This is to certify that the
dissertation entitled

ENVIRONMENTAL CONTROLS ON ALGAL COMMUNITY
STRUCTURE AND FUNCTION IN BOREAL WETLANDS

presented by

Kevin Howard Wyatt

has been accepted towards fulfillment
of the requirements for the

Ph.D. degree in Zoology and Ecology, Evolutionary Biology and Behavior

R. Jan Stevenson

Major Professor's Signature

November 19, 2010

ENVIRONMENTAL CONTROLS ON ALGAL COMMUNITY STRUCTURE AND FUNCTION IN BOREAL WETLANDS

By

Kevin Howard Wyatt

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Zoology
Ecology, Evolutionary Biology, and Behavior

2010

ABSTRACT

ENVIRONMENTAL CONTROLS ON ALGAL COMMUNITY STRUCTURE AND FUNCTION IN BOREAL WETLANDS

By

Kevin Howard Wyatt

Compared to lakes and streams, we know relatively little about algal ecology in freshwater wetlands. This discrepancy is particularly acute in boreal regions, where wetlands are abundant and processes related to climate change are expected to alter the hydrology, pH and nutrient concentrations of aquatic ecosystems.

To evaluate how accelerated nutrient inputs might affect algal structure and function in boreal wetlands, I enriched mesocosms in an Alaskan marsh with all possible combinations of nitrogen (N), phosphorus (P) and silica (Si). Algal growth was not stimulated following enrichment with any nutrient alone or with P and Si together, but increased significantly with the addition of N in any combination with P and Si. Water column concentration of dissolved organic carbon (DOC) increased linearly with algal biomass. The wetland algal community shifted from one dominated by *Euglena* and *Mougeotia* to small coccoid taxa (*Chroococcus* and *Gloeocystis*) and *Nitzschia* inside N-combination treatments. This study provides several lines of evidence for co-limitation, and the central importance of N as a co-limiting nutrient for the wetland algal community. Changes in algal dynamics with increased nutrient concentrations could have important implications for wetland food webs, and suggests that algae may provide a link between increasing nutrient inputs and altered wetland C cycling in this region.

In chapter 3, I examined the response of an algal community to a wide range of pH levels, both decreased and increased from ambient conditions in an Alaskan marsh.

Alkalinization resulted in an increase in the concentrations of inorganic nutrients and a significant increase in algal growth. There were distinct shifts in euglenoid taxa in the alkaline treatment, including an increase of *Trachelomonas* and a 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 C. Trends observed in this study indicate that alkalization may significantly alter algal community structure and loosen nutrient constraints on algal productivity, while acidification may reduce algal diversity in boreal wetlands.

In the final chapter, I monitored algal responses to a water table manipulation in an Alaskan fen to evaluate how changes in hydrology might affect C cycling and energy flow in boreal peatlands. I measured consistently higher algal productivity at sites exposed to seasonal drying than in ambient or flooded conditions. Approximately 18% of the C fixed by algae during photosynthesis was released into the overlying water column as DOC. At this rate, algae were contributing more than 6.84 mg DOC L^{-1} h^{-1} to the water column during peak productivity in the drought treatment. Approximately 25% of the algal exudates were carbohydrates, about 38% of which was glucose. I examined the biodegradability of algal exudates and found they were extremely labile, decreasing by more than 55% within the first 24 hours of incubation. Bacterial growth increased rapidly in the presence of algal exudates. These findings show that algae have the potential to contribute a significant amount of labile C to boreal peatlands, and may become increasingly important for energy flow in these ecosystems if seasonal drying trends become more frequent with future climate change.

ACKNOWLEDGEMENTS

I would like to thank my advisors, R. J. Stevenson and M. R. Turetsky for their direction and support of my dissertation work. Thank you to my dissertation guidance committee members, E. Litchman and D. W. Hyndman for valuable comments to the manuscripts. Thank you to E. Kane and D. Giroldo for assistance with the development of research hypotheses and methodology. Thank you to the faculty and staff at the University of Alaska-Fairbanks and the Bonanza Creek LTER, especially J. B. Jones. Thank you also to members of the Stevenson and Turetsky labs for help with fieldwork, labwork and logistics. I thank friends and family for their support. Most of all, I thank my wife, Allison, for your support and for the hundreds of hours we spent together in mosquito-filled wetlands in Alaska.

This research was supported by the College of Natural Science, Department of Zoology, Ecology Evolutionary Biology and Behavior Program and the Graduate School at Michigan State University, and Sigma Xi, Phycological Society of America, North American Benthological Society and the Wetland Foundation.

TABLE OF CONTENTS

LIST OF TABLES v

LIST OF FIGURES vi

CHAPTER 1
INTRODUCTION 1
    1.0 Wetland ecosystems 1
    1.1 Algal ecology in freshwater wetlands 2
    1.2 Environmental regulation of algae in wetlands: biomass, composition and function 4
    1.3 Potential anthropogenic disturbance and climate change effects 6
    1.4 Experimental manipulations to study wetland response to climate change 9

CHAPTER 2
THE IMPORTANCE OF NUTRIENT CO-LIMITATION IN REGULATING ALGAL COMMUNITY COMPOSITION, PRODUCTIVITY, AND ALGAL-DERIVED DOC IN AN OLIGOTROPHIC MARSH IN INTERIOR ALASKA19
    2.1 Introduction 19
    2.2 Methods 22
    2.3 Results 28
    2.4 Discussion 33

CHAPTER 3
EFFECTS OF ACIDIFICATION AND ALKALINIZATION ON A PERIPHYTIC ALGAL COMMUNITY IN AN ALASKAN WETLAND 56
    3.1 Introduction 56
    3.2 Methods 59
    3.3 Results 64
    3.4 Discussion 67

CHAPTER 4
LEGACY EFFECTS OF SEASONAL DRYING STIMULATE ALGAL PRODUCTIVITY FOLLOWING SPRING FLOODING IN AN ALASKAN PEATLAND: IMPLICATIONS FOR CARBON CYCLING IN THE BOREAL FOREST 86
    4.1 Introduction 86
    4.2 Methods 88
    4.3 Results 97
    4.4 Discussion 100

CHAPTER 5
CONCLUSION 121

LIST OF TABLES

Table 2.1 Comparison of nutrient data from freshwater habitats within the boreal region of western North America........39

Table 2.2 Mean (± S.E.) dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and silicate concentrations measured at open wetland sites and the control treatment (mesocosms without nutrient enrichment) measured every four days between June and July during each experiment, 2007 and 2008........40

Table 3.1 Mean values (± S.E.) of photosynthetically 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........73

Table 3.2 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........74

Table 4.1 Mean values (± 1 S.E.) of water table height, temperature, pH, dissolved oxygen (DO), dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and dissolved silica (SiO_2^-) in control, lowered and raised treatments.........107

Table 4.2 Bacterial degradation of the exudates released by algae measured by HPLC-PAD. The decay coefficients are shown for each monosaccharide, which compose the algal carbohydrate pool, and also for the total carbohydrates........108

Table 4.3 Carbohydrate composition (%) determined by HPLC-PAD of the polysaccharide released by algae and pore water collected from the APEX fen........109

LIST OF FIGURES

Figure 2.1 Dissolved inorganic N ($NO_3 + NO_2$-N), phosphate-P and silicate-Si concentrations among treatment enclosures following each nutrient addition during the 2007 experiment 41

Figure 2.2 Dissolved inorganic N ($NO_3 + NO_2$-N), phosphate-P and silicate-Si concentrations among treatment enclosures following each nutrient addition during the 2008 experiment 42

Figure 2.3 Comparison of mean chlorophyll-*a* concentration and g ash-free dry mass among treatment enclosures and the open wetland in 2007 and 2008 43

Figure 2.4 Comparison of mean total biovolume $\mu m^3\ cm^{-2}$ among treatment enclosures and the open wetland in 2007 and 2008 44

Figure 2.5 Comparison of algal N:P ratios among treatment enclosures and the open wetland in 2007 and 2008 45

Figure 2.6 Comparison of algal primary productivity mg C $m^{-2}\ h^{-1}$ among treatment enclosures and the open wetland in 2008 46

Figure 2.7 Comparison of water column dissolved organic carbon (DOC) mg L^{-1} among treatment enclosures and the open wetland in 2007 and 2008 47

Figure 2.8 Linear regression analysis between log (x+1) Chlorophyll-*a* mg m^{-2} and water column dissolved organic carbon (DOC) mg L^{-1} across all treatment enclosures and the open wetland in 2007 and 2008 48

Figure 2.9 Percent of total biovolume of dominant algal genera in the open wetland and treatment enclosures following 24 days of enrichment in 2007 and 2008 49

Figure 3.1 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 75

Figure 3.2 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) 76

Figure 3.3 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) 77

Figure 3.4 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) 78

Figure 4.1 Long term seasonal trends in water table heights across the control, lowered and raised water table treatments in interior, Alaska (negative values indicate water table position below the surface of the peat). Insert figure shows standard deviation in mean monthly water table position across the five years of study (total of 1938 individual water table measurements).............................. 110

Figure 4.2 Surface water temperature, pH, dissolved oxygen concentration (mg L^{-1}), dissolved organic carbon concentration (mg L^{-1}), soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) concentrations among the control, lowered and raised water table treatments on each sampling date in the APEX fen during the summer growing season in 2009 111

Figure 4.3 Mean algal primary productivity (mg C m^{-2} h^{-1}), ash-free dry mass and chlorophyll-*a* concentration in the control, lowered and raised water table plots on each sampling date in the APEX fen during the summer growing season in 2009 112

Figure 4.4 Linear regression analysis between gross primary productivity (mg C L^{-1} h^{-1}) and dissolved organic carbon concentration (mg C L^{-1} h^{-1}) during productivity measurements on 20 June 2007 (n = 24) 113

Figure 4.5 Dissolved organic carbon concentration (mg L^{-1}), specific UV-Vis absorption at $\lambda = 254$ nm of L mg C^{-1} m^{-1} and bacterial growth (10^6 cells mL^{-1}) in cultures set up with pore water from the APEX fen or from algal exudates during the incubation period (768 h).............................. 114

CHAPTER 1

INTRODUCTION

1.0 Wetland ecosystems

Wetlands are unique freshwater ecosystems that are defined by their hydrology, vegetation and soil characteristics. They are typically shallow, with the water table at or near the surface for at least some time during the growing season each year (Cowardin et al. 1979). Wetlands are characterized by vegetation able to withstand frequent, and sometimes persistent, fluctuations in water table and anoxic conditions associated with poorly drained soils. Wetlands occur on every continent except Antarctica and consist of a diversity of marshes, swamps, peatlands (bogs and fens) and coastal wetlands (Mitsch and Gosselink 2006). Collectively, wetlands comprise only about 6% of the Earth's surface, but their ecological importance is much greater than their surface area might suggest. The unique abiotic and biotic characteristics of wetlands provide many valuable ecosystem services including nutrient capture and retention (Mitsch and Gosselink 2006), carbon cycling and sequestration (Gorham 1991) and important habitat for often endemic flora and fauna, particularly waterfowl (Sedinger 1997).

1.1 Algal ecology in freshwater wetlands

Algae are abundant in wetlands and are a significant link in the physical, chemical and biological processes that characterize wetland ecosystems (Goldsborough and Robinson 1996, Wetzel 2006). The dynamic and shallow nature of wetland ecosystems provides a variety of substrates for algal growth (Ewe et al. 2006). The main growth form of algae in wetlands is periphytic or benthic algae, which are defined as those growing attached to, or loosely associated with, submersed substrata; the latter of which is often referred to as metaphyton, especially when it detaches from the bottom, or traps gases and forms a floating mat. In contrast to pelagic ecosystems, phytoplankton communities are often not well developed in wetlands, with the exception of those connected to large lakes, which serve as a source of plankton inocula (Goldsborough and Robinson 1996).

Algae typically have lower standing stocks of biomass compared to macrophytes in wetlands. However, since algal turnover rates are often measured in days rather than years, they can account for a significant amount of annual wetland primary production (Richardson 2009). In wetlands where sufficient light reaches the bottom, periphytic algae can account for more than half of the above ground biomass (see review in Goldsborough and Robinson 1996). When turnover rates are considered, annual rates of algal primary productivity can often surpass that of macrophytes in wetlands (Robinson et al. 2000).

Algae contribute significantly to the biogeochemical cycling within wetland environments. They can transform and regulate the fate of nutrients in wetlands and flowing through groundwaters by fixing atmospheric carbon and absorbing nutrients from the water column or leaking from plants and sediments (Burkholder 1996, Wetzel 1996).

Algae can directly contribute to nutrient cycling by "fixing" atmospheric nitrogen in low nitrogen conditions (Graham et al. 2009), or translocating nutrients from the water column to sediments where they can be taken up by plants. Algae attached to sediments can regulate nutrient cycling directly by assimilating nutrients and cycling them within the periphyton matrix (Kadlec 1986, Hansson 1989, Grimshaw et al. 1993), or indirectly, by oxygenating the sediment-water interface which can inhibit nutrient release into the water column (Carlton and Wetzel 1988).

Algal communities in wetlands are often diverse, and taxonomic diversity has important effects on ecosystem function because taxonomic groups of algae differ in their growth forms and ability to fix and store inorganic nutrients. For example, nitrogen fixation is limited to a few groups of cyanobacteria, including the family Nostocaceae which contain cells specialized for nitrogen fixation called heterocysts. Carbon production in cells and carbohydrates excreted into the overlying water column differs among algal groups (Graham et al. 2009), from starches in green algae and cyanobacteria to oils in diatoms (Giroldo and Vieira 2005). Thick mucilaginous cell walls occur in some growth forms, while spines are present in others (Graham et al. 2009). Carbon compounds produced by some algae are more labile for heterotrophic metabolism than others (Giroldo et al. 2005) and deviations in size structure associated with cell volume or filament size can affect ingestion and food quality for herbivores (Steinman 1996). Despite reviews stating the importance of algae for wetland ecology (Vymazal 1995, Goldsborough and Robinson 1996, Robinson et al. 2000, Richardson 2009), and known differences in algal functions related to taxonomic composition (Graham et al. 2009), there is little available information about the factors that regulate the distribution and abundance of algae in freshwater wetlands.

1.2 Environmental regulation of algae in wetlands: biomass, composition and function

Algal structure and function in wetlands is probably regulated by many of the same factors that are important in other aquatic ecosystems. Conceptual models attribute regional factors such as climate, geology and hydrology, coupled with local factors such as flood disturbance frequency, substrata type and size, water chemistry (especially pH and nutrient concentrations), canopy cover and light availability, and grazer density as strong influences on benthic algal structure and function. Much of our current understanding about these regulatory processes has been adapted from hypotheses generated in other aquatic ecosystems (Batzer et al. 2006).

Benthic algae are sensitive to changes in water quality, making nutrients an important factor regulating communities in freshwater habitats (Borchardt 1996). When nutrient conditions are low, nutrient deficiency can regulate algal growth or structure algal communities in favor of taxa tolerant of low nutrient conditions (McCormick et al. 1996, Pan et al. 2000). Nutrient enrichment can increase algal growth (McCormick et al. 1998), shift the taxonomic composition of algal communities (McCormick and O'Dell 1996) and change the chemical composition of algal tissue (Gaiser et al. 2006). In the Florida Everglades, for example, functional and structural changes in the benthic algal assemblage are correlated strongly with water column phosphorus (McCormick and

Stevenson 1998, McCormick et al. 2001). Enrichment with phosphorus leads to the loss of the naturally abundant calcium-precipitating cyanobacterial mats (McCormick et al. 2001, Gaiser et al. 2005, 2006), which play a unique role in the formation of marl sediments in the Everglades (Gleason and Spackman 1974). Other wetland studies, such as those conducted in southern Manitoba, Canada, have demonstrated the importance of both nitrogen and phosphorus in increasing benthic algal biomass (Murkin et al. 1994), or shifting a stable benthic algal community to one of metaphyton dominance (McDougal et al. 1997). Such changes can alter the habitat available for animals (Liston et al. 2008), the food quality for herbivores (Campeau et al. 1994) and the overall nutrient storage capacity of the wetland (Wu and Mitsch 1998).

The concentration of hydrogen ions is almost always considered among the most important factors regulating the distribution and diversity of algae in freshwater habitats (Wetzel 2001). An increase in hydrogen ion concentration can cause a decrease in the availability of dissolved inorganic carbon and increases in inorganic nitrogen concentrations (Planas 1996). Acidification often results in decreased species richness (e.g., Müller 1980, Turner et al. 1991) and an increase in biomass driven by aggregations of acidophilic algal species, particularly those in the family Zygnemataceae (e.g., Schindler et al. 1980, Turner et al. 1995a, b). However, laboratory investigations have demonstrated that several members of the Zygnemataceae can survive in extreme alkaline conditions (Graham et al. 1996, Arancibia-Avila et al. 2000), suggesting that this group may not be particularly acidophilic, but rather can tolerate both direct and indirect effects of reduced pH, including low concentrations of dissolved inorganic carbon (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.

Hydrology is perhaps the single most important factor regulating the establishment and maintenance of wetland ecosystems (Jackson 2006). Frequent water-level fluctuations is often considered the defining characteristic of wetland ecosystems and is responsible for regulating many of the physical and chemical conditions mentioned above, especially the movement of nutrients into and out of wetland ecosystems (Jonasson and Shaver 1999). Even small changes in depth can expose plant and animal communities to variations in nutrient concentrations, pH and dissolved gases which can induce significant changes in community metabolism (Browder et al. 1994, Kahn and Wetzel 1999, Gottlieb et al. 2005). Drought conditions can oxygenate anaerobic soils (Kadlec 1979, Schoenberg and Oliver 1988, Thomas et al. 2006), while re-inundation associated with seasonal flooding can reduce macrophyte abundance and release nutrients from dead vegetation and sediments, which often limit algal growth in the water column (Murkin 1989, Robinson et al. 2000).

1.3 Potential anthropogenic disturbance and climate change effects

Boreal regions cover a wide area (18.5 million km^2) that is distributed extensively throughout northern latitudes in Europe, Russia and North America (Gorham 1991, Kuhry and Turunen 2006, Vitt 2006). Globally, wetlands cover nearly a quarter of the boreal forest region (Vitt 2006, Wieder et al. 2006). In Alaska alone, wetlands make up more than 43 percent of the land area, which is approximately 60 percent of the total wetland area of the United States (Hall et al. 1994). Many of the wetlands serve as important freshwater habitat for endemic flora and fauna, including summer nursery and stopover habitat for migrating waterfowl (United States Fish and Wildlife Service 1985). Wetlands in boreal regions also serve as a global carbon reservoir (Gorham 1991). Currently, it is estimated that approximately 30% of the world's soil carbon is stored in boreal regions, mainly in poorly drained wetlands (Bridgham et al. 2006).

Climate models project that North American boreal regions will experience more warming than any other biome, with the greatest warming occurring in the continental interiors (National Research Council 2001). Interior Alaska is already experiencing large changes in climate including increases in surface annual temperatures (Serreze et al. 2000, Houghton et al. 2001, Hinzman et al. 2005, McGuire et al. 2007), increases in annual precipitation (Hinzman et al. 2005), longer growing seasons (Serreze et al. 2000, Goetz et al. 2005, Euskirchen et al. 2006) and altered snowpack dynamics (Dye 2002, Serreze et al. 2000).

Boreal wetlands are likely to be significantly altered by changes in climate because the average annual temperature of soils in this region, which constrain water at or near the surface, are close to that of the phase-change for water (Hinzman et al. 2006). Thus, even relatively small changes in temperature could have important implications for alternating freeze-thaw conditions (Boon 2006). In response to recent climatic change, the surface area of open water bodies within some wetland-rich landscapes in Alaska is expanding, likely due to permafrost thaw and increased runoff from surrounding uplands (Osterkamp et al. 2000). In other areas of Alaska, the surface area of open water is declining, likely due to increased summer moisture deficits and drainage related to permafrost thaw (Oechel et al. 2000, Yoshikawa and Hinzman 2003, Hinzman et al. 2005, Riordan et al. 2006). Increases in the extent of seasonal ice thaw and drought are predicted to increase microbial decomposition, which will probably promote nitrogen and phosphorus mineralization in the expanded active soil layer (Bridgham et al. 1995), as well as chemical weathering of parent rock material (Rouse et al. 1997). While regional variability of nutrient inputs may be significant, these changes are expected to have widespread impacts on nutrient concentrations of aquatic systems throughout the boreal forest (Rouse et al. 1997).

Disturbances associated with ongoing climate change (i.e., Rouse et al. 1997, Osterkamp et al. 2000, Hinzman et al. 2005), as well as human activities such as mining, peat excavation and fossil fuel combustion (i.e., Walker et al. 1987, Charman 2002, Hinzman et al. 2006), may also increase acid inputs into aquatic systems (Schindler 1998). In the interior of Alaska, 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). In a cool, wet climate, much of the anthropogenic emissions of sulfur oxides deposited by precipitation is reduced and stored as sulfur in the anoxic soils of wetland ecosystems (Schindler 1998). In future warmer, dryer conditions where wetland sediments are exposed to atmospheric oxygen, the stored sulfur is likely to reoxidize and result in the acidification of aquatic ecosystems throughout the boreal region (Schindler 1998).

1.4 Experimental manipulations to study wetland response to climate change

For my dissertation research, I studied wetlands located in the floodplain of the Tanana River just outside the boundaries of the Bonanza Creek Experimental Forest, situated approximately 35 km southeast of Fairbanks, Alaska. The Tanana River floodplain is located within an intermontane plateau characterized by wide alluvium-covered lowlands and underlain by discontinuous permafrost (Begét et al. 2006). Oxbows and thaw ponds dominate the floodplain landscape, and fluvial deposition and erosion are annual disturbance events. The area is classified as continental boreal, and experiences extremes in temperature (-50°C in January to +33°C in July), day length (more than 21 h on June 21 and less than 4 h on December 21), a short growing season (135 days or less from early May to mid-September) and minimum precipitation due to a montane rain shadow (Hinzman et al. 2006). The average precipitation is only 269 mm in Fairbanks, 30% of which falls as snow (Slaughter and Viereck 1986).

I evaluated the response of wetland algae to changes in nutrients, pH and hydrology expected with climate change, and I related algal responses to potential ecosystem functions associated with wetland carbon cycling. Chapter 2 of my dissertation describes the response of a wetland algal community to a two-year nutrient enrichment experiment. I measured changes in algal growth under different nutrient conditions and related changes in algal productivity associated with nutrient enrichment to water column dissolved organic carbon concentrations. Chapter 3 describes the response of a benthic algal community to a wide range of pH conditions in an *in situ* mesocosm experiment. In chapter 4, I monitored surface water chemistry and algal productivity in response to a water table manipulation in an Alaskan fen. Additionally, I estimated the amount of carbon that was released by algae into the water column as well as the chemical characteristics and biodegradability of algal exudates that may be transported to downstream ecosystems. Detailed hypotheses and predictions are described in sections 2.1, 3.1 and 4.1 of this dissertation. This is the first study to test hypotheses about the environmental factors that regulate the abundance and function of algae in Alaskan wetlands, and relates algal ecology to potential feedbacks on climate change processes through carbon cycling.

References

Arancibia-Avila, P., J. R. Coleman, W. A. Russin, L. W. Wilcox, J. M. Graham, and L. E. Graham. 2000. Effects of pH on cell morphology and carbonic anhydrase activity and localization in bloom-forming *Mougeotia* (Chlorophyta, Charophyceae). Canadian Journal of Botany 78: 1206–1214.

Batzer, D. P., R. Cooper, and S. A. Wissinger. 2006. Wetland animal ecology. p. 242–284. *In* D. P. Batzer and R. R. Sharitz (eds.) Ecology of Freshwater and Estuarine Wetlands. University of California Press, Los Angeles, CA, USA.

Begét, J. E., D. Stone, and D. L. Verbyla. 2006. Regional overview of interior Alaska. p. 12–20. *In* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Boon, P. I. 2006. Biogeochemistry and bacterial ecology of hydrologically dynamic wetlands. p. 115–176. *In* D. P. Batzer and R. R. Sharitz (eds.) Ecology of Freshwater and Estuarine Wetlands. University of California Press, Los Angeles, CA, USA.

Borchardt, M. A. 1996. Nutrients. p. 183–227. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Bridgham, S., D. Johnston, A. Carol, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience 45: 262–274.

Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. Trettin. 2006. The carbon balance of North American wetlands. Wetlands 26: 889–916.

Browder, J. A., P. J. Gleason, and D. R. Swift. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. p. 379–418. *In* S. M. Davis and J. C. Ogden (eds.) Everglades: The Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Burkholder, J. M. 1996. Interactions of Benthic Algae with Their Substrata. p. 253–297. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. Canadian Journal of Fisheries and Aquatic Science 51: 681–692.

Carlton, R. G. and R. G. Wetzel. 1988. Phosphorus flux from lake sediments: Effects of epipelic algal oxygen production. Limnology and Oceanography 33: 562–570.

Charman, D. 2002. Peatlands and environmental change. John Wiley, Sons, Inc., New York, USA.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. FWS/OBS-79/31, U.S. Fish and Wildlife Service, Washington, DC. p. 103.

Dye, D. G. 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972 – 2000. Hydrological Processes 16: 3065–3077.

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.

Ewe, S. M. L., E. E. Gaiser, D. L. Childers, D. Iwaniec, V. H. Rivera-Monroy, and R. R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. Hydrobiologia 569: 459–474.

Gaiser, E. E., J. C. Trexler, J. H. Richards, D. L. Childers, D. Lee, A. L. Edwards, L. J. Scinto, K. Jayachandran, G. B. Noe, and R. D. Jones. 2005. Cascading ecological effects of low level phosphorus enrichment in the Florida Everglades. Journal of Environmental Quality 34: 717–723.

Gaiser, E. E., D. L. Childers, R. D. Jones, J. H. Richards, L. J. Scinto, and J. C. Trexler. 2006. Periphyton responses to eutrophication in the Florida Everglades: cross-system patterns of structural and compositional change. Limnology and Oceanography 51: 617–630.

Giroldo, D. and A. A. H. Vieira. 2005. Polymeric and free sugars released by three phytoplanktonic species from a freshwater tropical eutrophic reservoir. Journal of Plankton Research 27: 695–705.

Giroldo, D., A. A. H. Vieira, and B. S. Paulsen. 2005. Microbial degradation of extracellular polysaccharides released by a tropical strain of Staurastrum orbiculare (Zygnematophyceae). Phycologia 44: 671–677.

Gleason, P. J., and W. Spackman. 1974. Calcareous periphyton and water chemistry in the Everglades. *In* P. J. Gleason (ed.) Environments of South Florida: present and past, memoir 2. Miami Geological Society, Miami, FL, USA.

Goetz, L. D., A. G. Bunn, G. J. Fiske, and R. A. Houghton. 2005. Satellite observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences 102(13): 521–525.

Goldsborough, L. G. and G. G. C. Robinson. 1996. Pattern in wetlands. p. 77–117. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Gorham, E. 1991. Northern peatlands: Role in the carbon-cycle and probable responses to climatic warming. Ecological Applications 1: 182–195.

Gottlieb, A., 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.

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, CA, USA.

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.

Grimshaw, H. J., M. Rosen, D. R. Swift, K. Rodberg, and J. M. Noel. 1993. Marsh phosphorus concentrations, phosphorus content and species composition of Everglades periphyton communities. Archiv für Hydrobiologie 128: 257–276.

Hansson, L. A. 1989. The influence of a periphytic biolayer on phosphorus exchange between substrate and water. Archiv für Hydrobiologie 115: 21–26.

Hall, J. V., W. E. Frayer, and B. O. Wilen. 1994. Status of Alaskan wetlands. U.S. Fish and Wildlife Service, Alaska Region, Anchorage, AK, USA.

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. p. 39–61. *In* F.S. Chapin, M.W. Oswood, K. Van Cleve, L.A. Viereck, and D.L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Houghton, J. T. Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu. 2001. Climate Change 2001: The scientific basis. Intergovernmental Panel for Climate Change. Cambridge University Press, UK. p. 944.

Jackson, M. B., E. M. Vandermeer, N. Lester, J. A. Booth, L. Molot, and I. M. Gray. 1990. Effects of neutralization and early reacidification on filamentous algae and macrophytes in Bowland Lake. Canadian Journal of Fisheries and Aquatic Sciences 47: 432–439.

Jackson, C. R. 2006. Wetland hydrology. p. 43–81. *In* D. P. Batzer and R. R. Sharitz (eds.) Ecology of Freshwater and Estuarine Wetlands. University of California Press, Los Angeles, CA, USA.

Jonasson, S. and G. R. Shaver. 1999. Within-stand nutrient cycling in arctic and boreal wetlands. Ecology 80: 2139–2150.

Kadlec, J. A. 1979. Nitrogen and phosphorus dynamics in inland freshwater wetlands. p. 17–41. *In* T. A. Boohout (ed.) Waterfowl and Wetlands: An Integrated Review. The Wildlife Society, Madison, WI, USA.

Kadlec, J. A. 1986. Effects of flooding on dissolved and suspended nutrients in small diked marshes. Canadian Journal of Fisheries and Aquatic Sciences 43: 1999–2008.

Kahn, W. E. and R. G. Wetzel. 1999. Effects of ultraviolet radiation and microscale water level fluctuations on periphytic microbiota. Microbial Ecology 38: 253–263.

Kuhry, P., and J. Turunen. 2006. The postglacial development of boreal and subarctic peatlands. p. 25–46. *In* R. K. Wieder and D. H. Vitt (eds.) Boreal Peatland Ecosystems. Springer, New York, USA.

Liston, S. E., S. Newman, and J. C. Trexler. 2008. Macroinvertebrate community response to eutrophication in an oligotrophic wetland: an in situ mesocosm experiment. Wetlands 28: 686-694.

McCormick, P. V. and M. B. O'Dell. 1996. Quantifying periphyton responses to phosphorus in the Florida Everglades: A synoptic-experimental approach. Journal of the North American Benthological Society 14: 450–468.

McCormick, P. V., P. S. Rawlik, K. Lurding, E. P. Smith, and F. H. Sklar. 1996. Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15: 433–449.

McCormick, P. V. and R. J. Stevenson. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology 34: 726–733.

McCormick, P. V., B. E. Robert, J. G. Shuford III, 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.

McCormick, P. V., M. B. O'Dell, R. B. E. Shuford III, J. G. Backus, and W. C. Kennedy. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. Aquatic Botany 71: 119–139.

McDougal, R. L., L. G. Goldsborough, and B. J. Hann. 1997. Responses of a prairie wetland to press and pulse additions of inorganic nitrogen and phosphorus: production by planktonic and benthic algae. Archiv für Hydrobiologie 140: 145–167.

McGuire, A. D., F. S. Chapin III, 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. p. 297–310. *In* J. G. Canadell, D. E. Pataki, and L. F. Pitelka (eds.) Terrestrial Ecosystems in a Changing World IGBP Series. Springer, Heidelberg.

Mitsch, W. J. and J. G. Gosselink. 2006. Wetlands, 4th edition. John Wiley and Sons, Inc., New York, USA.

Murkin, H. R. 1989. The basis for food chains in prairie wetlands. p. 316–338. *In* A.G. van der Valk (ed.) Northern prairie wetlands. Iowa State University Press, Ames, IA, USA.

Murkin, H. R., J. B. Pollard, M. P. Stainton, J. A. Boughen, and R. D. Titman. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of periodic additions throughout the growing season. Hydrobiologia 280: 483–495.

Müller, P. 1980. Effects of artifical acidification on the growth of periphyton. Canadian Journal of Fisheries and Aquatic Sciences 37: 355–363.

National Research Council, Committee on the Science of Climate Change, Division on Earth and Life Studies. 2001. Climate Change Science: An analysis of some key questions. National Academy Press, Washington D.C. USA.

Oechel, W. C, G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane. 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406: 978–981.

Osterkamp, T. E., L. Viereck, Y. Shur, M. T. Jorgenson, 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.

Pan, Y., R. J. Stevenson, P. Vaithiyanathan, J. Slate, and C. J. Richardson. 2000. Changes in algal assemblages along observed and experimental phosphorus gradients in a subtropical wetland, U.S.A. Freshwater Biology 44: 339–353.

Planas, D. 1996. Acidification effects. p. 497-530. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Richardson, C. J. 2009. The Everglades: North America's subtropical wetland. Wetlands Ecology and Management doi: 10.1007/s11273-009-9156-4.

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.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 2000. Algae in Prairie Wetlands. p. 163–198. *In* H. R. Murkin, A.G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

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. Rouet, 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., R. Wagemann, R. B. Cook, T. Ruszczynski, and J. Prokopowich. Exerimental acidification of lake 223, Experimental lakes area- Background data and the 1st three years of acidification. Canadian Journal of Fisheries and Aquatic Sciences 37: 342–354.

Schindler, D. W. 1988. Effects of acid rain on aquatic ecosystems. Science 239: 149–157.

Schindler, D. W. 1998. A dim future for boreal waters and landscapes. BioScience 48: 157–164.

Schoenberg, S. A. and J. D. Oliver. 1988. Temporal dynamics and spatial variation of algae in relation to hydrology and sediment characteristics in the Okefenokee Swamp, Georgia. Hydrobiologia 162: 1055–1063.

Sedinger, J. S. 1997. Waterfowl and wetland ecology in Alaska. p. 155–178. *In* M. A. Milner and M. W. Oswood (eds.) Freshwaters of Alaska-Ecological Synthesis. Vol. 119. Ecological Studies. Springer-Verlag, New York, USA.

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.

Slaughter, C. W. and L. A. Viereck. 1986. Climate characteristics of the taiga in interior Alaska. p. 9–21. *In* K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness (eds.) Forest Ecosystems in the Alaskan Taiga. Springer-Verlag, New York, USA.

Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. p. 341–373. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

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.

Turner, M. A., E. T. Howell, M. Summerby, R. H. Hesslein, D. L. Findlay, and M. B. Jackson. 1991. Changes in epilithon and epiphyton associated with experimental acidification of a lake to pH 5. Limnology and Oceanography 36: 1390–1405.

Turner, M. A., G. G. C. Robinson, B. E. Townsend, B. J. Hann, and J. A. Amaral. 1995a. Ecological effects of blooms of filamentous green algae in the littoral zone of an acid lake. Canadian Journal of Fisheries and Aquatic Sciences 52: 2264–2275.

Turner, M. A., D. W. Schindler, D. L. Findlay, M. B. Jackson, and G. G. C. Robinson. 1995b. Disruption of littoral algal associations by Experimental Lake acidification. Canadian Journal of Fisheries and Aquatic Sciences 52: 2238–2250.

United States Fish and Wildlife Service. 1985. Izembek National Wildlife Refuge – comprehensive conservation plan. U.S. Fish and Wildlife Service, Anchorage, Alaska. p. 270.

Vitt, D. H. 2006. Function characteristics and indicators of boreal peatlands. p. 9–24. *In* R. K. Wieder and D. H. Vitt (eds.) Boreal Peatland Ecosystems. Springer, New York, USA.

Vymazal, J. 1995. Algae and Element Cycling in Wetlands. Lewis Publishers, Ann Arbor, MI, USA.

Walker, D. A., P. J. Webber, E. F. Binnian, K. R. Everett, N. D. Lederer, E. A. Nordstrand, and M. D. Walker. 1987. Cumulative impacts of oil fields on northern Alaskan landscapes. Science 238: 757–761.

Wetzel, R. G. 2006. Wetland Ecosystem Processes. p. 285–312. *In* D. P. Batzer and R. R. Sharitz (eds.) Ecology of Freshwater and Estuarine Wetlands. University of California Press, Los Angeles, CA, USA.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems, 3rd edition. Academic Press, San Diego, CA, USA.

Wetzel, R. G. 1996. Benthic algae and nutrient cycling in lentic freshwater ecosystems. p. 641–667. *In* R. J. Stevenson, M.L. Bothwell, and R.L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Wieder, R. K., D. H. Vitt, and B. W. Benscoter. 2006. Peatlands and the boreal forest. p. 1–8. *In* R. K. Wieder and D. H. Vitt (eds.) Boreal Peatland Ecosystems. Springer, New York, USA.

Wu, X. and W. J. Mitsch. 1998. Spatial and temporal patterns of algae in newly constructed freshwater wetlands. Wetlands 18: 9–20.

Yoshikawa, K. and L. D. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. Permafrost and Periglacial Processes 14: 151–160.

CHAPTER 2

The importance of nutrient co-limitation in regulating algal community composition, productivity, and algal-derived DOC in an oligotrophic marsh in interior Alaska

2.1 Introduction

Wetlands are widely distributed freshwater habitats with important ecosystem functions (Mitsch and Gosselink 2006). Algal communities in wetlands are often taxonomically unique and important drivers of ecosystem function (Vymazal 1995, Goldsborough and Robinson 1996). In shallow wetlands, where sufficient light reaches the bottom, benthic algae can account for a significant amount of total primary production (Robinson et al. 1997b, McCormick et al. 2001), increase nutrient transformation and retention (Wetzel 1996, Inglett et al. 2004) and are habitat and food for a variety of organisms (Campeau et al. 1994, Liston et al. 2008). Despite their importance, the major factors controlling algal communities in freshwater wetlands continue to be poorly understood relative to other aquatic habitats such as lakes and rivers (Stevenson et al. 1996). This discrepancy is particularly acute in northern boreal regions, where wetlands are abundant and processes related to ongoing climate warming are expected to increase nutrient inputs into aquatic systems (Rouse et al. 1997).

Benthic algae are sensitive to changes in water quality, and nutrients are often the single most important factor regulating communities in freshwater habitats (Borchardt 1996). A review of the literature allows us to make broad generalizations as to the importance of nitrogen (N) and phosphorus (P) limitation of benthic algae in lakes

(Fairchild et al. 1985, Rodusky et al. 2001) and streams (Francoeur 2001, Tank and Dodds 2003), but there are too few data to make such generalizations about them in freshwater wetlands. Of the studies reviewed by Goldsborough and Robinson (1996), most investigations of N and P limitation of wetland algae have been limited to temperate and subtropical climes. Other potentially limiting nutrients, such as silica (Si), have received little attention in wetlands (but see Hooper-Reid and Robinson 1978) even though diatoms frequently dominate benthic habitats.

Research on the effects of nutrient enrichment on wetland algae has been driven primarily by the need for management strategies to mitigate human impairment of wetlands (see review in McCormick and Stevenson 1998). In the Florida Everglades, for example, there is an ongoing effort to develop algal-nutrient relationships to manage functional and structural changes in the native periphyton assemblage associated with agricultural and urban land use (Gaiser et al. 2004, 2006). In other regions, such as the northern boreal forest, algal-nutrient relationships in wetlands have been less studied, perhaps because it has been less directly impacted by human development. However, even in relatively remote areas of the boreal biome, such as the interior region of Alaska, anthropogenic sources of nutrient enrichment are apparent, as nitrate and ammonium concentrations in precipitation are enriched by six orders of magnitude relative to seawater (Hinzman et al. 2006). Boreal regions also are experiencing rapid climate change, which has led to a longer growing season with rising temperature (Chapin et al. 2006). Changes in thermal regime are expected to increase the extent of seasonal ice thaw, which will probably promote N and P mineralization in the expanded active soil layer (Bridgham et al. 1995), as well as chemical weathering of parent rock material

(Rouse et al. 1997). While regional variability of nutrient inputs may be significant, these changes are expected to have widespread impacts on nutrient concentrations of aquatic systems throughout the boreal forest (Rouse et al. 1997).

Wetlands are a dominant feature on the boreal landscape and may comprise the largest freshwater habitat directly affected by nutrient enrichment. In Alaska alone, wetlands make up more than 43% of the land surface, equivalent to approximately 60% of the total wetland area of the United States (Hall et al. 1994). Wetlands provide a number of ecosystem services for boreal regions, including important summer nursery and stopover habitat for migrating waterfowl (Sedinger 1997). Boreal wetlands also serve as an important global carbon reservoir (Bridgham et al. 2006), and there is an ongoing effort to identify processes that may alter carbon cycling in the region (Wickland et al. 2007). A better understanding of the effects of nutrient enrichment on algal structure and function in boreal wetlands may help to identify and forecast changes in primary production and biogeochemical cycling associated with climate warming and increased N deposition throughout the region.

In this study, I manipulated water column concentrations of N, P and Si in a completely crossed experimental design using mesocosms in an Alaskan marsh. I tested the hypothesis that nutrients are an important factor limiting algal biomass and constraining community structure in northern boreal wetlands, and that increases in algal biomass would be driven by taxa requiring high nutrient conditions. Additionally, since algae can release significant amounts of carbon fixed during photosynthesis into the water column as dissolved organic carbon (DOC) (Myklestad 1995), I hypothesized that water column DOC concentrations would be related to algal accrual, and increase with algal biomass following nutrient enrichment.

2.2 Methods

Site description

I conducted this study in a freshwater marsh located on the floodplain of the Tanana River (latitude 64°42′ N, longitude 148°18′ W) just outside the Bonanza Creek Experimental Forest, approximately 35 km southwest of Fairbanks, Alaska, U.S.A. This region within interior Alaska experiences a relatively short growing season (135 days or less) with more than 21 hours of light per day in June. The Tanana River floodplain is located within an intermontane plateau characterized by wide alluvium-covered lowlands and underlain by discontinuous permafrost (Begét et al. 2006). Oxbows and thaw ponds dominate the floodplain landscape, and fluvial deposition and erosion are annual disturbance events. The study site is characteristic of other marsh habitats that occur in oxbows along the flood plain, which are shallow with dense stands of beaked sedge (*Carex utriculata* Boott) and swamp horsetail (*Equisetum fluviatile* L.) surrounding open water pools with sparse (approximately 10% cover) emergent vegetation. The wetland supports a diverse grazer fauna, including wood frog tadpoles (*Rana sylvatica* LeConte) in early spring and high densities of the common pond snail (*Lymnaea spp.*) throughout the summer growing season. Background concentrations of inorganic nutrients were generally low during the study and within the range of other wetlands and lakes in the region (see Table 2.1). Phytoplankton biomass (measured as chlorophyll-*a*) was less than 0.28 μg L^{-1} throughout the growing season.

Nutrient enrichment

I manipulated nitrate, phosphate and silicate in a completely crossed design and *in situ* using mesocosms modified from the design described by Greenwood and Lowe (2006). A raised boardwalk was constructed prior to the beginning of the study to prevent the disturbance of wetland sediments during experimental set-up and regular sampling. I constructed 20 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. I deployed *Equisetum fluviatile* stems, cut into 10-cm segments from live plants, as a standard substratum for sampling benthic algae inside treatment enclosures. I suspended stems attached to paper clips that could be repositioned to maintain a consistent depth of 5 cm below the water surface inside each enclosure.

I added nutrients from a stock solution to achieve concentrations for nitrogen (+N) of 1,000 μg L^{-1} $NaNO_3$, phosphorus (+P) of 100 μg L^{-1} $NaPO_4$ and silica (+Si) of 20 mg L^{-1} Na_2O_3Si following each addition. I assumed these concentrations would saturate algal growth rates because they exceeded those reported to be limiting for benthic algae in studies reviewed by Borchardt (1996). My enrichments began after the seasonal thaw to simulate nutrient inputs from groundwater or surface water runoff (McDougal et al. 1997). My goals with enrichments were to ensure determination of which nutrient could be limiting and the potential magnitude of responses in an appropriate seasonal context.

Due to constraints on the area of the wetland that was suitable for experiments, I conducted half of the experiment during 2007 and half during 2008. My first objective was to determine if the wetland algal community was nutrient limited and, if so, whether it was limited by a single nutrient or some combination of nutrients. In 2007, I randomly assigned each enclosure to one of three single-nutrient treatments (+N, +P or +Si) or a combination treatment (+N+P+Si), with four replicates each. I added nutrient amendments to enclosures every four days for 20 days beginning on 29 June 2007. The second phase of the experiment was conducted in June 2008 to determine which combination of nutrients was co-limiting. I deployed fresh *Equisetum* stems and randomly assigned each enclosure to one of three pair-wise nutrient treatments (+N+P, +N+Si, +P+Si) or +N+P+Si, with four replicates each. I added nutrient amendments to enclosures every four days for 20 days beginning on 17 June 2008. During each experiment (2007 and 2008), I used four enclosures without nutrients as a control treatment and, to evaluate container effects, designated four sampling sites within the wetland without enclosures or nutrient additions (open wetland).

In both experiments, I monitored changes in water depth inside each enclosure as well as in open wetland sites with a metre stick, and measured conductivity, temperature and pH every four days using a calibrated model 556 YSI® Multi-Probe (YSI Incorporated, Yellow Springs, OH, U.S.A.). I collected and filtered water for dissolved nutrient analysis immediately following each nutrient addition (every four days for 20 days) using a 0.45 µm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, MA, U.S.A.). I later analyzed concentrations of dissolved inorganic N (DIN) as $NO_3 + NO_2$ in water samples following the cadmium reduction method, of silicate (SiO_2) following the molybdate method using a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands), and of soluble reactive P (SRP) using the ascorbic acid colorimetric method on a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, U.K.) (APHA 1998). A portion of the filtered sample collected on day 24 was acidified and placed on ice in the field for later DOC analysis using a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.).

Collection and processing of benthic algae

In both experiments, I allowed algae to colonize *Equisetum* stems inside treatment enclosures for 24 days. I assumed this length of colonization period allowed us to observe the algal response to nutrient inputs following the spring thaw, while minimizing container effects. I removed algae from stems with a soft toothbrush and homogenized the resulting algal slurry from each treatment in 100 mL of filtered water for subsequent analyses. I filtered a known volume of each homogenate onto a GF/F glass fiber filter (Whatman, Springfield Mill, U.K.) and stored filters frozen in the dark for chlorophyll-*a* analysis. I 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). I preserved a separate aliquot with 2.5% formalin for algal compositional analysis and ash-free dry mass (AFDM) and placed a known volume on ice for algal chemistry analysis. I determined AFDM following standard methods (APHA 1998). I dried samples at 105 °C for 48-72 h and then ashed them at 500 °C for 1 h in pre-weighed aluminium pans to measure dry mass and ashed mass, respectively. I analyzed algal chemistry for total P (TP) and total N (TN) by oxidizing particulate matter with persulphate and then analysing SRP following the ascorbic acid method and NO_3 following the second derivative UV spectroscopy method (APHA 1998). The proportion of N and P in samples was calculated by dividing the mass of N and P by AFDM and nutrient content was reported per unit dry mass.

I homogenized preserved algal samples and identified and counted at least 300 cells per sample to genus using a Palmer-Maloney nanoplankton counter chamber (Wildlife Supply Company, Buffalo, NY, U.S.A.) at 400 magnification with a Leica model DM LB light microscope (Leica Microsystems, Wetzler, Germany). Cell volume (μm^3 cm^{-2}) for each genus was determined by inserting average dimensions into geometric formulae from Hillebrand et al. (1999) and Wetzel and Likens (2000). I calculated the cell density (cells cm^{-2}) for each genus following Lowe and LaLiberte (2006), and then calculated total biovolume by multiplying cell density by estimated cell volume.

During the 2008 experiment, I split a portion of each homogenized sample into two separate biological oxygen demand (BOD) bottles to measure benthic algal productivity (mg C m^{-2} h^{-1}) following McCormick et al. (1998). I filled each BOD bottle with filtered water from the wetland and recorded initial DO using a Hach HQ 40d luminescent DO probe (Hach Company, Loveland, CO, U.S.A.). I wrapped one bottle from each set with aluminium foil for incubation in the dark and determined production by measuring oxygen changes produced by algal samples incubated *in situ* in light and dark bottles. Light and dark bottles were used to measure net primary productivity (NPP) and respiration, respectively. I calculated gross primary productivity (GPP) following Wetzel and Likens (2000) and converted GPP values into units carbon based on a C:O molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

Data analyses

My analyses focused on variables indicative of algal structure and function, including chlorophyll-*a*, ash-free dry mass, total cell biovolume, productivity, N:P ratio, DOC concentration and percent of total biovolume of common genera. 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.

Largely due to space constraints within my experimental study area, my nutrient manipulations were conducted across two separate study years. I analyzed the 2007 and 2008 experimental treatments separately using ANOVA models for two reasons. First, treatments were confounded with study year. Second, t-tests revealed differences in water-table between 2007 control data and 2008 control data, probably due to interannual variability in climate. Post hoc comparisons of means were performed using Tukey's tests. All analyses were performed using SYSTAT (version 11.0; SYSTAT, Evanston, IL, U.S.A.).

