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The effects of pH on a periphyton community in an acidic wetland, USA

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Abstract

Despite the importance of peatlands, the algal ecology of peatlands and the periphyton communities which are abundant in these habitats are relatively understudied. We performed an *in situ* manipulation of pH in an intermediate fen in northern lower Michigan in order to examine how hydrogen ion concentrations structure an epiphytic algal community. Levels of pH were manipulated in enclosures from the control level (pH = 5) to an acid treatment (pH = 4) by adding H_2SO_4 and a neutral treatment (pH = 7) by adding NaOH. Algal communities growing on sections of *Chamaedaphne calyculata* (L.) Moench stems were examined after 22 days of colonization. Chlorophyll *a* concentration was significantly greater only in the acid treatment (~5.5 mg m^{-2}) relative to the control (~3.5 mg m^{-2}). Taxa richness was lower in the acid treatment. The algal assemblages were dominated by filamentous green algae and a filamentous taxon, *Mougeotia* spp., was significantly greater in the acid treatment relative to the control. Increases in Zygnemataceae and *Oedogonium* spp. most likely account for the higher chlorophyll *a* in the acid treatment. Most treatment differences were detected in the neutral treatment, including increased abundances of *Closterium polystichum* Nygaard, *Cosmarium* sp., *Peridinium inconspicuum* Lemmermann, and *Synedra acus* Kütz. Unexpectedly, there was no strong response of the desmid community. These data can be informative in the development of algal monitoring programs in peatlands when assessment of acidification is desired.

Introduction

Peat-storing wetlands are important freshwater habitats. They are widely distributed, provide important habitats for often endemic flora and fauna and are in danger of destruction due to human uses, such as drainage for agriculture or excavation of peat (Parkyn et al., 1997; Charman, 2002). Benthic algal ecology in peatlands is drastically understudied compared to other aquatic systems such as lakes, streams, rivers, and non-peat-forming wetlands (Stevenson et al., 1996). Peatlands are physically and chemically unusual habitats, often with low pH levels and low nutrient and ion concentrations (Crum, 1988; Vitt, 2000). This unique chemistry results in a distinctive algal flora. In-depth descriptions of the unique and highly diverse algal assemblages from peatlands have been the topic of several floristic investigations describing patterns of species distribution and, often, correlations with physical variables (e.g., Flensburg & Malmer, 1970; Kingston, 1982a; Yung et al., 1986; Mataloni, 1999; Poulícková et al., 2004). There have been a few paleolimnological investigations of algal communities in peatlands to reconstruct the developmental history of a particular aquatic ecosystem (Kingston, 1982b; Rühland et al., 2000).

However, *in situ* experimental manipulations to study the mechanisms governing the distribution and composition of algal communities in peatlands are rare or non-existant. As the importance of using algae as biomonitors in wetlands increases (Stevenson et al., 2002), understanding the mechanisms driving algal community structure in peatlands also becomes more important.

An abiotic factor important in the classification of peatlands is pH (Crum, 1988; Vitt, 2000). However, the role of pH in structuring periphyton communities has rarely been examined explicitly in peatlands (but see van Dam et al., 1981; Bellemakers & van Dam, 1992). In recent years, examinations of the effect of pH on aquatic systems or algal communities have mostly addressed the effects of anthropogenic acidification of surface waters (see Planas, 1996 for a review). In contrast with peatland habitats, community changes of algal flora due to acidification have been extensively documented in lakes (Yan, 1979; Turner et al., 1987; Kingston et al., 1990; Turner et al., 1991) and streams (van Dam & Mertens, 1995; Verb & Vis, 2000).

Effects of acidification on algal communities have shown some general trends. Acidification often results in decreased species richness (e.g., Müller, 1980; Schindler et al., 1985; Turner et al., 1991). Also, acidification experiments in lakes often result in an increase in filamentous green algae in the family Zygnemataceae, especially the genera *Mougeotia*, *Spirogyra*, and *Zygogonium* (e.g., Turner et al., 1995a; Turner et al., 1995b). This increase has been attributed to an increased competitive advantage associated with decreased dissolved inorganic carbon at lower pH (Jackson et al., 1990; Klug & Fischer, 2000) or to a suppression of herbivores (Turner et al., 1987; Barmuta et al., 1990; Fairchild & Sherman, 1992). Generally, total algal biomass has been reported to increase in response to acidification (Müller, 1980), usually due to the blooms of filamentous green algae.

In the opposite direction on the pH spectrum, alkalinization (or neutralization) in lakes has also been examined. Neutralization is generally conducted as a process to mitigate impacts by recent anthropogenic acidification, generally by liming (Hultberg & Andersson, 1982; Fairchild & Sherman, 1990; Olem, 1991; Renberg & Hultberg, 1992; Hörnström, 2002). Neutralization can often reverse the changes in the algal community which resulted from acidification, again, particularly in the filamentous green algae. For example, several neutralization studies have found that *Mougeotia* is drastically reduced when pH is neutralized via liming from about pH 5 (Hultberg & Andersson, 1982; Jackson et al., 1990; Fairchild & Sherman, 1992).

