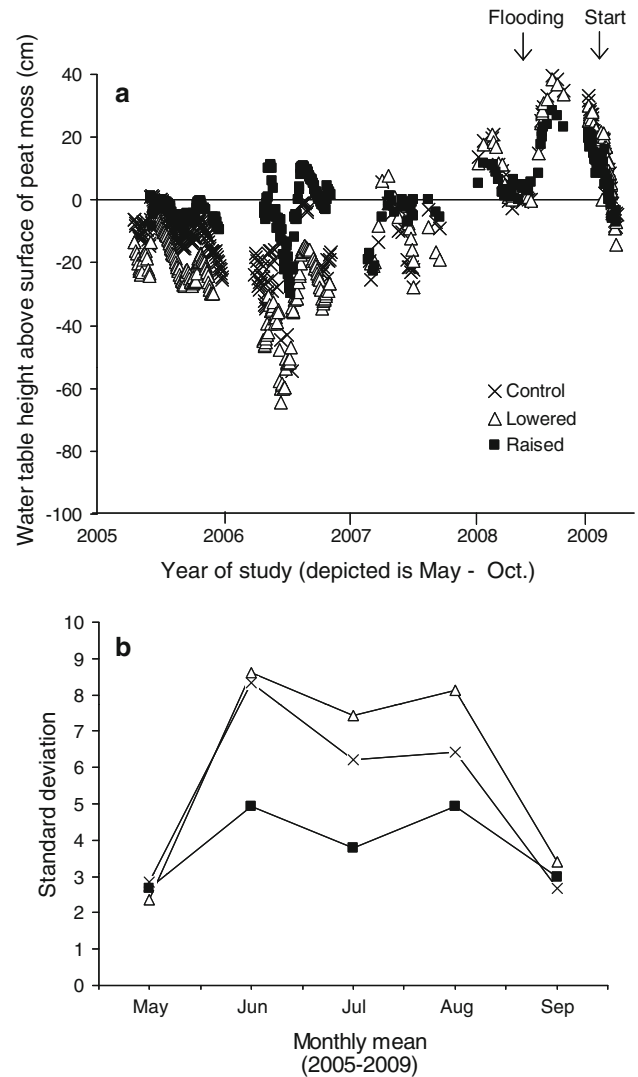


Fig. 1 **a** Long-term seasonal trends in water table heights across the control, lowered, and raised water table plots in the Alaska Peatland Experiment (APEX) site in interior Alaska during May–Oct 2005–2009. Negative values indicate water table position below the surface of the peat moss. Flooding in August 2008 is identified (Flooding) as is the initial study date in May 2009 (Start). **b** Standard deviation in mean monthly water table position across the 5 years of study from a total of 1,938 individual water table measurements

Program, station AK01). As a consequence, the region around the experimental plots became flooded during August and September 2008, and then flooded again following the spring thaw in 2009.

Surface water sampling

We monitored surface water nutrient concentrations as well as algal biomass and productivity within each of the water table plots each week beginning on 25 May 2009, shortly after the spring thaw and approximately 8 months after initial flooding of experimental plots, and then every

2 weeks beginning in July until the water table dropped below the peat surface in all treatment plots on 27 July 2009. The height of the water table relative to the peat surface was measured approximately weekly throughout the growing season inside polyvinyl chloride wells installed in each plot. Surface water temperature, dissolved oxygen (DO), and pH were measured using a calibrated model 556 YSI® Multi-Probe (YSI, Yellow Springs, OH, USA) on each sampling date. We filtered water for dissolved nutrient analysis using a 0.45- μm syringe-driven filter (Millipore, Bedford, MA, USA) into 120-mL acid-rinsed polyethylene bottles. Samples were stored on ice until returning to the laboratory, where a portion of each filtered sample was analyzed for DOC using a Shimadzu TOC-V analyzer (Shimadzu Scientific Instruments, Columbia, MD, USA). The remaining portion of each sample was frozen and stored until further analysis. We analyzed water samples for dissolved inorganic nitrogen (DIN) as $\text{NO}_3 + \text{NO}_2$ following the cadmium reduction method and for silica (SiO_2) following the molybdate method using a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands). Soluble reactive phosphorus (SRP) was measured following the ascorbic acid colorimetric method using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, UK) (APHA 1998).

Quantifying algal biomass, productivity and nutrient content

We sampled algae at eight randomly selected locations in each of the three water table plots for estimates of standing crop algal biomass and gross primary productivity (GPP) ($\text{mg C m}^{-2} \text{ h}^{-1}$). Each of the eight samples was a composite sample of four 25- cm^2 collections removed from the peat surface and, when present, the submersed portions of the dominant emergent macrophyte. Because the APEX site is part of a long-term study, we used non-destructive methods for removing algae from submersed surfaces. We used a plastic syringe to remove algae from each 25- cm^2 quadrat until there were no loosely attached algae or biofilms present on the peat surface. In cases where algae were attached to erect plant stems, we scraped the submersed portion of four stems clean with a plastic spoon, and adjusted the surface area in calculations. Each composite sample, which included algal material from stems and from the peat surface, was diluted to a measured volume with filtered water and gently inverted several times before separating for subsequent analyses. Measured aliquots of algal material were then removed for chlorophyll *a* (Chl *a*), dry mass, ash-free dry mass (AFDM), total P (TP), and GPP. Chl *a* was measured from a subsample collected on a Whatman GF/F glassfiber filter. Filters were

transported to the laboratory on ice and in the dark where they were frozen. Chl *a* was measured within a week of collection using a Turner model 700 fluorometer (Turner Designs, Sunnyvale, CA, USA) after extraction with 90% ethanol and correction for phaeophytin (APHA 1998). Two subsamples of homogenized algal material were dried at 105°C for 48–72 h and weighed. One dried sample was combusted in a muffle furnace at 500°C for 1 h in a pre-weighed aluminum pan for the estimation of mineral mass. AFDM was calculated as the difference between the dry and mineral mass. The second dried subsample was analyzed for TP by oxidizing particulate matter with persulphate and then analyzing SRP following the ascorbic acid method (APHA 1998). The proportion of P in each sample was calculated by dividing the mass of P by dry mass, and nutrient content of algae was reported per unit dry mass.

