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ARTICLE

Effects of Acidification and Alkalinization on a Periphytic Algal Community in an Alaskan Wetland

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Abstract Experimental research examining how algal communities respond to changes in pH is sparse in the wetland literature. In this study, we used a mesocosm experiment to examine the response of a periphytic algal community to a wide range of pH levels, both decreased to pH 5 (acid treatment) and increased to pH 9 (alkaline treatment) from ambient conditions (pH 7) in an Alaskan marsh. We examined algal communities growing on stems of *Equisetum fluviatile* (L.) after 24 days of colonization at experimental pH levels. Alkalinization resulted in a two-fold increase in concentrations of inorganic nutrients (dissolved inorganic N, soluble reactive P, SiO_2) and a significant increase in algal accrual relative to the control. There were distinct shifts in euglenoid taxa in the alkaline treatment, including a significant increase of *Trachelomonas* and a significant decrease of *Euglena* relative to the control. Acidification resulted in an increase of *Mougeotia* (Chlorophyta, Zygnemataceae) and a decrease in overall taxa richness, which coincided with a significant reduction in concentrations of dissolved inorganic carbon. Trends observed in our study indicate that alkalization may significantly alter algal community structure and loosen nutrient restraints on algal productivity, while acidification may reduce algal diversity in boreal wetlands.

Keywords Benthic algae · Boreal · Dissolved inorganic carbon · Marsh · *Mougeotia* · pH

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Introduction

Algae are an ecologically important component of many wetland ecosystems (Goldsborough and Robinson 1996). In shallow wetlands, periphytic algae, or those growing attached to submerged substrata, can account for a significant amount of total wetland primary productivity (McCormick et al. 1998; Ewe et al. 2006), increase nutrient cycling and retention (Wetzel 1996; Inglett et al. 2004), and serve as an important base of the wetland food web (Murkin 1989; Campeau et al. 1994). Algal communities are sensitive to changes in water quality, and many ecosystem services provided by algae in wetlands (i.e., nitrogen-fixation, soils formation) are related to taxonomic composition (Goldsborough and Robinson 1996). Environmental stressors related to human disturbance can lead to homogenization of wetland algal communities (Lougheed et al. 2008), and thus alter their role in wetland ecosystem function (Sklar et al. 2005). Despite extensive reviews stating the importance of algae for wetland ecology (Vymazal 1995; Robinson et al. 2000; Richardson 2009) and known differences in algal functions related to taxonomic composition (Graham et al. 2009), little information is available about the factors that regulate algal communities in wetlands.

The concentration of hydrogen ions is among the most important factors regulating the distribution and diversity of algae in freshwater habitats (Planas 1996). Acidification of freshwaters, generally associated with mineral acid inputs, can occur either naturally (i.e., volcanic emissions, bog water drainage inflow) or through human disturbance. Most recent studies in freshwater systems have focused on anthropogenic causes of acidification (i.e., acid mine drainage, sulfur and nitrogen oxide emissions), with extensive documentation of algal community changes

following acid inputs into lakes (Turner et al. 1987, 1991) and rivers (van Dam and Mertens 1995; Smucker and Vis 2009). In lakes, conditions associated with low pH often reduce species richness (e.g., Müller 1980; Turner et al. 1991) and diverse communities are frequently replaced by homogeneous assemblages dominated by filamentous green algae, especially those in the family Zygnemataceae (Müller 1980; Turner et al. 1995a, b).

At the opposite end of the pH range, the effects of alkalization on algal communities have also been investigated, generally as part of restoration measures to mitigate impacts of anthropogenic acidification (Fairchild and Sherman 1990; Hörnström 2002). In lakes, research has confirmed that many of the changes observed following acidification are reversed when acid waters are neutralized, generally by liming (see review in Olem 1991). Several studies have found that bloom-forming filamentous green algae, particularly *Mougeotia* (Chlorophyta, Zygnemataceae) are considerably reduced when pH is neutralized from about pH 5 (Hultberg and Andersson 1982; Jackson et al. 1990; Fairchild and Sherman 1992). However, laboratory investigations have demonstrated that *Mougeotia* can survive in extreme alkaline conditions (Graham et al. 1996; Arancibia-Avila et al. 2000), suggesting that it may not be particularly acidophilic, but rather can tolerate both direct and indirect effects of reduced pH, including low concentrations of dissolved inorganic carbon (DIC) (Jackson et al. 1990; Turner et al. 1991; Graham et al. 1996). Such discrepancies suggest that algal responses to pH may depend strongly on environmental conditions and vary by habitat type and geographic region of the water body.