In addition to the approach outlined above, I also evaluated differences in algal assemblages among treatments with an Analysis of Similarities (ANOSIM) using PRIMER for Windows (version 5.2.9; PRIMER-E Ltd., Plymouth, U.K.). ANOSIM operates directly on a dissimilarity matrix and tests whether there is a significant difference between two or more groups of sampling units. I used Bonferroni corrections for the algal assemblage analyses to preserve the experiment-wise Type I error rate of $P = 0.05$ (Zar 1999). Finally, I used linear regression analysis to examine the relationship between algal biomass and water column DOC following nutrient enrichment.

2.3 Results

Physical conditions and nutrient concentrations

Standing water ranged from 44 - 49 cm (mean 46 ± 1.60 cm) between June-July 2007, and from 14 - 28 cm (mean 22 ± 0.76 cm) between June-July 2008, and differences between seasons were statistically significant ($t = -13.54$, $P < 0.0001$). Background concentrations of inorganic nutrients in the control treatment were similar to the open wetland during each season (t-test, $P > 0.05$; Table 2.2). Conductivity, temperature and pH varied over time during each experiment, but did not differ significantly among treatments (ANOVA, $P > 0.05$; data not shown).

In 2007, DIN in the +N+P+Si treatment increased to target concentrations following each N addition over 20 days whereas, in the +N treatment, DIN began to accumulate following enrichment on day 12, increasing to a mean of 4,984.40 ± 459.90 $\mu g\ N\ L^{-1}$ on day 20 (Figure 2.1). Following the second P addition, mean SRP concentrations increased to 184.98 ± 31.45 $\mu g\ P\ L^{-1}$ and 132.78 ± 25.26 $\mu g\ P\ L^{-1}$ in +P and +N+P+Si treatments, respectively, but then increased to near target values throughout the remainder of the study (Figure 2.1). Silicate concentrations in +Si and +N+P+Si treatments met or exceeded target values following each addition over 20 days (Figure 2.1).

In 2008, DIN increased to near target concentrations following each N addition over 20 days (Figure 2.2). SRP exceeded target concentrations with P enrichment, especially in the +P+Si treatment where SRP began to accumulate following enrichment on day 4, reaching 680.44 ± 74.76 $\mu g\ P\ L^{-1}$ on day 20 (Figure 2.2). Silicate concentrations met or exceeded target values following each addition over 20 days (Figure 2.2).

Benthic algae biomass, stoichiometry and productivity

Benthic algal biomass (chlorophyll-*a* concentration, g AFDM and total biovolume) was similar between the open wetland and the control treatment during each experiment (2007 and 2008) ($P > 0.05$; Figures 2.3 and 2.4). In 2007, there was no increase in algal biomass with either nutrient alone ($P > 0.05$), but there was a significant increase in chlorophyll-*a* concentration ($F_{5,18} = 29.29$, $P < 0.0001$), g AFDM ($F_{5,18} =$

32.68, $P < 0.0001$), and total biovolume ($F_{5, 18} = 6.76$, $P = 0.0010$) in the +N+P+Si treatment compared to the control treatment (Figures 2.3 and 2.4).

In 2008, chlorophyll-*a* concentration ($F_{5, 18} = 26.12$, $P < 0.0001$) and total biovolume ($F_{5, 18} = 14.76$, $P < 0.0001$) were significantly greater in +N+P, +N+Si and +N+P+Si treatments compared to +P+Si and control treatments (Figures 2.3 and 2.4). Ash-free dry mass was also significantly higher in +N+P and +N+P+Si treatments compared to +P+Si and control treatments ($F_{5, 18} = 16.90$, $P < 0.0001$; Figure 2.3). Although mean AFDM was higher in the +N+Si treatment than in the control treatment, differences were not statistically significant ($P = 0.145$). All measures of algal biomass (chlorophyll-*a*, g AFDM, total biovolume) were similar between the +P+Si treatment and the control treatment ($P > 0.05$; Figures 2.3 and 2.4).

In 2007, algal N:P ratios in the +N (21.59:1 ± 3.68) and +N+P+Si (14.48:1 ± 0.97) treatments were not significantly different on a mass basis, but both were higher compared to treatments without N addition (< 5:1) ($F_{5, 18} = 21.29$, $P < 0.0001$; Figure 2.5). In 2008, algal N:P ratios were significantly higher in the +N+Si treatment (31.27:1 ± 0.23) and lower in the +P+Si treatment (7.15:1 ± 0.47) compared to the control treatment ($F_{5, 18} = 34.71$, $P < 0.0001$); and they were similar among +N+P (15.18:1 ± 2.05) and +N+P+Si (16.91:1 ± 1.14) treatments (Figure 2.5).

In 2008, benthic algal productivity (mg C $m^{-2} h^{-1}$) in the +N+P+Si treatment (127.98 ± 22.32) was significantly greater compared to +N+P and +N+Si treatments (73.59 ± 10.43 and 57.84 ± 9.53, respectively), and productivity rates in all N treatments were significantly higher compared to +P+Si (27.53 ± 5.16) and control (20.55 ± 5.32) treatments ($F_{5, 18} = 13.82$, $P < 0.0001$; Figure 2.6). Algal productivity was similar among the +P+Si treatment, control treatment and the open wetland ($P > 0.05$).

In 2007, water column DOC concentration (mg L^{-1}) was similar among individual nutrient treatments and the control treatment ($P > 0.05$), but DOC concentration was significantly higher in the +N+P+Si treatment (43.96 ± 1.50) than in the control treatment (20.72 ± 0.31) ($F_{5, 18} = 400.98$, $P < 0.0001$; Figure 2.7). In 2008, DOC concentration was significantly greater in +N+P (49.61 ± 2.58) and +N+P+Si (47.49 ± 1.63) treatments than in the +N+Si treatment (39.56 ± 1.72), and DOC concentrations in all N-combination treatments (+N+P, +N+Si, +N+P+Si) were significantly greater compared to +P+Si (25.94 ± 1.06) and control (28.62 ± 0.80) treatments ($F_{5, 18} = 31.89$, $P < 0.0001$; Figure 2.7). There was no difference in DOC concentration among the +P+Si treatment, control treatment and the open wetland ($P > 0.05$). Water column DOC increased linearly with increasing standing algal biomass in 2007 ($r^2 = 0.89$, $P < 0.0001$) and 2008 ($r^2 = 0.74$, $P < 0.0001$; Figure 2.8).

Benthic algal community response to nutrient enrichment

Of the 43 genera identified in 2007 and 2008, seven comprised > 80% of the total biovolume in both seasons (Figure 2.9). Multivariate analysis (ANOSIM) indicated differences in the composition of benthic algal assemblages occurring in different nutrient treatments in 2007 (Global R = 0.510, $P < 0.001$) and 2008 (Global R = 0.311, $P < 0.001$). In 2007, the algal community in the open wetland was comprised primarily of

Mougeotia (Chlorophyta), *Euglena* (Euglenophyta), *Anabaena* (Cyanobacteria) and *Gloeocystis* (Chlorophyta), which made up approximately 39%, 25%, 13% and 12% of the total biovolume, respectively (Figure 2.9). ANOVA indicated that all taxa represented a similar percent of total biovolume in the control treatment compared to the open wetland, except that *Mougeotia* ($F_{5, 18} = 9.77$, $P < 0.0001$) was significantly lower, and *Euglena* ($F_{5, 18} = 43.27$, $P < 0.0001$) significantly greater, in the control treatment than the open wetland. All taxa occurred at similar percent of total biovolume among individual nutrient treatments (+N, +P, +Si) and the control treatment (ANOVA, $P > 0.05$). In the +N+P+Si treatment, the percent of total biovolume of *Gloeocystis* ($F_{5, 18} = 12.76$, $P < 0.0001$) and *Chroococcus* ($F_{5, 18} = 7.66$, $P < 0.0001$) were significantly greater, and *Euglena* ($F_{5, 18} = 43.27$, $P < 0.0001$) and *Mougeotia* ($F_{5, 18} = 9.77$, $P < 0.0001$) significantly lower, than in the control treatment (Figure 2.9).

In 2008, the percent of total biovolume of all taxa was similar between the open wetland and the control treatment (ANOVA, $P > 0.05$), and comprised primarily of *Mougeotia* (70% and 67%, respectively), *Euglena* (7% and 6%) and *Nitzschia* (Bacillariophyceae) (7% and 8%) (Figure 2.9). *Nitzschia* increased to 56% and 71% of the total biovolume in +N+Si and +N+P+Si treatments, respectively, which were significantly greater than the control treatment ($F_{5, 18} = 20.74$, $P < 0.0001$). The percent of total biovolume of *Gloeocystis* was significantly greater in the +N+P treatment compared to the control treatment ($F_{5, 18} = 77.27$, $P < 0.0001$), and *Mougeotia* was significantly lower in all N-addition treatments (+N+P, +N+Si, +N+P+Si) than in the control treatment ($F_{5, 18} = 8.19$, $P = 0.0004$; Figure 2.9). There were no differences in the percent of total biovolume of any taxa between the +P+Si and control treatments (ANOVA, $P > 0.05$).

2.4 Discussion

My results provide several lines of evidence for nutrient co-limitation and the central importance of N limitation for regulating algal production and taxonomic composition in the wetlands of interior Alaska. Nutrient co-limitation was indicated by low background DIN and SRP concentrations in wetland water during each summer growing season and the lack of treatments responses to any nutrient alone. Additionally, algal N:P ratios increased to approximately 16:1 with the addition of N and P together, but were symptomatic of N limitation with the addition of P without N, and P limitation with the addition of N without P. It was only in treatments with the highest N:P ratio (N treatments without P) that a pool of DIN remained unexploited, and in treatments with the lowest N:P ratio (P treatments without N) that PO_4 began to accumulate in the water column. The central importance of N limitation was indicated by significant increases in algal biomass and productivity with the addition of N in any combination with P and Si, but no biomass and productivity responses were observed in the +P+Si treatment.

Following Liebig's Law of the Minimum, I would expect algal growth to be regulated by the scarcest available resource, or a single limiting nutrient (Liebig 1855). Simultaneous limitation by multiple nutrients, i.e., co-limitation (Borchardt 1996), has been observed in freshwater systems occurring across high latitude regions, where combined N and P enrichment results in a larger increase in algal accrual than enrichment with either nutrient alone (Elser et al. 2007). More specific to wetland studies, similar results have been reported from Delta Marsh in southern Manitoba, Canada (see review in Robinson et al. 2000) and in the southeast United States (Scott et al. 2005), where enrichment with either N or P alone induces limitation by the alternative nutrient. In contrast, my findings are markedly different from those for the Florida Everglades, which are naturally P limited and enrichment results in the decrease in algal biomass as a result of the loss of the native cyanobacterial mat (see review in McCormick and Stevenson 1998, Gaiser et al. 2005, 2006, Richardson 2009).

I observed a significant shift in community composition in response to nutrient enrichment, which reflects the interaction between nutrient limitation and resource competition. In 2007, nutrient effects on the algal community were strongest in the +N+P+Si treatment, where *Euglena* was almost completely displaced by a combination of *Chroococcus* and *Gloeocystis*. Although similar shifts in response to nutrient enrichment have not been widely reported from other wetland studies, high abundances of *Chroococcus* have been reported in shallow lakes with high nutrient concentrations across North America (Komarek and Anagnostidis 1998). The increase in *Gloeocystis* with nutrient enrichment is interesting, as it has been argued that mucilaginous taxa are good competitors for nutrients in shallow oligotrophic lakes and wetlands (McCormick et al. 1996). Their increase in relative biovolume in my study may reflect a high latitude community adapted to sequester available nutrients rapidly during the short summer growing season.

In 2008, the increase in diatom taxa following enrichment with Si along with N or N and P was surprising, since background concentrations of Si were an order of magnitude higher than those known to be growth saturating for phytoplankton (Hecky and Kilham 1988). Diatom growth was constrained in the control and +N+P treatments, in which the filamentous green alga *Mougeotia* was abundant. The increase of *Nitzschia* with the addition of Si with N and/or P does offer support for early culturing experiments, which show that some benthic diatoms grow best when Si concentrations are greater than 30 mg L^{-1} (Chu 1942). Higher Si concentrations may be needed to satisfy demand of benthic versus planktonic algae because a) densities of algae are higher on substrata than suspended in water, and b) high algal density on substrata severely constrains nutrient supply because nutrient uptake rates exceed diffusion and mixing rates (Stevenson and Glover 1993).

Although functional responses of the algal community as a whole were quite similar among years, seasonal shifts in community composition demonstrate the importance of temporal variability in shaping algal responses to nutrient inputs in the region. Shifts in community composition may reflect interannual variability in timing and concurrence of antecedent seasonal conditions, such as changes in the water-table resulting from seasonal drying and rewetting from seasonal flood pulses (*sensu* Junk et al. 1989). The water table at my study site varied between the two study years, and was on average 50% lower during the 2008 study. In particular, shallow wetlands such as my study site tend to be highly variable. Shallow conditions during the second year may have favoured filamentous taxa over euglenoid flagellates in the control treatment (i.e., Robinson et al. 1997a) and aided the resuspension of diatom cells from the sediments.

Ambient rates of algal productivity in the wetland (20 mg C m^{-2} h^{-1}) were similar to values reported from marshes in temperate climates (see review in Goldsborough and

Robinson 1996). Following enrichment with N in any combination with P and Si, productivity increased significantly and became more similar to daily values reported from oligotrophic subtropical wetlands (McCormick et al. 1998, Ewe et al. 2006). Assuming that peak macrophyte biomass at my site (47.23 g C m^{-2}; unpublished data) is equivalent to annual net productivity (g m^{-2} yr^{-1}), my measured values of 52 - 341 g C m^{-2} yr^{-1} for benthic algae (based on 135 day ice-free period) are notably higher. These results offer evidence in support of the hypothesis that algal productivity in wetlands can be as significant as that of macrophytes (Robinson et al. 2000), and as such, may support significant proportions of the secondary production in boreal wetlands.

The strong positive relationship between increasing algal biomass and water column DOC concentration suggest that a significant portion of the carbon fixed by algae during photosynthesis was released into the water column as carbon exudates. It is widely accepted that phytoplankton lose significant amounts (5-35%) of photoassimilated carbon as organic compounds, much of which (80-90%) is often carbohydrates (Myklestad 1995). However, there have been discussions in the literature as to whether this is a normal process performed by healthy cells or an overflow mechanism in response to low nutrient conditions (Sharp 1977). I observed a significant increase in DOC concentration with high algal biomass resulting from nutrient enrichment (N:P ratio of approximately 16:1), suggesting that algae in high nutrient conditions may release significant amounts of DOC in boreal wetlands.

Many areas of the boreal biome, such as western North America have undergone rapid climate warming in recent years and climate models predict that temperatures will continue to increase with human activity (Serreze et al. 2000). There is uncertainty with respect to how some aspects of climate change will affect aquatic systems, but there is consensus that processes such as increased organic matter mineralization and mineral weathering will lead to increased nutrient cycling and nutrient inputs into aquatic ecosystems (Carpenter et al. 1992, Rouse et al. 1997). My findings suggest that an increase in N and P availability will probably increase benthic algal biomass and productivity, and alter their community structure in northern boreal wetlands. Although the quantitative significance of algae as a food source has not been established for wetlands in this region, its potential importance is evident from the gut contents of animals from other wetland ecosystems (Browder et al. 1994). From a management standpoint, alteration of the proportions and biomass of algal assemblages may be important because algal groups differ in their relative utilization by consumers (Lamberti and Moore 1984). Shifts in taxonomic composition, especially an increase in diatom abundance, may have important implications for secondary production in the wetland food web.

The results of this study are limited in scope as they only show algal response to nutrient enrichment in a single wetland complex within interior Alaska. Although background concentrations of inorganic nutrients at my study site are within the range of other wetlands and shallow lakes in the region, wetlands across the boreal biome will almost certainly respond to nutrients in different ways. Future research should include additional wetland sites that may vary in geology, food-web structure, energy and nutrient inputs. Also, research is needed to understand more completely the consequences of altered algal community dynamics for wetland secondary production (Sedinger 1997), as well as the role of algal-derived DOC in wetland biogeochemistry

(Reddy and DeLaune 2008). This, coupled with a better understanding of permafrost degradation effects on water table position and nutrient cycling, will help predict the consequences of climate change for the structure and function of wetlands, which are the most common freshwater ecosystem in this region.

Table 2.1 Comparison of nutrient data from freshwater habitats within the boreal region of western North America

Habitat type	Country Region/province	n	DIN $\mu g\ L^{-1}$	TN $\mu g\ L^{-1}$	SRP $\mu g\ L^{-1}$	TP $\mu g\ L^{-1}$	SiO_2 $mg\ L^{-1}$	Ref. No
Fen (riverine)	Alberta, Canada	1	16.2 ± 2.3		14.9 ± 3.9	102.4 ± 21.0		1
Fen (floating)	Alberta, Canada	1	22.0 ± 5.2		6.0 ± 1.0	95.0 ± 13.1		1
Marsh (lacustrine)	Alberta, Canada	1	265.7 ± 90.9		69.7 ± 26.2	354.7 ± 51.9		1
Marsh (riverine)	Alberta, Canada	1	95.8 ± 41.3		9.1 ± 2.9	157.8 ± 16.9		1
Wetland Lake	Alberta, Canada	148	17.9 (0.2-218.9)		35.2 (0.0-617.6)	123.2 (15.7-726.6)		2
Lake (boreal-forest)	Yukon & Northwest Territories, Canada	17	21.5 (BD-220.0)	722.4 (259.0-1585.0)	1.9 (BD-7.5)	14.3 (4.3-35.4)	4.46 (0.17-12.47)	3
Lake (boreal-forest)	Northwest Territories, Canada	4	18.0 (2.0-29.0)	373.5 (247-478)	0.7 (0.6-0.8)	8.1 (3.9-9.6)	0.68 (0.92-0.41)	4
Fen (moderate-rich)	Interior Alaska, USA	2	11.9 (7.8-15.9)	1795.0 (1090.0-2500.0)	2.8 (2.5-3.24)	35.0 (30.0-40.0)	3.22 (3.11-3.32)	5
Marsh (riverine)	Interior Alaska, USA	4	17.38 (5.0-33.0)	2000.0 (1120.0-3510.0)	2.54 (1.9-3.3)	32.2 (20.0-50.0)	6.23 (1.93-9.23)	5
Marsh (riverine)	Interior Alaska, USA (This Study)	1	6.6 (5.3-21.2)	1232.0 (960.1-1412.2)	9.1 (2.91-20.4)	23.3 (18.4-63.4)	9.4 (2.23-14.47)	6
Lake (northern-southern forest)	Alaska, USA	26	30.6 (16.0-385.0)	835.5 (208.0-2833.0)		37.2 (3.3-475.8)	2.69 (0.08-10.80)	7

Reference numbers *1* Bayley and Mewhort (2004); *2* Bayley and Prather (2003); *3* Pienitz, Smol and Lean (1997a); *4* Pienitz, Smol and Lean (1997b); *5* K.H. Wyatt, unpublished data; *6* This study; *7* Gregory-Eaves *et al.*, (2000); *DIN* dissolved inorganic N; *TDN* total dissolved N; *TN* total N; *SRP* soluble reactive P; *TP* total P; *BD* below detection; *n* number of sites; mean and ± SE or range are given based on available information.

Table 2.2 Mean (± S.E.) dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and silicate concentrations measured at open wetland sites and the control treatment (mesocosms without nutrient enrichment) measured every four days between June and July during each experiment, 2007 and 2008

	n	DIN (μg L^{-1})	SRP (μg L^{-1})	Silicate (mg L^{-1})
2007				
Open wetland	28	8.02 ± 1.28	8.69 ± 1.28	12.09 ± 0.49
Control treatment	28	13.85 ± 1.63	8.37 ± 1.77	7.53 ± 0.55
2008				
Open wetland	28	5.25 ± 1.25	9.98 ± 0.96	4.10 ± 0.37
Control treatment	28	9.75 ± 1.75	13.07 ± 1.98	3.09 ± 0.57

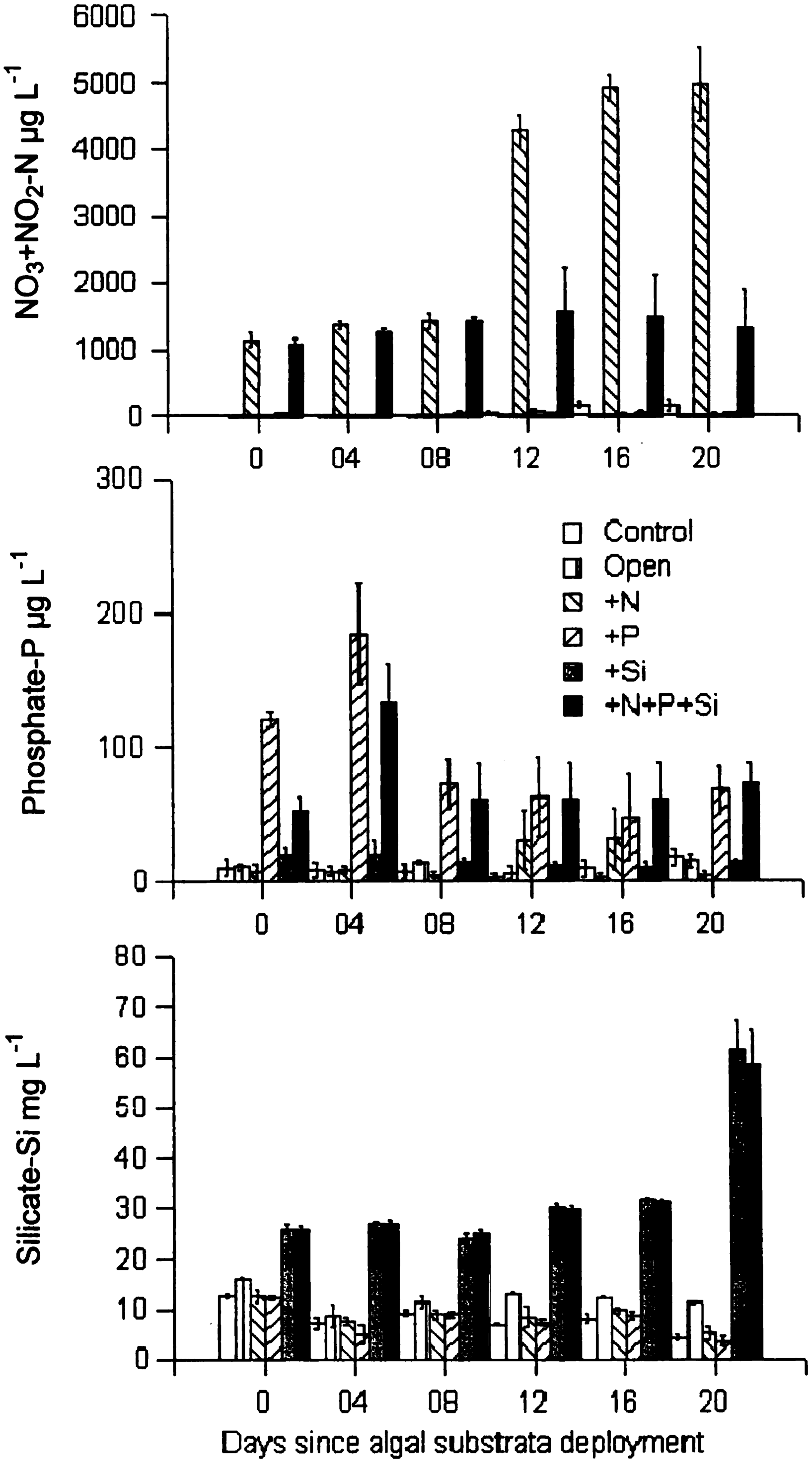

Figure 2.1 Dissolved inorganic N (NO_3 + NO_2-N), phosphate-P and silicate-Si concentrations among treatment enclosures following each nutrient addition during the 2007 experiment. Points are means of four replicates ± S.E.