A final subsample was divided and immediately placed into two separate biological oxygen demand (BOD) bottles in situ and then used to estimate algal GPP ($\text{mg C m}^{-2} \text{ h}^{-1}$) following McCormick et al. (1998). We filled each BOD bottle with filtered water from the wetland and recorded initial DO using a Hach model 40d luminescent DO probe (Hach, Loveland, CO, USA). Bottles were sealed without trapping gas bubbles that would contribute to the initial oxygen concentration. We wrapped one bottle from each set with aluminum foil for incubation in the dark, and determined productivity by measuring oxygen changes produced by algal samples incubated in light and dark bottles. Bottles incubated light and dark were used to measure net ecosystem productivity and respiration, respectively. Bottles were incubated for approximately 2 h during midday hours and at similar depths to provide the most accurate daily productivity rates. We calculated GPP and converted GPP values into units C based on a C:O molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

Quantification, characterization, and degradation of algal exudates

We evaluated changes in DOC concentrations in light bottles during productivity measurements on 20 June to evaluate the proportion of C fixed by algae during photosynthesis that was released into the overlying water column. We chose this sampling date because of the noticeable differences in standing stock algal biomass among treatment plots, which we expected to produce a wide range of productivity rates (see “Results”). Prior to light–dark bottle incubations, we filtered pore water through a 0.2- μm VacuCap filter (Pall Life Sciences, Ann Arbor, MI, USA) to eliminate most bacteria from solution, and then incubated algal samples for measures of GPP as described above. After the final DO reading, we filtered

and acidified water from each light bottle for measurements of DOC concentration, and related changes in DOC concentration to measures of algal GPP during the 2 h incubation.

We performed a laboratory incubation to evaluate the chemical characteristics and biodegradability of algal exudates. We collected algal exudates by incubating samples in an open-top polyethylene container filled with 0.2 μm filtered water in the sunlight for 12 h. The incubation process was not sterile, but bacterial densities were less than 1×10^5 bacteria L^{-1} , which we assumed to have a low impact on the amount and quality of the DOC. We filtered algal exudates through a 0.2- μm VacuCap filter into an acid-washed flask, and then further diluted the solution using milli-Q water to approximately the same DOC concentration as the pore water of the APEX fen (25 mg L^{-1}). We also collected and filtered 2 L of pore water through a 0.2- μm VacuCap filter for characterization and degradation patterns of ambient pore water DOC. We prepared a bacterial inoculum by filtering a portion of pore water through a 0.7- μm Whatman GF/F filter. Other studies have shown that approximately 80% of bacterial cells pass through 0.7- μm pore-size filters (Giroldo et al. 2007). Water samples were kept at a constant temperature (ca. 21°C) until the start of the experiment (2 h).

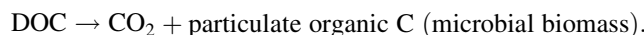
We made two treatments for relative comparisons of degradation rates: (1) 0.2- μm -filtered algal exudates, and (2) 0.2- μm -filtered pore water from the APEX fen. We pipetted 1 mL of the bacterial inoculum (0.7- μm -filtered pore water) into eight 300-mL glass flasks and filled the remaining volume of each flask with either algal exudates or 0.2- μm -filtered pore water, for a total of $n = 4$ for each treatment. We incubated the cultures in the dark and the temperature was kept constant throughout the experiment (ca. 21°C). We sampled flasks at 0, 12, 24, 48, 72, 192 (day 8), 384 (day 16) and 768 h (day 32) for measures of specific UV absorbance at $\lambda = 254$ nm (SUVA), DOC concentration, carbohydrate composition- and bacteria abundance.

We analyzed samples during the incubation for UV-Vis absorption at $\lambda = 254$ nm, the wavelength associated with aromatic compounds (Chin et al. 1994) using a Shimadzu UV-Mini model 1240 spectrophotometer (Shimadzu Scientific Instruments-). We analyzed the samples for DOC and calculated SUVA by dividing UV-Vis absorbance at $\lambda = 254$ nm by DOC concentration. SUVA gives an “average” molar absorptivity for all the molecules contributing to the DOC in a sample, and has been used as a measure of DOC aromaticity (Chin et al. 1994).

The compositions of polymeric and free carbohydrates in pore water and algal exudates were analyzed during the incubation using high performance liquid chromatography coupled to pulse amperometric detection (HPLC-PAD).

The HPLC-PAD analyses were performed on a Dionex model DX500 (Dionex-, Sunnyvale, CA, USA). Samples were divided into two fractions before analysis: total dissolved carbohydrates (TDCHOs) and free dissolved carbohydrates (FDCHOs). Polymeric dissolved carbohydrates (PDCHOs) were calculated by subtracting FDCHOs from TDCHOs. The FDCHO samples were injected directly into the HPLC system, while TDCHOs were hydrolyzed prior to injection (Gremm and Kaplan 1997).

A first-order decay equation was used to describe the degradation of DOC and extracellular polysaccharides in algal exudates assuming the following reaction:



The decay coefficients of DOC, the total polysaccharide pool- and each monomer were calculated using the following equation:

$$A_t = A_0 e^{-kt}$$

where A_t is the carbohydrate concentration, A_0 is the initial carbohydrate concentration, k is the decay coefficient (day^{-1}), e is the base of natural logarithms and t is time. Nonlinear regression (Levenberg-Marquardt algorithm) was used to calculate decay rates (Press et al. 1993).

Bacterial growth was evaluated by direct counts using a Nikon Eclipse E800 epifluorescence microscope with UV (Nikon Instruments, Melville, NY, USA) after staining the cells with DAPI (4', 6-diamino-2-phenylindole) and filtered on 0.2- μm black filters (Osmonic, Livermore, USA) (Porter and Feig 1980). At least 300 bacteria or 25 fields were counted per filter.

Statistical analyses

We used univariate repeated measures analysis of variance (RM ANOVA) models with an adjusted Bonferroni significance level ($P < 0.016$) and Tukey's test for post hoc comparison of means to determine if algal productivity and biomass were different among water table treatments. We used a linear mixed model that included environmental variables (water depth, water temperature, DO, DIN, SRP) and water table treatment to predict changes in algal productivity and biomass. We determined which environmental variables to include in the model using univariate RM ANOVAs with an adjusted Bonferroni significance level. We used a Tukey's test to discriminate between different treatments. Although environmental variables were significantly different among treatments, they were not significant predictors of algal biomass or productivity within treatments. We evaluated the relationship between algal productivity and DOC concentration during light-bottle incubations using linear regression analysis.