Although pH is frequently observed as an important factor regulating algal species composition in large surveys of wetlands (Pan and Stevenson 1996; Stevenson et al. 1999; Negro et al. 2003), experimental research examining how algal communities respond to changes in pH is sparse in the wetland literature (but see van Dam et al. 1981; Greenwood and Lowe 2006). This is particularly true for boreal regions, where wetlands are abundant and processes related to increasing human activity (i.e., Walker et al. 1987; Charman 2002; Chapin et al. 2006) will likely alter the pH of aquatic ecosystems. In the interior region of Alaska, indications of human disturbance are already apparent, as sulfate and nitrate concentrations are enriched in precipitation by six orders of magnitude relative to sea water (Hinzman et al. 2006). These compounds, which are typically derived from industrial sources, are precursors of strong acids that have contributed to the acidification of surface waters globally (Schindler 1988). The boreal region is also experiencing rapid climate change (Hinzman et al. 2005), which has led to increased seasonal ice thaw and permafrost collapse (Hinzman et al. 2006). The expansion of open water areas due to permafrost thaw and increased surface water runoff from uplands (Osterkamp et al. 2000), may increase chemical weathering and alkalinization of surrounding wetlands, similar to those expected for lakes in the region (Schindler 1997). A better understanding of the effects of pH on algal communities will help to forecast and monitor wetland ecosystem health in boreal regions (i.e., McCormick and Stevenson 1998; Stevenson et al. 1999), especially in Alaska, where approximately 90% of the wetland area is under public management (Hall et al. 1994).

In this study, we examined the response of a periphytic algal community to a wide experimental pH range, both decreased (pH 5) and increased (pH 9) from ambient levels (pH 7) in an Alaskan marsh. Based on results from studies cited above, we hypothesized that increasing acidity would result in an overall decrease in taxa richness and result in a wetland algal community with greater total biomass comprised of acidophilic taxa, mainly those in the family Zygnemataceae. In contrast, we expected that alkaline condition would result in an algal community including few acidophilic taxa. We also expected that some of the changes in taxonomic structure that commonly occur in acid conditions would be explained by the response of algae (or lack thereof) to environmental conditions associated with the alkaline treatment (i.e., Graham et al. 1996).

Methods

Study Location

We conducted this study in a freshwater marsh located within an undeveloped area of the Tanana River floodplain situated approximately 35 km southwest of Fairbanks, Alaska, U.S.A. (latitude 64°42′ N, longitude 148°18′ W). This region experiences a relatively short growing season (135 days or less) with more than 21 hours of light per day in June. The flood plain is located within an intermontane plateau characterized by wide alluvium-covered lowlands with poorly drained, shallow soils over discontinuous permafrost (Begét et al. 2006). The region within interior Alaska has not experienced glaciation, and consequently, the area has a highly weathered geology (Hinzman et al. 2006). Oxbows and thaw ponds dominate the floodplain landscape, and fluvial deposition and erosion are annual disturbance events (Begét et al. 2006). The site is characteristic of other marsh wetlands that occur along the flood plain, which are shallow with dense stands of beaked sedge (*Carex utriculata* Boott) and swamp horsetail (*Equisetum fluviatile* L.) surrounding areas of open water with sparse emergent vegetation. Other vascular plants are also present at the site, including water parsnip (*Sium suave* Walter), flat leaved bladderwort (*Utricularia intermedia* Hayne), narrow leaved bur-reed (*Sparganium angustifolium*

Michaux), broad leaved water plantain (*Alisma plantago-aquatica* L.) and common mare's tail (*Hippuris vulgaris* L.). We conducted research in an open water area of the wetland (1494 m^2) with approximately 10% vegetation cover and a water depth of 44–49 cm.

pH Manipulation

We manipulated pH in situ using mesocosms modified from the design described by Greenwood and Lowe (2006). A raised boardwalk was built prior to beginning the study to prevent the disturbance of wetland sediments during experimental set-up and regular sampling. We constructed mesocosm enclosures by rolling welded wire mesh into a cylinder (40 cm in diameter), and enclosing each cylinder with a layer of 0.1 mm thick clear window vinyl. Enclosures were evenly spaced throughout an area of the wetland with open canopy and pushed into the sediments so that approximately 15 cm extended above the water surface. This design allowed water inside enclosures to be in contact with sediments and also kept natural vegetation intact to simulate natural wetland conditions more effectively.

We established three treatments: acid (pH=5), alkaline (pH=9) and the control (pH=7.2), with four replicates each. For the acid treatment, an average of 6.25 ml of 2.5% solution of H_2SO_4 was required to initially decrease the pH to or below 5, and an average of 5 ml of 2.5% solution of NaOH to initially raise the pH to or above 9 in the alkaline treatment. We monitored pH inside each enclosure every two days using a calibrated model 556 YSI meter (YSI Incorporated, Yellow Springs, OH, U.S.A.) and adjusted as needed with enough 2.5% H_2SO_4 or 2.5% NaOH to maintain experimental pH levels. We added an average of 2.5 ml 2.5% H_2SO_4 every two days over the first 12 days to maintain pH 5, and an average of 2 ml 2.5% NaOH every two days for the first 10 days of enclosure deployment to maintain pH 9. The acid treatment required approximately 1.5 ml 2.5% H_2SO_4 on days 6, 12, 16, 20, and 22 during the algal colonization period to maintain pH 5 (Fig. 1). For the alkaline treatment, approximately 0.5 ml of 2.5% NaOH was added on days 2, 4, 12, and 18 to maintain pH 9.