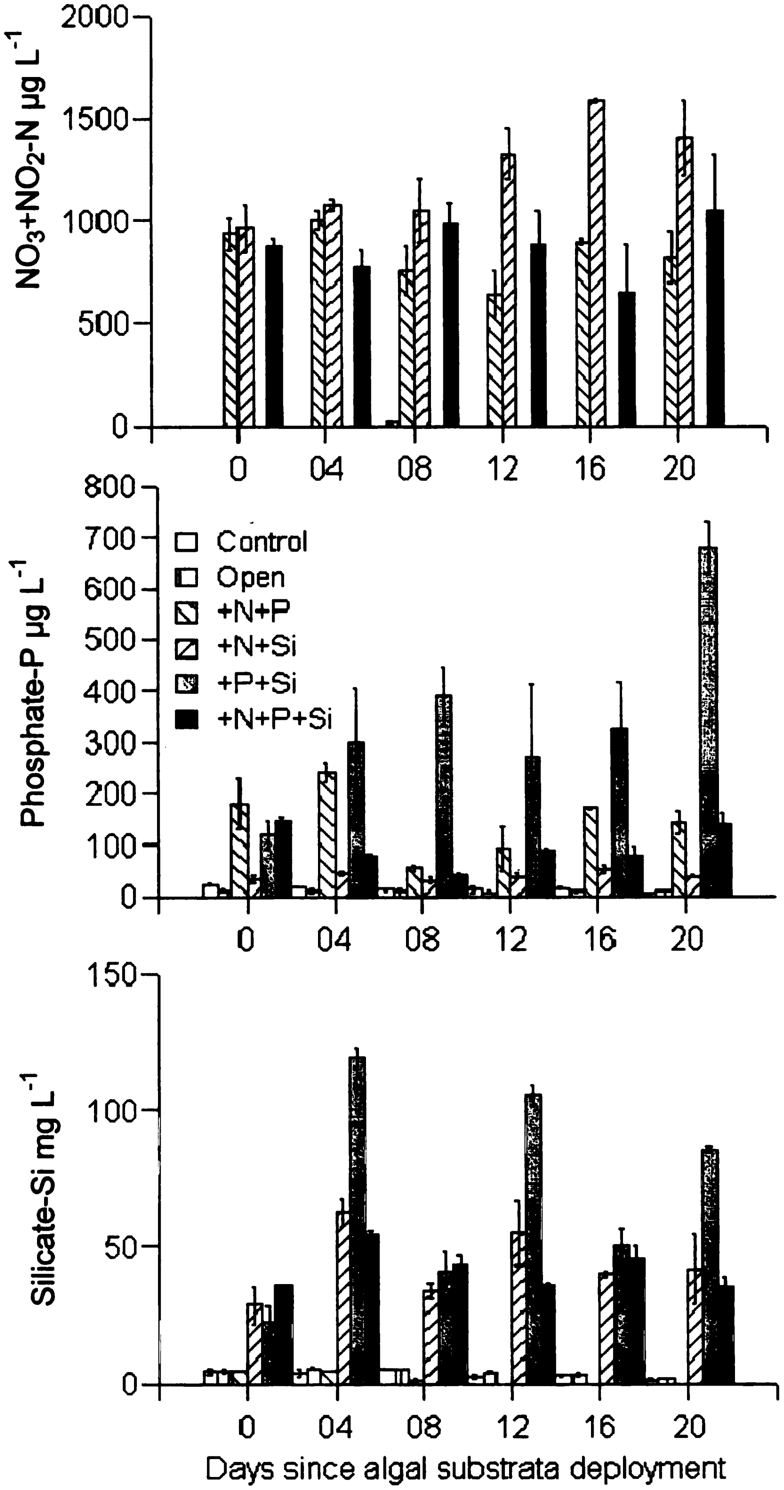

Figure 2.2 Dissolved inorganic N (NO_3 + NO_2-N), phosphate-P and silicate-Si concentrations among treatment enclosures following each nutrient addition during the 2008 experiment. Points are means of four replicates ± S.E.

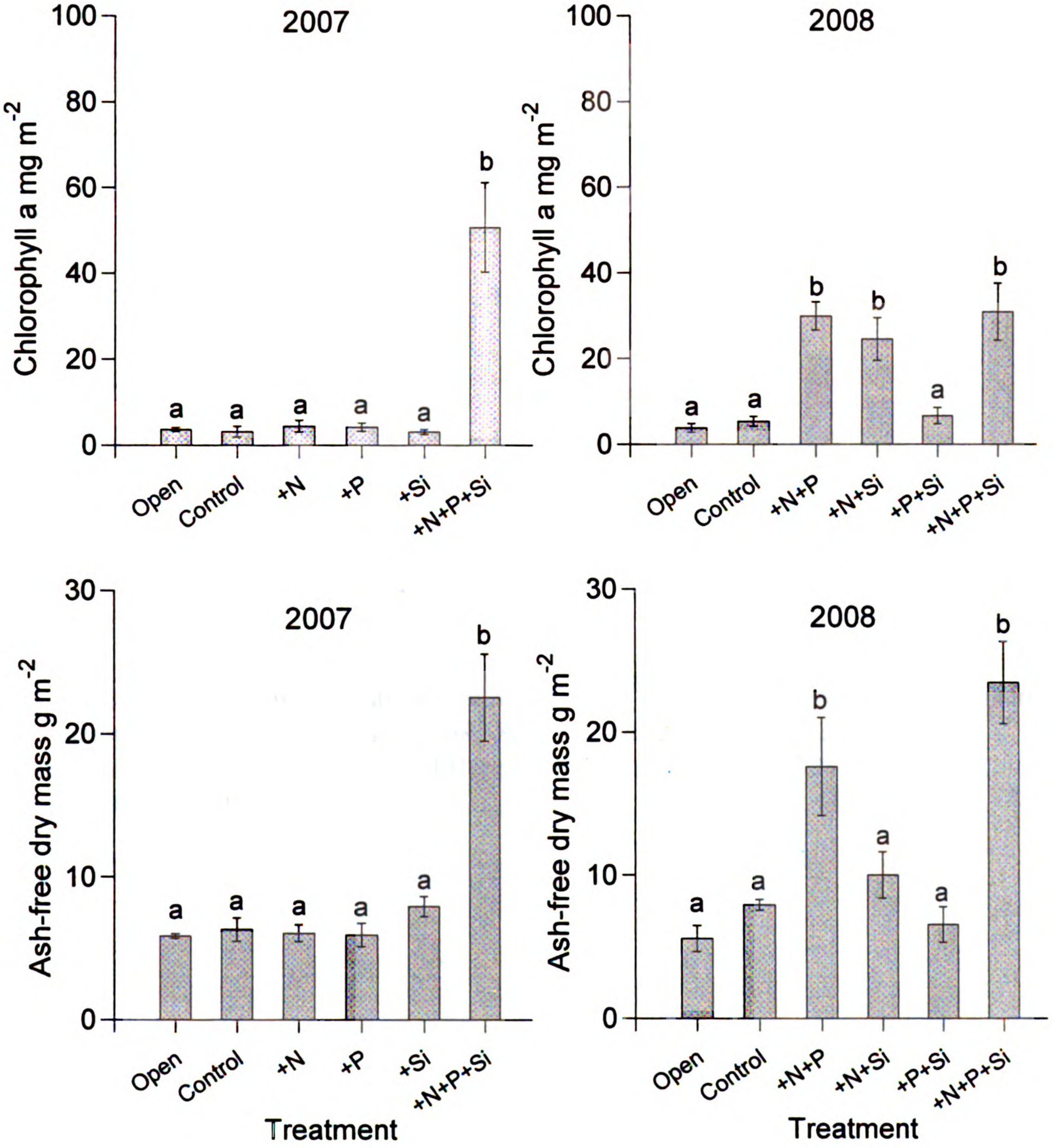

Figure 2.3 Comparison of mean chlorophyll-*a* concentration and g ash-free dry mass among treatment enclosures and the open wetland in 2007 and 2008. Bars are means of four replicates ± S.E. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

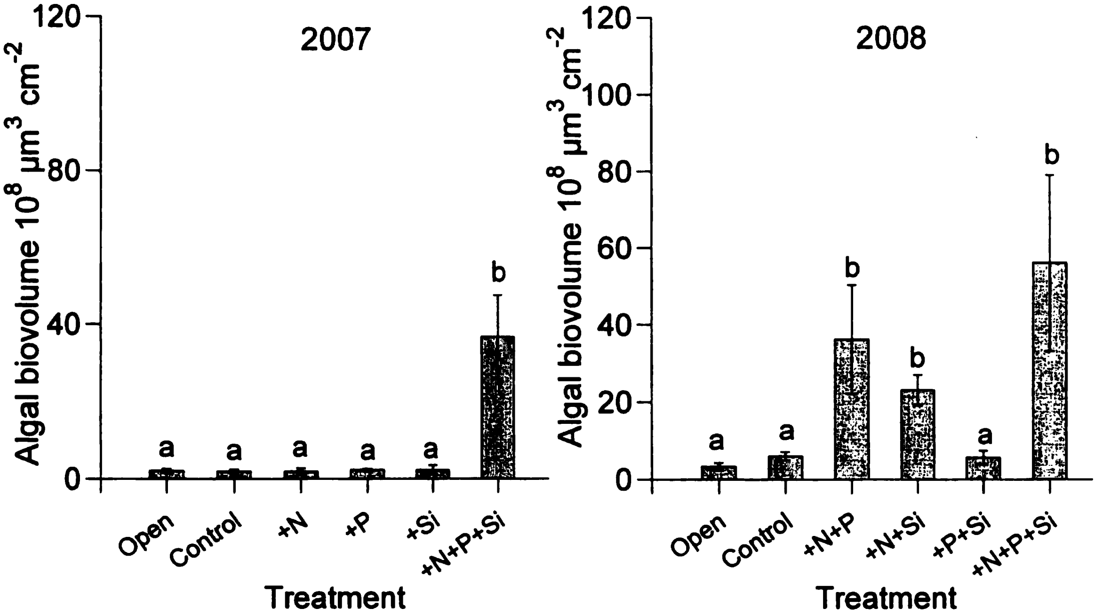

Figure 2.4 Comparison of mean total biovolume µm^3 cm^{-2} among treatment enclosures and the open wetland in 2007 and 2008. Bars are means of four replicates ± S.E. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

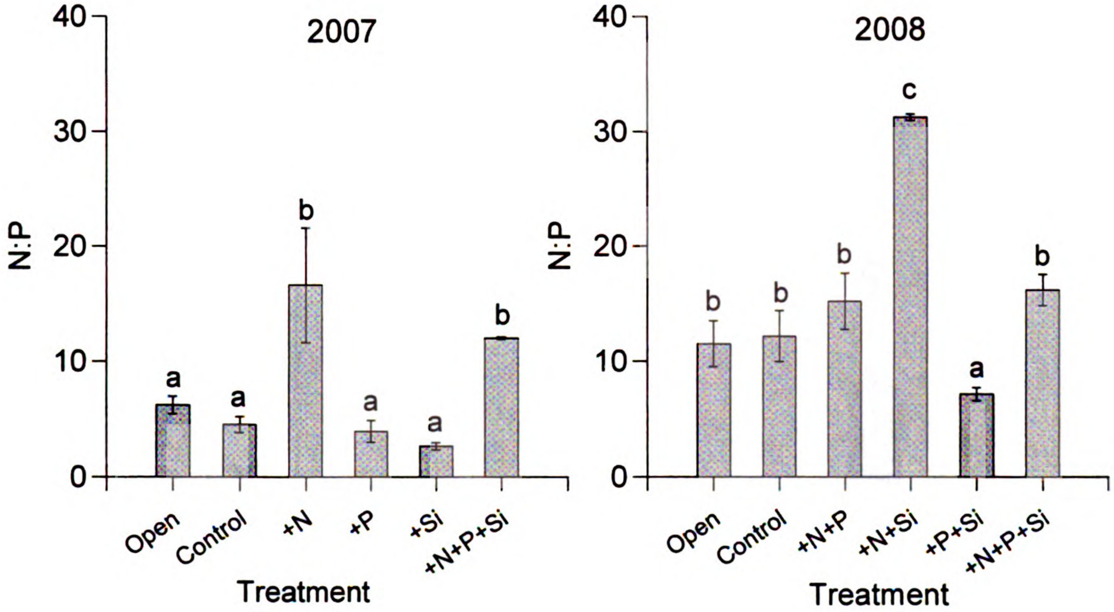

Figure 2.5 Comparison of algal N:P ratios among treatment enclosures and the open wetland in 2007 and 2008. Bars are means of four replicates ± S.E. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

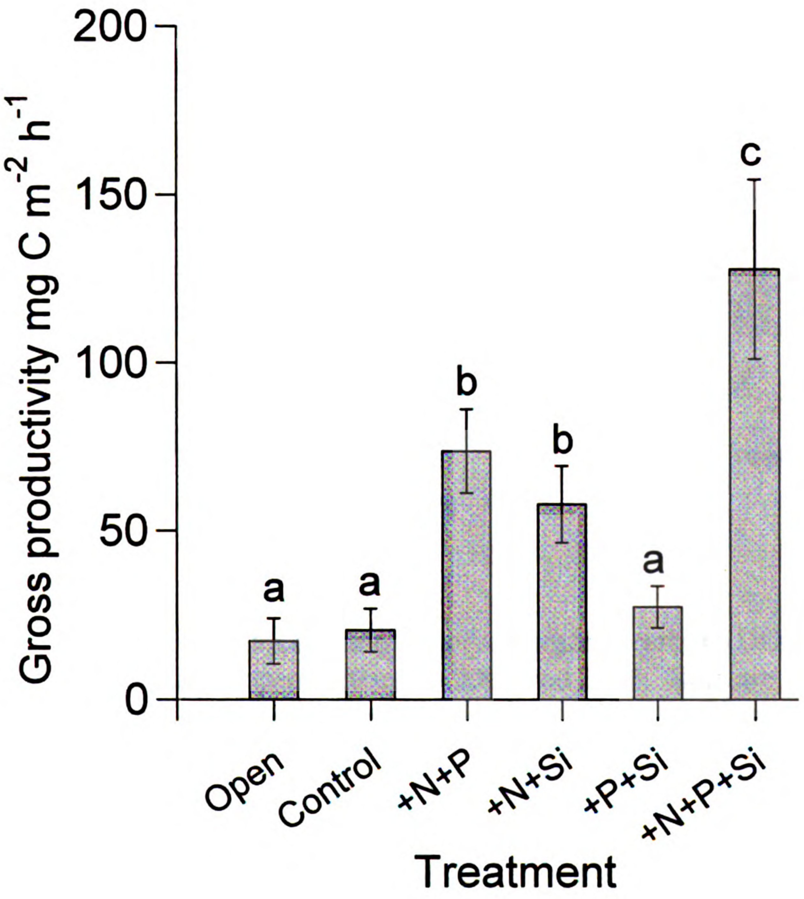

Figure 2.6 Comparison of algal primary productivity mg C m^{-2} h^{-1} among treatment enclosures and the open wetland in 2008. Bars are means of four replicates ± S.E. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

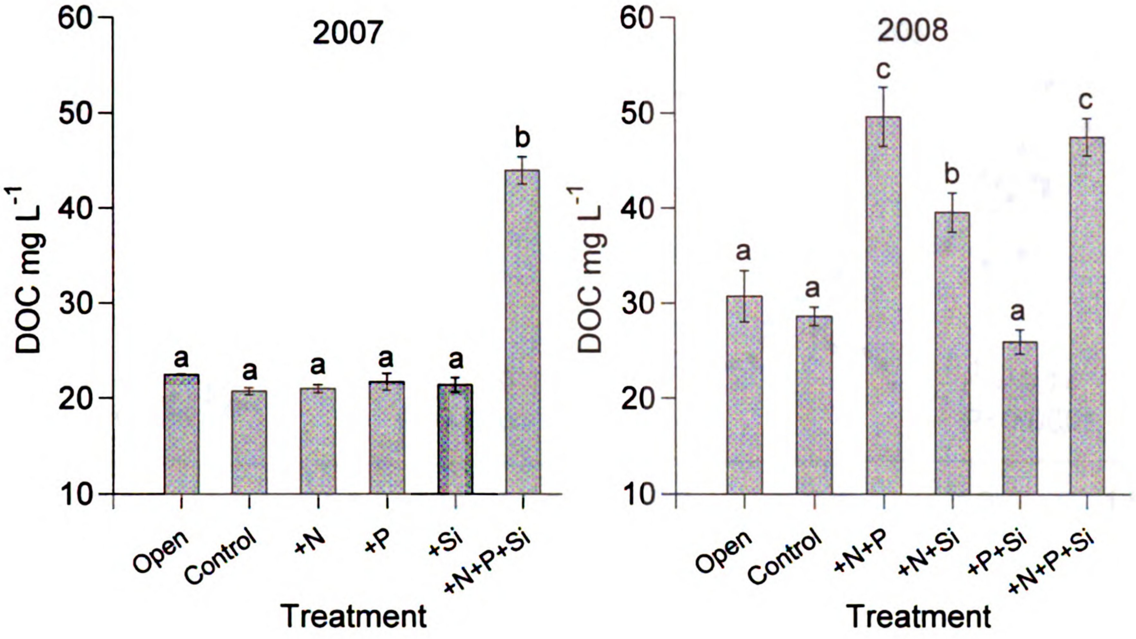

Figure 2.7 Comparison of water column dissolved organic carbon (DOC) mg L^{-1} among treatment enclosures and the open wetland in 2007 and 2008. Bars are means of four replicates ± S.E. Significant difference indicated by different letters above bars (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

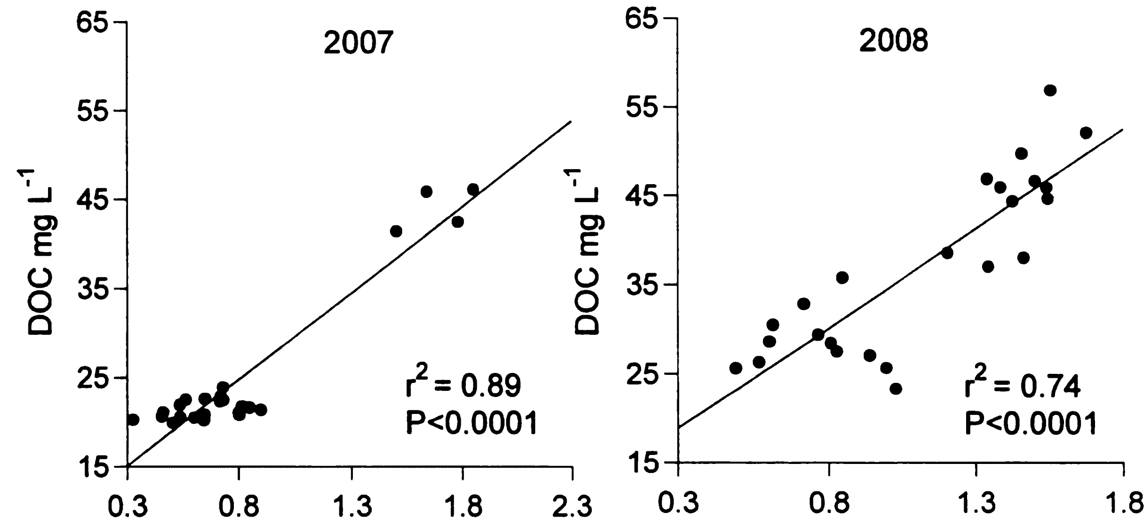

Figure 2.8 Linear regression analysis between log (x+1) Chlorophyll-*a* mg m^{-2} and water column dissolved organic carbon (DOC) mg L^{-1} across all treatment enclosures and the open wetland in 2007 and 2008.

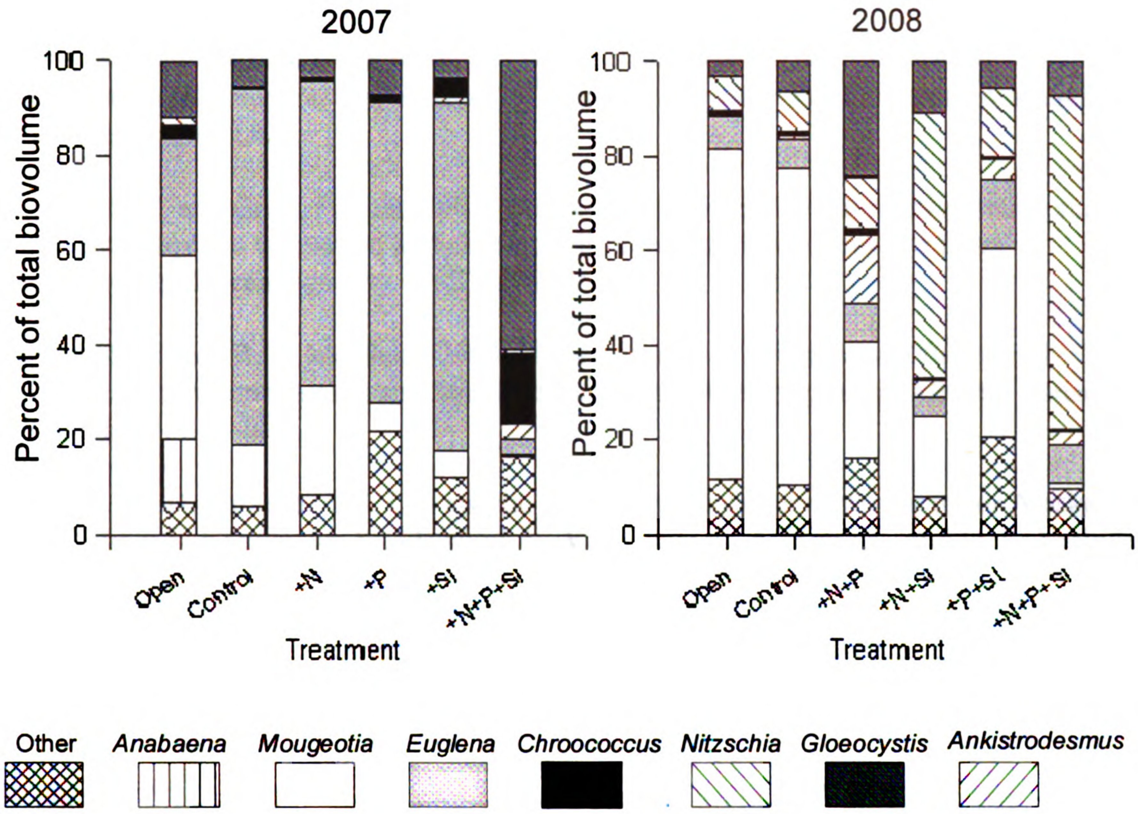

Figure 2.9 Percent of total biovolume of dominant algal genera in the open wetland and treatment enclosures following 24 days of enrichment in 2007 and 2008.

References

American Public Heath Association (APHA). 1998. Standard methods for the examination of water and wastewater, 20th edition. American Public Health Association, Washington, DC, USA.

Bayley, S. E. and C. M. Prather. 2003. Do wetland lakes exhibit alternative stable states? Submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. Limnology and Oceanography 48: 2335–2345.

Bayley, S. E. and R. L. Mewhort. 2004. Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24: 277–294.

Begét, J. E., D. Stone, and D. L. Verbyla. 2006. Regional overview of interior Alaska. p. 12–20. *In* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Borchardt, M. A. 1996. Nutrients. p. 183–227. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Bridgham, S., D. Johnston, A. Carol, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience 45(4): 262–274.

Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. Trettin. 2006. The carbon balance of North American wetlands. Wetlands 26: 889–916.

Browder, J. A., P. J. Gleason, and D. R. Swift. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. p. 379–418. *In* S. M. Davis and J.C. Ogden (eds.) Everglades, the Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. Canadian Journal of Fisheries and Aquatic Science 51: 681–692.

Carpenter, S. R., S. G. Fisher, N. B. Grimm, and J. F. Kitchell. 1992. Global change and freshwater ecosystems. Ecology and Systematics 23: 119–139.

Chapin, F. S. III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) 2006. Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Chu, S. P. 1942. The influence of the mineral composition of the medium on the growth of planktonic diatoms: methods and culture media. Journal of Ecology 30: 284–325.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10: 1135–1142.

Ewe, S. M. L., E. E. Gaiser, D. L. Childers, D. Iwaniec, V. H. Rivera-Monroy, and R. R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. Hydrobiologia 569: 459–474.

Fairchild, G. W., R. L. Lowe, and W. B. Richardson. 1985. Algal periphyton growth on nutrient-diffusing substrates: an in situ bioassay. Ecology 66: 465–472.

Francoeur, S. N. 2001. Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. Journal of the North American Benthological Society 20: 358–368.