Differences in DOC concentration, SUVA and bacterial abundance between pore water and algal exudates during the degradation experiment were analyzed with *t* tests. All statistical analyses were performed using general linear models in SPSS 18 (SPSS, Chicago, IL, USA). The distributions of variables were $\log(x + 1)$ transformed if necessary to correct for non-normal distribution and unequal variances among treatments prior to analysis. It is also important to note that water table treatment was not replicated, and, thus, location is confounded with water table plot. The effects of the water table treatment were tested with a small number of degrees of freedom and some caution is warranted due to the lack of true replicates.

Results

Physical and chemical conditions

From May to July 2009, water table position in the APEX plots was not well regulated by draining and active pumping, but instead was controlled by the natural flood (Fig. 1). Water table height above the peat surface decreased with time across all water table plots following the spring snowmelt (Fig. 1), but it was not significantly different among plots ($P > 0.05$). Water temperature increased in all plots over time (Fig. 2a), but was consistently lower in the raised plot compared to the control and lowered plots (RM ANOVA, $F_{2,21} = 271.1$, $P < 0.001$). Dissolved oxygen concentrations peaked in mid-June and were significantly greater only in the lowered plot ($F_{2,21} = 5.3$, $P = 0.014$), where levels reached $12.7 \pm 0.15 \text{ mg L}^{-1}$ on 10 June before decreasing thereafter (Fig. 2b).

Surface water nutrient concentrations were higher in the lowered plot relative to the control and raised plots following the spring thaw in 2009 (Fig. 2). In each plot, water column nutrient concentrations peaked in early June and then decreased sharply (Fig. 2e, f). Averaged across all sampling dates, levels of SRP (RM ANOVA, $F_{2,21} = 78.9$, $P < 0.0001$) and DIN ($F_{2,21} = 332.2$, $P < 0.0001$) varied among plots, with greater mean concentrations in the lowered plot relative to the control plot. SiO_2 concentrations were below detection in all plots throughout the growing season. Dissolved organic C concentrations tended to increase, and water column pH decreased with time across all plots (Fig. 2c, d), but on average there were no differences in these variables among water table plots ($P > 0.05$).

Algae biomass, productivity and nutrient content

Algal productivity ($\text{mg C m}^{-2} \text{ h}^{-1}$) peaked immediately following the maxima in nutrient concentrations, and was

consistently higher in the lowered plot ($5.18 \pm 1.8\text{--}37.99 \pm 13.4$) compared to the control ($2.6 \pm 0.9\text{--}13.8 \pm 4.9$) and raised plots ($0.12 \pm 0.04\text{--}12.1 \pm 4.3$) (Fig. 3c). Averaged across sampling dates, measures of algal biomass and GPP were significantly higher in the lowered plot than in the other plots (RM ANOVA; Chl *a*: $F_{2,21} = 83.6$, $P < 0.0001$; AFDM: $F_{2,21} = 113.8$, $P < 0.0001$; GPP: $F_{2,21} = 55.7$, $P < 0.0001$; (Fig. 3a–c).

The concentration of P in algal material ($\mu\text{g P g}^{-1}$ dry mass) increased with the initial spike in water column P concentration, and was consistently higher in the lowered plot ($161 \pm 7\text{--}674 \pm 15$) compared to the raised ($47 \pm 4\text{--}125 \pm 6$) and control ($49 \pm 6\text{--}127 \pm 9$) plots throughout the summer growing season (RM ANOVA, $F_{2,21} = 404.6$, $P < 0.0001$; Fig. 3d).

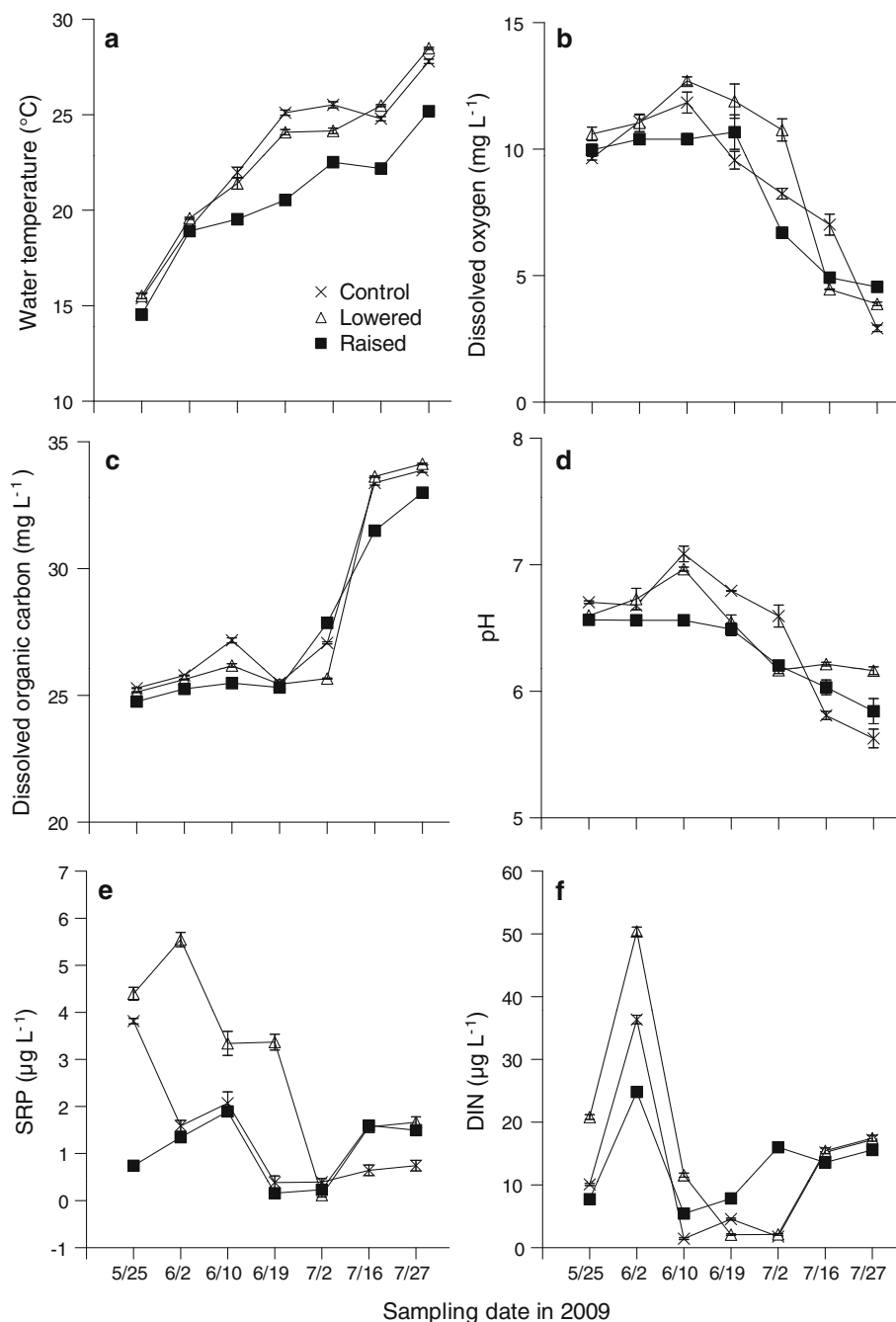
Characterization and degradation of algal exudates