After experimental pH levels within the enclosures stabilized (day 12) (Fig. 1), we placed stems of *Equisetum fluviatile*, cut from live plants, as a standard substratum for sampling periphytic algae inside each enclosure. This native plant dominated the submerged macrophyte community, and we observed algae growing on submerged stalks of *Equisetum* in the open water area of the wetland. We suspended eight stems (10 cm-length segments) attached to paper clips that could be repositioned to maintain a consistent depth of 5 cm below the water surface inside each enclosure. We allowed algae to colonize on stems inside enclosures with stabilized experimental pH levels for 24 days (4–28 July 2007). Stems

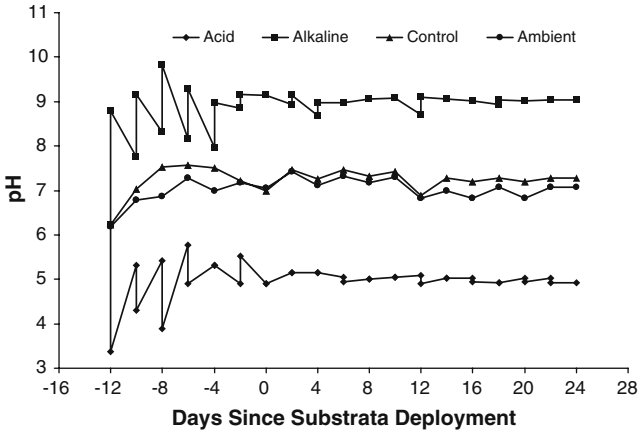

Fig. 1 Mean pH levels during the stabilization period before algal substrata were deployed and during substrata deployment in the acid, alkaline, and control treatment enclosures and in the surrounding water (ambient). Days with two data points connected with a line in acid and alkaline treatments indicate pH levels before and after acid and base additions, respectively. Points are means of four replicates

remained sturdy during the colonization period without noticeable differences in texture among stems removed from different treatment enclosures.

We monitored changes in water depth inside each enclosure with a meter stick, and measured temperature and pH every four days using a calibrated model 556 YSI® Multi-Probe. After 24 days, we measured light transparency as photosynthetic active radiation (PAR) (μmol quanta $m^{-2}s^{-1}$) using a LI-COR quantum sensor (LI-COR, Lincoln, NE, U.S.A). We filtered water directly from enclosures using a 0.45 μm syringe-driven filter unit and collected two unfiltered water samples for nutrient analysis in 125-ml acid-rinsed polyethylene bottles. To evaluate container effects, we designated four sampling sites within the open wetland (ambient) and measured physical and chemical parameters following methods described for treatment enclosures. Water samples were stored on ice until returning to the lab, where a portion of each filtered sample was analyzed for dissolved inorganic carbon (DIC) with a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.). The remaining nutrient samples were frozen and stored until analysis. We analyzed water samples for NO_3 + NO_2-N (NO_x) 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 method using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, U.K.). Alkalinity was measured following standard methods (APHA 1998). To determine total P (TP) and total N (TN) concentrations, particulate matter in water samples was oxidized with persulfate; then SRP was analyzed following the ascorbic

acid method and NO_x was analyzed following the second derivative UV spectroscopy method (APHA 1998).

Following 24 days of exposure to stabilized experimental pH levels, we randomly selected four *Equisetum* stems from each enclosure and pooled them to produce one replicate for measurements of algal accumulation. Stems were carefully removed from enclosures using forceps, brushed clean with a toothbrush, and rinsed thoroughly with filtered water into a 120 ml sample bottle for subsequent analyses. We filtered a known volume of each homogenate onto a glass fiber filter (Whatman GF/F) and stored filters frozen in the dark for chlorophyll *a* analysis. We later measured chlorophyll *a* using a TD-700 fluorometer (Turner Designs, Sunnyvale, CA, U.S.A.) after extraction with 90% ethanol and corrected for phaeophytin (APHA 1998). We preserved a separate aliquot with 2.5% formalin for algal compositional analysis and ash-free dry mass (AFDM). We determined AFDM following standard methods (APHA 1998). We dried samples at 105°C for 48–72 h and then ashed them at 500°C for 1 h in pre-weighed aluminum pans to measure dry mass and ashed mass, respectively. We later identified and counted between 300 and 500 algal cells or colonies per preserved sample using a Palmer-Maloney nanoplankton counter chamber at 400× magnification with taxonomy following Prescott (1962) and Komárek and Anagnostidis (1998, 2005). For diatom compositional analysis, we acid-cleaned an aliquot of each sample and mounted cleaned diatoms to a microslide using NAPHRAX® mounting medium. We identified and enumerated diatom valves at 1000× magnification following Kramer and Lange-Bertalot (1986, 1988, 1991a, b). Cell volume ($\mu m^3 cm^{-2}$) for each genus was determined by inserting average dimensions into geometric formulae from Hillebrand et al. (1999). We calculated the cell density (cells cm^{-2}) for each genus, and then calculated total biovolume by multiplying cell density by estimated cell volume.