In contrast to the applied research on the effects of anthropogenic acidification in lentic systems, empirical research on how algal communities respond to effects of pH levels in peatlands has not been thoroughly examined. This experiment was designed to examine the response of a peatland algal community to a range of pH regimes, increased and decreased from ambient levels. The changes in periphyton algal assemblages resulting from variation in pH were examined in enclosures in Waldron Fen, an acidic peatland in northern lower Michigan. We hypothesized that increasing acidity would increase algal biomass due to increased filamentous green algal abundance, and would result in a decrease in species richness and a shift toward more acidophilic or acidobiontic species, especially desmids or acidophilic diatoms. We also hypothesized that neutralization would result in an increase in taxa richness and a decrease in algal biomass due to decreases in filamentous green algae.

Materials and methods

Study site

Waldron Fen is located in northern lower Michigan (Fig. 1) approximately 17 km northeast of Petoskey (45°23′ N, 84°46′ W). This wetland is an "intermediate fen" (Crum, 1988) where minerals and nutrients are scarce, and the open water has a pH of approximately 5. The common vascular plant flora is indicative of fen-type peat-storing wetlands. *Chamaedaphne calyculata* (L.) Moench and the sedge, *Carex lasiocarpa* Ehrh. are dominant species within the *Sphagnum* lawn which surrounds the pond of open water. Other vascular plants such as *Vaccinium* spp., *Sarracenia purpurea* L., *Drosera* spp., and *Dulichium arundinaceum* (L.)

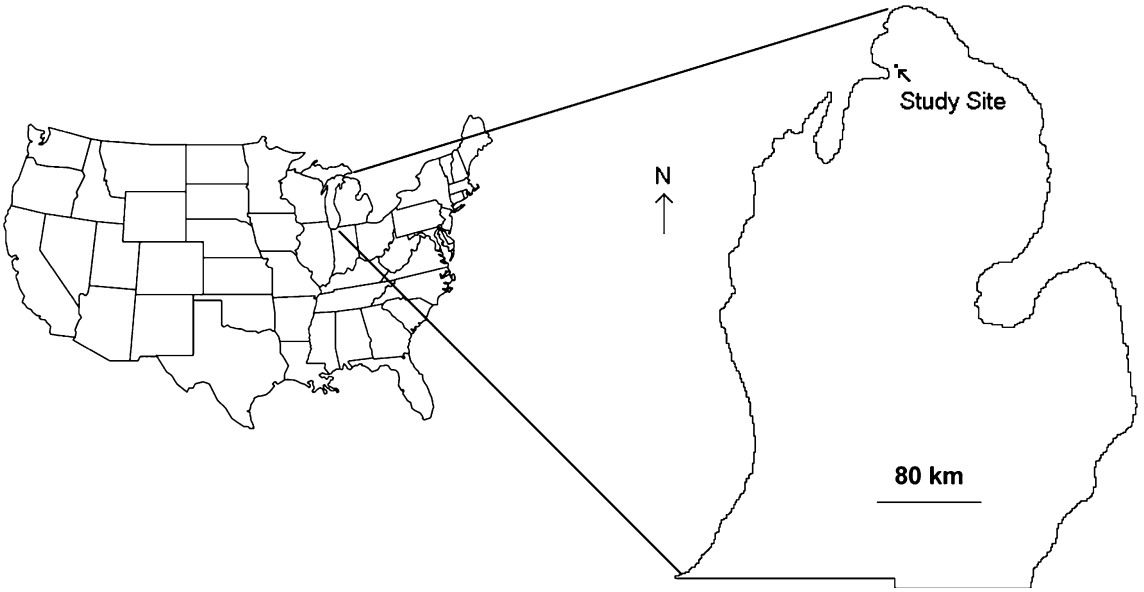

Figure 1. Map of location of study site.

Britton are also present. Experiments were performed in an open water area of the fen. Here, phytoplankton densities were very low, and the dominant substrata for periphyton were *Nymphaea odorata* Aiton and *Nuphar variegate* Durand stems and underleaves, and submerged stems of *C. calyculata* dominated the margin of the open water.

pH manipulation

Hydrogen ion concentration was manipulated in open-ended cylindrical enclosures which were embedded in the bottom of the fen (Fig. 2). Enclosures were constructed from welded wire fabric, 30 cm in diameter and 1.5 m tall. The top 1.1 m of the inside of the enclosures was lined with 4-mil (approximately 0.1 mm thick) window vinyl which was glued at the seams and attached to the wire fabric with clear silicone sealant. Enclosures were embedded approximately 20 cm into the sediment. Approximately 20 cm of the bottom of the enclosure remained open to the environment between the bottom of the vinyl lining and the sediment surface after enclosures were deployed in the fen. This allowed some interaction with the natural environment, while maintaining experimental pH levels. Flocculent sediment filled the first 70 cm of enclosure, with about 50 cm of transparent water above the flock. Approximately 10 cm of the enclosure extended above the water surface.

