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Algal community response to experimental and interannual variation in hydrology in an Alaskan boreal fen

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Abstract. Floristic studies indicate the abundance of microalgae in northern boreal peatlands, but we know relatively little about their ecology or how they will respond to changes in environmental conditions expected in this region as climate changes. We examined changes in algal community structure at sites exposed to a long-term water-table manipulation, including drought (lowered water-table treatment), flooding (raised water-table treatment), and control (no manipulation) treatments in an Alaskan fen. In previous years, continuous algal colonization typically would have occurred only in the raised water-table treatment, but a spring flood inundated experimental plots and provided a unique opportunity to examine algal community response to rewetting after long-term drought. This event allowed us to investigate how much ecosystem memory of the antecedent water-table manipulations regulated the ability of taxa to recolonize sites after prolonged drought compared to sites that had been continuously flooded. Despite no differences in water-table position among treatments at the time of sampling, surface-water nutrient concentrations were higher in the lowered water-table treatment relative to the other treatments after the spring thaw. This difference corresponded with greater algal abundance and biovolume in the lowered water-table treatment relative to the control and raised water-table treatments. Higher abundance and biovolume was driven mainly by filamentous green algae (Chlorophyta), especially *Oedogonium*, *Spirogyra*, and *Microspora*. Diatoms were most abundant in the raised water-table treatment, whereas chrysophytes were most abundant in the control treatment. Across all water-table treatments, N-fixing cyanobacteria increased as nutrients and water-table position declined over time. The differences in algal community structure among water-table treatments suggest that alternating drought and flooding events expected with climate change may significantly alter algal-driven functions in boreal wetlands.

Key words: algae, climate change, hydrology, peatland, taxonomic composition, wetland.

Algae can be abundant in wetlands and can contribute significantly to many of the physical, chemical, and biological processes that characterize wetland

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ecosystems (Goldsborough and Robinson 1996, Wetzel 2006). Many of the processes carried out by algae in wetlands (e.g., N-fixation, soil formation) are related to taxonomic composition (Goldsborough and Robinson 1996, Inglett et al. 2004). Despite literature describing the importance of algae for wetland ecosystem processes (Vymazal 1995, Robinson et al. 2000, Richardson 2010) and known differences in algal functions related to taxonomic composition (Graham et al. 2009), relatively little is known about the factors that regulate algal communities in wetlands. This issue is particularly significant in boreal regions, where wetlands are

abundant and processes related to ongoing climate change are expected to have widespread effects on aquatic ecosystems (Rouse et al. 1997, Schindler 1998).

Hydrology probably is the single most important factor regulating the establishment and maintenance of wetland ecosystems (Mitsch and Gosselink 2006). Frequent water-level fluctuations influence many of the physical and chemical factors characteristic of wetland habitats (e.g., nutrients, light, temperature, substrate availability), and therefore, algal communities (Goldsborough and Robinson 1996). Much of the research examining how algae respond to changes in hydrology was done in the Florida Everglades (McCormick et al. 1998, Gottlieb et al. 2005, 2006, Iwaniec et al. 2006), where wetland hydrology has been significantly altered by human development (Sklar et al. 2005). The effects of hydrology on wetland algal communities have been less studied in northern latitudes. Changes in boreal wetland hydrology are particularly significant, in part because temperatures that have constrained water at or near the surface of permanently frozen soils are increasing rapidly in the region. Climate models predict that temperatures in the region will continue to increase during this century (Serreze et al. 2000, Hinzman et al. 2005, McGuire et al. 2007).

Peatlands may be particularly sensitive to global change because water level is highly dependent on changes in rates of precipitation and evapotranspiration (Hinzman et al. 2006, Sulman et al. 2010). Peatlands cover extensive portions of interior Alaska where the surface areas of open water bodies in wetland-rich landscapes are already declining, probably because of increased evapotranspiration with longer, drier growing seasons (Serreze et al. 2000, Euskirchen et al. 2006), drainage after permafrost thaw (Hinzman et al. 2005, Riordan et al. 2006), or encroachment of wetland vegetation (Roach et al. 2011). However, some wetland areas in Alaska are expanding because of hydrologic upwelling and increased flooding from meltwater runoff from surrounding uplands (Osterkamp et al. 2000).

Increased frequency of drought and flooding events associated with climate change probably will alter the physical and chemical conditions of aquatic ecosystems in the boreal region, including the movement of limiting nutrients into and out of wetlands (Rouse et al. 1997). Seasonal drought and exposure of sediments probably will oxygenate anaerobic soils and stimulate microbial decomposition, thereby facilitating nutrient remineralization. Flooding of previously dried soils may release available nutrients into the overlying water column (Boon 2006, Thomas et al. 2006). Algae in shallow wetlands are sensitive to

changes in hydrology and water chemistry. Even small changes in water depth can result in desiccation (Thomas et al. 2006) or can expose algal communities to environmental conditions that may induce significant changes in community structure.

We monitored changes in algal community composition in response to an ecosystem-scale water-table manipulation that included drought (lowered water-table treatment) and flooding (raised water-table treatment) conditions in a rich fen in interior Alaska. Surface water conditions typically would allow continuous algal colonization only in the raised water-table treatment, but a significant flooding event provided a unique opportunity to examine algal community response at sites previously exposed to long-term drought. We investigated how much ecosystem memory of the antecedent water-table manipulations regulated the ability of taxa to recolonize sites after prolonged drought compared to sites that had been continuously flooded. In a concurrent study, we reported on surface-water chemistry and algal community metabolism after rewetting (Wyatt et al. 2012). Here, we evaluate the effects of rewetting on algal community structure.

Methods

Study site and experimental design

The APEX (Alaska Peatland Experiment) site is in the Tanana River floodplain just outside the Bonanza Creek Experimental Forest, ~35 km southeast of Fairbanks, Alaska (lat 64°82'N, long 147°87'W). This region of interior Alaska has large temperature fluctuations, mean annual temperature = -2.9°C, and low precipitation (269 mm/y) (Hinzman et al. 2006). The growing season is short (<135 d) and the region experiences >21 h of light/d in June. The site used in our study is a rich fen that receives water from surface-water runoff, precipitation, and to a small extent, groundwater. Vegetation at the site is dominated by brown moss, *Sphagnum*, and emergent vascular flora, including *Equisetum*, *Carex*, and *Potentilla*.