A portion of C fixed by algae during photosynthesis was released into the overlying water column as DOC. During in situ incubations, DOC concentration increased with algal GPP ($r^2 = 0.85$, $P < 0.0001$; Fig. 4). By dividing the average rate of DOC flux ($0.36 \text{ mg L}^{-1} \text{ h}^{-1}$) by the average GPP ($1.93 \text{ mg L}^{-1} \text{ h}^{-1}$), we calculated that algae released 19% (range 9–29%) of fixed C into the water column. At this rate, algae attached to the peat surface contributed $0.93 \pm 0.31\text{--}6.84 \pm 2.28 \text{ mg C L}^{-1} \text{ h}^{-1}$ to the overlying water column in the lowered plot, $0.47 \pm 0.03\text{--}2.48 \pm 0.83 \text{ mg C L}^{-1} \text{ h}^{-1}$ in the control plot, and $0.02 \pm 0.01\text{--}2.17 \pm 0.73 \text{ mg C L}^{-1} \text{ h}^{-1}$ in the raised plot for each m^2 of submersed substrate during the growing season.

Algal exudates were more labile than pore water DOC during biodegradability assays. Algal exudates decreased by 56% within the first 24 h of incubation and SUVA levels increased by 38% over the same period (Fig. 5). Bacterial growth in algal exudates increased from 0.73 ± 0.004 to $3.65 \pm 0.03 \cdot 10^6 \text{ cells mL}^{-1}$ and reaching maximum density after 24 h of incubation (Fig. 5c). Bacterial growth in algal exudates slowed when SUVA values reached between 2.3 and $2.5 \text{ L mg C}^{-1} \text{ m}^{-1}$, but maintained a consistently higher bacterial density over 32 days compared to the pore water treatment (Fig. 5). SUVA levels in the pore water remained near $2.5 \text{ L mg C}^{-1} \text{ m}^{-1}$, which corresponded to low *k* values (0.001 day^{-1}) relative to algal exudates (0.018 day^{-1}) and low bacterial density ($<1.38 \pm 0.03 \cdot 10^6 \text{ cells mL}^{-1}$) throughout the incubation (Fig. 5b).

The most labile carbohydrates made up the greatest proportion of algal exudates. HPLC–PAD analysis showed that 5.57 mg L^{-1} or 25% of the total algal exudates were composed of carbohydrates compared to 2.75 mg L^{-1} or 10.7% of the pore water DOC. A

Fig. 2 Surface water **a** temperature, **b** dissolved oxygen concentration, **c** dissolved organic carbon concentration, **d** pH, **e** soluble reactive phosphorus (*SRP*), **f** dissolved inorganic nitrogen (*DIN*) concentrations among the control, lowered, and raised water table plots on each sampling date in the APEX fen during the summer growing season in 2009 (mean \pm SE, $n = 8$)



combination of glucose, mannose, and fructose made up 60% of the total carbohydrate composition of algal exudates (Table 2). These sugars had a higher k value ($>0.034 \text{ day}^{-1}$) compared to arabinose, fucose, N-acetyl-glucosamine, rhamnose, galacturonic acid, xylose, and galactose which made up 56.8% of the total carbohydrate composition of pore water DOC (Table 1). No free monosaccharide was detected, and thus the total carbohydrates were composed entirely of polymeric carbohydrates.

Discussion

The ecosystem memory of drought and implications for algae

Prior to the onset of this study, there were significant differences in pore water nutrient concentrations among the water table treatments at the APEX fen, including higher concentrations of total dissolved N in the lowered water table plot relative to the raised and control plots (Kane

Fig. 3 Algal **a** chlorophyll *a* concentration, **b** ash-free dry mass, **c** gross primary productivity, **d** total phosphorus (*TP*) in the control, lowered, and raised water table plots on each sampling date in the APEX fen during the summer growing season in 2009 (mean \pm SE, $n = 8$)