Gaiser, E. E., L. J. Scinto, J. H. Richards, K. Jayachandran, D. L. Childers, J. C. Trexler, and R. D. Jones. 2004. Phosphorus in periphyton mats provides the best metric for detecting low-level P enrichment in an oligotrophic wetland. Water Research 38: 507–516.

Gaiser, E. E., J. C. Trexler, J. H. Richards, D. L. Childers, D. Lee, A. L. Edwards, L. J. Scinto, K. Jayachandran, G. B. Noe, and R. D. Jones. 2005. Cascading ecological effects of low level phosphorus enrichment in the Florida Everglades. Journal of Environmental Quality 34: 717–723.

Gaiser, E. E., D. L. Childers, R. D. Jones, J. H. Richards, L. J. Scinto, and J. C. Trexler. 2006. Periphyton responses to eutrophication in the Florida Everglades: cross-system patterns of structural and compositional change. Limnology and Oceanography 51: 617–630.

Goldsborough, L. G. and G. G. C. Robinson. 1996. Pattern in wetlands. p. 77–117. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

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.

Gregory-Eaves, I., J. P. Smol, B. P. Finney, D. R. S. Lean, and M. E. Edwards. 2000. Characteristics and variation in lakes along a north–south transect in Alaska. Archiv für Hydrobiologie 147: 193–223.

Hall, J. V., W. E. Frayer, and B. O. Wilen. 1994. Status of Alaskan Wetlands. U.S. Fish and Wildlife Services, Alaska Region, Anchorage.

Hecky, R. E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence of the effects of enrichment. Limnology and Oceanography 33: 796–822.

Hillebrand, H., C. D. Durselen, D. Kirschtel, U. Pollingher, and T. Zohary. 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of Phycology 35: 403–424.

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. p. 39–61. *In* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Hooper-Reid, N. M. and G. G. C. Robinson. 1978. Seasonal dynamics of epiphytic algal growth in a marsh pond: composition, metabolism, and nutrient availability. Canadian Journal of Botany 56: 2441–2448.

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.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems.p. 110–127. *In* D. P. Lodge (ed.) Proceedings of the International Large River Symposium (LARS). Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110-127.

Komárek, J. and K. Anagnostidis. 1998. *Cyanoprokaryota 1. Teil: Chroococcales, Süsswasserflora von Mitteleuropa 19/1.* Fischer Verlag, Stuttart.

Lamberti, G. A. and J. W. Moore. 1984. Aquatic insects as primary consumers. p. 164–195. *In* V. H. Resh and D. M. Rosenberg (eds.) The Ecology of Aquatic Insects. Praeger Publishers, New York, USA.

Liebig, J. V. 1855. Principles of Agricultural Chemistry with Special Reference to the Late Researches Made in England. Dowden, Hutchinson and Ross, Stroudsburg.

Liston, S. E., S. Newman, and J. C. Trexler. 2008. Macroinvertebrate community response to eutrophication in an oligotrophic wetland: an in situ mesocosm experiment. Wetlands 28: 686–694.

Lowe, R. L. and G. D. Laliberte. 2006. Benthic stream algae: distribution and structure. p. 327–356. *In* F. R. Hauer and G.A. Lamberti (eds.) Methods in Stream Ecology, 2nd edition. Academic Press, San Diego, CA, USA.

McCormick, P. V., P. S. Rawlik., K. Lurding, E. P. Smith, and F. H. Sklar. 1996. Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15: 433–449.

McCormick, P. V. and R. J. Stevenson. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology 34: 726–733.

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

McCormick, P. V., M. B. O'Dell, R. B. E. Shuford III, J. G. Backus, and W. C. Kennedy. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. Aquatic Botany 71: 119–139.

McDougal, R. L., L. G. Goldsborough, and B. J. Hann. 1997. Responses of a prairie wetland to press and pulse additions of inorganic nitrogen and phosphorus: production by planktonic and benthic algae. Archiv für Hydrobiologie 140: 145–167.

Mitsch, W. J. and J. G. Gosselink. 2006. Wetlands 4th edition. John Wiley and Sons, Inc., New York, USA.

Myklestad, S. M. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. The Science of the Total Environment 165: 155–164.

Pienitz, R., J. P. Smol, and D. R. S. Lean. 1997a. Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). Canadian Journal of Fisheries and Aquatic Sciences 54: 330–346.

Pienitz, R., J. P. Smol, and D. R. S. Lean. 1997b. Physical and chemical limnology of 24 lakes located between Yellowknife and Contwoyto Lake, Northwest Territories (Canada). Canadian Journal of Fisheries and Aquatic Sciences 54: 347–358.

Reddy, K. R. and R. D. DeLaune. 2008. Biogeochemistry of Wetlands. CRC Press, Boca Raton, FL, USA.

Richardson, C. J. 2009. The Everglades: North America's subtropical wetland. Wetlands Ecology and Management doi 10.1007/s11273-009-9156-4.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 1997a. The 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. 1997b. The primary productivity of benthic and planktonic algae in a prairie wetland under controlled water-table regimes. Wetlands 17: 182–194.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 2000. Algae in Prairie Wetlands. p. 163–199. *In* H. R. Murkin, A.G. van der Valk, and W.R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

Rodusky, A. J., A. D. Steinman, T. L. East, B. Sharfstein, and R. M. Meeker. 2001. Periphyton nutrient limitation and other potential growth-controlling factors in Lake Okeechobee, USA. Hydrobiologia 448: 27–39.

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. Rouet, and J. P. Smol. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrological Processes 11: 873–902.

Scott, J. T., R. D. Doyle, and C. T. Filstrup. 2005 Periphyton nutrient limitation and nitrogen fixation potential along a wetland nutrient-depletion gradient. Wetlands 25: 439–448.

Sedinger, J. S. 1997. Waterfowl and wetland ecology in Alaska. p. 155–178. *In* A. M. Milner and M. W. Oswood (eds.) Freshwaters of Alaska: Ecological Syntheses. Springer-Verlag, New York, USA.

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.

Sharp, J. H. 1977. Excretion of organic matter by marine phytoplankton: do healthy cells do it? Limnology and Oceanography 22: 381–399.

Stevenson, R. J. and R. Glover. 1993. Effects of algal density and current on ion transport through periphyton communities. Limnology and Oceanography 38: 1276–1281.

Stevenson, R. J., M. L. Bothwell, and R. L. Lowe (eds.). 1996. Algal Ecology: FreshwaterBenthic Ecosystems. Academic Press, New York, USA.

Tank, J. L. and W. K. Dodds. 2003. Nutrient limitation of epilithic and epixylic biofilms in 10 North American streams. Freshwater Biology 48: 1031–1049.

Vymazal, J. 1995. Algae and Element Cycling in Wetlands. Lewis Publishers, Ann Arbor, MI, USA.

Wetzel, R. G. 1996. Benthic algae and nutrient cycling in lentic freshwater ecosystems. p. 641–667. *In* R. J. Stevenson, M.L. Bothwell, and R.L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Wetzel, R. G. and G. E. Likens. 2000. Limnological Analyses, 3rd edition. Springer-Verlag, New York, USA.

Wickland, K. P., J. C. Neff, and G. R. Aiken. 2007. Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems 10: 1323–1340.

Zar, J. H. 1999. Biostatistical Analysis. Prentice Hall, Upper Saddle River, NJ, USA.

CHAPTER 3

Effects of acidification and alkalinization on a periphytic algal community in an Alaskan wetland

3.1 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, I 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, I 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, I expected that alkaline condition would result in an algal community comprising few acidophilic taxa. I 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).

3.2 Methods

Study Location

I 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.). I 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

I 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. I 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.

I 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. I 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. I added an average of 2.5 ml 2.5% H_2SO_4 every 2 days over the first 12 days to maintain pH 5, and an average of 2 ml 2.5% NaOH every 2 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 (Figure 3.1). 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) (Figure 3.1), I 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 I observed algae growing on submerged stalks of *Equisetum* in the open water area of the wetland. I 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. I allowed algae to colonize on stems inside enclosures with stabilized experimental pH levels for 24 days (4 – 28 July 2007). Stems remained sturdy during the colonization period without noticeable differences in texture among stems removed from different treatment enclosures.

I 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, I measured light transparency as photosynthetically active radiation (PAR) (μmol quanta m^{-2} s^{-1}) using a LI-COR quantum sensor (LI-COR, Lincoln, NE, U.S.A). I filtered water directly from enclosures using a 0.45 μm syringe-driven filter unit and collected 2 unfiltered water samples for nutrient analysis in 125-ml acid-rinsed polyethylene bottles. To evaluate container effects, I 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. I 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. Soluble reactive phosphorus (SRP) was measured following the ascorbic acid method using a Genesys™ 2 UV-Vis spectrophotometer. 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, I 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. I 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. I later measured chlorophyll-*a* fluorometrically after extraction with 90% ethanol and corrected for phaeophytin (APHA 1998). I preserved a separate aliquot with 2.5% formalin for algal compositional analysis and ash-free dry mass (AFDM). I determined AFDM following standard methods (APHA 1998). I 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. I later identified and counted between 300-500 algal cells or colonies per preserved sample using a Palmer-Maloney nanoplankton counter chamber at 400x magnification with taxonomy following Prescott (1962) and Komárek and Anagnostidis (1998, 2005). For diatom compositional analysis, I acid-cleaned an aliquot of each sample and mounted cleaned diatoms to a microslide using NAPHRAX® mounting medium. I identified and enumerated diatom valves at 1000x 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). I 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. I 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. My 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. I 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, I used a Tukey's test to calculate which treatments were significantly different.

3.3 Results

Water depth and temperature varied over time during each experiment, but did not differ significantly among treatments ($P > 0.05$). After exposure to 24 days of experimental pH levels, alkalinity ($F_{2,9} = 4278.52$, $P < 0.0001$) and DIC ($F_{2,9} = 8309.49$,

$P < 0.0001$) were significantly lower in the acid treatment compared to the alkaline and control treatments (Table 3.1). Photosynthetically 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 3.1). 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 3.1), 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 ($F_{2,9} = 6.43$, $P = 0.0185$), g AFDM ($F_{2,9} = 14.39$, $P = 0.0016$) and total biovolume ($F_{2,9} = 5.54$, $P = 0.0270$) were significantly greater in the alkaline treatment compared to the acid and control treatments (Figure 3.2). Algal cell density was significantly greater in the alkaline treatment compared to the control ($F_{2,9} = 4.50$, $P = 0.0441$), but not significantly different compared to the acid treatment (Figure 3.2). 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 ($F_{2,9} = 4.96$, $P = 0.0353$; Figure 3.3).

Cyanobacteria, green algae (Chlorophyta) and euglenoids (Euglenophyta) comprised approximately 32, 28 and 38%, respectively, of the total cell density in the control treatment (Figure 3.4). 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 (Figure 3.4). 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 (ANOVA, Bonferroni adjusted: $P_{significant} < 0.005$). The relative abundance of a diatom *Achnanthidium* (mainly *A. minutissimum* (Kützing) Czarnecki) ($F_{2,9} = 9.36$, $P = 0.0043$) was significantly greater, and *Anabaena* (Cyanobacteria) ($F_{2,9} = 17.86$, $P = 0.0007$), *Gloeocystis* (Chlorophyta) ($F_{2,9} = 10.06$, $P = 0.0043$) and *Euglena* (Euglenophyta) ($F_{2,9} = 11.67$, $P = 0.0032$) were significantly lower in the acid treatment compared to the control treatment (Table 3.2). In the alkaline treatment, the relative abundance of *Nitzschia* (mainly *N. linearis* W. Smith) ($F_{2,9} = 15.97$, $P = 0.0011$) and *Chroococcus* (Cyanobacteria) ($F_{2,9} = 10.04$, $P = 0.0041$) were significantly greater, and *Limnothrix* (Cyanobacteria) ($F_{2,9} = 10.82$, $P = 0.0046$) and *Euglena* ($F_{2,9} = 11.67$, $P = 0.0032$) were significantly lower compared to the control treatment (Table 3.2).

Euglenoids represented the greatest percentage of total biovolume among treatment enclosures, comprising approximately 63, 62 and 79% in alkaline, acid and control treatments, respectively (Figure 3.4). The proportion of algal groups was similar among treatments (ANOVA, Bonferroni adjusted: $P_{significant} < 0.013$), but there were significant differences at the genus level (ANOVA, Bonferroni adjusted: $P_{significant} < 0.005$). The relative biovolume of *Nitzschia* ($F_{2,9} = 18.11$, $P = 0.0007$) and *Trachelomonas* (Euglenophyta) ($F_{2,9} = 17.6576$, $P = 0.0014$) were significantly greater, and *Euglena* ($F_{2,9} = 14.78$, $P = 0.0026$) was significantly lower in the alkaline treatment compared to the control treatment (Table 3.2). In the acid treatment, the relative biovolume of *Mougeotia* (Chlorophyta, Zygnemataceae) was significantly greater ($F_{2,9}$ = 13.29, P = 0.0021), and *Anabaena* was significantly lower ($F_{2,9}$ = 17.80, P = 0.0007) compared to the control treatment (Table 3.2).

3.4 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 my 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, which generally proliferate in conditions of low pH.

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, I 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 I observed in the water column of the alkaline treatment (i.e., Hörnström 1999).

I 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% reduction in taxa richness that I 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 my 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 (i.e., 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 my 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 ($< 127\ \mu m^3$), 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 4.46 and 7.29. I 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 concentration (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 (i.e., 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 my 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. I 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.

Table 3.1 Mean values (± S.E.) of photosynthetically 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.

Table 3.2 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

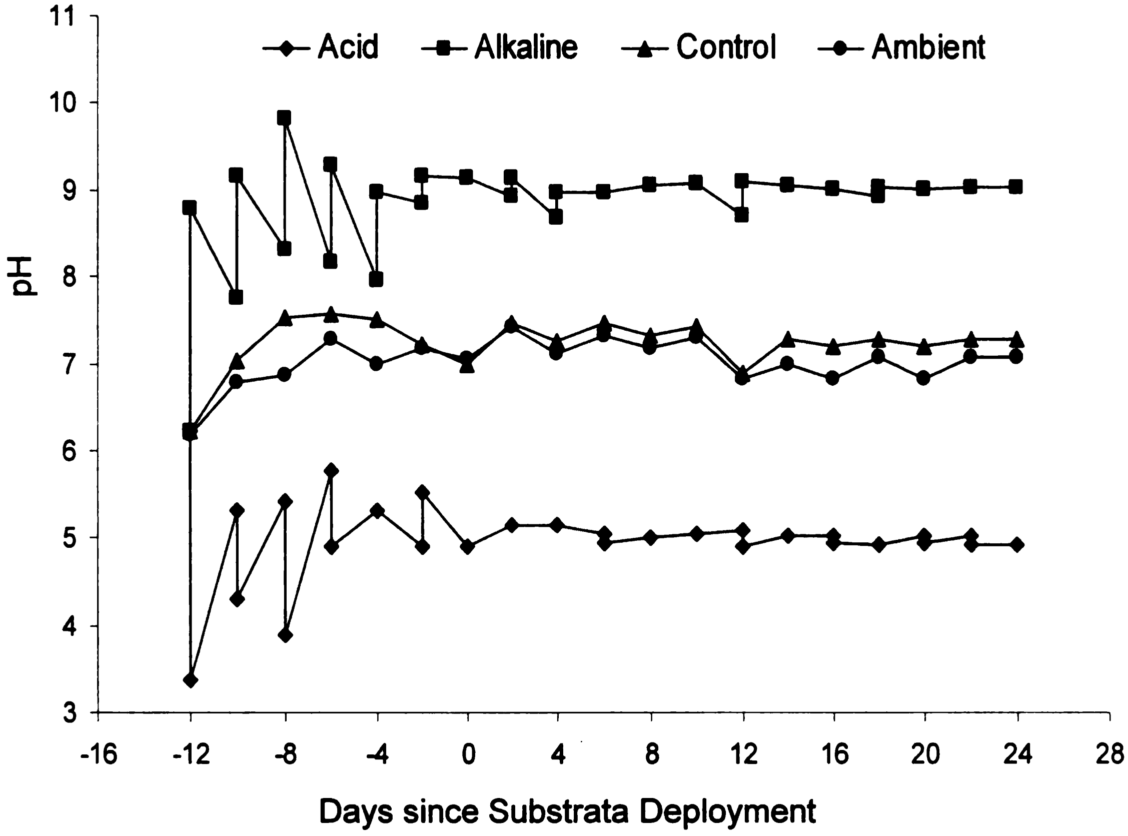

Figure 3.1 Mean pH levels during the stabilization period before algal substrata were deployed and during substrata deployment in the acid, alkaline, and control treatment enclosures and in the surrounding water (ambient). Days with two data points connected with a line in acid and alkaline treatments indicate pH levels before and after acid and base additions, respectively. Points are means of four replicates.

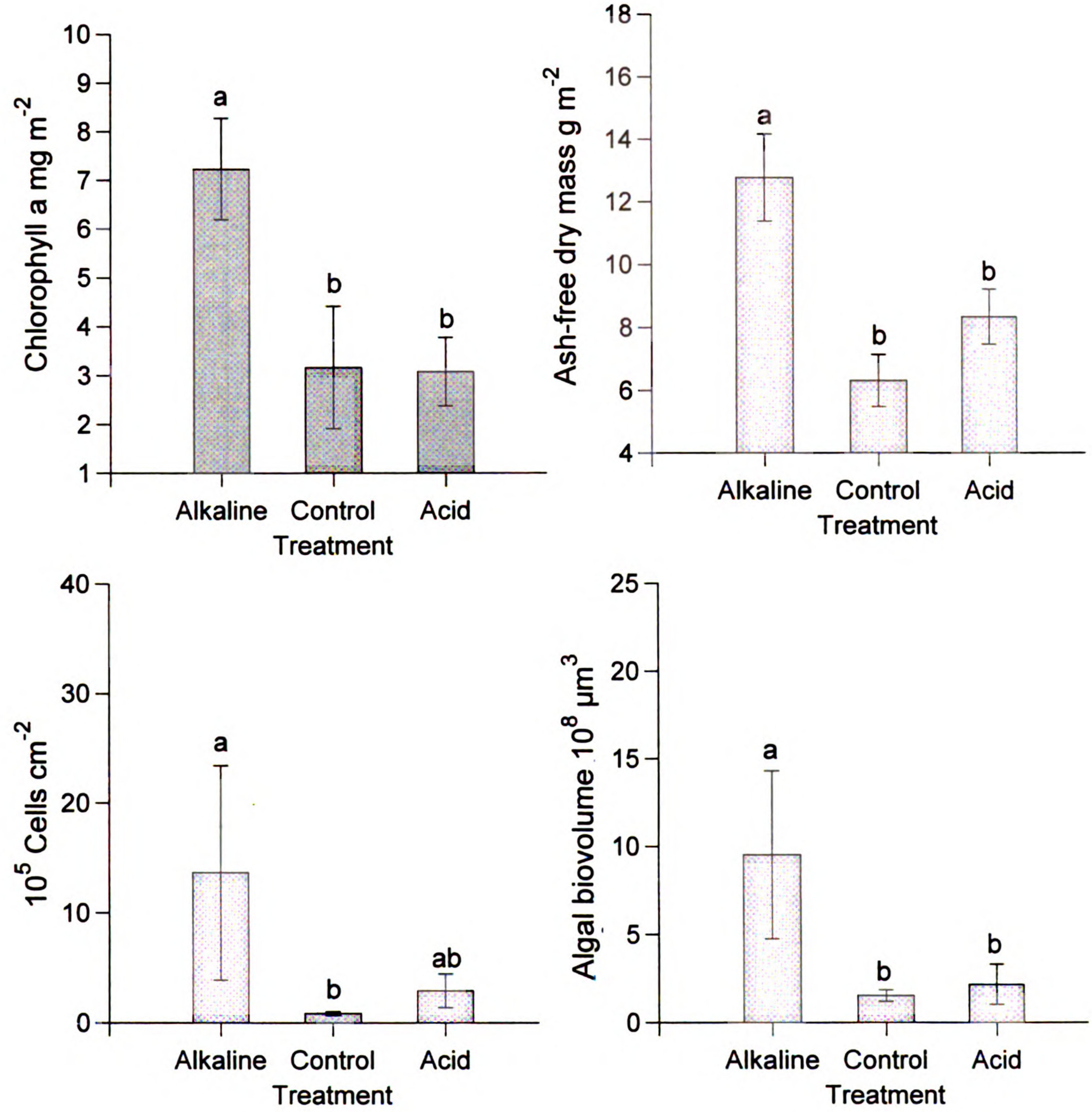

Figure 3.2 Comparison of mean chlorophyll-*a* concentration, ash-free dry mass, algal cell abundance and biovolume among the control (pH = 7.2) and pH manipulated enclosures (Acid: pH = 5.0; Alkaline: pH = 9.0). Bars are means of four replicates ± S.E. Bars with the same letters are not significantly different (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

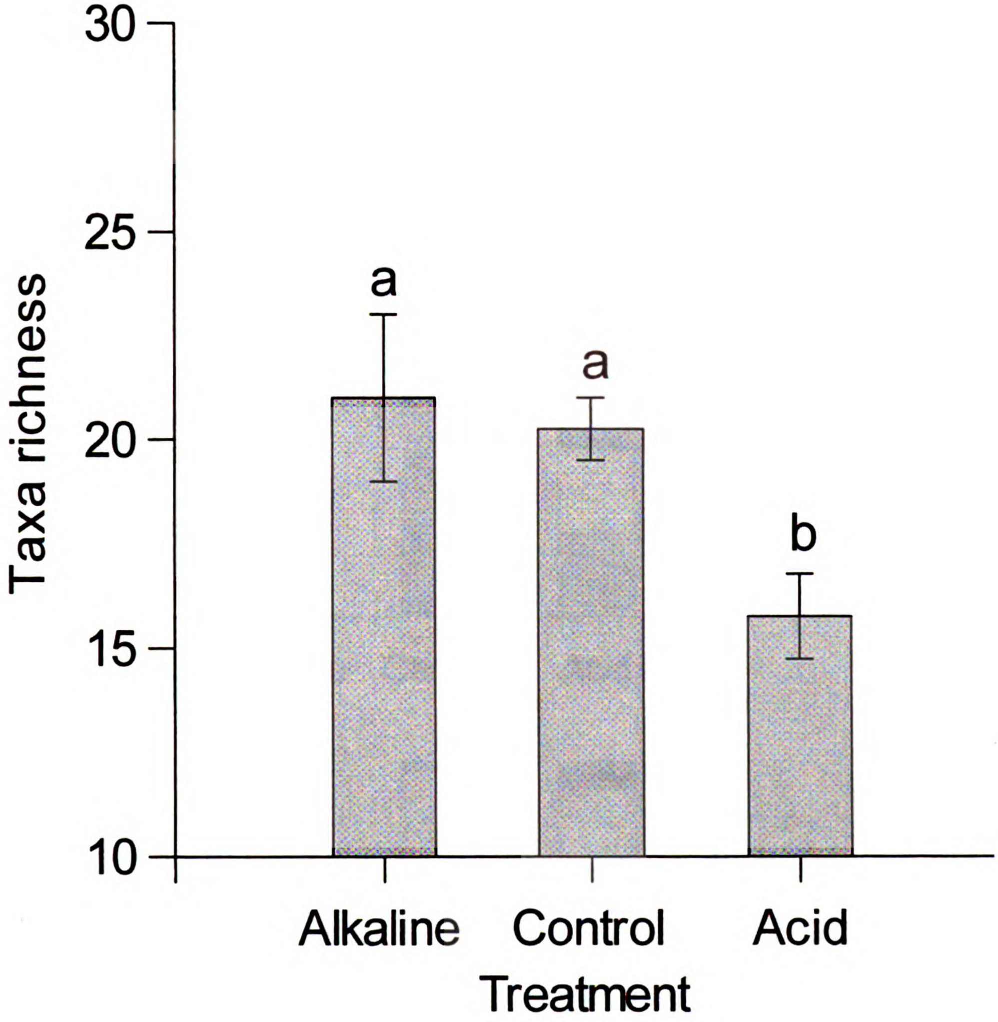

Figure 3.3 Mean taxa richness from substrata exposed for 24 days in pH-manipulated enclosures (Acid: pH = 5.0; Control: pH = 7.2; Alkaline: pH = 9.0). Bars are means of four replicates ± S.E. Bars with the same letters are not significantly different (ANOVA, $P < 0.05$, Tukey's test $P < 0.05$).