Data Analyses

All statistical analyses were done with SYSTAT (version 11.0; SYSTAT, Evanston, IL, U.S.A.). 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. We used one-way analysis of variance (ANOVA) to evaluate differences in environmental conditions (water depth, temperature, PAR, alkalinity, nutrients) and algal parameters among treatment enclosures. Our analyses of algal parameters included chlorophyll *a*, AFDM, cell density, total cell biovolume, taxa richness, and the proportion of the 11 most common genera to determine if changed experimental conditions led to changes in algal biomass and taxonomic structure. We used Bonferroni corrections for multiple comparisons to preserve the experiment-wise Type I error rate of $p=0.05$. In instances when ANOVA indicated significant differences among treatments, we used a Tukey's test to calculate which treatments were significantly different.

Results

Water depth and temperature varied over time during each experiment, but did not differ significantly among treatments (ANOVA, $p>0.05$). After exposure to 24 days of experimental pH levels, alkalinity (ANOVA, $F_{2,9}=4278.5$, $p<0.0001$) and DIC ($F_{2,9}=8309.5$, $p<0.0001$) were significantly lower in the acid treatment compared to the alkaline and control treatments (Table 1). Photosynthetic active radiation was approximately 10% greater in the acid treatment and 23% less in the alkaline treatment compared to the control, but differences were not statistically significant (Table 1). Concentrations of DIN, TP, SRP, and SiO_2 were more than two-fold greater in the alkaline treatment compared to the acid and control treatments (Table 1), but differences were not statistically significant ($p>0.05$). All physical and chemical variables were similar between the control treatment and ambient conditions in the wetland without treatment enclosures ($p>0.05$).

Mean chlorophyll *a* concentration ($F_{2,9}=6.4$, $p=0.0185$), g AFDM ($F_{2,9}=14.4$, $p=0.0016$), and total biovolume ($F_{2,9}=5.5$, $p=0.0270$) were significantly greater in the alkaline treatment compared to the acid and control treatments (Fig. 2). Algal cell density was significantly greater in the alkaline treatment compared to the control ($F_{2,9}=4.5$, $p=0.0441$), but not significantly different compared to the acid treatment (Fig. 2). All measures of algal accrual were similar between the acid and control treatments ($p>0.05$). Taxa richness was significantly lower in the acid treatment (mean 16.00±1.08) compared to the alkaline (mean 21.00± 1.68) and control (mean 20.25±0.63) treatments ($F_{2,9}=5.0$, $p=0.0353$; Fig. 3).

Cyanobacteria, green algae (Chlorophyta), and euglenoids (Euglenophyta) comprised approximately 32, 28, and 38%, respectively, of the total cell density in the control treatment (Fig. 4). Cyanobacteria comprised approximately 68% and 63% of the total cell density in alkaline and acid treatments, respectively, and euglenoids represented less than 15% in each treatment (Fig. 4). Differences in the proportion of algal groups were not statistically different among treatments (ANOVA, Bonferroni adjusted: $p_{significant}<0.013$), but there were significant shifts at the genus level (Bonferroni adjusted: $p_{significant}<0.005$). The relative abundance of a diatom *Achnanthidium* (mainly *A. minutissimum* (Kützing) Czarnecki) ($F_{2,9}=9.4$, $p=0.0043$) was significantly greater, and *Anabaena* (Cyanobacteria) ($F_{2,9}=17.9$, $p=0.0007$), *Gloeocystis* (Chlorophyta) ($F_{2,9}=10.1$, $p=$

Table 1 Mean values (±S.E.) of photosynthetic active radiation (PAR), alkalinity, dissolved inorganic carbon (DIC), total nitrogen (TN), dissolved inorganic nitrogen (DIN), total phosphorus (TP), soluble reactive phosphorus (SRP), and dissolved silica (Si) in acid (pH=5), alkaline (pH=9), and control (pH=7.2) treatments and ambient conditions