In 2005, 3 treatment plots (control, lowered, and raised water-table treatments) were established in the rich fen (Conlin 2008, Turetsky et al. 2008). Treatment plots are 120 m² in area and are ~25 m apart. Each treatment plot is surrounded by a permanent, raised boardwalk. Before the initiation of the water-table manipulation in 2005, early growing-season water-table position and plant species composition did not differ among treatments (Turetsky et al. 2008). A series of drainage canals (40 cm wide, 1 m deep) divert water from the lowered treatment. Surface water from a nearby well is pumped into the raised

treatment at a rate of ~ 10 cm/d by solar-powered bilge pumps. The chemistry of water added to the raised treatment is similar to ambient pore water in terms of pH, electrical conductivity, and concentrations of anions/cations, and organic acids (Turetsky et al. 2008). A data-logger communication system maintains natural fluctuations in the water table in the treatments based on fluctuations associated with precipitation and seasonal drying trends in the control treatment.

Throughout all 4 y of manipulation, mean water-table height relative to the surface of the peat was consistently lower in the lowered water-table treatment and consistently higher in the raised water-table treatment than in the control treatment (Fig. 1; Kane et al. 2010). The mean ($\pm$ SE) monthly water-table position during the growing season across all 4 y of manipulation was 7.2 ± 3.2 and 10.0 ± 3.8 cm beneath the surface of the peat in the control and lowered water-table treatments, respectively, and 0.1 ± 2.2 cm above the peat surface in the raised water-table treatment. Lowering the position of the water table increased variability in water-table height, whereas raising the position of the water table reduced fluctuations in water-table height in June, July and August (Fig. 1; Kane et al. 2010).

However, from May to July 2009, water-table height in treatment plots was not well regulated by experimental manipulation, but instead was affected by a flood that occurred at the end of summer 2008. Between May and October 2008, >275 mm of precipitation fell in interior Alaska (National Atmospheric Deposition Program, station AK01). Therefore, all 3 treatments were flooded in August to September 2008 and remained flooded during the spring thaw in 2009 (Fig. 1). Water-table height above the peat surface decreased with time in all water-table treatments after the spring snowmelt, but did not differ between treatments ($p > 0.05$; Fig. 1). After the spring flood, water-column nutrient concentrations peaked in early June in all treatments and then decreased sharply (Fig. 2A, B). Averaged across all sampling dates (mean $\pm$ SE), dissolved inorganic N (DIN) and soluble reactive P (SRP) were consistently higher in the lowered treatment (SRP = 2.86 ± 0.24 $\mu\text{g/L}$, DIN = 17.12 ± 2.05 $\mu\text{g/L}$) compared to in the raised (SRP = 1.07 ± 0.09 $\mu\text{g/L}$, DIN = 12.9 ± 0.84 $\mu\text{g/L}$) or control (SRP = 1.38 ± 0.16 $\mu\text{g/L}$, DIN = 12.4 ± 1.54 $\mu\text{g/L}$) treatments ($p < 0.0001$; Fig. 2A, B; Wyatt et al. 2012).

Benthic algal biomass measured as chlorophyll *a* and ash-free dry mass (AFDM) peaked after the maxima in nutrient concentrations (Wyatt et al. 2012). Averaged across all sampling dates (mean $\pm$ SE),

chlorophyll *a* concentration and AFDM were higher in the lowered treatment (chl *a* = 23.3 ± 3.69 mg/m^2 , AFDM = 2.889 ± 0.30 g/m^2) than in the control (chl *a* = 2.46 ± 0.44 mg/m^2 , AFDM = 0.84 ± 0.09 g/m^2) or raised (chl *a* = 2.42 ± 0.43 mg/m^2 , AFDM = 0.78 ± 0.06 g/m^2) treatments ($p < 0.0001$).

Sampling methods

In May 2009, we began monitoring algal variables in each treatment weekly, and then every 2 wk from July to August to evaluate algal responses to altered water-table position. We sampled algae at 8 randomly selected locations in each treatment to estimate algal density, biovolume, and taxonomic composition. The APEX site is part of a long-term study, so we used nondestructive methods to remove algae from submersed surfaces. Each sample consisted of four 25-cm² subsamples collected from peat surface and the submersed portions of 4 stems of the dominant emergent macrophyte. We used a plastic syringe to remove algae from each 25-cm² quadrat until no loosely attached algae or biofilms were present on the peat surface. We scraped the submersed portion of 4 stems clean with a plastic spoon. We estimated the surface area sampled based on water depth and measurements of the plant stem made with a caliper. We diluted each composite sample, which included algal material from stems and from the peat surface, to a known volume with filtered water and gently inverted the sample several times before separating subsamples for subsequent analyses. We preserved each algal sample with 2% formalin for taxonomic analysis.

We used standard protocols to characterize algal taxonomic composition. We counted ≥ 300 natural units or colonies per sample in a Palmer–Maloney nanoplankton counting chamber and identified algae to genus at 400 $\times$ magnification (Charles et al. 2002). For diatom compositional analysis, we acid-cleaned an aliquot of each sample and mounted cleaned diatoms on a microslide in NAPHRAX[®] mounting medium. We identified and enumerated diatom valves at 1000 $\times$ magnification. We quantified benthic algal abundance (cells/cm² of substrate) with the formula provided by Lowe and Laliberte (2006) and calculated biovolume ($\mu\text{m}^3/\text{cm}^2$ of substrate) by multiplying algal cell density by the estimated cell volume based on geometric formulae published by Hillebrand et al. (1999).

Data analysis

We log($x + 1$)-transformed data if necessary for statistical analyses to correct for nonnormal distribution

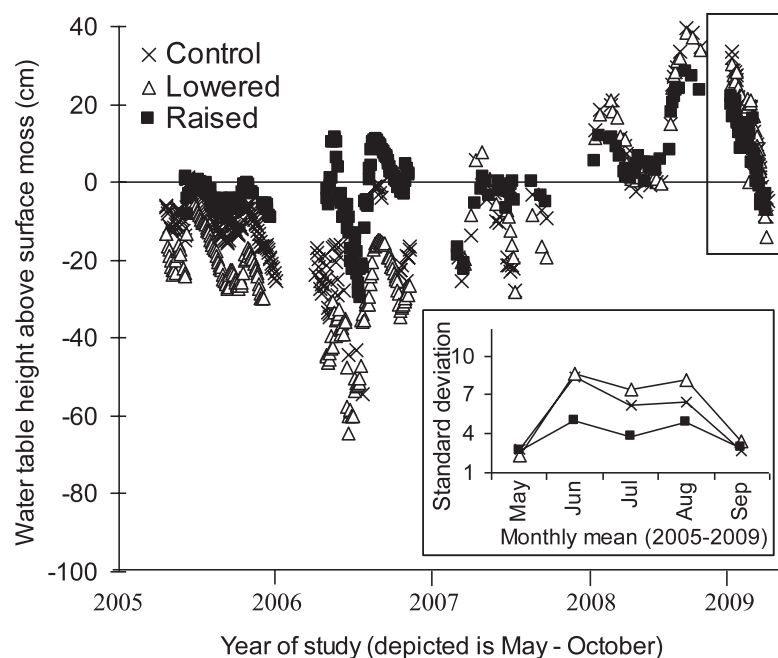


FIG. 1. Long-term seasonal trends in water-table heights in the control, lowered, and raised water-table treatments in interior Alaska (from Kane et al. 2010). Negative values indicate water-table position below the surface of the peat. Outlined values indicate water-table measurements made during our study. Insert shows standard deviation in mean monthly water table position across the 5 y of study (1938 individual water-table measurements).