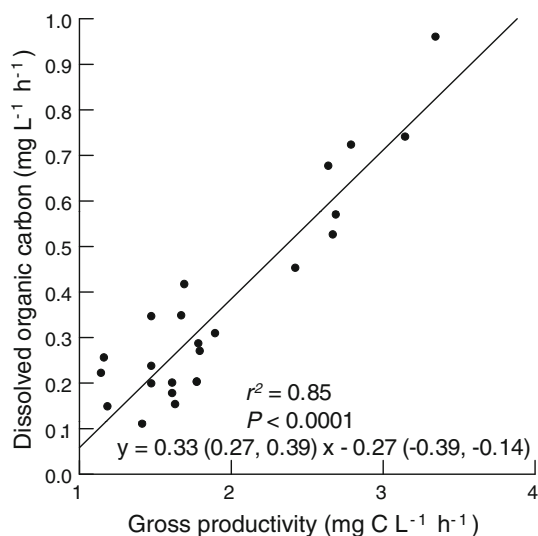
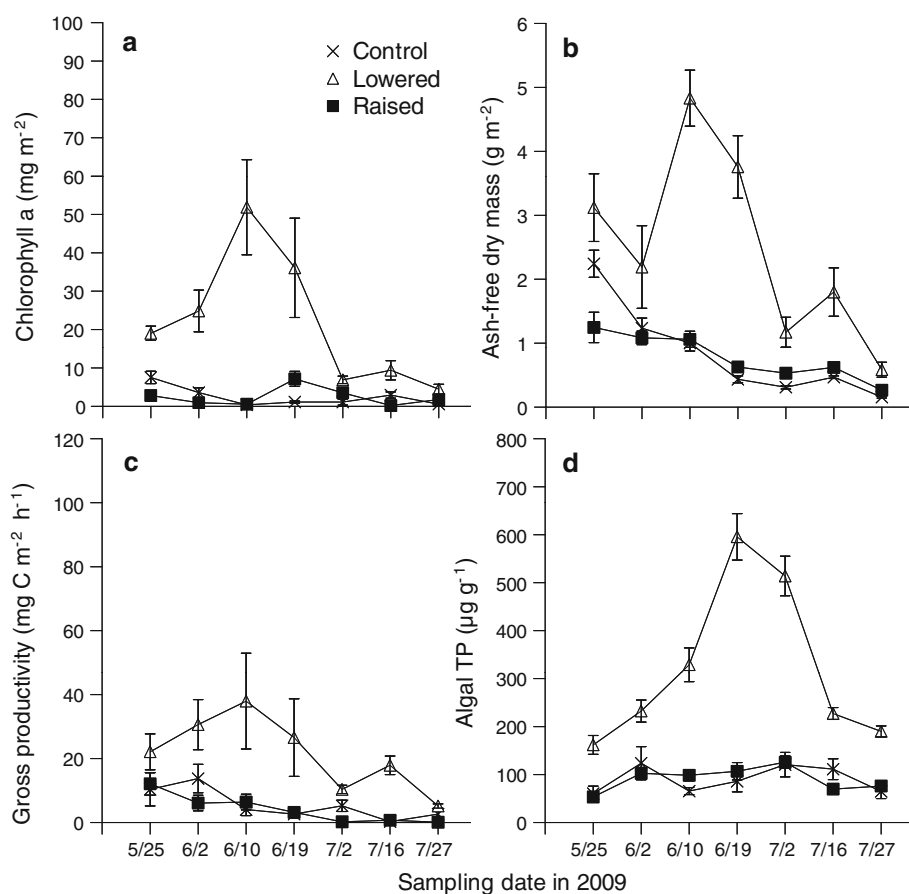


Fig. 4 Linear regression analysis between gross productivity ($\text{mg C L}^{-1} \text{ h}^{-1}$) and dissolved organic carbon flux ($\text{mg C L}^{-1} \text{ h}^{-1}$) inside light bottles during productivity measurements (95% CI of coefficients, $n = 24$)

et al. 2010). The summer of 2008 was one of the wettest for interior Alaska, and, as a consequence, the entire rich fen including all three experimental plots became flooded during the fall, and flooding persisted through the

following spring. We anticipated that flooding over the plots might simply re-set the ecosystem to conditions present before the hydrological manipulations, in which case algae would most likely respond to current water status with no memory of the antecedent water table manipulations. Instead, we quantified higher surface water nutrient concentrations in the lowered water table plot relative to the other plots following the spring thaw in 2009, approximately 9 months after rewetting. Since mean water table position did not vary among plots during the natural flooding period in this study, the high nutrient concentrations in the lowered plot can be attributed to the antecedent effects of drying during the previous four growing seasons, which carried over to influence nutrient dynamics after rewetting. In general, our results agree with other studies that have shown that drought can increase organic matter decomposition, triggering a pulse of nutrients from sediments into the overlying water column with re-inundation (Boon 2006).

The length of time that nutrient concentrations remained elevated in the lowered plot was likely prolonged by ice cover which occurred shortly after the flood and persisted until the spring thaw. The rapid reduction in nutrient levels that occurred in the lowered plot following the spring peak was likely the result of assimilation by the algae, which

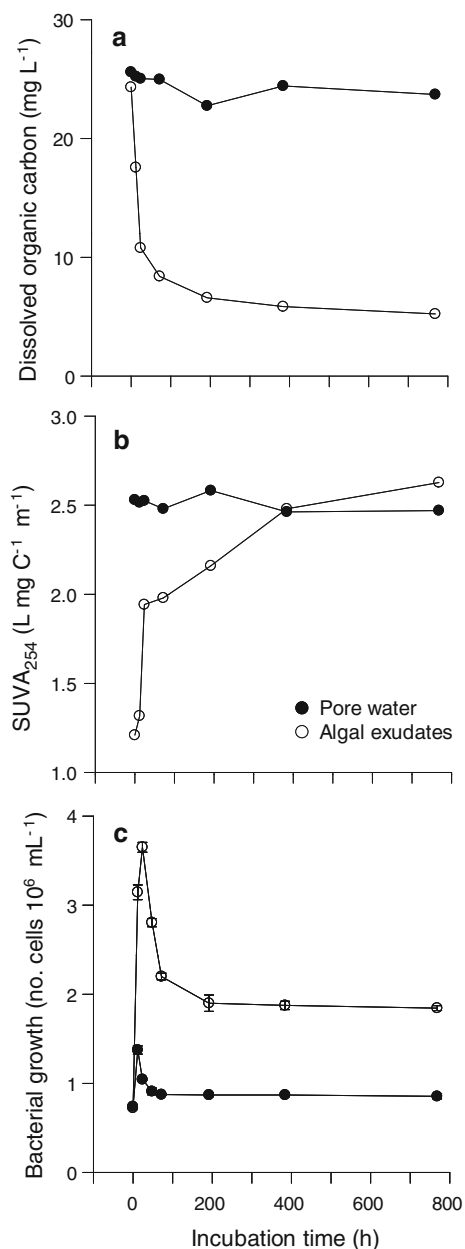


Fig. 5 Comparison of degradation rates of **a** dissolved organic carbon concentration, **b** specific UV-Vis absorption at $\lambda = 254$ nm (SUVA₂₅₄, L mg C⁻¹ m⁻¹), **c** bacterial growth in cultures of algal exudates or pore water from the APEX fen during 32 days (768 h) incubation period (mean \pm SE, $n = 4$)

were available to utilize nutrients after ice-thaw owing to a high, yet ephemeral, water table. This scenario, where nutrients are not sequestered until algae can grow after ice-thaw, presents an interesting contrast to lower latitudes where algae are available to assimilate nutrients year-round (i.e., Thomas et al. 2006). Our hypothesis that nutrient drawdown was due to algal sequestration is supported by the increase in algal productivity and nutrient content immediately following the spike in nutrient levels, and then

by the rapid reduction in water-column nutrient levels following the increase in algal productivity. The ability of algae to rapidly respond to and assimilate nutrients from the water column has been well documented in wetlands receiving external nutrient inputs (Richardson 2010; Rober et al. 2011). In the Florida Everglades, algae can sequester P rapidly (Noe et al. 2001), making it almost undetectable in the water column only a few meters from the source (Gaiser et al. 2004). When we relate measures of algal biomass in the lowered plot (0.59 ± 0.31 – 5.34 ± 1.12 g m⁻²) to the average P content per g dry mass (161 ± 8 – 674 ± 16 μ g P g⁻¹), we see the potential for algae to sequester a large amount of P, especially during peak biomass ($1,756 \pm 71$ μ g P m⁻²).