Three pH treatments: pH = 4, pH = 7 and the control, pH = 5, with four replicates each, were established. Enclosures were placed in areas of the fen that had similar depths, currents, and distance from the margin of the fen. About 5 ml of 2.5% solutions of H_2SO_4 (for the pH = 4 treatment) and NaOH (for the pH = 7 treatment) were required to initially change the pH within the enclosures. The pH of each enclosure was checked every 2–3 days with a Corning Model 6 portable pH meter and adjusted as needed with enough 2.5% H_2SO_4 or 2.5% NaOH to maintain experimental pH levels. Water in the enclosure was stirred 10 times with a meter stick after dosing or at each visit if additional acid or base was not added. Algal substrata were deployed (see below) after pH within the enclosures stabilized. Macro-herbivores were not observed in the enclosures during the experiment.

Chamaedaphne calyculata stems were employed as a standard substratum for sampling periphyton. This ericaceous shrub dominated the margin of the open water, and stems that were submerged often had thick growths of green algae. The other potential natural algal substrata to use from the open water area of the fen, *Nymphaea* or *Nuphar* plants,

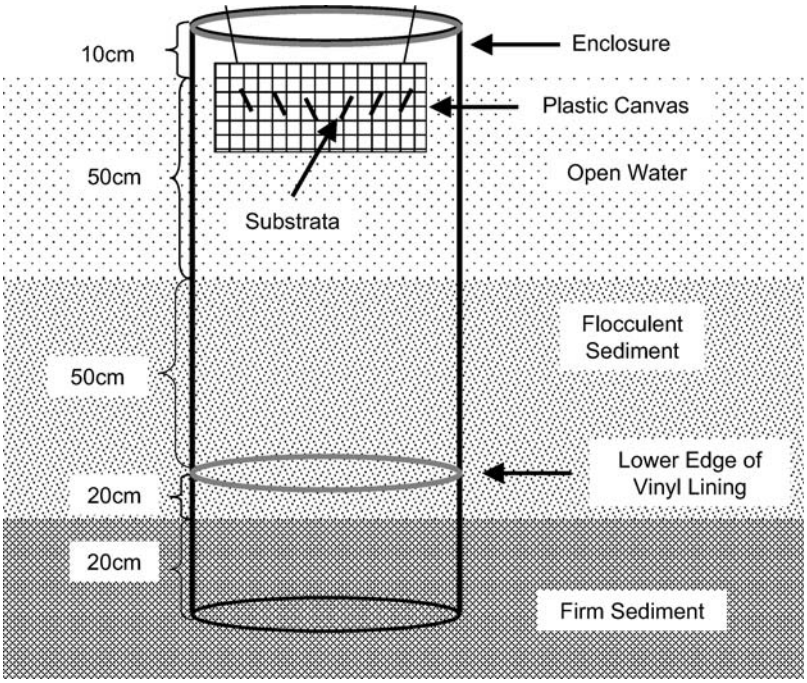

Figure 2. Enclosures used in pH manipulation (not to scale).

would have decomposed more quickly than *Chamaedaphne* stems, potentially confounding experimental effects. The *Chamaedaphne* stems were also smooth and sturdy, providing a replicable yet natural substratum for algal colonization. Aerial *Chamaedaphne* stems (i.e., stems were not previously submerged and did not have periphyton growth) 4–6 mm in diameter were removed from live plants and cut into approximately 10 cm length segments. Sheets of 55×30 cm plastic canvas positioned vertically inside the enclosure on the northern side (to maximize direct sun exposure and minimize light interference from the vinyl lining) were used to stabilize the horizontal position of the stems by inserting one end of the stem into an opening in the canvas, allowing the stem to extend horizontally toward the center of the enclosure at more or less a right angle to the sheet of canvas. The plastic canvas was tied to the enclosure with strings and could be repositioned within the enclosure to maintain a consistent depth of the substrata of 5 cm from the surface. Algae were allowed to colonize for 22 days (July 28–August 19, 1996). A longer colonization period was infeasible for logistical reasons. Of ten stems deployed, three randomly selected stems were harvested for sampling from each enclosure and pooled to produce one replicate.

All samples were processed on 19 August 1996. *Chamaedaphne* stems were brushed clean with a toothbrush and rinsed thoroughly with deionized water. The resulting algal slurry (usually 50–100 ml) was homogenized with a tissue miser. For chlorophyll *a* analysis, between 20–50 ml of algal slurry was filtered through a Millipore 0.45 μm filter, filters were sonicated in 90% acetone buffered with magnesium carbonate for 10 min, then extracted in a dark freezer for 24 h. The pigment concentration was measured on a Turner 10-000R fluorometer and corrected for phaeophytin (APHA, 1998). For algal community analysis, 20 ml were preserved in 2.5% formalin and samples were analyzed by counting at least 500 cells or colonies per sample in a Palmer-Maloney nannoplankton counting chamber. Algal cells were identified to the lowest taxonomic level possible at 400$\times$ using Prescott (1962), Patrick & Reimer (1966, 1975), and Prescott et al. (1975–1983).