and unequal variances among treatments before analysis. We used repeated measures analysis of variance (rmANOVA) with an adjusted Bonferroni significance level and Tukey's test for post hoc comparison of means to test the null hypothesis that water-table treatment had no effect on algal cell density and biovolume. We used a repeated measures multivariate analysis of variance (rmMANOVA) and Tukey's post hoc comparisons of means test to evaluate differences in algal taxonomic composition among water-table treatments. We identified 78 genera that were included in statistical analyses for cell density within phyla. We included individual taxa in analyses only when they were present at >5% relative abundance. We calculated biovolume only for taxa present at >5% relative abundance.

Water temperature ($21.1 \pm 0.3^\circ\text{C}$), dissolved O_2 (DO; $9.52 \pm 0.2 \text{ mg/L}$), and pH (6.51 ± 0.03) varied among treatments but were not significant predictors of algal biomass or taxonomic composition within treatments ($p > 0.05$; data not shown). A detailed description of the physical and chemical variables in the APEX site during our study was reported by Wyatt et al. (2012). We did statistical analyses with general linear models in SPSS 18 (SPSS, Chicago, Illinois).

Results

Algal taxonomic composition

Mean algal cell density (10^4 cells/cm^2) peaked immediately after the maximum in nutrient concentrations, and was nearly $3\times$ higher in the lowered (21.14 ± 2.9) than in the control (6.76 ± 1.31) or raised (8.39 ± 1.02) water-table treatments ($F_{2,15} = 8.88$, $p = 0.003$; Fig. 3A). The absolute abundance of almost all taxa was greater in the lowered water-table treatment than in the others because of greater overall biomass, but the relative abundances of taxa differed among treatments ($F_{22,180} = 5.95$, $p < 0.0001$; Fig. 4A–C).

Chrysophytes were significantly more abundant in the control treatment than in the lowered or raised water-table treatments ($F_{2,75} = 36.525$, $p < 0.0001$; Fig. 4A). *Dinobryon* was the dominant chrysophyte in the control treatment ($F_{2,180} = 68.18$, $p < 0.0001$; Fig. 5A). Cyanobacteria made up a greater proportion of total cell density in the raised (22–62%) and control (22–53%) water-table treatments than in the lowered (10–48%) water-table treatment ($F_{2,75} = 11.21$, $p < 0.0001$; Fig. 4A–C). *Nostoc* was the dominant cyanobacteria in all water-table treatments and increased in abundance as nutrient concentration and water-table position declined (Fig. 5A–F). Diatom relative abundance peaked in the

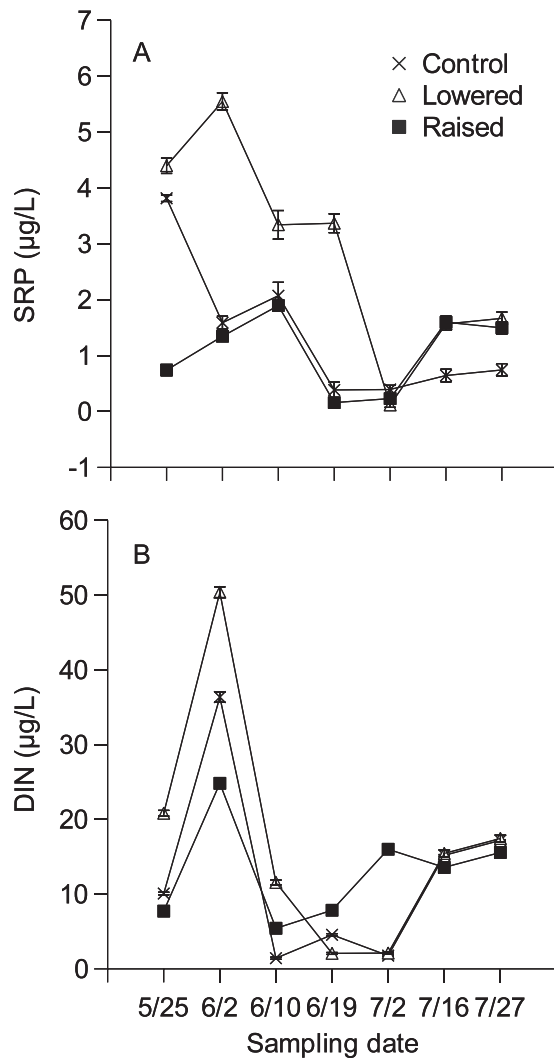


FIG. 2. Mean (± 1 SE; $n = 8$) soluble reactive P (SRP) (A) and dissolved inorganic N (DIN) (B) concentrations in control, lowered, and raised water-table treatments on each sampling date in the Alaska Peatland Experiment (APEX) fen during the summer 2009 growing season (from Wyatt et al. 2012).

middle of the growing season in all treatments, but was consistently greater in the raised (9–28%) than in the lowered (7–10%) or control (1–19%) water-table treatments ($F_{2,75} = 13.75$, $p < 0.0001$; Fig. 4A–C). The increase in diatom relative abundance in all treatments was driven by an increase in the abundance of *Tabellaria*, which was greater in the raised than in the lowered or control water-table treatments ($F_{2,180} = 25.13$, $p < 0.0001$; Fig. 5C). The green algae (Chlorophyta) were more abundant in the lowered than in the raised or control water-table treatments ($F_{2,75} = 54.42$, $p < 0.0001$; Fig. 4B). The lowered water-table treatment was dominated by large filamentous green algae *Oedogonium* ($F_{2,180} = 6.62$, $p = 0.002$; Fig. 5B), *Spirogyra* ($F_{2,180} = 9.37$,