In addition to nutrient storage, it is likely that algae were recycling nutrients internally within the periphyton matrix (i.e., Wetzel 1996), which allowed them to maintain relatively high rates of productivity after water column nutrients were depleted. This process was recently demonstrated in the Everglades, where periphyton quickly removed P from the water column of an enclosure within a 2-day period following rewetting, but maintained similar levels of productivity without an increase in nutrient concentrations for the duration of a 20-day study (Thomas et al. 2006). The offset timing of the nutrient release from peat and the subsequent increase in algal productivity, as well as nutrient storage and internal cycling, may explain why water column nutrients were not significant predictors of algal productivity during the growing season in the APEX fen.

The abundance of algae in the water column had several effects on the physical and chemical environment that may, in turn, affect other wetland ecosystem processes. Dissolved oxygen concentrations were near saturation levels during peak algal productivity in the lowered treatment, and greater than those in adjacent water table treatments. These findings are similar to those reported from the Everglades, where algal photosynthesis in sloughs can raise daytime DO concentrations to levels much higher than those in nearby sawgrass stands with lower algal biomass (Belanger et al. 1989; Richardson 2010). Wetlands with low daily oxygen levels generally show reduced respiration and a shift to anaerobic processes due to the lack of available oxygen to support aerobic metabolism (McCormick et al. 1997). Thus, saturating levels of DO, which occurred with greater algal production in the lowered plot, could have important implications for community metabolism, especially during peak productivity.

Contribution of algal productivity to GPP and DOC production

Rates of algal productivity in the control plot were low, indicating that flooding of unmanipulated soils (i.e., with

Table 1 Bacterial degradation of the exudates released by algae measured by HPLC–PAD

Monosaccharides	<i>K</i>	<i>r</i> ²
<i>N</i> -acetyl-galactosamine	–	–
Arabinose	0.002 (0.001)	0.72
Fucose	0.002 (0.001)	0.66
<i>N</i> -acetyl-glucosamine	0.002 (0.001)	0.72
Rhamnose	0.004 (0.002)	0.67
Galacturonic acid	0.004 (0.005)	0.66
Xylose	0.005 (0.004)	0.58
Galactose	0.009 (0.003)	0.76
Glucose	0.034 (0.012)	0.88
Mannose	0.041 (0.016)	0.83
Ribose	0.044 (0.023)	0.73
Glucuronic acid	0.067 (0.031)	0.67
Fructose	0.090 (0.001)	0.99
Total	0.018 (0.008)	0.82

The decay coefficients are shown for each monosaccharide, which compose the algal carbohydrate pool, and also for the total carbohydrates; *n* = 4 ± SD

Table 2 Carbohydrate composition (%) determined by HPLC–PAD of the polysaccharide released by algae and pore water collected from the APEX fen; *n* = 4 ± SD

Monosaccharides	Pore water	Algae
<i>N</i> -acetyl-galactosamine	0.61 (0.59)	0.06 (0.03)
Arabinose	6.65 (0.03)	2.83 (0.57)
Fucose	6.50 (1.95)	2.85 (0.80)
<i>N</i> -acetyl glucosamine	2.31 (0.52)	1.34 (0.42)
Rhamnose	9.90 (2.92)	7.53 (3.37)
Galacturonic acid	2.19 (1.33)	1.18 (0.54)
Xylose	14.17 (4.02)	5.68 (2.82)
Galactose	15.08 (3.22)	12.96 (4.44)
Glucose	19.64 (2.63)	38.39 (8.96)
Mannose	13.74 (0.88)	13.18 (8.34)
Ribose	2.10 (0.20)	3.54 (0.18)
Glucuronic acid	4.10 (0.65)	2.54 (0.47)
Fructose	2.98 (1.45)	7.92 (1.72)
Total	100.00%	100.00%

no enhanced nutrient pool) does not stimulate algae productivity enough to affect total primary productivity in this boreal fen. Using GPP data reported by Chivers et al. (2009), we estimate that our measurements of mean algal productivity in the control plot represented about 7% of the total ecosystem GPP during the early part of the growing season. However, algal productivity was more important to ecosystem GPP in the lowered plot, representing approximately 31% of early season GPP, due to the enhanced nutrient supply triggered by the previous 4 years of

experimental drought. These results show that algae may become a more important component of total primary productivity in northern peatlands if drying–rewetting events become more common in the region and/or if land use or climate change leads to high nutrient supply and saturated conditions in northern wetlands.

In addition to the C that was present as algal biomass on the peat surface, algae released at least 19% of their photosynthate directly into the overlying water column. While several factors such as temperature can influence the relationship between DOC and GPP, our estimate of exudates release is within the range (5–35%) of those reported for phytoplankton in other aquatic ecosystems (Myklestad 1995). When this estimate is extrapolated to measures of algal GPP in the lowered treatment, we calculated that algae were contributing up to 26% of the total DOC pool per hour during peak productivity. It is, however, important to note that we measured algal exudates released immediately following the maxima in nutrient concentrations. The release of DOC, which is thought to function as an overflow mechanism to avoid damage of the photosynthetic apparatus (Smith and Underwood 2000), tends to increase with decreasing nutrient availability (Fogg 1983). Thus, our estimates of exudates release rates may have underestimated the amount of C that was released into the water column during the latter part of the growing season when nutrient concentrations were low.

Despite the substantial release of algal exudates, there were no differences in water column DOC concentrations among the experimental plots, even during periods of peak algal productivity in the lowered water table plot. Generally, algal exudates are produced and consumed by accumulating microbes at similar rates (Søndergaard et al. 1995), and we would not expect exudates to accumulate in the water column except during very brief periods of grazer control of the microbial community (i.e., Wright 1988). The high *k* values during the decomposition experiment support this hypothesis and indicated that algal exudates were degraded by a microbial inoculum much more quickly than fen pore water DOC. HPLC–PAD analysis showed that a large proportion of algal exudates was comprised of carbohydrates, dominated by glucose, mannose, and fructose, with *k* values greater than arabinose, fucose, rhamnose, galacturonic acid, xylose, and galactose, which comprised a large proportion of fen pore water DOC.