Variable	Units	Acid	Alkaline	Control	Ambient
Photosynthetic active radiation (PAR)	μmol m^{-2} s^{-1}	200.6 (23.14)	143.29 (38.67)	185.12 (27.12)	177.12 (22.23)
Alkalinity	mg L^{-1}	0.50 (0.28) [a]	202.0 (4.0) [b]	197.5 (6.1) [b]	194.3 (7.7) [b]
Dissolved inorganic carbon (DIC)	mg L^{-1}	2.25 (0.32) [a]	49.11 (0.27) [b]	49.65 (0.22) [b]	49.57 (0.19) [b]
Total nitrogen (TN)	mg L^{-1}	1.13 (0.15)	1.57 (0.27)	1.61 (0.23)	1.11 (0.06)
Dissolved inorganic nitrogen (DIN)	μg L^{-1}	5.38 (3.20)	9.93 (1.10)	1.93 (0.90)	3.57 (2.94)
Total phosphorus (TP)	μg L^{-1}	22.03 (4.79)	47.82 (12.74)	27.19 (4.94)	26.16 (4.62)
Soluble reactive phosphorus (SRP)	μg L^{-1}	3.60 (1.55)	7.03 (2.43)	2.13 (1.39)	3.31 (2.50)
Dissolved silica (SiO_2)	mg L^{-1}	5.21 (3.18)	10.56 (1.35)	4.52 (0.96)	11.81 (0.52)

n=4 for all values. Different letters indicate significant differences (ANOVA, $p<0.05$, Tukey's test $p<0.05$) within each parameter among the treatments and ambient conditions

0.0043) and *Euglena* (Euglenophyta) ($F_{2,9}$=11.7, p=0.0032) were significantly lower in the acid treatment compared to the control treatment (Table 2). In the alkaline treatment, the relative abundance of *Nitzschia* (mainly *N. linearis* W. Smith) ($F_{2,9}$=16.0, p=0.0011) and *Chroococcus* (Cyanobacteria) ($F_{2,9}$=10.0, p=0.0041) were significantly greater, and *Limnothrix* (Cyanobacteria) ($F_{2,9}$=10.8, p=0.0046) and *Euglena* ($F_{2,9}$=10.2, p=0.0041) were significantly lower compared to the control treatment (Table 2).

Euglenoids represented the greatest percentage of total biovolume among treatment enclosures, comprising approximately 63, 62, and 79% in alkaline, acid and control