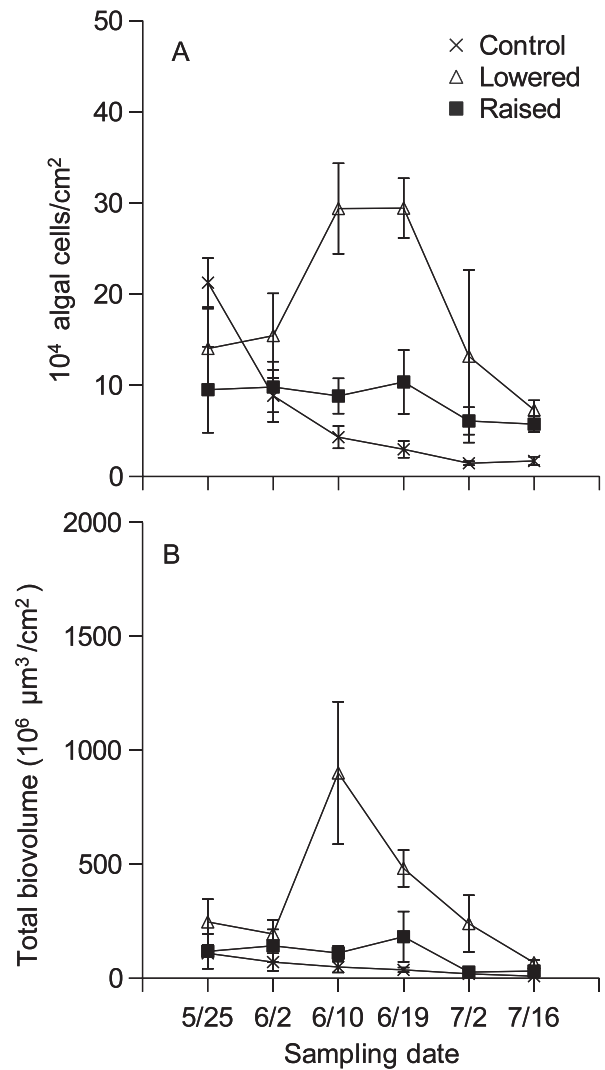


FIG. 3. Mean (± 1 SE; $n = 8$) algal cell density (A) and total biovolume (B) in the control, lowered, and raised water-table treatments on each sampling date in the Alaska Peatland Experiment (APEX) fen during the summer 2009 growing season.

$p < 0.0001$; Fig. 5B), and *Microspora* ($F_{2,180} = 5.54$, $p = 0.005$; Fig. 5B). Small coccoid taxa, many of which were present at $< 5\%$ relative abundance, made up the greatest proportion of green algae in raised and control water-table treatments (“other” in Fig. 5A, C). Relative abundances of the green algae *Gloeocystis*, *Bambusina*, *Ulothrix*, and *Zygnema* did not differ significantly between treatments at any time during the study (Fig. 5A–C). Of the 78 genera identified, 76% were present in all 3 water-table treatments.

Algal biovolume

Total algal biovolume was significantly greater in the lowered than in the raised or control water-table

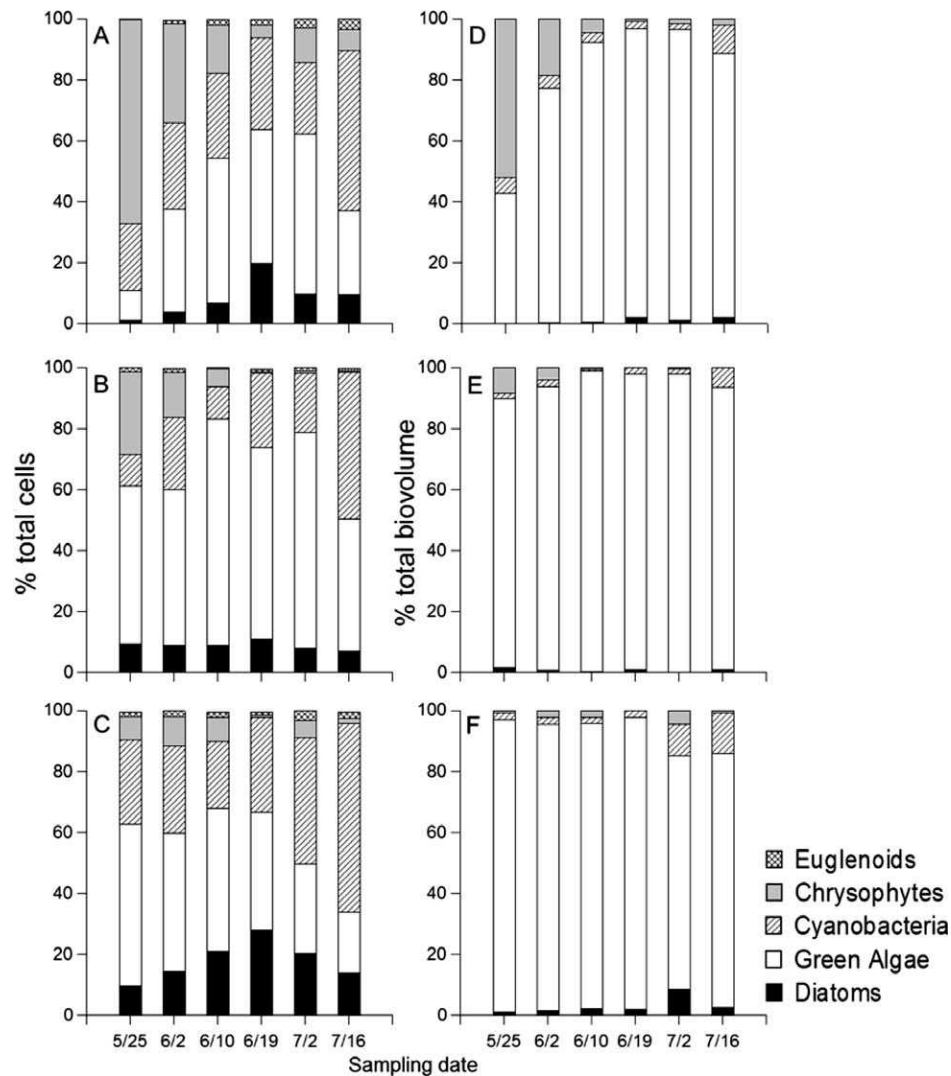


FIG. 4. Percent of total cells (A–C) and %total biovolume (D–F) in functional groups in the control (A, D), lowered (B, E), and raised (C, F) water-table treatments on each sampling date in the Alaska Peatland Experiment (APEX) fen during the summer 2009 growing season.