When we consider that algal productivity values in the lowered water table plot remained above 5.18 mg C m⁻² h⁻¹ while water was above the peat surface, algae were likely an important energy source for heterotrophic metabolism throughout the growing season following rewetting. The increase in bacterial density in the presence of algal exudates could have important indirect effects on

other ecosystem functions driven by microbes in boreal peatlands. For example, increases in microbial density could increase the ability of the bacterial community to decompose other, more recalcitrant C substrates that are already present in solution, or any new C substrates added to solution (i.e., Hamer and Marschner 2005). This process has been well documented in soils (see Kuzyakov et al. 2000 for a review), where a relatively small amount of labile C substrate can cause a disproportionate turnover of more recalcitrant organic matter (i.e., the priming effect). Despite the recent revival of interest in the priming effect in terrestrial ecosystems, it has been almost totally ignored in freshwater ecosystems (Guenet et al. 2010), especially in peatlands, where heterotrophic metabolism is often limited by available C substrate (Bergman et al. 1998).

In many regions, northern wetlands are expected to experience altered hydrology under climate change and with increasing human activity (i.e., Walker et al. 1987; Chapin et al. 2006). Drought associated with increased evapotranspiration or drainage from permafrost degradation or human development, coupled with longer and warmer growing seasons (Serreze et al. 2000), will likely increase decomposition in an expanded active layer in boreal wetlands (e.g., Bridgman et al. 1995). An increase in annual precipitation and altered flow-paths-associated runoff with permafrost degradation may result in greater flooding in regions previously exposed to seasonal drought (e.g., Hinzman et al. 2005). While drought may directly lead to algal desiccation, subsequent rewetting may increase algal productivity due to greater nutrient availability and the ability of algae to rapidly assimilate available nutrients in the water column. We suggest that, since water table drawdown typically increases solute loading, one memory effect of drought is the increase in nutrient supply that serves to stimulate algal production following rewetting. How important this effect is to other aspects of biological activity in peatlands is not yet clear.

The results of this study are limited in scope as they only show algal response to drying–rewetting in a single rich fen occurring within interior Alaska. Peatlands occurring across the boreal biome will almost certainly respond in different ways depending on length of drying and timing of rewetting. In light of the magnitude of algal productivity demonstrated here, and the high degree of algal exudates incorporated in wetland bacteria, more detailed investigations are warranted. The relationship between algal community composition and the chemical composition of exudates should be investigated, as well as the changes in the bacterial community during the degradation of algal exudates. Studies correlating bacterial dynamics to the composition and structure of polysaccharides released by algae would supply important information about the possible roles of these extracellular compounds for C cycling in this region.

Acknowledgments This research was supported by a Hensley Fellowship from MSU and a Sigma Xi Grant-in-Aid of Research Fellowship awarded to K.H.W. This research was also supported by the National Science Foundation Grant DEB-0425328, and the Bonanza Creek Long-Term Ecological Research Program (US Forest Service grant number PNW01-JV11261952-231 and National Science Foundation grant number DEB-0080609).

References

- APHA (1998) Standard methods for the examination of water and wastewater, 20th edn. American Public Health Association, Washington, DC
- Baines SB, Pace ML (1991) The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnol Oceanogr* 36:1078–1090
- Belanger TV, Scheidt DJ, Platko JR II (1989) Effects of nutrient enrichment on the Florida Everglades. *Lake Reserv Manag* 5:101–111
- Bergman I, Svensson BH, Nilsson MN (1998) Regulation of methane production in Swedish acid mire by pH, temperature and substrate. *Soil Biol Biochem* 30:729–741
- Boon PI (2006) Biogeochemistry and bacterial ecology of hydrologically dynamic wetlands. In: Batzer DP, Sharitz RR (eds) Ecology of freshwater and estuarine wetlands. University of California Press, Los Angeles, pp 115–176
- Bridgman SD, Johnston CA, Pastor J, Updegraff K (1995) Potential feedbacks of northern wetlands on climate change. *BioScience* 45:262–274
- Chapin FS, Oswood MW, Van Cleve K, Viereck LA, Verbyla DL (eds) (2006) Alaska's changing boreal forest. Oxford University Press, New York
- Chin YP, Aiken GR, O'Loughlin E (1994) Molecular weight, polydispersity, and spectroscopic properties of aquatic humic substances. *Environ Sci Technol* 28:1853–1858
- 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
- Fogg GE (1983) The ecological significance of extracellular products of phytoplankton photosynthesis. *Bot Mar* 26:3–14
- Gaiser EE, Scinto LJ, Richards JH, Jayachandran K, Childers DL, Trexler JD, Jones RD (2004) Phosphorus in periphyton mats provides best metric for detecting low level P enrichment in an oligotrophic wetland. *Water Res* 38:507–516
- Giroldo D, Ortolano PIC, Vieira AAH (2007) Bacteria–algae association in batch cultures of phytoplankton from a tropical reservoir: the significance of algal carbohydrates. *Freshwat Biol* 52:1281–1289
- Goldsborough LG, Robinson GGC (1996) Patterns in wetlands. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology: freshwater benthic ecosystems. Academic, San Diego, pp 77–117
- Gorham E (1991) Northern peatlands—Role in the carbon-cycle and probable responses to climatic warming. *Ecol Appl* 1:182–195
- Gottlieb A, Richards J, Gaiser E (2005) Effects of desiccation duration on the community structure and nutrient retention of short and long-hydroperiod Everglades periphyton mats. *Aquat Bot* 82:99–112
- Gremm TJ, Kaplan TJ (1997) Dissolved carbohydrates in streamwater determined by HPLC–PAD and pulse amperometric detection. *Limnol Oceanogr* 42:385–393
- Guenet B, Danger M, Abbadie L, Lacroix G (2010) Priming effect: bridging the gap between terrestrial and aquatic ecology. *Ecology* 91:2850–2861