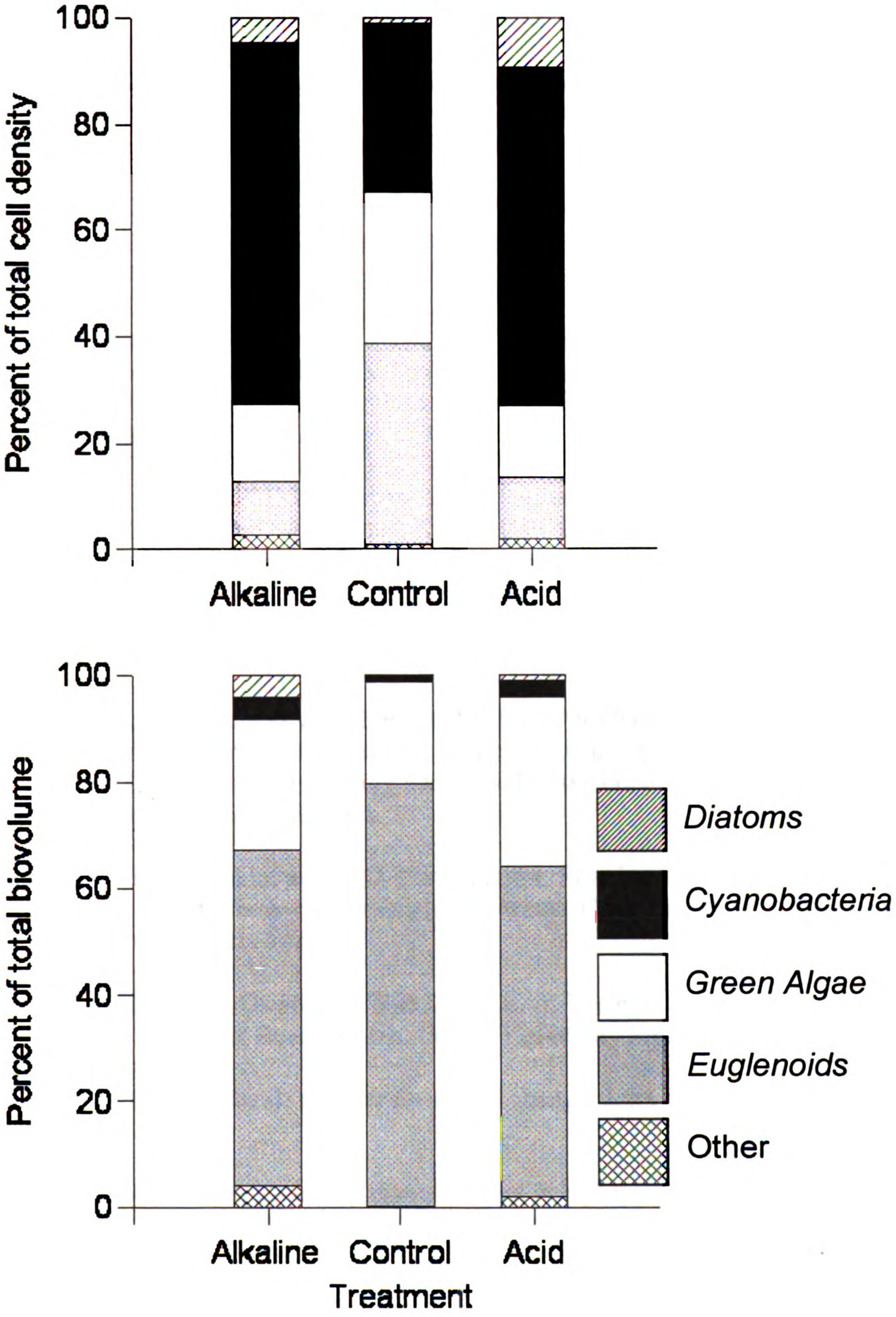

Figure 3.4 The structure of main algal groups on substrata exposed for 24 days in the control treatment (pH = 7.2) and pH-manipulated enclosures (Acid: pH = 5.0; Alkaline: pH = 9.0).

References

Almer, B., W. Dickson, C. Ekström, and E. Hörnström. 1978. Sulfur pollution and the aquatic ecosystem. p. 271–311. *In* J. O. Nriagu (ed.) Sulfur in the Environment. Part 2. Ecological Impacts. Wiley, New York, USA.

American Public Health Association (APHA). 1998. Standard Methods for the Examination of Water and Wastewater, 20th edition. American Public Health Association, Washington, DC, USA.

Arancibia-Avila, P., J. R. Coleman, W. A. Russin, L. W. Wilcox, J. M. Graham, and L. E. Graham. 2000. Effects of pH on cell morphology and carbonic anhydrase activity and localization in bloom-forming *Mougeotia* (Chlorophyta, Charophyceae). Canadian Journal of Botany 78: 1206–1214.

Begét, J. E., D. Stone, and D. L. Verbyla. 2006. Regional overview of interior Alaska. p. 12–20. *In* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Brock, T. D. 1973. Lower pH limit for the existence of blue-green algae: evolutionary and ecological implication. Science 179: 480–483.

Browder, J. A., P. J. Gleason, and D. R. Swift. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. p. 379–418. *In* S. M. Davis and J. C. Ogden (eds.) Everglades: The Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. Canadian Journal of Fisheries and Aquatic Sciences 51: 681–692.

Chapin, F. S. III, M. W. Oswood, K Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.). 2006. Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Charman, D. 2002. Peatlands and environmental change. John Wiley, Sons, Inc., New York, USA.

DeNicola, D. M. 2000. A review of diatoms found in highly acidic environments. Hydrobiologia 433: 111–122.

Ewe, S. M. L., E. F. Gaiser, D. L. Childers, V. H. Rivera-Monroy, D. Iwaniec, J. Fourquerean, and R. R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) in the Florida Coastal Everglades LTER (2001-2004). Hydrobiologia 569: 459–474.

Fairchild, G. W. and J. W. Sherman. 1990. Effects of liming on nutrient limitation of epilithic algae in an acid lake. Water, Air, and Soil Pollution 52: 133–147.

Fairchild, G. W. and J. W. Sherman. 1992. Linkage between epilithic algal growth and water column nutrients in softwater lakes. Canadian Journal of Fisheries and Aquatic Sciences 49: 1641–1649.

Fritz, S. C., A. M. Kreiser, P. G. Appleby, and R. W. Battarbee. 1990. Recent acidification of upland lakes in North Wales: Paleolimnological evidence. p. 27–37. *In* K. W. Edwards, A. S. Gee, and J. H. Stoner (eds.) Acid Water in Wales. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Goldsborough, L. G. and G. G. C. Robinson. 1996. Patterns in wetlands. p. 77–117. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

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, CA, USA.

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.

Hall, J. V., W. E. Frayer, and B. O. Wilen. 1994. Status of Alaskan wetlands. U.S. Fish and Wildlife Service, Alaska Region, Anchorage, AK, USA.

Hecky, R. E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence of the effects of enrichment. Limnology and Oceanography 33: 796–822.

Hillebrand, H., C. D. Dürselen, D. B. Kirschtel, U. Pollingher, and T. Zohary. 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of Phycology 35: 403–424.

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. p. 39–61. *In* F. S. Chapin, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Hörnström, E. 1999. Long-term phytoplankton changes in acid and limed lakes in SW Sweden. Hydrobiologia 394: 93–102.

Hörnström, E. 2002. Phytoplankton in 63 limed lakes in comparison with the distribution in 500 untreated lakes with varying pH. Hydrobiologia 470: 115–126.

Hultberg, H. and I. B. Andersson. 1982. Liming of acidified lakes: induced long-term changes. Water, Air, and Soil Pollution 18: 311–331.

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.

Jackson, M. B., E. M. Vandermeer, N. Lester, J. A. Booth, L. Molot, and I. M. Gray. 1990. Effects of neutralization and early reacidification on filamentous algae and macrophytes in Bowland Lake. Canadian Journal of Fisheries and Aquatic Sciences 47: 432–439.

Klug, J. K. and J. M. Fischer. 2000. Factors influencing the growth of Mougeotia in experimentally acidified mesocosms. Canadian Journal of Fisheries and Aquatic Sciences 57: 538–547.

Komárek, J. and K. Anagnostidis. 1998. Cyanoprokaryota 1. Teil: Chroococcales, Süsswasserflora von Mitteleuropa 19/1. Fischer Verlag, Stuttart, Germany.

Komárek, J. and K. Anagnostidis. 2005. Cyanoprokaryota 2. Teil: Oscillatoriales, Spektrum Akademischer Verlag 19/2. Elsevier GmbH, München.

Krammer, K. and H. Lange-Bertalot. 1986. Bacillariophyceae, teil 1. Naviculaceae. Spektrum Akademischer Verlag, Heidelberg, Germany.

Krammer, K. and H. Lange-Bertalot. 1988. Bacillariophyceae, teil 2. Epithemiaceae, Bacillariophyceae, Surirellaceae. Spektrum Akademischer Verlag, Heidelberg, Germany.

Krammer, K. and H. Lange-Bertalot. 1991a. Bacillariophyceae, teil 3. Centrales, Fragilariaceae, Eunotiaceae, Achnanthaceae. Spektrum Akademischer Verlag, Heidelberg, Germany.

Krammer, K. and H. Lange-Bertalot. 1991b. Bacillariophyceae, teil 4. Achnanthaceae, kritische erganzungen zu *Navicula* (lineolate) und *Gomphonema*. Spektrum Akademischer Verlag, Heidelberg, Germany.

Lackey, J. B. 1968. Ecology of *Euglena*. p. 27–44. *In* D. E. Buetow (ed.) The Biology of Euglena, Vol. 1. Academic Press, New York, USA.

Lamberti, G. A. and J. W. Moore. 1984. Aquatic insects as primary consumers. p. 164–195. *In* V. H. Resh and D. M. Rosenberg (eds.) The Ecology of Aquatic Insects. Praeger Publishers, New York, USA.

Lazarek, S. 1982. Structure and function of a cyanophyton mat community in an acidified lake. Canadian Journal of Botany 60: 2235–2240.

Lougheed, V. L., M. D. McIntosh, C. A. Parker, and R. J. Stevenson. 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. Freshwater Biology 53: 2402–2413.

McCormick, P. V. and R. J. Stevenson. 1998. Periphyton as a tool for ecological assessment and management in the Florida Everglades. Journal of Phycology 34: 726–733.

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.

Müller, P. 1980. Effects of artifical acidification on the growth of periphyton. Canadian Journal of Fisheries and Aquatic Sciences 37: 355–363.

Murkin, H. R. 1989. The basis for food chains in prairie wetlands. p. 316-338. *In* A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Negro, A. I., C. DeHoyos, and J. J. Aldasoro. 2003. Diatom and desmid relationships with the environment in mountain lakes and mires of NW Spain. Hydrobiologia 505: 1–13.

Olaveson, M. M. and C. Nalewajko. 2000. Effects of acidity on the growth of two *Euglena* species. Hydrobiologia 433: 39–56.

Olem, H. 1991. Liming Acidic Surface Waters. Lewis Publishers, Chelsea, MI, USA.

Olsson, H. 1983. Origin and production of phosphatases in the acid Lake Gardsjon. Hydrobiologia 101: 49–58.

Osterkamp, T. E., L. Viereck, Y. Shur, M. T. Jorgenson, 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.

Pan, Y. D. and R. J. Stevenson. 1996. Gradient analysis of diatom assemblages in western Kentucky wetlands. Journal of Phycology 32: 222–232.

Planas, D. 1996. Acidification effects. p. 497–530. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Prescott, G. W. 1962. The Algae of the Western Great Lakes Area, With an Illustrated Key to the Genera of Desmids and Freshwater Diatoms. Wm. C. Brown Company, Dubuque, IA, USA.

Richardson, C. J. 2009. The Everglades: North America's subtropical wetland. Wetlands Ecology and Management doi: 10.1007/s11273-009-9156-4.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 2000. Algae in prairie wetlands. p. 163–198. *In* H. R. Murkin, A. G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

Rosowski, J. R. 2003. Photosynthetic englenoids. p. 383–416. *In* J. D. Wehr and R. G. Sheath (eds.) Freshwater Algae of North America: Ecology and Classification. Academic Press, New York, USA.

Schindler, D. W. 1988. Effects of acid rain on aquatic ecosystems. Science 239:149–157.

Schindler, D. W. 1997. Widespread effects of climate warming on freshwater ecosystems of North America. Hydrological Processes 11: 1043–1067.

Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. Science 228: 1395–1401.

Sedinger, J. S. 1997. Waterfowl and wetland ecology in Alaska. p. 155–178. *In* M. A. Milner and M. W. Oswood (eds.) Freshwaters of Alaska-Ecological Synthesis. Vol. 119. Ecological Studies. Springer-Verlag, New York, USA.

Sklar, F. H., M. J. Chimney, S. Newman, P. 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.

Smol, J. P., R. W. Battarbee, R. B. Davis, and J. Meriläinen (eds.). 1986. Diatoms and Lake Acidity. Junk Publishers, Dordrecht, The Netherlands.

Smucker, N. J. and M. L. Vis. 2009. Use of diatoms to assess agricultural and coal mining impacts on streams and a multiassemblage case study. Journal of the North American Benthological Society 28: 659–675.

Stevenson, R. J., R. Singer, D. A. Roberts, and C. W. Boylen. 1985. Patterns of epipelic algal abundance with depth, trophic status, and acidity of poorly buffered New Hampshire lakes. Canadian Journal of Fisheries and Aquatic Science 42: 1501–1512.

Stevenson, R. J., P. R. Sweets, Y. Pan, and R. E. Schultz. 1999. Algal community patterns in wetlands and their use as indicators of ecological conditions. p. 517–527. *In* A. J. McComb and J. A. Davis (eds.) Proceedings of INTECOL's Vth International Wetland Conference. Gleneagles Press, Adelaide, Australia.

Stumm, W. and J. J. Morgan. 1996. Aquatic Chemistry, 3rd edition. John Wiley and Sons, Inc., New York, USA.

Sullivan, T. J. 2000. Aquatic Effects of Acidic Deposition. Lewis Publishers, Boca Raton, FL, USA.

Turner, M. A., M. B. Jackson, D. L. Findlay, R. W. Graham, E. R. DeBruyn, and E. M. Vandermeer. 1987. Early Responses of Periphyton to Experimental Lake Acidification. Canadian Journal of Fisheries and Aquatic Sciences 44: 135–149.

Turner, M. A., E. T. Howell, M. Summerby, R. H. Hesslein, D. L. Findlay, and M. B. Jackson. 1991. Changes in epilithon and epiphyton associated with experimental acidification of a lake to pH 5. Limnology and Oceanography 36: 1390–1405.

Turner, M. A., G. G. C. Robinson, B. E. Townsend, B. J. Hann, and J. A. Amaral. 1995a. Ecological effects of blooms of filamentous green algae in the littoral zone of an acid lake. Canadian Journal of Fisheries and Aquatic Sciences 52: 2264–2275.

Turner, M. A., D. W. Schindler, D. L. Findlay, M. B. Jackson, and G. G. C. Robinson. 1995b. Disruption of littoral algal associations by Experimental Lake acidification. Canadian Journal of Fisheries and Aquatic Sciences 52: 2238–2250.

van Dam, H., G. Suurmond, and C. J. F. ter Braak. 1981. Impact of acidification on diatoms and chemistry of Dutch moorland pools. Hydrobiologia 83: 425–459.

van Dam, H. and A. Mertens. 1995. Long-term changes of diatoms and chemistry in headwater streams polluted by atmospheric deposition of sulphur and nitrogen compounds. Freshwater Biology 34: 579–600.

Vymazal, J. 1995. Algae and Element Cycling in Wetlands. Lewis Publishers, Ann Arbor, MI, USA.

Walker, D. A., P. J. Webber, E. F. Binnian, K. R. Everett, N. D. Lederer, E. A. Nordstrand, and M. D. Walker. 1987. Cumulative impacts of oil fields on northern Alaskan landscapes. Science 238: 757–761.

Wetzel, R. G. 1996. Benthic algae and nutrient cycling in lentic freshwater ecosystems. p. 641–667. *In* R. J. Stevenson, M. L. Bothwell and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Wright, R. F. 1985. Chemistry of Lake Hovvatn, Norway, following liming and reacidification. Canadian Journal of Fisheries and Aquatic Sciences 42: 1103–1113.

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.

CHAPTER 4

Legacy effects of seasonal drying stimulate algal productivity following spring flooding in an Alaskan peatland: implications for carbon cycling in the Boreal Forest

4.1 Introduction

A pertinent issue in global change biology is to understand how climate change will affect carbon (C) cycling and energy flow in boreal peatlands. As a consequence, considerable effort has been made to quantify primary production in boreal peatlands, and to better understand environmental factors that influence this key ecosystem functional property (Wieder 2006). For the most part, estimates of primary production in these ecosystems have focused on submerged and emergent macrophytes (i.e., Thormann and Bayley 1997). As of yet, the contribution of other primary producers such as algae to the C pool of boreal peatlands is largely unknown, as is their response to the fluctuations in water level that is expected for this region with climate change (i.e., Hinzman et al. 2005).

Wetlands in boreal regions are experiencing significant changes in hydrology, in part because temperature regimes that have constrained water at or near the surface of permanently frozen soils in the region are increasing rapidly, and 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. 2002, 2007). Across the interior region of Alaska, the surface areas of open water bodies are already declining, likely due to increased summer moisture deficits associated with increased evapotranspiration, or drainage after permafrost thaw (Oechel et al. 2000, Yoshikawa and Hinzman 2003, Hinzman et al. 2005, Riordan et al. 2006). Alaskan wetlands are also strongly influenced by landscape topography, and thus some areas have experienced increased flooding from permafrost thaw and melt-water runoff from surrounding uplands (Osterkamp et al. 2000).

Changes in hydrology are likely to alter the chemical and physical conditions of aquatic ecosystems in the boreal region, including the movement of limiting nutrients into and out of wetland ecosystems (Rouse et al. 1997). Seasonal drought and exposure of sediments will likely oxygenate anaerobic soils and stimulate microbial decomposition, while flooding may release nutrients from sediments into the overlying water column (Schoenberg and Oliver 1988, Reddy et al. 1999, Thomas et al. 2006). Algae are sensitive to changes in hydrology as well as water quality, and thus, even small changes in water depth can result in desiccation (Thomas et al. 2006) or expose wetland algal communities to environmental conditions that can induce significant changes in community metabolism (Kahn and Wetzel 1999).

Algae are inextricably linked to fundamental processes in wetlands, and thus, may exert considerable control over energy flow. Few studies have traced the fate of algal C in wetlands, but it is generally considered more labile for heterotrophic metabolism than macrophyte tissue (i.e., Hart and Lovvorn 2003). A significant portion of C fixed by algae is excreted into the ambient water column as carbohydrates and other relatively available sugars (Giroldo et al. 2005, 2007). Several studies have shown the importance of algal exudates for heterotrophic metabolism in lakes and oceans (Jensen 1983, Baines and Pace 1991, Giroldo and Vieira 2005), but there is no information on their availability, or utilization as an energy source in boreal peatlands.

In this study, I monitored surface water chemistry and algal parameters following a spring flooding event at sites previously exposed to a four-year, ecosystem-scale water table manipulation in an Alaskan fen to test the hypothesis that hydrology is an important factor regulating algal productivity in boreal peatlands. Previous papers on this experiment have reported on the effect of water-table levels on peat nutrient cycling and transport (Kane et al. 2010), net primary productivity and plant community composition (Chivers et al. 2009) and CH_4 and CO_2 fluxes (Turetsky et al. 2008, Chivers et al. 2009). Here, I report the effect of these treatments on water column nutrient cycling and algal primary productivity. I expected that sites exposed to long-term drought would experience a flush of nutrients into the water column and increase algal productivity with reflooding. Additionally, I estimated the amount of C that is released by algae into the water column as well as the chemical characteristics and biodegradability of algal exudates that may be transported to downstream ecosystems.

4.2 Methods

Site description and water-table manipulation

This study was conducted at the Alaska Peatland Experiment (APEX) site, located on the floodplain of the Tanana River near the Bonanza Creek Experimental Forest, approximately 35 km southeast of Fairbanks, Alaska (64.82 °N, 147.87 °W). The area within interior Alaska is classified as continental boreal, with a mean annual temperature of –2.9°C and mean annual precipitation of 269 mm (Hinzman et al. 2006). The region experiences a relatively short growing season (135 days or less) with more than 21 h of light per day in June. The APEX site is a rich fen, which is the most common peatland type in western North America (Vitt 2006). The site lacks trees and is dominated by brown moss, *Sphagnum* and emergent vascular flora, including *Equisetum*, *Carex* and *Potentilla*.

The APEX study site is made up of three 120 m^2 plots including a control, lowered and raised water table treatment (Turetsky et al. 2008). Plots are located approximately 25 m apart and outlined by a raised boardwalk. Prior to water table manipulation in 2005, there were no significant differences in early growing season water table position or plant species composition across these three plots (Turetsky et al. 2008). A series of drainage canals (40 cm wide, 1 m deep) divert water from the lowered water table plot to a small holding trench down slope. Solar powered bilge pumps transport water into the raised water table treatment from a surface well at a rate of approximately 10 cm d^{-1}. The chemistry of water additions is similar to ambient pore water in the raised plot, with no significant differences in pH, electrical conductivity and concentrations of anions-cations or organic acids (Turetsky et al. 2008). A datalogger communication system maintains natural fluctuations in water table levels in the experimental treatments based on fluctuations in the control plot associated with precipitation and seasonal drying trends.

Throughout all four years of manipulation, the drained plot had a consistently lower water table height relative to the surface of the peat than the control plot, and the raised treatment plot has been consistently wetter (Figure 4.1; Kane et al. 2010). The mean (± standard error) monthly water table position during the growing season for the control and drained plots across all four years of manipulation was 7.2 ± 3.2 and 10.0 ± 3.8 cm beneath the surface of the peat, respectively, whereas the raised water table treatment had water 0.1 ± 2.2 cm above the peat surface on average (Kane et al. 2010). The water table position at the drained treatment is also generally more variable than at the control plot, whereas experimentally raising the water table height at the raised plot reduces fluctuations in water table height within the months of June, July and August.

While water table position is controlled to some degree within the experimental treatments, the considerable seasonal variation in water table height that is typical for this ecosystem continued to occur across all plots (Figure 4.1). In particular, the end of the summer in 2008 was one of the wettest on record, with over 275 mm of precipitation falling in interior Alaska between the months of May and October (National Atmospheric Deposition Program, station AK01). As a consequence of this, the region around the experimental plots became flooded in August-September 2008 and consequently, resulted in a subsequent flooding event following the spring thaw in 2009. While surface water conditions would only typically allow for continuous algal production at the raised water table treatment in previous years, this flooding event afforded a unique opportunity to examine the legacy effects of drainage on surface water chemistry and algal production, and the implications of this for DOC dynamics.

Surface water sampling

I monitored surface water chemistry and algal parameters within each of the water table treatments each week beginning on 25 May 2009, and then every two weeks beginning in July until the water table dropped below the peat surface on 27 July 2009. The height of the water table relative to the peat surface was measured inside polyvinyl chloride wells installed in each plot approximately weekly throughout the growing season. Surface water temperature, dissolved oxygen (DO) and pH were measured using a calibrated model 556 YSI® Multi-Probe (YSI Incorporated, Yellow Springs, OH, U.S.A.) on each sampling date. I filtered water for dissolved nutrient analysis using a 0.45 µm Millex®-HA syringe-driven filter unit (Millipore Corporation, Bedford, MA, U.S.A.) into 120 mL acid-rinsed polyethylene bottles. Samples were stored on ice until returning to the lab, where a portion of each filtered sample was analyzed for DOC using a Shimadzu TOC-V carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, U.S.A.). The remaining portion of each sample was frozen and stored until analysis. I analyzed water samples for dissolved inorganic nitrogen (DIN) as $NO_3 + NO_2$ following the cadmium reduction method and for silica (SiO_2) following the molybdate method using a Skalar® auto-analyzer (Skalar Analytical, Breda, Netherlands). Soluble reactive phosphorus (SRP) was measured following the ascorbic acid colorimetric method using a Genesys™ 2 UV-Vis spectrophotometer (Spectronic Analytical Instruments, Garforth, U.K.) (APHA 1998).