treatments ($F_{2,15} = 25.89$, $p < 0.0001$; Fig. 3B). Greater biovolume in the lowered water-table treatment was driven by *Oedogonium* ($F_{2,180} = 12.9$, $p < 0.0001$), *Spirogyra* ($F_{2,180} = 9.9$, $p < 0.0001$), and *Microspora* ($F_{2,180} = 4.6$, $p = 0.011$) (Fig. 5E). Filamentous green algae did not constitute a large proportion of the relative abundance of the algal community in raised or control water-table treatments (Fig. 5A, C), but they had larger cell sizes compared to many of the diatoms, chrysophytes, and cyanobacteria that were present in greater relative abundance. Therefore, despite the low abundance of *Oedogonium*, *Spirogyra*, and *Bambusina* in raised and control water-table treatments (Fig. 5A, C), they made up a significant portion of total algal biovolume ($p < 0.05$; Fig. 5D, F).

These results are limited to the high-biovolume taxa (i.e., filaments) because they made up a portion of the cell density in all treatments (Fig. 4D–F) and have much greater cell sizes than many of the smaller taxa.

Discussion

Algal community structure differed significantly among water-table treatments, even during the early part of the growing season when the water table did not differ among treatments. Differences in community composition were manifested mostly by changes in relative abundance rather than the presence/absence of individual taxa. The presence of most taxa in all 3 treatments suggests that the long-term natural variation in water-table position that occurs in the

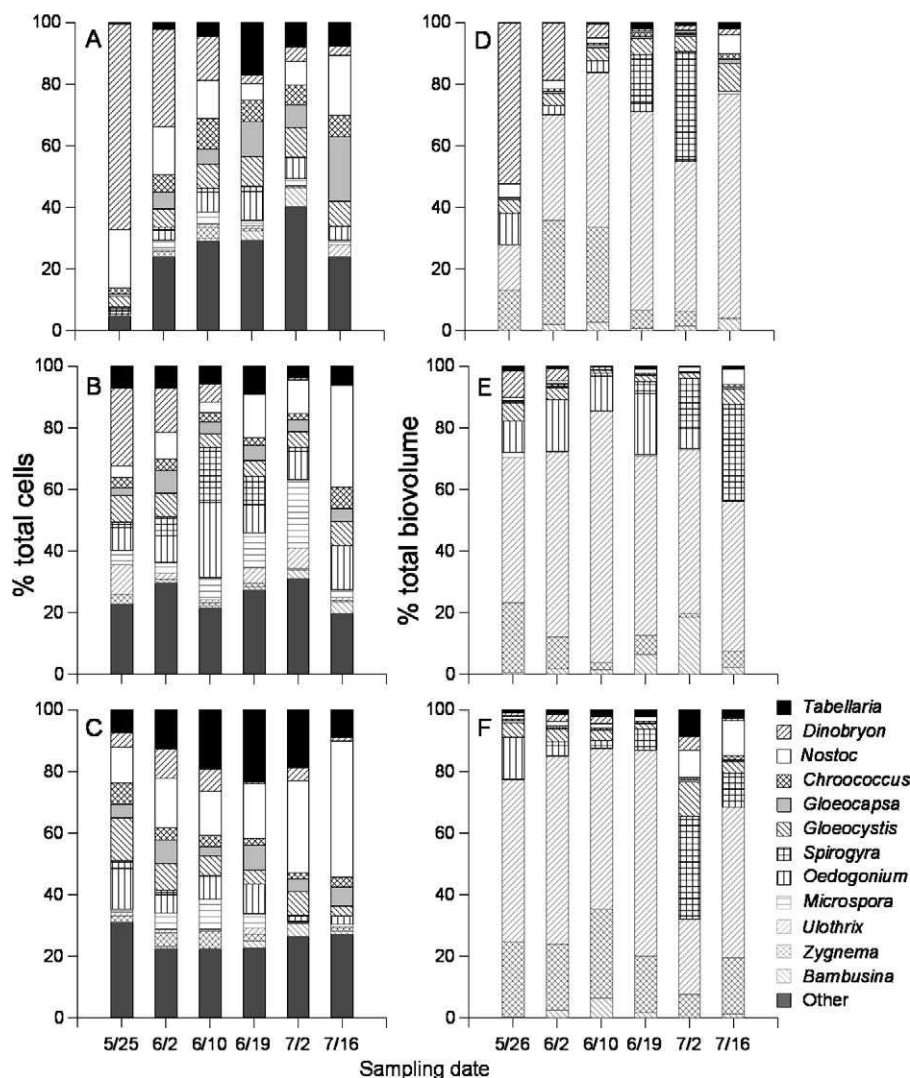


FIG. 5. Algal taxonomic composition as relative abundance (A–C) and % total biovolume (D–F) of dominant algal genera in the control (A, D), lowered (B, E), and raised (C, F) water-table treatments on each sampling date in the Alaska Peatland Experiment (APEX) fen during the summer 2009 growing season.

control and experimental plots with spring flooding, precipitation events, and seasonal drawdown, and similar regional environmental conditions regulates species membership of the algal community (sensu Pickett and McDonnell 1989, Stevenson 1997). However, altered nutrient dynamics associated with rewetting of previously dried soils probably regulate the density and relative abundance of taxa that are available to colonize substrates. Thus, antecedent conditions probably are acting on the algal community in 2 ways, first by limiting the taxa that are available in the seed bank to colonize substrates and then by increasing nutrient concentrations after rewetting, which shapes the relative abundance of taxa present on the peat surface.

The abundance of green algae across all water-table treatments is consistent with the literature from a survey of North American peatlands (Yung et al. 1986). Many species of green algae have an affinity for low pH conditions (Graham et al. 1996, Greenwood and Lowe 2006, Wyatt and Stevenson 2010), making them well adapted to acidic conditions in peatland ecosystems. The presence of filamentous green algae in Alaskan wetlands also has been attributed to their ability to tolerate the extreme fluctuations in temperature that occur at this latitude (Prescott 1963). The increase in filamentous taxa in the lowered water-table treatment probably was a response to increased nutrient availability after the spring thaw because some green algae are capable of exploiting available

nutrients and outcompeting other taxa for light and space (Graham et al. 1996). Our results are consistent with those reported in previous studies done in the Tanana River floodplain where filamentous green algae increased in biomass following nutrient enrichment (Wyatt et al. 2010, Rober et al. 2011), the Saskatchewan River Delta in northern Canada (Watchorn 2011) and Delta Marsh, Manitoba, where filamentous green algae contributed ~87% of the total algal biomass after a wetland was reflooded after experimental drawdown (Robinson et al. 1997).