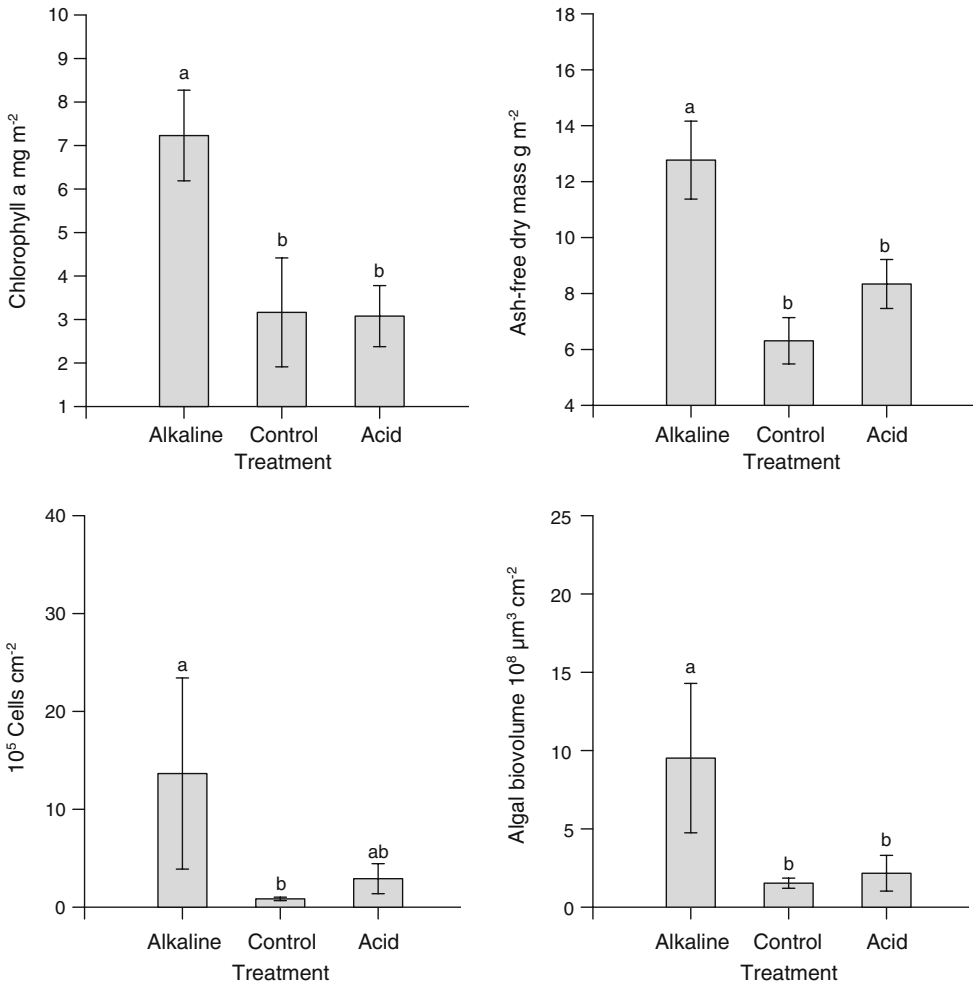

Fig. 2 Comparison of mean chlorophyll *a* concentration, ash-free dry mass, algal cell abundance and biovolume among the control (pH=7.2) and pH manipulated enclosures (Acid: pH=5.0; Alkaline: pH=9.0). Bars are means of four replicates ±S.E. Bars with the same letters are not significantly different (ANOVA, $p<0.05$, Tukey's test $p<0.05$)

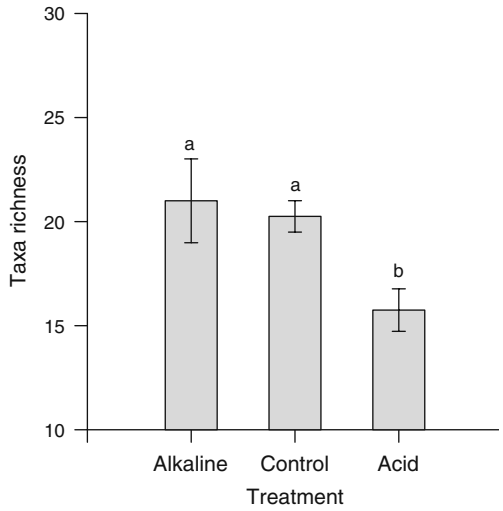

Fig. 3 Mean taxa richness from substrata exposed for 24 days in pH-manipulated enclosures (Acid: pH=5.0; Control: pH=7.2; Alkaline: pH=9.0). Bars are means of four replicates ±S.E. Bars with the same letters are not significantly different (ANOVA, $p<0.05$, Tukey's test $p<0.05$)

treatments, respectively (Fig. 4). The proportion of algal groups was similar among treatments (Bonferroni adjusted: $p_{significant}<0.013$), but there were significant differences at the genus level (Bonferroni adjusted: $p_{significant}<0.005$). The

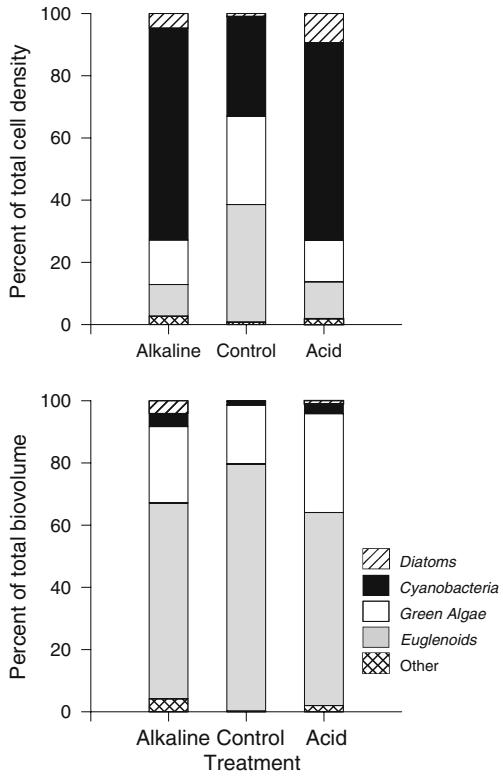

Fig. 4 The structure of main algal groups on substrata exposed for 24 days in the control treatment (pH=7.2) and pH-manipulated enclosures (Acid: pH=5.0; Alkaline: pH=9.0)

relative biovolume of *Nitzschia* ($F_{2,9}$=18.1, p=0.0007) and *Trachelomonas* (Euglenophyta) ($F_{2,9}$=17.7, p=0.0014) were significantly greater, and *Euglena* ($F_{2,9}$=14.8, p=0.0026) was significantly lower in the alkaline treatment compared to the control treatment (Table 2). In the acid treatment, the relative biovolume of *Mougeotia* (Chlorophyta, Zygnemataceae) was significantly greater ($F_{2,9}$=13.3, p=0.0021), and *Anabaena* was significantly lower ($F_{2,9}$=17.8, p=0.0007) compared to the control treatment (Table 2).