Calcium (Ca), Soluble reactive phosphorus (SRP), nitrate-nitrogen (NO_3–N) ammonia nitrogen (NH_3–N) and silica (SiO_2) were measured in all enclosures and in 4 areas in the open water on 8

August 1996. Concentrations were determined with a Technicon® II Autoanalyzer (APHA, 1998).

Differences among treatments in nutrients, chlorophyll *a*, taxa richness and absolute abundances of taxa were determined with ANOVA, and multiple comparisons were performed with a Tukey test with JMP (Release 5.0.1a, SAS Institute, Inc., 2002). All non-nutrient data were log-transformed prior to analysis. Below detection values for nutrients were considered zeroes during analysis. Only taxa and groups of taxa that were > 5% relative abundance were included in the analysis. The Bonferroni procedure was used in algal assemblage analysis to preserve the experimentwise Type I error rate of $p = 0.05$ (Ott & Longnecker, 2001).

Results

Enclosures were deployed for 21 days to allow pH levels to stabilize before adding the algal substrata (Fig. 3). For the acid treatment, an average of 3 ml of H_2SO_4 were required to initially decrease the pH to 4, with pH maintenance requiring an additional 0.5 ml every 2–3 days. For the neutral treatment, an average of 6 ml of NaOH were required to initially raise the pH to or above 7, with maintenance requiring an additional 3 ml every 2–3 days for the first 10 days of enclosure deployment. During the algal colonization period, approximately 0.5 ml of NaOH were added on the 3rd and 19th day to maintain pH = 7.

Mineral and nutrient concentrations were relatively low in all samples (Table 1). Concentrations of Ca, SRP, NH_3–N and SiO_2 were significantly different between ambient condition, control and treatments (Table 1) (ANOVA Ca: $p = 0.02$; SRP: $p < 0.0001$; NH_3–N: $p = 0.0003$, SiO_2: $p = 0.03$). NO_3–N was not detected in any of the enclosures or in the ambient water column.

Mean chlorophyll *a* levels were approximately double in the acid treatment compared to the control (ANOVA, $p = 0.05$, Fig. 4). Chlorophyll *a* concentration in the neutral treatment was not significantly different from the acid or control treatment. The average taxa richness was significantly lower in the acid treatment compared to the neutral treatment (ANOVA, $p = 0.03$, Fig. 5). The total number of taxa identified (47 for all treatments) in composited treatment samples was lower in the acid treatment (27 taxa identified) compared with the neutral (35 taxa) and control (32 taxa) treatments.

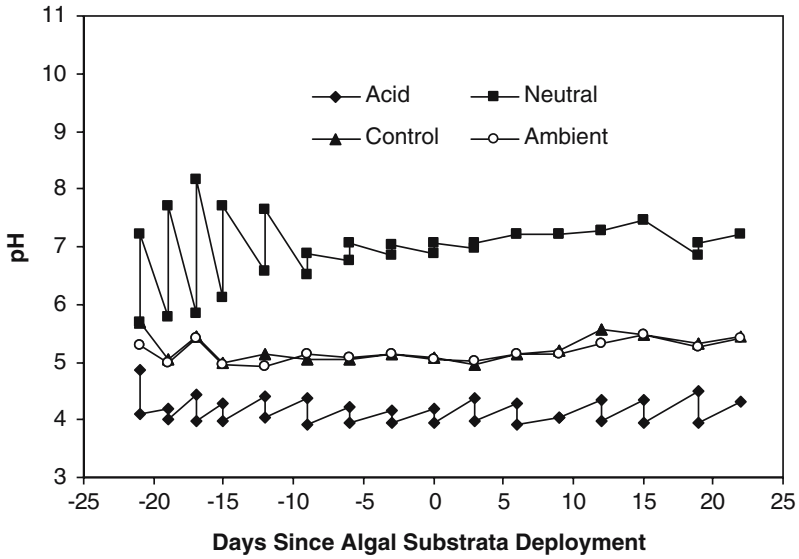

Figure 3. Average pH levels in enclosures during the stabilization period before algal substrata were deployed and during algal substrata deployment in the acid, control, and neutral treatment enclosures and in the surrounding water (ambient). For each data point, $n = 4$.