The increase in the abundance of *Nostoc* as nutrient concentrations declined in all water-table treatments suggests that it can survive in low-nutrient environments. *Nostoc* is commonly found living endosymbiotically in moss tissues (Granhall and Selander 1973, DeLuca et al. 2002) and as epiphyton attached to moist moss surfaces in peatlands (Basilier 1980). *Nostoc* is capable of fixing atmospheric N, thereby making it biologically available for moss and vascular plant uptake and for microbial decomposition (DeLuca et al. 2002). N-fixation by cyanobacteria is the most important source of N to many arctic and boreal regions and contributes as much as 80% of total annual ecosystem N (Solheim et al. 2006). A considerable amount of research has been done in arctic and boreal regions to assess the importance of N-fixation in boreal forests (DeLuca et al. 2002, Uliassi and Ruess 2002, Hobara et al. 2006), but to our knowledge, the N-fixation potential of peatland cyanobacteria has not been quantified under different water-table regimes. Our results suggest that changes in water-table position will influence the abundance of N-fixing cyanobacteria and, therefore, probably the amount of N being fixed under differing hydrologic conditions. This effect may be particularly significant under hydrologic conditions similar to those in the raised water-table treatment, where continuously saturated soils reduce nutrient availability in the water column.

Diatoms are sensitive to desiccation stress, and the lower abundance of diatoms in the lowered compared to the control and raised water-table treatments is consistent with results from the Everglades, where diatom abundance decreased in areas that experienced more frequent drought (Browder et al. 1981, Gottlieb et al. 2006). Desiccation sensitivity also may explain the greater abundance of diatoms in the raised water-table treatment, which had been flooded during the previous 4 growing seasons and consistently had less variability than other treatments in water-table position (Kane et al. 2010). Overall, diatoms did not contribute greatly to total cell abundance or biovolume in our study. This group of algae, which use Si to build their cell walls, may have been limited by Si

concentrations that were below detection throughout much of the summer growing season (Wyatt et al. 2012). This result is consistent with those of other studies in which Si was a limiting nutrient for algae in peatland ecosystems (Struyf and Conley 2009).

Chrysophytes are widely distributed and commonly are found in oligotrophic habitats, especially at northern latitudes (Wehr and Sheath 2003). The abundance of chrysophytes, particularly *Dinobryon*, in our study is consistent with results of a previous study in Alaska (Hilliard 1968). This alga is mixotrophic and can switch between autotrophic and heterotrophic metabolism (Wehr and Sheath 2003). Therefore, it may be able to maintain metabolic activity in low-light conditions or under ice (Wiedner and Nixdorf 1998), which may explain its abundance early in the growing season after the spring thaw. However, the lower abundance of *Dinobryon* in the raised and lowered water-table treatments than in the control suggests that chrysophytes may be particularly sensitive to changes in hydrology and could decline in boreal peatlands as fluctuations in water-table position become more frequent with climate change.

Algal function in an ecosystem can be related to the overall abundance of a particular taxonomic group, so we used estimates of algal abundance as an indication of their functional importance. Filamentous green algae (*Oedogonium*, *Spirogyra*, *Microspora*) made up a substantial proportion of the algal cell density in the lowered water-table treatment and were dominant when measured by biovolume. Therefore, filamentous green algae probably will play an increasingly important role in wetland ecosystem function with increasing frequency of drying and rewetting events. This increase in importance may be particularly strong in shallow wetlands, which we would expect to experience more frequent fluctuations in water table. This shift in community composition probably will have ecosystem-level consequences given the significant amount of labile dissolved organic C released from filamentous green algae in the lowered water-table treatment and its use by bacterial communities (Wyatt et al. 2012).

Cell volume and abundance data were not consistent in raised and control water-table treatments where cyanobacteria made up a significant proportion of the algal community. These taxa (*Nostoc*, *Chroococcus*, and *Gloeocapsa*) are small coccoid cells that have much smaller cell volumes than the filamentous green taxa. Therefore, the dominance of filamentous green algae in terms of biovolume in raised and control water-table treatments was disproportionate relative to their absolute abundance. This mismatch between abundance and biovolume could mislead conclusions

regarding the function of the algal community within these sites because cyanobacteria, like *Nostoc*, may be important for ecosystem function.

Compared to the extensive literature on benthic algae in lakes and streams, few studies of the benthic algal assemblages of freshwater wetlands or the factors that regulate their structure and function have been published (Robinson et al. 2000). This discrepancy is particularly problematic for northern boreal regions where wetlands are abundant and extremely vulnerable to disturbances associated with climate change. Our results provide evidence that hydrology is an important factor regulating benthic algal community structure in a northern boreal peatland and adds to a growing literature on the role of algae in wetland ecosystems. The observed differences in algal taxonomic composition in response to fluctuations in water table suggests that increased frequency of drought and flooding events expected with climate change may significantly alter algal community structure and function in boreal wetlands from the expected natural peatland algal community (i.e., control treatment). This shift may be particularly important when hydrologic conditions influence nutrient mineralization and availability in surface soils. Furthermore, the similarity in taxa found in our study and those found in other floristic studies of peatlands (Yung et al. 1986, Mataloni 1999, Greenwood and Lowe 2006) indicate that the effect of altered hydrology on algal community structure could be applicable to peatland ecosystems beyond those in Alaska.