Quantifying algal biomass and productivity

I sampled algae at eight randomly selected locations in each of the three water table treatments for estimates of standing crop algal biomass and gross primary productivity (GPP) (mg C $m^{-2} h^{-1}$). Each of the eight samples was a composite sample of four 25 cm^2 collections removed from the peat surface and, when present, the submersed portions of the dominant emergent macrophyte. Because the APEX site is part of a long-term study, I used non-destructive methods for removing algae from submersed surfaces. I used a plastic turkey baster to remove algae from each 25 cm^2 quadrant until there were no loosely attached algae or biofilm present on the peat surface. In cases where algae were attached to erect plant stems, I scraped the submersed portion of four stems clean with a plastic spoon, and adjusted the surface area in subsequent calculations. Each algal sample was homogenized in 120 mL of water for analyses. I filtered ¼ volume of each homogenate onto a GF/F glass fiber filter and stored filters frozen in the dark for chlorophyll-*a* analysis, and I preserved ¼ for ash-free dry mass (AFDM). I 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). I determined AFDM following standard methods (APHA 1998). I 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.

I split ½ of each homogenized sample into two separate biological oxygen demand (BOD) bottles and estimated algal GPP (mg C $m^{-2} h^{-1}$) following McCormick et al. (1998). I filled each BOD bottle with filtered water from the wetland and recorded initial DO using a Hach HQ 40d luminescent DO probe (Hach Company, Loveland, CO, U.S.A.). Bottles were sealed without trapping gas bubbles that would contribute to the initial oxygen concentration. I wrapped one bottle from each set with aluminum foil for incubation in the dark and determined productivity by measuring oxygen changes produced by algal samples incubated *in situ* in light and dark bottles. Bottles incubated uncovered and dark were used to measure net primary productivity and respiration, respectively. Bottles were incubated for 1–3 hours during midday hours, and at similar depths to provide the most accurate daily productivity rates. I calculated GPP following Wetzel and Likens (2000) and converted GPP values into units C based on a C:O molar ratio of 0.375 and a photosynthetic quotient of 1.2 (Wetzel and Likens 2000).

Quantifying algal-derived DOC

I evaluated changes in DOC concentrations in light bottles during productivity measurements on 20 June to evaluate the proportion of C fixed by algae during photosynthesis that was released into the overlying water column. I chose this sampling date because of the noticeable differences in standing stock algal biomass among plots, which I expected to produce a wide range of productivity rates (see results). Prior to light-dark bottle incubations, I filtered pore water through a 0.2 µm filter (VacuCap filters, Gelman Science) to eliminate most bacteria from solution, and then incubated algal samples for measures of GPP as described above. After the final DO reading, I filtered and acidified water from each light bottle for measurements of DOC concentration, and related changes in DOC concentration to measures of algal GPP during the 2 h incubation.

Characterization and degradation of algal exudates

I performed a laboratory incubation to evaluate the chemical characteristics and biodegradability of algal exudates. I collected algal exudates by incubating samples collected on 20 June in a clear polyethylene container filled with sterile milli-Q water in the sunlight for 12 h. The incubation process was not sterile, but bacterial densities were less than 1×10^5 bacteria L^{-1}, which I assumed to have a low impact on the amount and quality of the DOC. I filtered algal exudates through a 0.2 μm filter (VacuCap filters, Gelman Science) into an acid-washed flask, and then further diluted the solution using Milli-Q water to approximately the same DOC concentration as the pore water of the APEX fen (25 mg L^{-1}). I also collected and filtered 2 L of pore water through a 0.2 μm filter for characterization and degradation patterns of ambient pore water DOC. I prepared a bacterial inoculum by filtering a portion of pore water through a 0.7 μm filter (GF/F filter, Whatman type). Other studies have shown that approximately 80% of bacterial cells pass through 0.7-μm pore size filters (Giroldo et al. 2007). Water samples were kept at a constant temperature (ca. 21°C) until the start of the experiment (2 h).

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

I analyzed samples during the incubation for UV-Vis absorption at λ =254 nm, the wavelength associated with aromatic compounds (Chin et al. 1994) using a UV-Mini 1240 Spectrophotometer (Shimadzu Scientific Instruments, Inc., Columbia, MD, U.S.A). I analyzed the samples for DOC and calculated SUVA by dividing UV-Vis absorbance at λ =254 nm by DOC concentration. SUVA of DOC is reported in units of L mg C^{-1} m^{-1}. It gives an "average" molar absorptivity for all the molecules contributing to the DOC in a sample, and it has been used as a measure of DOC aromaticity (Chin et al. 1994, Weishaar et al. 2003, Wickland et al. 2007).

The compositions of polymeric and free carbohydrates in pore water and algal exudates during the incubation were analyzed using high performance liquid chromatography coupled to pulse amperometric detection (HPLC–PAD) (Wicks et al. 1991, Gremm and Kaplan 1997). Samples were divided into two fractions before analysis: total dissolved carbohydrates (TDCHOs) and free dissolved carbohydrates (FDCHOs). Polymeric dissolved carbohydrates (PDCHOs) were determined by subtracting FDCHOs from TDCHOs. The FDCHO samples were injected directly into the HPLC system, while TDCHOs were hydrolyzed prior to injection (Gremm and Kaplan 1997).

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

$$\text{Degradation} \rightarrow CO_2 + \text{particulate organic C (microbial biomass)}$$

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

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

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

Bacterial growth was evaluated by direct counts using a Nikon Eclipse E800 epifluorescence microscope with UV and a light source after staining the cells with 4', 6-diamino-2-phenylindole (DAPI) (Porter and Feig 1980). At least 300 bacteria or 25 fields were counted per filter.

Data Analysis

All statistical analyses were performed using general linear models in SPSS 18 (SPSS inc., Chicago, 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. I used univariate repeated measures ANOVAs (rmANOVA) with an adjusted Bonferroni significance level ($P < 0.016$) and Tukey's test for post hoc comparison of means to determine if algal productivity and biomass were different among water table treatments. I used a linear mixed model that included environmental variables (water depth, water temperature, DO, DIN, SRP) and water table treatment to predict changes in algal productivity and biomass. I determined which environmental variables to include in the model using univariate repeated measures ANOVAs with an adjusted Bonferroni significance level. I used a Tukey's test to discriminate between different treatments. Although environmental variables were significantly different among treatments, they were not significant predictors of algal biomass or productivity within treatments; therefore I did not include results from the mixed model.

I evaluated the relationship between algal productivity and changes in DOC concentrations inside light bottle incubations using linear regression analysis. Differences in DOC concentration, SUVA and bacterial abundances among pore water and algal exudates during the degradation experiment were analyzed with t tests.

4.3 Results

Physical and Chemical Conditions

From May to July 2009, water table height in the APEX plots was not well regulated by draining and active pumping, but instead by variability associated with the spring flooding event (Figure 4.1). Water table depth above the peat surface decreased with time across all water table treatments following the spring snowmelt (Figure 4.1), but it was not significantly different among water table treatment plots ($P > 0.05$; Table 4.1). Water temperature increased in all treatments over time (Figure 4.2), but was consistently lower in the raised treatment compared to the control and lowered water table treatments ($F_{2,21} = 271.05$, $P < 0.001$; Table 4.1). Dissolved oxygen concentrations peaked in mid June, and were significantly greater only in the lowered water table treatment ($F_{2,21} = 5.29$, $P = 0.014$), where levels reached 12.7 ± 0.15 mg L^{-1}on 10 June before decreasing in all treatments thereafter (Figure 4.2).

Dissolved organic C concentrations tended to increase, and water column pH decreased with time across all treatments (Figure 4.2), but on average there were no differences in these variables among water table treatments (Table 4.1). Water column nutrient concentrations tended to peak in early June in all water table treatments (Figure 4.2). Nutrient levels decreased sharply in all treatments following the early season maxima, and remained similar among treatments for the remainder of the study (Figure 4.2). However, averaged across all sampling dates, levels of SRP ($F_{2,21} = 78.87$, $P < 0.0001$) and DIN ($F_{2,21} = 332.23$, $P < 0.0001$) varied among water table treatments, with greater mean concentrations in the lowered water table treatment relative to the control treatment (Table 4.1). SiO_2 levels were below detection in all treatments throughout the summer growing season.

Algal Biomass, Productivity and Algal Exudates

Averaged across sampling date, algal GPP (mg C m^{-2} h^{-1}), g AFDM and chlorophyll-*a* concentration were consistently higher in the lowered water table treatment than in the control or raised water table treatments (Figure 4.3; GPP - $F_{2,21} = 55.70$, $P < 0.0001$; AFDM - $F_{2,21} = 113.79$, $P < 0.0001$; chlorophyll-*a* $F_{2,21} = 83.62$, $P < 0.0001$). Measures of algal biomass and GPP peaked immediately following the maxima in nutrient concentrations (Figure 4.3). Nutrient concentrations then fell sharply immediately following the maxima in algal biomass (Figure 4.2), especially in the lowered water table treatment.

Dissolved organic C concentration (mg C L^{-1} h^{-1}) increased with algal GPP (mg C L^{-1} h^{-1}) during *in situ* incubations ($R^2 = 0.847$, $P < 0.0001$; Figure 4.4). By dividing the rate of DOC change by GPP, I calculated that algae released 0.18 ± 0.06 mg DOC L^{-1} h^{-1} into the water column for each mg C fixed during photosynthesis. When this rate is extrapolated to *in situ* measures of GPP, algae contributed 0.93 ± 0.31 – 6.84 ± 2.28 mg C L^{-1} h^{-1} to the overlying water column in the lowered water table treatment, 0.47 ± 0.03 – 2.48 ± 0.83 mg C L^{-1} h^{-1} in the control treatment and 0.02 ± 0.01 – 2.17 ± 0.73 mg C L^{-1} h^{-1} in the raised water table treatment for each m^2 of submersed substrate.

Characterization and degradation of algal exudates

Algal exudates decreased by 56% within the first 24 hours of incubation with the bacteria inoculum (Figure 4.5). SUVA levels increased by 38% over the same period in the algae treatment (Figure 4.5). Bacterial growth in algal exudates was significant (Figure 4.5), increasing from 0.73 ± 0.004 to 3.65 ± 0.030 10^6 cells mL^{-1}, reaching maximum density at 24 hours of incubation (3×10^6 bacteria mL^{-1}). Bacterial growth in algal exudates slowed when SUVA values reached between 2.3 and 2.5 L mg C^{-1} m^{-1}, but maintained a consistently higher bacterial density over 32 days compared to the pore water treatment (Figure 4.5). SUVA levels in the pore water remained near 2.5 L mg C^{-1} m^{-1}, which corresponded to low k values (0.00094 d^{-1}) relative to algal exudates (0.01818 d^{-1}), and low bacterial density (< 1.38 ± 0.025 10^6 cells mL^{-1}) throughout the incubation (Figure 4.5).

HPLC- PAD analysis showed that 5.57 mg L^{-1} or 25% of the total algal exudates were comprised of carbohydrates compared to 2.75 mg L^{-1} or 10.7% of the pore water. The decay coefficients for each monosaccharide, and also for the total carbohydrate pool released by algae are shown in Table 4.2. A combination of glucose, mannose and fructose made up 60% of the total carbohydrate composition of algal exudates (Table 4.3). These sugars had a higher k value (> 0.03435 d^{-1}) compared to arabinose, fucose, N-acetyl-glucosamine, rhamnose, galacturonic acid, xylose and galactose which made up 56.8% of the total carbohydrate composition of pore water (Table 4.2). No free monosacharide was detected, thus, the total carbohydrates were diagnosed as polymeric carbohydrates.

4.4 Discussion

This study adds to a growing pool of literature evaluating algal biomass and productivity in wetland ecosystems globally (Goldsborough and Robinson 1996, McCormick et al. 1998, 2001, Robinson et al. 2000, Ewe et al. 2006) and provides the first estimates of algal productivity for a rich fen in the boreal region of Alaska. These data allow us to make cross-system comparisons of algal productivity among different

wetland types in the boreal region (i.e., Wyatt et al. 2010) and to those occurring at lower latitudes (see review in Goldsborough and Robinson 1996). Compared to daily values reported for peatlands occurring at temperate climates (1.75–11.49 g C m^{-2} d^{-1}; McCormick et al. 1998), ambient rates of algal productivity in the APEX fen were lower (0.07 – 0.19 g C m^{-2} d^{-1}) and indicate that under current conditions, algae may contribute only a minor portion of overall primary productivity in boreal peatlands. Algal productivity at sites previously exposed to seasonal drought (0.12 – 0.80 g C m^{-2} d^{-1}) was consistently greater than for flooding and control treatments, suggesting that algae may become an increasingly important part of the C cycle in boreal peatlands with more variable hydrology expected for this region with future climate change.

During all four years of manipulation, differences in water table position have resulted in significant alteration of pore water chemistry among the treatment plots, including higher concentrations of total dissolved N in water samples collected from wells at the lowered water table plot relative to the raised and control plots (Kane et al. 2010). I anticipated that flooding over the APEX plots might simply re-set the ecosystem to conditions present before experimental manipulation. Instead, there was a sharp increase in surface water nutrient concentrations across experimental plots, especially in the lowered water table treatment. Since water table position was not hydrologically distinct among plots during the time of sampling, the significant increase in nutrient concentrations in the drought treatment points to the importance of drying during the previous growing seasons as being an important factor regulating nutrient dynamics following the spring thaw. Other studies have shown that drought can increase organic matter decomposition and translate into a pulse of nutrients from sediments into the overlying water column with re-inundation (see review in Boon 2006). Briggs et al. (1985) demonstrated this by collecting soils from a temporary wetland and immersing them in tanks in a glasshouse. In the Briggs et al (1985) study, concentrations of nitrate and inorganic P increased after 4 days of rewetting, but the response was short lived and there was no further net increase in nutrient concentrations up to 130 days of inundation.

The rapid reduction in nutrient levels that occurred in the lowered water table treatment after the early June peak was likely the result of assimilation by algae. This hypothesis is supported by an increase in algal productivity immediately following the spike in nutrient levels, and then by the rapid reduction in nutrient levels following the increase in algal productivity. The ability of algae to rapidly respond to, and assimilate nutrients from the water column has been well documented in wetlands receiving external nutrient inputs (Richardson 2009). In the Florida Everglades, algae can sequester P rapidly, making it almost undetectable in the water column only a few meters from the source (Gaiser et al. 2004). When I relate measures of algal biomass in the APEX fen to the average P content of algae per unit g dry mass reported from the Everglades (30 – 3750 μg P g^{-1}) (summarized by Noe et al. 2001), even at the extreme low end of this range, the potential for algae to sequester a significant amount of P during peak biomass in the drought treatment (160 – 20,025 μg P m^{-2}) becomes apparent.

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

Dissolved oxygen concentrations were near saturation levels during peak algal productivity in the drought treatment, and greater than those in adjacent water table treatments. These findings are similar to those reported from the Everglades, where algal photosynthesis in sloughs can raise daytime dissolved oxygen concentrations to levels much higher than those in nearby sawgrass stands with lower algal biomass (Richardson 2009). Wetlands with low daily oxygen levels generally show reduced respiration, and a shift to anaerobic processes due to the lack of available oxygen to support aerobic metabolism (McCormick et al. 1997). Likewise, greater rates of algal photosynthesis and higher water column dissolved oxygen concentrations typically indicate a photosynthesis to respiration (P/R) ratio greater than one (McCormick et al. 1997). The increase in photosynthesis that I observed in the lowered water table treatment indicates a P/R ratio greater than one and community metabolism dependent on autochthonous production.

The increase in DOC concentrations during light bottle incubations indicates that a significant portion of photo-assimilated C was released by algae into the ambient water column. My estimates of 18% exudates release are within the range (5-35%) of those reported for phytoplankton in other aquatic ecosystems (Myklestad 1995). When this estimate is extrapolated to measures of algal GPP in the drought treatment, I calculated that algae were contributing up to 26% of the DOC pool per hour during peak algal productivity. It is however, important to note that I measured algal exudates release immediately following the maxima in nutrient concentrations. The release of organic C, which is thought to work as an overflow mechanism to avoid damage of the photosynthetic apparatus (Smith and Underwood 2000), tends to increase with decreasing nutrient availability (Fogg 1983). Thus, my estimates may have underestimated the exudates release rate under nutrient limited conditions during the latter part of the growing season.

Despite the potential for algae to contribute to the peatland DOC pool, there were no differences in water column DOC concentrations among treatment plots during the growing season, even during periods of peak algal productivity in the drought treatment. Generally, algal exudates are produced and consumed by accumulating microbes at similar rates (Søndergaard et al. 1995), and I would not expect exudates to accumulate in the water column except during very brief periods of grazer control of the microbial community (Wright 1988). The high k values that I observed during the decomposition experiment confirmed this hypothesis, and indicated that algal exudates were degraded by a microbial inoculum much more quickly than fen porewater. HPLC-PAD analysis showed that a significant portion of algal exudates was comprised of carbohydrates, dominated by glucose, mannose and fructose, with k values an order of magnitude greater than arabinose, fucose, rhamnose, galacturonic acid, xylose and galactose, which made up a significant proportion of fen porewater.

When I consider that algal productivity values in the lowered water table treatment remained above 5.18 mg C $m^{-2} h^{-1}$ when water was above the peat surface, algae were likely an important energy source for heterotrophic metabolism throughout the growing season in the drought treatment. The increase in bacterial density that I observed in the presence of algal exudates could have important indirect effects on other ecosystem functions driven by microbes in boreal peatlands. For example, increases in microbial density could impact the ability of the bacterial community to decompose other, more recalcitrant substrates that are already present in solution, or any new substrates added to solution (i.e., Hamer and Marschner 2005). This process has been documented in soils (Kuzyakov et al. 2000), where a relatively small amount of labile substrate can result in a disproportionate turnover of more recalcitrant compounds C (i.e., the priming effect). The addition of algal exudates may be especially important for the microbial loop in boreal peatlands (i.e., Gilbert et al. 1998), where heterotrophic metabolism is often limited by available substrate, and the addition of labile materials such as glucose tends to increase decomposition (Bergman et al. 1998).

In many regions, northern wetlands are expected to experience warmer and drier climatic conditions under climate change. Interior Alaska already is experiencing changes in climate including increases in annual temperatures, increases in annual precipitation, longer growing seasons and altered snowpack dynamics (Serreze et al. 2000, Hinzman et al. 2005). Increased drought associated with increased evapotranspiration or drainage from permafrost degradation, coupled with a longer growing season (Serreze et al. 2000, Goetz et al. 2005, Euskirchen et al. 2006) and warmer temperatures (Serreze et al. 2000, Hinzman et al. 2005, McGuire et al. 2002, 2007) will likely increase microbial decomposition in the expanded active layer in boreal wetlands (e.g., Bridgham et al. 1995). Increased precipitation (e.g., Hinzman et al. 2005) and altered flow-paths associated increased runoff with permafrost degradation may result in greater flooding in regions previously exposed to seasonal drought (e.g., Osterkamp et al. 2000). While directly, drought will likely lead to algal desiccation and low overall productivity, subsequent flooding may increase algal productivity at sites previously exposed to drought due to the ability of algae to rapidly sequester available nutrients in the water column.

As new, more complex models of peatland C cycling are developed, a more comprehensive view of peatland primary productivity will be needed. While algae are not likely to contribute directly to long-term C storage in boreal peatlands, they may provide a new pathway for processes related to future climate change to alter energy flow within these ecosystems, as well as the quality of C exported to downstream ecosystems. In view of the magnitude of algal productivity demonstrated here and the acceptability of algal exudates to wetland bacteria, more detailed investigations of the role of algae in boreal peatland C cycling are warranted. The relationship between changes in algal community composition and changes in the chemical composition of algal exudates release should become a focus, as well as the changes in the bacterial community during the degradation of algal exudates. Studies correlating bacterial dynamics to the composition and structure of polysaccharides released by algae would supply important information about the possible extracellular roles of these compounds.

Table 4.1 Mean values (± 1 S.E.) of water table height, temperature, pH, dissolved oxygen (DO), dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP) and dissolved silica (SiO_2^-) in control, lowered and raised treatments.

Variable	Units	Control	Lowered	Raised
Water table height	cm	13.05 (2.01)	14.47 (2.23)	8.78 (1.35)
Temperature	°C	22.80 (0.54) ^{a}	22.67 (0.53) ^{a}	21.48 (0.43) ^{b}
pH		6.47 (0.07)	6.48 (0.14)	6.32 (0.14)
Dissolved oxygen (DO)	mg L^{-1}	8.61 (0.39) ^{a}	9.33 (0.47) ^{b}	8.23 (0.36) ^{a}
Dissolved organic carbon (DOC)	mg L^{-1}	28.72 (0.44)	28.33 (0.62)	27.59 (0.31)
Dissolved inorganic nitrogen (DIN)	μg L^{-1}	11.66 (1.57) ^{a}	17.12 (2.05) ^{b}	12.28 (0.95) ^{a}
Soluble reactive phosphorus (SRP)	μg L^{-1}	1.38 (0.16) ^{a}	2.86 (0.24) ^{b}	1.07 (0.09) ^{a}
Dissolved silica (SiO_2^-)	mg L^{-1}	BD	BD	BD

n = 42 for all values. Different letters indicate significant differences (Repeated Measures ANOVA, $P < 0.05$, Tukey $P < 0.05$) within each parameter among the treatments.

Table 4.2 Bacterial degradation of the exudates released by algae measured by HPLC-PAD. The decay coefficients are shown for each monosaccharide, which compose the algal carbohydrate pool, and also for the total carbohydrates. n = 4 ± SD.

Monosaccharides	**K**	**R^2**
N-acetyl-galactosamine	-	-
Arabinose	0.00151 (0.00057)	0.72
Fucose	0.00151 (0.00067)	0.66
N-acetyl-glucosamine	0.00227 (0.00096)	0.72
Rhamnose	0.00355 (0.00186)	0.67
Galacturonic acid	0.00409 (0.00452)	0.66
Xylose	0.00506 (0.00373)	0.58
Galactose	0.00873 (0.00276)	0.76
Glucose	0.03435 (0.01211)	0.88
Mannose	0.04071 (0.01551)	0.83
Ribose	0.04390 (0.02308)	0.73
Glucuronic acid	0.06729 (0.03057)	0.67
Fructose	0.08962 (0.00621)	0.99
Total	0.01818 (0.00758)	0.82

Table 4.3 Carbohydrate composition (%) determined by HPLC-PAD of the polysaccharide released by algae and pore water collected from the APEX fen. n = 4 ± SD.

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

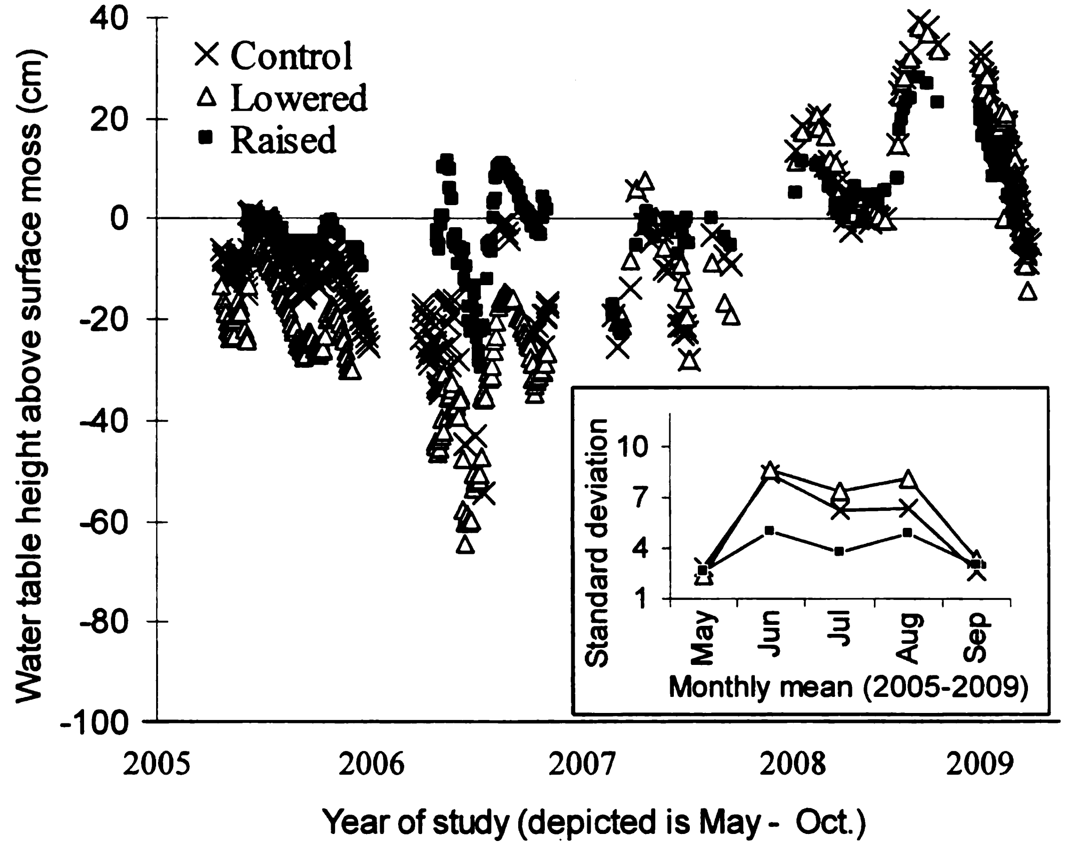

Figure 4.1 Long term seasonal trends in water table heights across the control, lowered and raised water table treatments in interior, Alaska (negative values indicate water table position below the surface of the peat). Insert figure shows standard deviation in mean monthly water table position across the five years of study (total of 1938 individual water table measurements).