Table 1. Average concentrations and range of concentrations (in parentheses) of calcium (Ca), soluble reactive phosphorus (SRP), nitrate-nitrogen (NO_3–N) ammonia nitrogen (NH_4–N) and silica (SiO_2) in the open water of Waldron Fen (Ambient) and in the experimental enclosures on 8 Aug 1996

	Ca (mg l^{-1})	SRP (μg l^{-1})	NO_3–N (μg l^{-1})	NH_3–N (μg l^{-1})	SiO_2 (μg l^{-1})
Ambient	2.25 A (2.0–3.0)	2.6 A (2.0–3.2)	bd (bd)	25 A (20–30)	bd A (bd)
Acid	2.26 A (0.05–3)	bd B (bd)	bd(bd)	bd B (bd)	60 B (bd-130)
Control	1.51 AB (0.05–2)	2.45 A (2–2.6)	bd (bd)	bd B (bd-23)	Bd A(bd)
Neutral	0.05 B (0.05–0.05)	3.8 C (3.2–4.4)	bd (bd)	bd B (bd)	bd A (bd)

bd = below detection and $n = 4$ for all values. Capital letters indicate significant differences (ANOVA $p < 0.05$, Tukey $p < 0.05$) within each mineral or nutrient among the treatments and ambient concentrations.

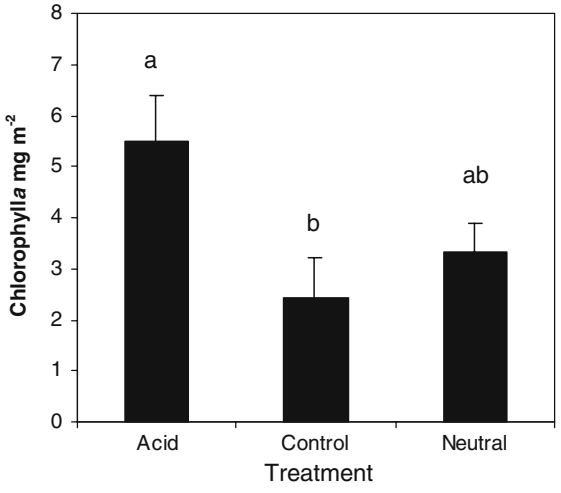

Figure 4. Mean (± 1 standard error) chlorophyll *a* concentration (mg m^{-2} of substratum) from substrata in pH-manipulated enclosures in Waldron Fen (Acid: pH = 4.0; Control: pH = 5.2; Neutral: pH = 7.0). Significant difference indicated by different letters (ANOVA, $p = 0.05$, Tukey $p < 0.05$). For each treatment, $n = 4$.

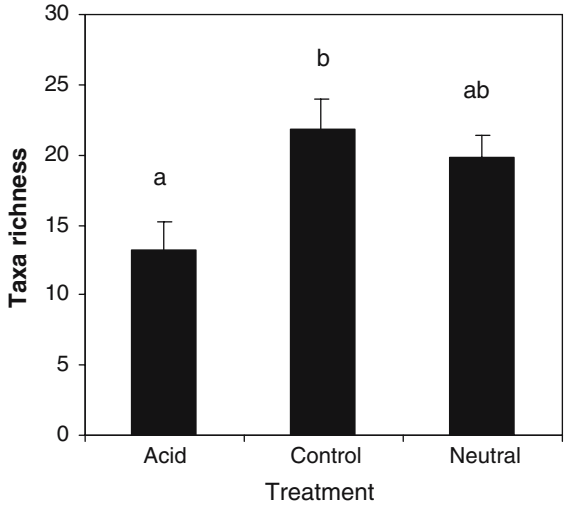

Figure 5. Mean taxa richness (± 1 standard error) from substrata exposed for three weeks in pH-manipulated enclosures in Waldron Fen (Acid: pH = 4.0; Control: pH = 5.2; Neutral: pH = 7.0). Significant differences indicated by different letters above bars (ANOVA, $p < 0.05$, Tukey $p < 0.05$). For each treatment, $n = 4$.

There were no significant differences in total algal abundance between treatments, although total abundance tended to be higher in the acid treatment (Fig. 6, ANOVA $p > 0.05$). Responses of taxa to the treatments were analyzed only in individual taxa or groups of taxa (Cyanobacteria, dinoflagellates, diatoms, chrysophytes, Chlorococcales, Oedogoniales, Zygnematales, unicellular desmids, and filamentous desmids) that had greater than 5% relative abundance in any one replicate (Table 2). There were no significant differences in absolute abundances of the total number of cells for any of the groups of algae (Fig. 7). The only species that was more abundant in the acid treatment relative to the control was *Mougeotia* sp.3 (ANOVA $p = 0.005$, Fig. 8a). There were significantly lower cell densities in the acid treatment of the species *Closterium polystichum* Nygaard (ANOVA $p = 0.002$, Fig. 8b), *Cosmarium* sp.1 (ANOVA $p < 0.001$, Fig. 8c), *Peridinium inconspicuum* Lemmermann (ANOVA $p = 0.0009$, Fig. 8d), and *Synedra acus* Kützing (ANOVA $p = 0.0005$, Fig. 8e).