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Literature Cited

- BASILIER, K. 1980. Fixation and uptake of nitrogen in *Sphagnum* blue-green algae associations. *Oikos* 34: 239–242.
- BOON, P. I. 2006. Biogeochemistry and bacterial ecology of hydrologically dynamic wetlands. Pages 115–176 in D. P. Batzer and R. R. Sharitz (editors). *Ecology of freshwater and estuarine wetlands*. University of California Press, Los Angeles, California.
- BROWDER, J. A., S. BLACK, M. BROWN, M. NEWMAN, D. COTTRELL, D. BLACK, R. POPE, AND P. POPE. 1981. Perspectives on the ecological causes and effects of the variable algal composition of southern Everglades periphyton. Report T-643. South Florida Research Center, Homestead, Florida. (Available from: <http://ufdc.ufl.edu/ed1/sfrc>)
- CHARLES, D. F., C. KNOWLES, AND R. S. DAVIS. 2002. Protocols for the analysis of algal samples collected as part of the U.S. Geological Survey National Water-Quality Assessment program. Report No. 02–06. Academy of Natural Sciences, Philadelphia, Pennsylvania. (Available from: <http://water.usgs.gov/nawqa/protocols/algprotocol>)
- CONLIN, M. R. 2008. Soil hydroclimate, vegetation, and substrate controls on carbon flux in an Alaskan fen. MS Thesis, Michigan State University, East Lansing, Michigan.
- DELUCA, T. H., O. ZACKRISSON, M. NILSSON, AND A. SELLSTEDT. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature* 419:917–920.
- EUSKIRCHEN, E. S., A. D. MCGUIRE, D. W. KICKLIGHTER, Q. ZHUANG, J. S. CLEIN, R. J. DARGAVILLE, D. G. DYE, J. S. KIMBALL, K. C. McDONALD, J. M. MELILLO, V. E. ROMANOVSKY, AND N. V. SMITH. 2006. Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Global Change Biology* 12:731–750.
- GOLDSBOROUGH, L. G., AND G. G. C. ROBINSON. 1996. Patterns in wetlands. Pages 77–117 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (editors). *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York.
- GOTTLIEB, A. D., J. RICHARDS, AND E. E. GAISER. 2005. Effects of desiccation duration on the community structure and nutrient retention of short and long-hydroperiod Everglades periphyton mats. *Aquatic Botany* 82:99–112.
- GOTTLIEB, A. D., J. H. RICHARDS, AND E. E. GAISER. 2006. Comparative study of periphyton community structure in long and short-hydroperiod Everglades marshes. *Hydrobiologia* 569:195–207.
- GRAHAM, J. M., P. ARANCIBIA-AVILA, AND L. E. GRAHAM. 1996. Effects of pH and selected metals on growth of the filamentous green alga *Mougeotia* under acidic conditions. *Limnology and Oceanography* 41:263–270.
- GRAHAM, L. E., J. M. GRAHAM, AND L. W. WILCOX. 2009. *Algae*. 2nd edition. Benjamin Cummings, San Francisco, California.
- GRANHALL, U., AND H. SELANDER. 1973. Nitrogen fixation in a subarctic mire. *Oikos* 24:8–15.
- GREENWOOD, J. L., AND R. L. LOWE. 2006. The effects of pH on a periphyton community in an acidic wetland, USA. *Hydrobiologia* 561:71–82.
- HILLEBRAND, H., C. D. DÜRSELEN, D. B. KIRSCHTEL, U. POLLINGER, AND T. ZOHARY. 1999. Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology* 35:403–424.
- HILLIARD, D. K. 1968. Seasonal variation in some *Dinobryon* species (Chrysophyceae) from a pond and a lake in Alaska. *Oikos* 19:28–38.

- HINZMAN, L. D., N. D. BETTEZ, W. R. BOLTON, F. S. CHAPIN, M. B. DYURGEROV, C. L. FASTIE, B. GRIFFITH, R. D. HOLLISTER, A. HOPE, H. P. HUNTINGTON, A. M. JENSEN, G. J. JIA, T. J. GENSON, D. L. KANE, D. R. KLEIN, G. KOFINAS, A. H. LYNCH, A. H. LLOYD, A. D. MCGUIRE, F. E. NELSON, W. C. OECHEL, T. E. OSTERKAMP, C. H. RACINE, V. E. ROMANOVSKY, R. S. STONE, D. A. STOW, M. STURM, C. E. TWEEDIE, G. L. VOURLITIS, M. WALKER, D. A. WALKER, P. J. WEBBER, J. M. WELKER, K. S. WINKER, AND K. YOSHIKAWA. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72:251–298.
- HINZMAN, L. D., L. A. VIERECK, P. C. ADAMS, V. E. ROMANOVSKY, AND K. YOSHIKAWA. 2006. Climate and permafrost dynamics of the Alaskan boreal forest. Pages 39–61 in F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (editors). *Alaska's changing boreal forest*. Oxford University Press, New York.
- HOBARA, S., C. MCCALLEY, K. Koba, A. E. GIBLIN, M. S. WEISS, G. M. GETTEL, AND G. R. SHAVER. 2006. Nitrogen fixation in surface soils and vegetation in an arctic tundra watershed: a key source of atmospheric nitrogen. *Arctic, Antarctic, and Alpine Research* 38:363–372.
- INGLETT, P. W., K. R. REDDY, AND P. V. MCCORMICK. 2004. Periphyton chemistry and nitrogenase activity in a northern Everglades ecosystem. *Biogeochemistry* 67:213–233.
- IWANIEC, D. M., D. L. CHILDERS, D. RONDEAU, C. J. MADDEN, AND C. SAUNDERS. 2006. Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. *Hydrobiologia* 569:223–235.
- KANE, E. S., M. R. TURETSKY, J. HARDEN, A. D. MCGUIRE, AND J. M. WADDINGTON. 2010. Seasonal ice and hydrologic controls on dissolved organic carbon and nitrogen concentrations in a boreal rich fen. *Journal of Geophysical Research: Biogeosciences*. doi:10.1029/2010JG001366
- LOWE, R. L., AND G. D. LALIBERTE. 2006. Benthic stream algae: distribution and structure. Pages 327–356 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. 2nd edition. Academic Press, San Diego, California.
- MATALONI, G. 1999. Ecological studies on algal communities from Tierra del Fuego peat bogs. *Hydrobiologia* 391:157–171.
- MCCORMICK, P. V., R. B. E. SHUFORD, J. G. BACKUS, AND W. C. KENNEDY. 1998. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, U.S.A. *Hydrobiologia* 362:185–208.
- MCGUIRE, A. D., F. S. CHAPIN, C. WIRTH, M. A. APPS, J. BHATTI, T. V. CALLAGHAN, T. R. CHRISTENSEN, M. FUKUDA, J. CLEIN, T. MAXIMOV, A. ONUCHIN, A. SHVIDENKO, AND E. VAGANOV. 2007. Responses of high latitude ecosystems to global change: potential consequences for the climate system. Pages 297–310 in J. G. Canadell, D. E. Pataki, and L. F. Pitelka (editors). *Terrestrial ecosystems in a changing world*. International Geosphere–Biosphere Programme Series. Springer-Verlag, Heidelberg, Germany.
- MITSCH, W. J., AND J. G. GOSSELINK. 2006. *Wetlands*. 4th edition. John Wiley and Sons, New York.
- OSTERKAMP, T. E., L. VIERECK, Y. SHUR, M. T. JORGENSEN, C. RACINE, A. DOYLE, AND R. D. BOONE. 2000. Observations of thermokarst and its impact on boreal forests in Alaska, USA. *Arctic, Antarctic, and Alpine Research* 32:303–315.
- PICKETT, S. T. A., AND M. J. McDONNELL. 1989. Changing perspectives in community dynamics: a theory of successional forces. *Trends in Ecology and Evolution* 4:241–245.
- PRESCOTT, G. W. 1963. Ecology of Alaskan freshwater algae II. Introduction: general considerations. *Transactions of the American Microscopical Society* 82:83–98.
- RICHARDSON, C. J. 2010. The Everglades: North America's subtropical wetland. *Wetlands Ecology and Management* 18:517–542.
- RIORDAN, B., D. VERBYLA, AND A. D. MCGUIRE. 2006. Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research: Biogeosciences*. doi:10.1029/2005JG000150
- ROACH, J., B. GRIFFITH, D. VERBYLA, AND J. B. JONES. 2011. Mechanisms influencing changes in lake area in Alaskan boreal forest. *Global Change Biology*. doi:10.1111/j.1365-2486.2011.02446.x
- ROBER, A. R., K. H. WYATT, AND R. J. STEVENSON. 2011. Regulation of algal structure and function by grazing and nutrients in a boreal wetland. *Journal of the North American Benthological Society* 30:787–796.
- ROBINSON, G. G. C., S. E. GURNEY, AND L. G. GOLDSBOROUGH. 1997. Response of benthic and planktonic algal biomass to experimental water-level manipulation in a prairie lakeshore wetland. *Wetlands* 17:167–181.
- ROBINSON, G. G. C., S. E. GURNEY, AND L. G. GOLDSBOROUGH. 2000. Algae in prairie wetlands. Pages 163–198 in H. R. Murkin, A. G. van der Valk, and W. R. Clark (editors). *Prairie wetland ecology: the contribution of the Marsh Ecology Research Program*. Iowa State University Press, Ames, Iowa.
- ROUSE, W. R., M. S. V. DOUGLAS, R. E. HECKY, A. E. HERSHEY, G. W. KLING, L. LESACK, P. MARSH, M. McDONALD, B. J. NICHOLSON, N. T. ROULET, AND J. P. SMOL. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. *Hydrological Processes* 11:873–902.
- SCHINDLER, D. W. 1998. A dim future for boreal waters and landscapes. *BioScience* 48:157–164.
- SERREZE, M. C., J. E. WALSH, F. S. CHAPIN, T. OSTERKAMP, M. DYURGEROV, V. ROMANOVSKY, W. C. OECHEL, J. MORISON, T. ZHANG, AND R. G. BARRY. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46:159–207.
- SKLAR, F. H., M. J. CHIMNEY, S. NEWMAN, P. V. MCCORMICK, D. GAWLIK, S. MIAO, C. MCVoy, W. SAID, J. NEWMAN, C. CORONADO, G. CROZIER, M. KORVELA, AND K. RUTCHEY. 2005. The ecological–societal underpinnings of Everglades restoration. *Frontiers in Ecology and the Environment* 3:161–169.
- SOLHEIM, B., M. ZIELKE, J. W. BJERKE, AND J. ROZEMA. 2006. Effects of enhanced UV-B radiation on nitrogen fixation in arctic ecosystems. *Plant Ecology* 182:109–118.
- STEVENSON, R. J. 1997. Scale-dependent determinants and consequences of benthic algal heterogeneity. *Journal of the North American Benthological Society* 16:248–262.
- STRUYF, E., AND D. J. CONLEY. 2009. Silica: an essential nutrient in wetland biogeochemistry. *Frontiers in Ecology and the Environment* 7:88–94.