Discussion

As predicted from survey data of other wetlands (Pan and Stevenson 1996; Stevenson et al. 1999; Negro et al. 2003) and experimental evidence from lakes (Turner et al. 1987, 1991), changes in pH levels resulted in changes in the taxonomic structure of periphytic algae in a northern boreal wetland. Contrary to our expectations, algal biomass did not increase following acidification, which commonly occurs in lakes when pH levels are decreased from above 6 to less than 5 (Müller 1980). In addition to low DIC levels in the acid treatment, concentrations of N and P were extremely low and may have limited the growth of some acidophilic algal species.

An increase in algal accrual in the alkaline treatment may have been due, in part, to the increase in nutrient concentrations that occurred at pH 9. In a concurrent study, we documented a significant increase in overall algal biomass following N and P additions to mesocosms during the summer growing season (Wyatt et al. 2010). Similar increases in nutrient levels, particularly P, have been related to an increase in algal biomass following liming to neutralize acidic lakes (Olem 1991). Phosphorus enrichment is often attributed to reduced P precipitation by aluminum (Almer et al. 1978), increased phosphatase activity (Olsson 1983), or an increase in sediment respiration, which can release organic substances to the overlying water column (Wright 1985). This release may have led to the reduction in light transparency that we observed in the water column of the alkaline treatment (e.g., Hörnström 1999).

We anticipated a decrease in taxa richness in the acid treatment, as similar reductions have been reported in lakes influenced by acid precipitation or experimental acidification (Schindler et al. 1985; Turner et al. 1991). In a similar mesocosm study, Greenwood and Lowe (2006) reported a significant decrease in taxa richness following experimental acidification of a peatland in northern Michigan. Although they did not directly measure physiological stressors associated with low pH conditions, they hypothesized that factors such as reduced bicarbonate availability may have been responsible for the loss of algal taxa following acidification. The 20%

Table 2 Percent of total cell density and total biovolume of genera with >5% relative abundance in acid (pH=5), alkaline (pH=9), and control (pH=7.2) treatments. Values in bold indicate statistical significance compared to the control (ANOVA, Bonferroni adjusted: $p_{significant}<0.005$, Tukey's test, $p<0.05$)

Taxon and taxonomic groups	Percent of total cell density			Percent of total biovolume		
	Alkaline	Control	Acid	Alkaline	Control	Acid
Bacillariophyceae						
Achnanthidium	0.19	0.19	7.99	0.01	0.02	0.27
Nitzschia	5.43	0.70	1.06	4.09	0.20	0.75
Cyanobacteria						
Anabaena	3.38	5.03	1.21	1.28	0.60	0.06
Aphanocapsa	5.06	6.60	8.42	0.03	0.19	0.04
Cyanosarcina	8.63	0.28	11.63	0.99	0.11	1.02
Chroococcus	41.29	7.74	22.74	8.20	0.48	3.45
Limnothrix	0.55	6.23	19.08	0.04	0.13	0.99
Chlorophyta						
Gloeocystis	8.68	16.11	1.89	9.24	5.36	1.53
Mougeotia	1.79	10.68	8.73	6.91	12.91	25.81
Euglenophyta						
Euglena	2.80	33.42	8.61	20.17	75.42	47.43
Trachelomonas	8.01	4.39	3.13	42.78	4.01	14.63
Other	14.19	8.63	5.51	6.26	0.57	4.02

reduction in taxa richness that we observed in the acid treatment, which coincided with lower DIC concentrations, supports their hypothesis and suggests that acidification may lead to a significant loss of algal taxa in boreal wetlands.

With respect to biovolume, euglenoids dominated algal assemblages at both ends of the pH range. Although euglenoids are often important members of the periphyton community in shallow, isolated aquatic habitats (Rosowski 2003), their occurrence or ecology in wetlands is not well understood. The presence of euglenoids in both acid and alkaline conditions in our study verifies reports in the literature that the group has a wide pH tolerance (Olaveson and Nalewajko 2000). Although *Euglena* was reduced in the acid treatment, it was not surprising that it existed in conditions of pH 5, as some taxa are considered indicators of acidification in regions receiving acid mine drainage (Lackey 1968). From an autecological perspective, the shift from *Euglena* to *Trachelomonas* in the alkaline treatment is particularly interesting as it is among the first reports of a preference for alkaline conditions for any of the euglenoid taxa.

The increase in biovolume of *Mougeotia* in the acid treatment was similar to those reported in lakes (Schindler et al. 1985; Jackson et al. 1990) and wetlands (Greenwood and Lowe 2006) following acid inputs. In addition to having a low pH optimum (i.e., Müller 1980), an increase of *Mougeotia* is often attributed to a competitive advantage for the uptake of DIC (Jackson et al. 1990; Turner et al. 1991; Graham et al. 1996), which generally decreases along with pH due to the transformation of bicarbonate to carbon dioxide (Stumm and Morgan 1996). Although it is likely that a combination of environmental factors were responsible for the increase of *Mougeotia* following acidification, including low DIC (e.g., Klug and Fischer 2000), its decrease in abundance at pH 9 highlights the importance of pH independent of inorganic carbon concentration.