Discussion

This study is one of the first to examine the effects of acidification and neutralization simultaneously in periphyton from a peatland. Changes in pH

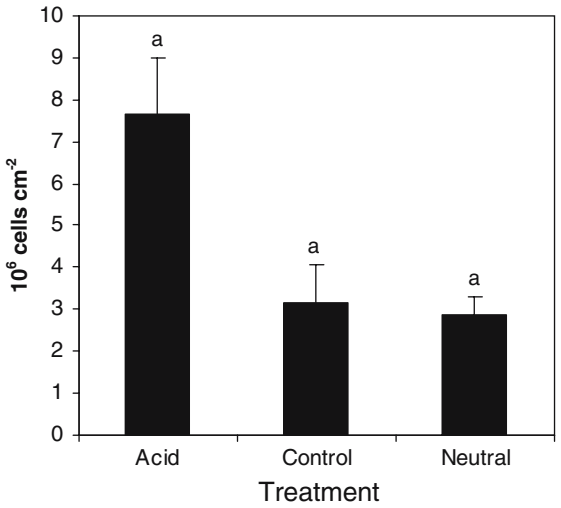

Figure 6. Total abundance (± 1 standard error) in cells cm^{-2} of substratum from substrata exposed for 22 days in pH-manipulated enclosures in Waldron Fen (Acid: pH = 4.0; Control: pH = 5.2; Neutral: pH = 7.0). There were no significant differences within groups among the treatments (ANOVA $p > 0.05$). For each treatment, $n = 4$.

resulted in significant changes in the biomass and species composition of an attached algal community. The increase in biomass as chlorophyll *a* may have been due to increases in some filamentous green algae in the acid treatment, particularly *Mougeotia* spp. (Fig. 8a) and *Oedogonium* spp. (Fig. 7). *Mougeotia* spp. is consistently found to increase in response to acidification in many lake studies (Turner et al., 1987; Klug & Fischer, 2000), so the increase in *Mougeotia* in our study is not surprising. The results from our measures of abundance were likely more conservative than biovolume measurements would have been since a large proportion of cell densities were composed of high biovolume taxa, i.e. filaments. Also, algal assemblage data from peatlands are relatively unavailable; we are unaware of published biomass data for periphyton from peatlands.

The lower taxa richness in the acid treatment was also anticipated (Fig. 5). A pH of 4.0 is a physically stressful habitat for many taxa due to

Table 2. Average cell density of taxa and taxon groups with > 5% relative abundance

Cells cm^{-2}	Acid	Control	Neutral
Filamentous Desmids	1345167	1107313	182040
Bambusina brebissonii Kütz.	374967	82694	18595
Desmidium baileyi (Ralfs) Norstedt	329074	962389	163446
Desmidium grevellii (Kütz) De Bary	465242	45964	0
Hyalotheca dissilens (Smith) Bréb. ex Ralfs	175884	16266	0
Unicellular Desmids	49058	179513	558570
**Closterium polystichum* Nygaard	0	38715	159056
**Cosmarium* sp.1	0	14850	165532
Staurastrum sp.6	22695	73562	96560
Zygnemataceae	1540524	172541	243830
Mougeotia sp.2	1114885	163332	159556
**Mougeotia* sp.3	165852	0	13323
Spirogyra sp.	226738	9209	69682
Oedogoniales	4372764	1545725	1449259
Oedogonium sp.2	921640	1388052	302752
Oedogonium sp.3	3309282	112864	1146507
Diatoms	35856	79589	207023
**Synedra acus* Kütz.	0	6795	188940
Chrysophytes	131716	44563	7614
Dinobryon sp.	70207	40913	6345
Dinoflagellates	12452	1808	144129
**Peridinium inconspicuum* Lemm.	0	1808	137097

*$p < 0.05$, ANOVA in enclosures from the acid, control and neutral treatments.