- SULMAN, B. N., A. R. DESAI, N. Z. SALIENDRA, P. M. LAFLEUR, L. B. FLANAGAN, O. SONNENTAG, D. S. MACKAY, A. G. BARR, AND G. VAN DER KAMP. 2010. CO₂ fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table. *Geophysical Research Letters*. doi:10.1029/2010GL044018
- THOMAS, S., E. E. GAISER, M. GANTAR, AND L. J. SCINTO. 2006. Quantifying the responses of calcareous periphyton crusts to rehydration: a microcosm study (Florida Everglades). *Aquatic Botany* 84:317–323.
- TURETSKY, M. R., C. C. TREAT, W. P. WALDROP, J. M. WADDINGTON, J. W. HARDEN, AND A. D. MCGUIRE. 2008. Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research: Biogeosciences*. doi:10.1029/2007JG000496
- ULIASSI, D. D., AND R. W. RUESS. 2002. Limitations to symbiotic nitrogen fixation in primary succession on the Tanana River floodplain. *Ecology* 83:88–103.
- VYMAZAL, J. 1995. *Algae and element cycling in wetlands*. Lewis Publishers, Ann Arbor, Michigan.
- WATCHORN, K. E. 2011. Effects of water level management on water chemistry and primary production of boreal marshes in northern Manitoba, Canada. MS Thesis, University of Manitoba, Winnipeg, Manitoba.
- WEHR, J. D., AND R. G. SHEATH. 2003. *Freshwater algae of North America: ecology and classification*. Academic Press, San Diego, California.
- WETZEL, R. G. 2006. Wetland ecosystem processes. Pages 285–312 in D. P. Batzer and R. A. Sharitz (editors). *Ecology of freshwater and estuarine wetlands*. University of California Press, Los Angeles, California.
- WIEDNER, C., AND B. NIXDORF. 1998. Success of chrysophytes, cryptophytes and dinoflagellates over blue-greens (cyanobacteria) during an extreme winter (1995/96) in eutrophic shallow lakes. *Hydrobiologia* 369/370: 229–235.
- WYATT, K. H., AND R. J. STEVENSON. 2010. Effects of acidification and alkalization on a periphytic algal community in an Alaskan wetland. *Wetlands* 30:1193–1202.
- WYATT, K. H., R. J. STEVENSON, AND M. R. TURETSKY. 2010. The importance of nutrient co-limitation in regulating algal community composition, productivity, and algal-derived DOC in an oligotrophic marsh in interior Alaska. *Freshwater Biology* 55:1845–1860.
- WYATT, K. H., M. R. TURETSKY, A. R. ROBER, D. GIROLDI, E. S. KANE, AND R. J. STEVENSON. 2012. 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. *Oecologia (Berlin)* 169: 821–832.
- YUNG, Y. K., P. STOKES, AND E. GORHAM. 1986. Algae of selected continental maritime bogs in North America. *Canadian Journal of Botany* 64:1825–1833.

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