- Hamer U, Marschner B (2005) Priming effects in soils after combined and repeated substrate additions. *Geoderma* 128:38–51
- Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyrugerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Genson TJ, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker M, Walker DA, Webber PJ, Welker JM, Winker KS, Yoshikawa K (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Clim Change* 72:251–298
- Hinzman LD, Viereck LA, Adams PC, Romanovsky VE, Yoshikawa K (2006) Climate and permafrost dynamics of the Alaskan boreal forest. In: Chapin FS, Oswood MW, Van Cleve K, Viereck LA, Verbyla DL (eds) *Alaska's changing boreal forest*. Oxford University Press, New York, pp 39–61
- Kane ES, Turetsky MR, Harden JW, McGuire AD, Waddington JM (2010) Seasonal ice and hydrologic controls on dissolved organic carbon and nitrogen concentrations in a boreal rich fen. *J Geophys Res Biogeosci*. doi:10.1029/2010JG001366
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biol Biochem* 32:1485–1498
- Lang S, Cornelissen JHC, Klahn T, van Logtestijn RSP, Broekman R, Schweikert W, Aerts R (2009) An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *J Ecol* 97:886–900
- McCormick PV, Chimney MJ, Swift DR (1997) Diel oxygen profiles and water column community metabolism in the Florida Everglades. *USA Arch Hydrobiol* 140:117–129
- McCormick PV, Shuford RBE, Backus JG, Kennedy WC (1998) Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, USA. *Hydrobiologia* 362:185–208
- Molot LA, Dillon PJ (1996) Storage of terrestrial carbon in boreal lake sediments and evasion to the atmosphere. *Glob Biogeochem Cy* 10:483–492
- Mykkestad SM (1995) Release of extracellular products by phytoplankton with special emphasis on polysaccharides. *Sci Total Environ* 165:155–164
- Noe GB, Childers DL, Jones RD (2001) Phosphorus biogeochemistry and the impact of phosphorus enrichment: why the Everglades is so unique? *Ecosystems* 4:603–624
- Osterkamp TE, Viereck L, Shur Y, Jorgenson MT, Racine C, Doyle A, Boone RD (2000) Observations of thermokarst and its impact on boreal forests in Alaska, USA. *Arct Alp Res* 32:303–315
- Porter KG, Feig Y (1980) The use of DAPI for identification and enumeration of bacteria and blue green algae. *Limnol Oceanogr* 25:943–948
- Press WH, Teukolsky SA, Vetterling WT, Flannery BP (eds) (1993) *Numerical recipes: the art of scientific computing*. Cambridge University Press, New York
- Richardson CJ (2010) The Everglades: North America's subtropical wetland. *Wetl Ecol Manag* 18:517–542
- Roach J, Griffith B, Verbyla D, Jones J (2011) Mechanisms influencing changes in lake area in Alaskan boreal forest. *Glob Change Biol*. doi:10.1111/j.1365-2486.2011.02446.x
- Rober AR, Wyatt KH, Stevenson RJ (2011) Regulation of algal structure and function by nutrients and grazing in a boreal wetland. *J N Am Benthol Soc* 30:787–796
- Robinson GGC, Gurney SE, Goldsborough LG (1997) The primary productivity of benthic and planktonic algae in a prairie wetland under controlled water-table regimes. *Wetlands* 17:182–194
- Serreze MC, Walsh JE, Chapin FS III, Osterkamp T, Dyrugerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46:159–207
- Sheffield J, Wood EF (2008) Global trends and variability in soil moisture and drought characteristics, 1950–2000, from observation-driven simulations of the terrestrial hydrologic cycle. *J Clim* 21:432–458
- Søndergaard M, Hansen B, Markager S (1995) Dynamics of dissolved organic carbon lability in a eutrophic lake. *Limnol Oceanogr* 40:46–54
- Smith LC, Sheng Y, MacDonald GM, Hinzman LD (2005) Disappearing Arctic lakes. *Science* 308:1429
- Smith DJ, Underwood GJC (2000) The production of extracellular carbohydrates by estuarine benthic diatoms: the effects of growth phase and light and dark treatment. *J Phycol* 36:321–333
- Sulman BN, Desai AR, Saliendra NZ, Lafleur PM, Flanagan LB, Sonnentag O, Mackay DS, Barr AG, van der Kamp G (2010) CO₂ fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table. *Geophys Res Lett*. doi:10.1029/2010GL044018
- Tarnocai CJ, Canadell G, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Glob Biogeochem Cy* 23:GB2023. doi:10.1029/2008GB003327
- Thomas S, Gaiser EE, Gantar M, Scinto LJ (2006) Quantifying the responses of calcareous periphyton crusts to rehydration: a microcosm study (Florida Everglades). *Aquat Bot* 84:317–323
- Thormann MN, Bayley SE (1997) Above ground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecol* 131:1–16
- Turetsky MR, Treat CC, Waldrop MP, Waddington JM, Harden JW, McGuire AD (2008) Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *J Geophys Res Biogeosci* 113:doi:10.1029/2007JG000496
- Turetsky MR, Mack MC, Hollingsworth T, Harden JW (2010) Patterns in moss productivity, decomposition, and succession: implications for the resilience of Alaskan ecosystems. *Can J For Res* 40:1237–1264
- Urban NR, Bayley SE, Eisenreich SJ (1989) Export of dissolved organic carbon and acidity from peatlands. *Water Resour Res* 25:1619–1628
- Walker DA, Webber PJ, Binnian EF, Everett KR, Lederer ND, Nordstrand EA, Walker MD (1987) Cumulative impacts of oil fields on northern Alaskan landscapes. *Science* 238:757–761
- 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
- Wetzel RG (1996) Benthic algae and nutrient cycling in lentic freshwater ecosystems. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) *Algal ecology: freshwater benthic ecosystems*. Academic, San Diego, pp 641–667
- Wetzel RG, Likens GE (eds) (2000) *Limnological analyses*, 3rd edn. Springer, New York
- Wieder RK (2006) Primary production in boreal peatlands. In: Wieder RK, Vitt DH (eds) *Boreal peatland ecosystems*. Springer, New York, pp 145–164
- Woo MK, Lewkowicz AG, Rouse WR (1992) Response of the Canadian permafrost environment to climate change. *Phys Geogr* 13:287–317
- Wright RT (1988) Methods for evaluating the interaction of substrate and grazing as factors controlling planktonic bacteria. *Arch Hydrobiol Monogr Beit* 31:229–242
- Wyatt KH, Stevenson RJ, Turetsky MR (2010) The importance of nutrient co-limitation in regulating algal community composition, productivity, and algal-derived DOC in an oligotrophic marsh in interior Alaska. *Freshw Biol* 55:1845–1860