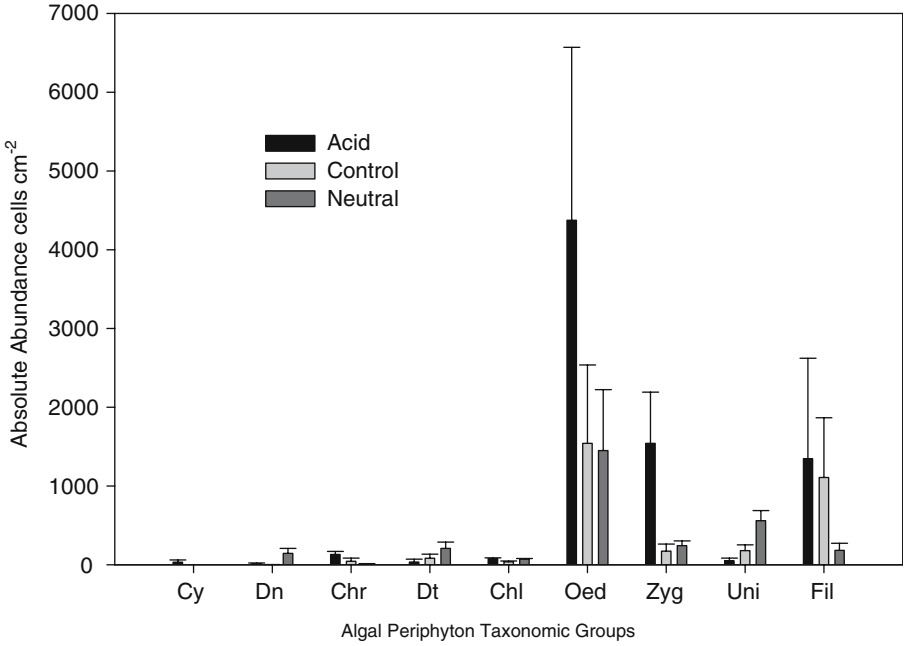

Figure 7. Mean absolute abundance (±1 standard error) of Cyanobacteria (Cy), dinoflagellates (Dn), chrysophytes (Chr), Chlorococcales (Chl), Oedogoniales (Oed), Zygnematales (Zyg), unicellular desmids (Uni), and filamentous desmids (Fil) in cells cm^{-2} of substratum from substrata exposed for 22 days in pH-manipulated enclosures in Waldron Fen (Acid: pH = 4.0; Control: pH = 5.2; Neutral: pH = 7.0). There were no significant differences within groups among the treatments (ANOVA $p > 0.05$). For each treatment, $n = 4$.

such factors as increased metal toxicity or reduced bicarbonate availability, an important source of carbon for algae. Also, phosphorus concentrations were lower in the acid treatment, potentially affecting taxa richness. Further, lower taxa richness may have resulted from the dominance of filamentous green algae (Zygnemataceae, Oedogoniales, and desmids) in the acid treatment. This may create a situation where encountering new taxa during identification will be less likely since the counts will be saturated by the dominant filaments. There were no increases or appearances of known acidophilic or acidobiontic species (i.e., diatoms).

Effects on individual algal species seemed strongest in the neutral treatment. *Peridinium inconspicuum* showed an increase in cell density with increasing pH (Fig. 8d) which is contrary to findings in previous acidification studies (Dixit & Smol, 1989; Hörnström, 1999). Also, Yan (1979) considered this taxon indicative of acidic lakes if it constituted a large part of the phytoplankton (evidence from Canada and Sweden). Further, Hultberg & Andersson (1982) found a decrease in *P. inconspicuum* in the plankton from limed lakes in Sweden. Perhaps the changes in *P. inconspicuum* are not a result of pH preferences. This taxon may be indifferent and/or tolerant of low pH levels, and may be able to exploit niches left open by pH-sensitive taxa that were eliminated during acidification or neutralization. However, *P. inconspicuum* was part of the periphyton (i.e., not plankton) in this study. It is not clear if this taxon is tychoplanktonic or if perhaps it was physiologically stressed in the neutral treatment during the experiment and settled onto the substrata. Also, the lack of current in the enclosures may have reduced the suspension of cells, increasing settling onto the substrata. However, plankton samples were depauperate of algal cells, making comparisons between planktonic and periphytic community composition difficult.

Diatoms were relatively rare and no well documented acidophilic or acidobiontic diatoms species appeared in the acid treatment. This is not surprising considering that SiO_2 levels were below detection, except in the acid treatment, and potentially limiting to diatom growth (Table 1). The higher concentrations of silica