The diatoms are among the best documented algal groups with regard to changes in pH. High relative abundances of certain diatom species have been reported at very low pH (van Dam and Mertens 1995), and acid-tolerant taxa are widely used as indicators of acidification in paleolimnological studies of lakes (Smol et al. 1986; Fritz et al. 1990). The diatom response to pH in our study was more muted than expected. As a group, the diatoms maintained relatively low cell numbers in all treatments and comprised a small component of total algal biomass. This finding was surprising considering that SiO_2 levels were an order of magnitude greater than those known to be growth limiting for diatoms in plankton studies of lakes (Hecky and Kilham 1988). *Achnanthidium* (mainly *A. minutissimum*), which increased in abundance in the acid treatment, has been widely reported in other benthic habitats with low pH (DeNicola 2000) and may be an important indicator of acid conditions for wetlands in this region. In contrast, the increase of *Nitzschia* (mainly *N. linearis*) in the alkaline treatment may have been driven more by an increase in nutrient concentration than an increase in pH, as it is commonly reported in wetlands with high nutrient content (see review in Browder et al. 1994) and it was a dominate taxon in a concurrent nutrient enrichment study (Wyatt et al. 2010).

Cyanobacteria comprised a large portion of total cell density in all treatments, but many of the taxa were small

(<127 μm^3), so they did not make up a significant component of the total biomass in any treatment. Following an extensive survey of lakes and rivers of different pH, Brock (1973) reported a tolerance limit for cyanobacteria of about pH 4.8. Their presence in the acid treatment appears to challenge the hypothesis that acidification is detrimental to cyanobacteria. Lazarek (1982) reported a similar finding in lakes with a pH between 4.3 and 4.7, and Stevenson et al. (1985) did not find a strong correlation between the presence of Oscillatoriaceae and pH in their study of 20 lakes with a pH range between 4.5 and 7.3. We observed a significant reduction of *Anabaena* in the acid treatment, similar to those reported by Turner et al. (1987, 1991) following lake acidification. Given the importance of N-fixing cyanobacteria for N cycling in wetlands with low N concentrations (Inglett et al. 2004), a reduction of *Anabaena* following acid inputs in boreal wetlands could have important implications for biogeochemical cycling in this region.

Much of the wetland landscape the interior region of Alaska serves as important freshwater habitat for endemic flora and fauna, including summer nursery and stopover habitat for migrating waterfowl (Sedinger 1997). Although the quantitative significance of algae as a food source has not been established for northern boreal wetlands, its potential importance is evident from the analysis of gut contents of common invertebrates from other wetland ecosystems (Browder et al. 1994). From a management standpoint, alteration of the proportions and biomass of algal assemblages with changes in pH levels may have important implications for the wetland food web because algal taxa differ in their relative utilization by consumers (Lamberti and Moore 1984). Shifts in the composition of algal communities to include more filamentous green algae following acidification may impact secondary production, as they are considered inedible for many grazers (Robinson et al. 2000). Further studies that clarify major pathways of energy flow and grazing rates and preferences of aquatic herbivores are needed to determine the significance of taxonomic shifts in the algal assemblage to trophic dynamics in boreal wetlands.

This study of an Alaskan marsh adds to a growing pool of literature showing the effects of pH disturbance on aquatic ecosystems globally (Sullivan 2000), and contributes to a small number of empirical studies of pH effects on algal community ecology in wetlands (e.g., van Dam et al. 1981; Greenwood and Lowe 2006). While wetland algal communities are generally highly diverse and heterogeneous under pristine conditions (Goldsborough and Robinson 1996), trends observed in our study indicate that changes associated with acidification may reduce algal diversity in boreal wetlands. On the other hand, alkalization may significantly alter algal community structure and loosen nutrient restraints on wetland algal productivity. Together, these findings suggest that changes at either end of the pH spectrum could have significant effects on algal dynamics in boreal wetland ecosystems, which will likely affect carbon cycling in interior Alaska as well. Relatively small changes in the functioning of these boreal wetlands could have large scale effects on ecosystem processes in Alaska, owing to the extensive coverage of wetland ecosystems in this region. While we did find significant experimental effects with our short-term mesocosm experiment, a larger scale study with a longer colonization period would better predict the effects of pH on algal communities in boreal wetlands. We suggest that future research focusing on how both acidification and alkalization affects algal community structure and productivity in a variety of boreal wetland types is necessary to understand consequences of altered pH for the functioning of these aquatic systems.

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