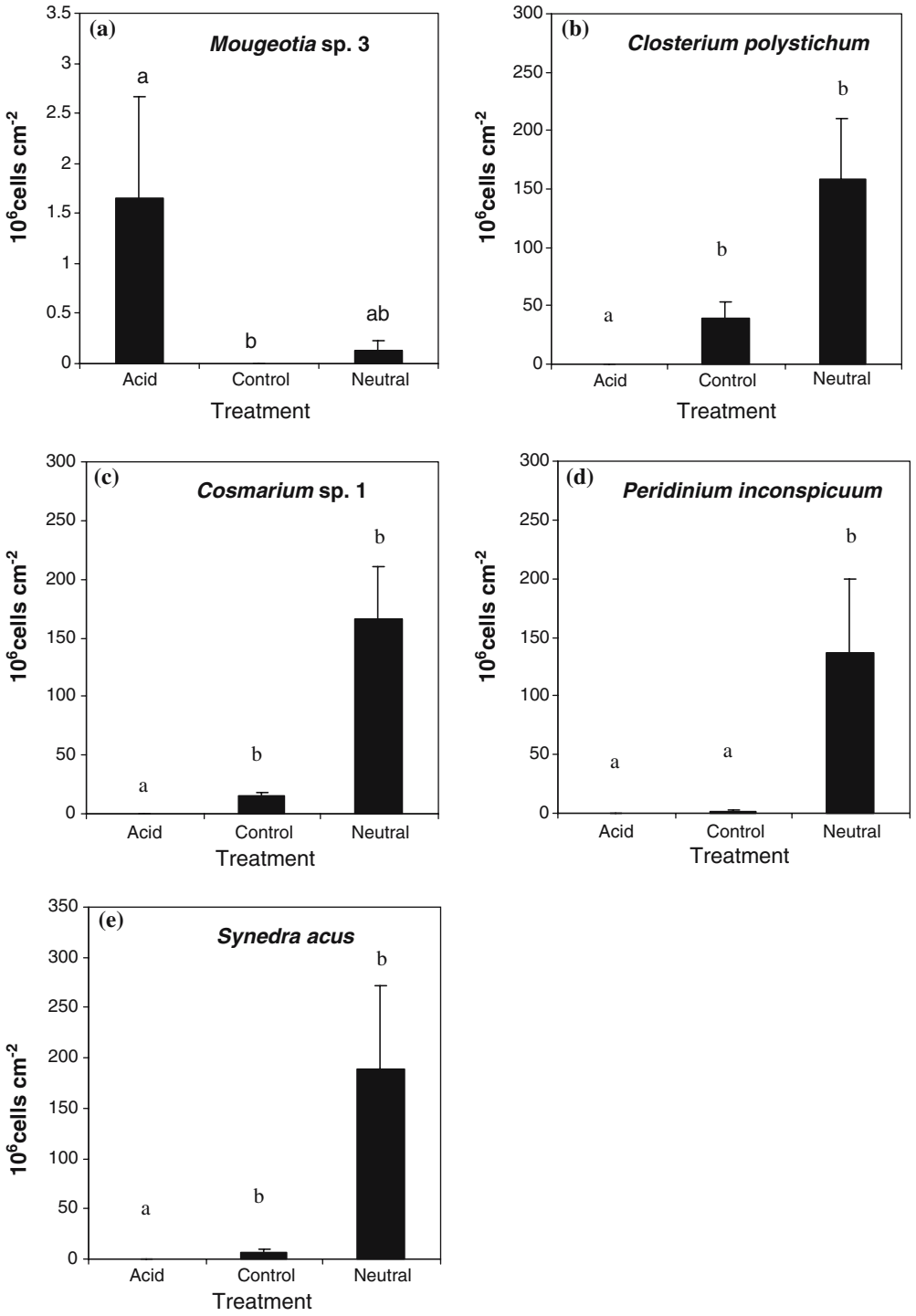

Figure 8. Mean absolute abundance (±1 standard error) in cells cm^{-2} of substratum of the taxa *Mougeotia* sp. 3 (a), *Closterium polystichum* (b), *Cosmarium* sp. 1 (c), *Peridinium inconspicuum* (d), and *Synedra acus* (e) with significant differences between absolute abundances of taxa. Samples were from substrata exposed for three weeks in pH-manipulated enclosures in Waldron Fen (Acid: pH = 4.0; Control: pH = 5.2; Neutral: pH = 7.0). Significant difference indicated by different letters above bars (ANOVA, $p < 0.05$, Tukey $p < 0.05$). For each treatment, $n = 4$.

observed in the acid treatment, however, did not result in increases in diatoms, although chryophyte levels tended to be higher. Another consideration is that diatoms may have grown better under a lower light environment relative to the enclosures (Hill, 1996). However, in a related study of shade effects on algal communities in the fen, decreased light intensities did not result in increases in diatoms (Greenwood, 1998). In our study, there was an increase in *Synedra acus* (Fig. 8e) in the neutral treatment which corroborates previous findings. Renberg and Hultberg (1992) found an increase in *S. acus* in lakes in Sweden that had been limed with $CaCO_3$ to a pH of 7.5. This taxon is also considered planktonic and, like *P. inconspicuum*, reasons for its presence on experimental substrata are unceratain.

Desmids, as a group, show the highest diversity in acidic, low-nutrient habitats (Brook, 1981; Coesel, 1981; Coesel, 1982). In this study, filamentous desmids did show a trend of lower cell density with increasing pH. However, densities of 2 unicellular desmids, *Closterium polystichum* (Fig. 8b), and *Cosmarium* sp. 1 (Fig. 8c) were significantly higher in the neutral treatment. Even though there are species which are found in higher nutrient environments (Gerrath, 2003), it is interesting that there was not more of a decrease in unicellular desmid cell density with neutralization. There was a non-significant decrease in filamentous desmids with neutralization, including the complete disappearance of *Desmidium grevellii* and *Hyalotheca dissilens*. However the overall response of desmids to changes in pH were relatively more muted than expected. Potentially, the length of the experiment was insufficient for the algal community to fully respond to changes in pH. Response from the desmids and other algae may have been more robust with a longer colonization period. However, our results do suggest that periphyton community structure can change with changes in pH.

Conclusion

We successfully changed attached algal assemblages with *in situ* manipulations of pH. Many of our results were consistent with findings from acidification and acidification mitigation studies, with higher algal biomass measured as chlorophyll *a* and filamentous green algal cell density and lower taxa richness with decreasing pH. Cell densities of taxa usually considered acidophilic were lower in response to neutralization. These data could potentially be informative in the development of algal monitoring programs in peatlands when assessment of acidification is desired. With our short-term, small scale experiment, we did see significant experimental effects, however, a longer-term, larger scale study would better predict the effects of pH change on periphytic algal communities in a peatland.

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