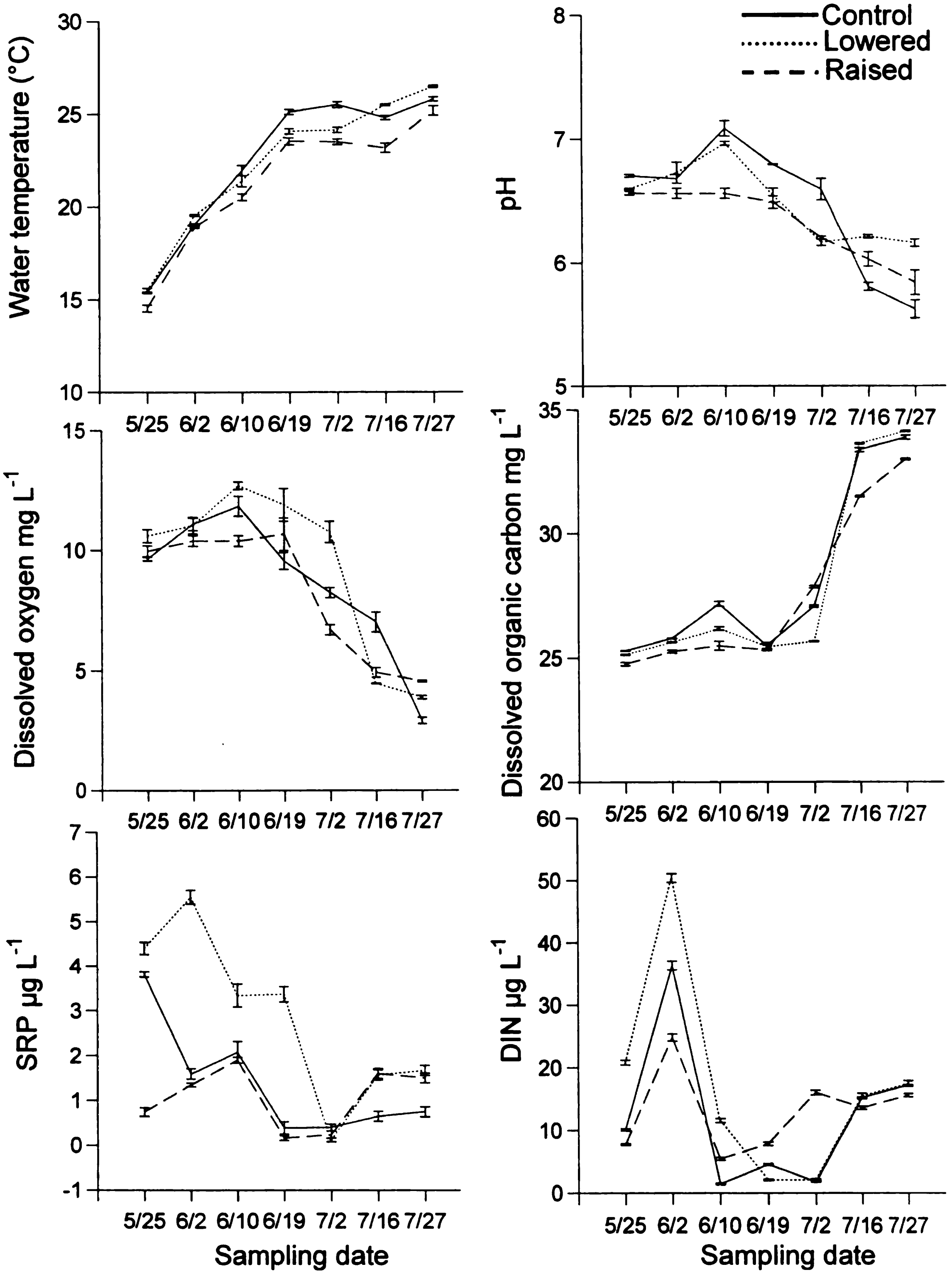

Figure 4.2 Surface water temperature, pH, dissolved oxygen concentration (mg L^{-1}), dissolved organic carbon concentration (mg L^{-1}), soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) concentrations among the control, lowered and raised water table treatments on each sampling date in the APEX fen during the summer growing season in 2009. Points are means of eight replicates ± S.E.

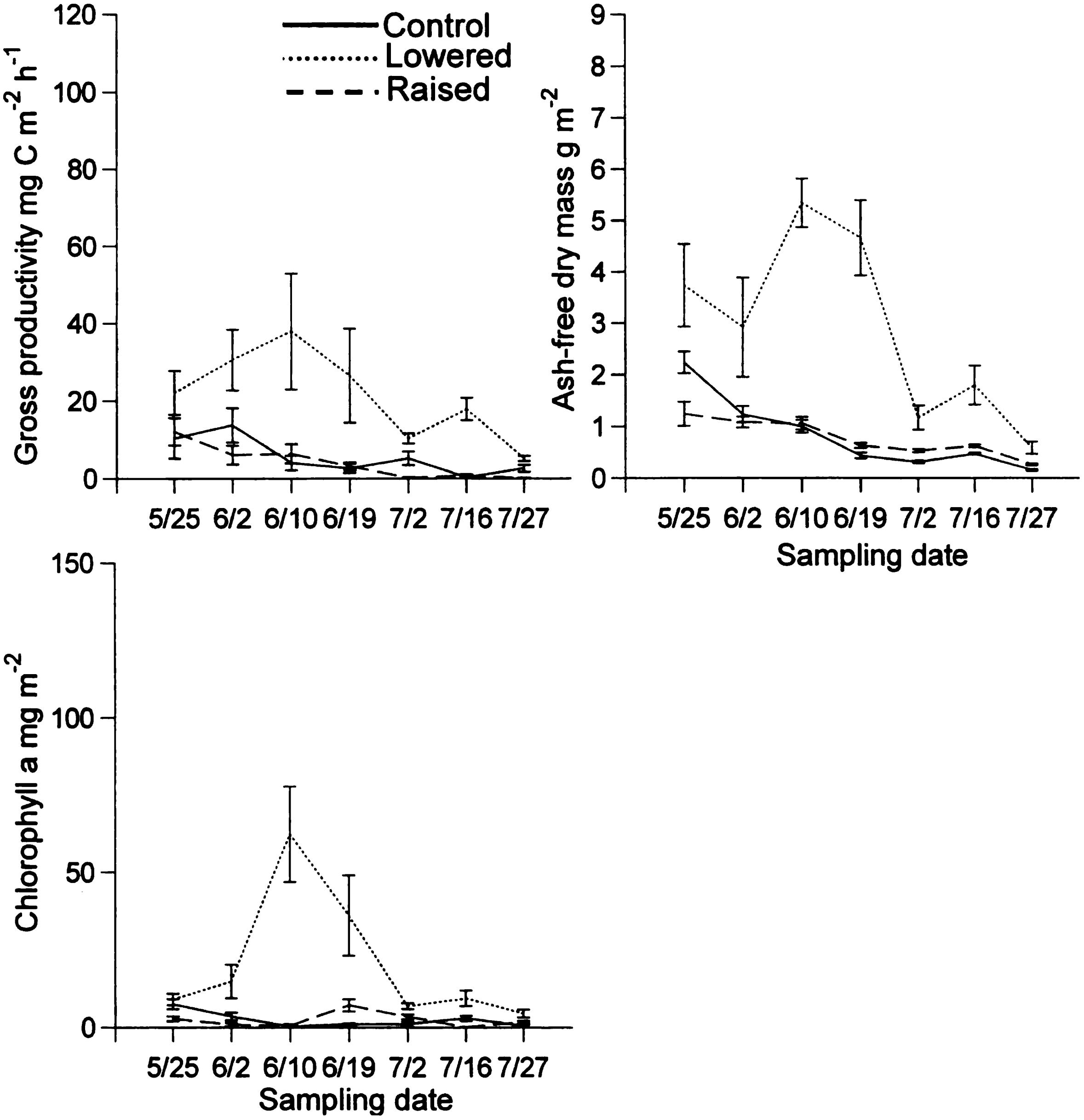

Figure 4.3 Mean algal primary productivity (mg C m^{-2} h^{-1}), ash-free dry mass and chlorophyll-*a* concentration in the control, lowered and raised water table plots on each sampling date in the APEX fen during the summer growing season in 2009. Bars are means of eight replicates ± S.E.

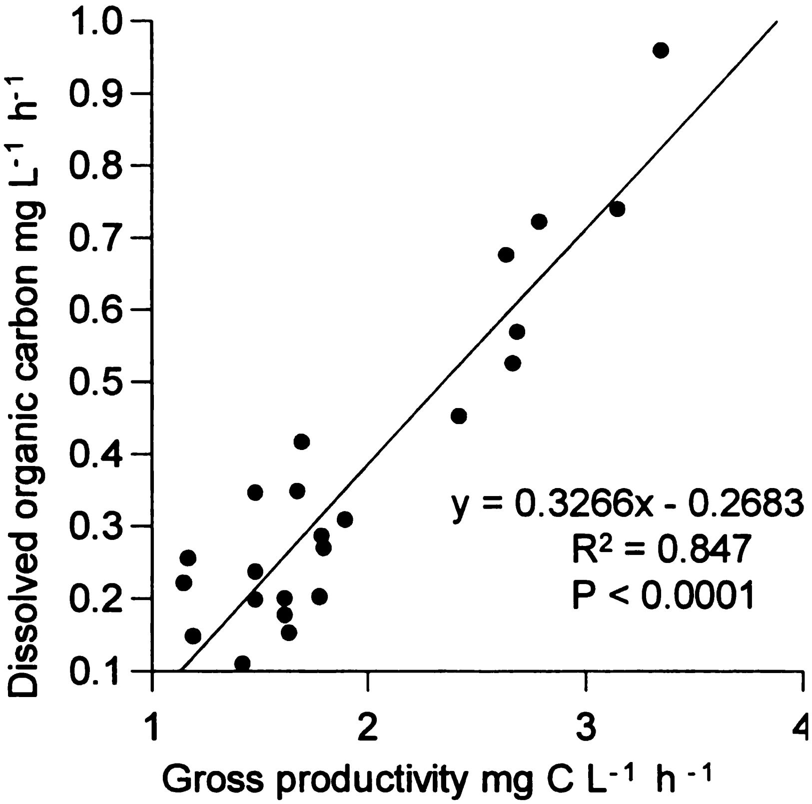

Figure 4.4 Relationship between gross primary productivity (mg C L^{-1} h^{-1}) and dissolved organic carbon concentration (mg C L^{-1} h^{-1}) during productivity measurements on 20 June 2007 (n = 24).

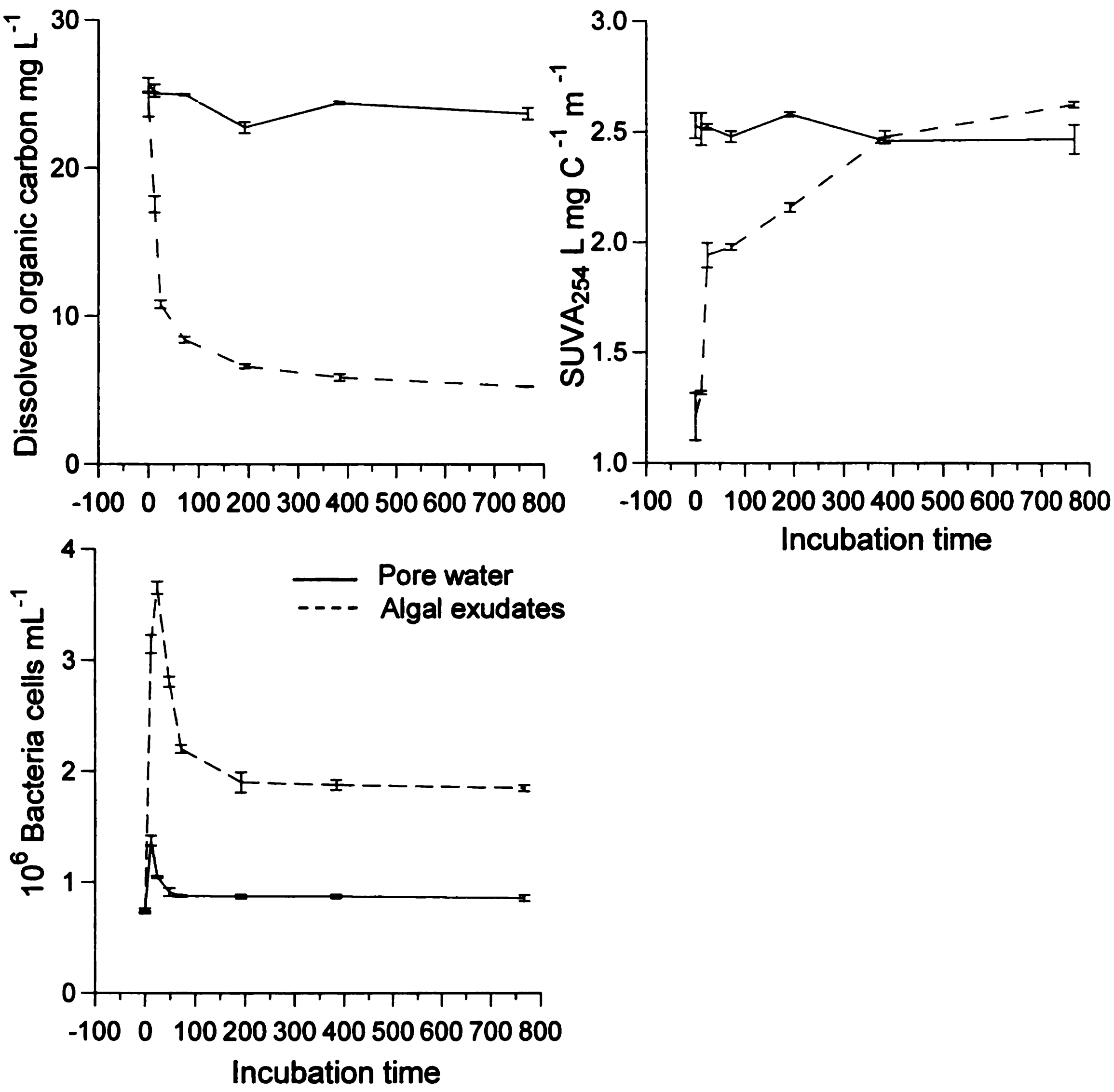

Figure 4.5 Dissolved organic carbon concentration (mg L^{-1}), specific UV-Vis absorption at λ = 254 nm of L mg C^{-1} m^{-1} and bacterial growth (10^6 cells mL^{-1}) in cultures set up with pore water from the APEX fen or from algal exudates during the incubation period (768 h). Points are mean (± S.E., n = 4).

References

American Public Health Association (APHA). 1998. Standard Methods for the Examination of Water and Wastewater, 20th edition. American Public Health Association, Washington, DC, USA.

Baines, S. B. and M. L. Pace. 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: Patterns across marine and freshwater systems. Limnology and Oceanography 36: 1078–1090.

Bergman, I., B. H. Svensson, and M. N. Nilsson. 1998. Regulation of methane production in Swedish acid mire by pH, temperature and substrate. Soil Biology and Biochemistry 30: 729–741.

Boon, P. I. 2006. Biogeochemistry and bacterial ecology of hydrologically dynamic wetlands. p. 115-176. *In* D. P. Batzer and R. R. Sharitz (eds.) Ecology of Freshwater and Estuarine Wetlands. University of California Press, Los Angeles, CA, USA.

Bridgham, S. D., C. A. Johnston, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience 45: 262–274.

Briggs, S. V., M. T. Maher, and S. M. Carpenter. 1985. Limnological studies of waterfowl habitat in south-western New South Wales. I. Water chemistry. Australian Journal of Marine and Freshwater Research 36: 59–67.

Chin, Y. P., G. R. Aiken, and E. O'Loughlin. 1994. Molecular weight, polydispersity, and spectroscopic properties of aquatic humic substances. Environmental Science and Technology 28:1853–1858.

Chivers, M. R., M. R. Turetsky, J. M. Waddington, J. W. Harden, and A. D. McGuire. 2009. Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO_2 Fluxes in an Alaskan Rich Fen. Ecosystems 12: 1329–1342.

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.

Ewe, S. M. L., E. E. Gaiser, D. L. Childers, V. H. Rivera-Monroy, D. Iwaniec, J. Fourquerean, and R. R. Twilley. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) in the Florida Coastal Everglades LTER (2001-2004). Hydrobiologia 569: 459–474.

Fogg, G. E. 1983. The ecological significance of extracellular products of phytoplankton photosynthesis. Botanica Marina 26: 3–14.

Gaiser, E. E., L. J. Scinto, J. H. Richards, K. Jayachandran, D. L. Childers, J. D. Trexler, and R. D. Jones. 2004. Phosphorus in periphyton mats provides best metric for detecting low level P enrichment in an oligotrophic wetland. Water Research 38: 507–516.

Gilbert, D., C. Amblard, G. Bourdier, and A. J. Francez. 1998. The microbial loop at the surface of a peatland: Structure, function, and impact of nutrient input. Microbial Ecology 35: 83–93.

Giroldo, D. and A. A. H. Vieira. 2005. Polymeric and free sugars released by three phytoplanktonic species from a freshwater tropical eutrophic reservoir. Journal of Plankton Research 27: 695–705.

Giroldo, D., A. A. H. Vieira, and B. S. Paulsen. 2005. Microbial degradation of extracellular polysaccharides released by a tropical strain of Staurastrum orbiculare (Zygnematophyceae). Phycologia 44: 671–677.

Giroldo, D., P. I. C. Ortolano, and A. A. H. Vieira. 2007. Bacteria–algae association in batch cultures of phytoplankton from a tropical reservoir: the significance of algal carbohydrates. Freshwater Biology 52: 1281–1289.

Goetz, L. D., A. G. Bunn, G. J. Fiske, and R. A. Houghton. 2005. Satellite observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences 102: 521–525.

Goldsborough, L. G. and G. G. C. Robinson. 1996. Patterns in wetlands. p. 77–117. *In* R. J. Stevenson, M. L. Bothwell, and R. L. Lowe (eds.) Algal Ecology: Freshwater Benthic Ecosystems. Academic Press, New York, USA.

Gremm, T. J. and T. J. Kaplan. 1997. Dissolved carbohydrates in streamwater determined by HPLC-PAD and pulse amperometric detection. Limnology Oceanography 42: 385–393.

Hamer, U. and B. Marschner. 2005. Priming effects in soils after combined and repeated substrate additions. Geoderma 128: 38–51.

Hart, E. A. and J. R. Lovvorn. 2003. Algal vs. macrophyte inputs to food webs of inland saline wetlands. Ecology 84: 3317–3326.

Hinzman, L. D., N. D. Bettez, W. R. Bolton, F. S. Chapin III, 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. p. 39–61. *In* F. S. Chapin, M.W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, USA.

Jensen, L. M. 1983. Phytoplankton release of extracellular organic carbon, molecular weight and bacterial assimilation. Marine Ecology Progress Series 11: 39–48.

Kahn, W. E. and R. G. Wetzel. 1999. Effects of microscale water level fluctuations and altered ultraviolet radiation on periphytic microbiota. Microbial Ecology 38: 253–263.

Kane, E. S., M. R. Turetsky, J. Harden, A. D. McGuire, and J. M. Waddington. 2010. Seasonal ice and hydrolic controls on dissolved organic carbon and nitrogen concentrations in a boreal rich fen. Journal of Geophysical Research - Biogeosciences doi:10.1029/2010JG001366.

Kuzyakov, Y., J. K. Friedel, and K. Stahr. 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biogeochemistry 32: 1485–1498.

McCormick, P. V., M. J. Chimney, and D. R. Swift. 1997. Diel oxygen profiles and water column community metabolism in the Florida Everglades, U.S.A. Archiv für Hydrobiologie 140: 117–129.

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.

McCormick, P. V., M. B. O'Dell, R. B. E. Shuford III, J. G. Backus, and W. C. Kennedy. 2001. Periphyton responses to experimental phosphorus enrichment in a subtropical wetland. Aquatic Botany 71: 119–139.

McGuire, A. D., C. Wirth, M. A Apps, J. Beringer, J. Clein, H. E. Epstein, D. W. Kicklighter, J. Bhatti, F. S. Chapin III, B. deGroot, D. Efremov, W. Eugster, M. Fukuda, T. Gower, L. D. Hinzman, B. Huntley, G. J. Jia, E. S. Kasischke, J. M. Melillo, V. E. Romanovsky, A. Shvidenko, E. Vaganov, and D. A. Walker. 2002. Environmental variation, vegetation distribution, carbon dynamics, and water/energy exchange in high latitudes. Journal of Vegetation Science 13: 301–314.

McGuire, A. D., F. S. Chapin III, 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. p. 297–310. *In* J. G. Canadell, D. E. Pataki, and L.

F. Pitelka (eds.) Terrestrial Ecosystems in a Changing World IGBP Series. Springer, Heidelberg.

Myklestad, S. M. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. The Science of the Total Environment 165: 155–164.

Noe, G. B., D. L. Childers, and R. D. Jones. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: why the Everglades is so unique? Ecosystems 4: 603–624.

Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane. 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406: 978–981.

Osterkamp, T. E., L. Viereck, Y. Shur, M. T. Jorgenson, 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.

Porter, K. G. and Y. Feig. 1980. The use of DAPI for identification and enumeration of bacteria and blue green algae. Limnology and Oceanography 25: 943–948.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1993. p. 994. Numerical Recipes: the Art of Scientific Computing. Cambridge University Press, New York, USA.

Reddy, K. R., R. H. Kadlec, E. Flaig, and P. M. Gale. 1999. Phosphorus retention in streams and wetlands: A review. Critical Reviews in Environmental Science and Technology 29: 83–146.

Richardson, C. J. 2009. The Everglades: North America's subtropical wetland. Wetlands Ecology and Management doi: 10.1007/s11273-009-9156-4.

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.

Robinson, G. G. C., S. E. Gurney and L. G. Goldsborough. 2000. Algae in Prairie Wetlands. p. 163–198. *In* H. R. Murkin, A. G. van der Valk and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

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. Rouet, and J. P. Smol. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrological Processes 11: 873–902.

Schoenberg, S. A. and J. D. Oliver. 1988. Temporal dynamics and spatial variation of algae in relation to hydrology and sediment characteristics in the Okefenokee Swamp, Georgia. Hydrobiologia 162: 123–133.

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.

Søndergaard, M., B. Hansen, and S. Markager. 1995. Dynamics of dissolved organic carbon lability in a eutrophic lake. Limnology and Oceanography 40: 46–54.

Smith, D. J. and G. J. C. Underwood. 2000. The production of extracellular carbohydrates by estuarine benthic diatoms: The effects of growth phase and light and dark treatment. Journal of Phycology 36: 321–333.

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.

Thormann, M. N. and S. E. Bayley. 1997. Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. Plant Ecology 131: 1–16.

Turetsky, M. R., C. C. Treat, M. 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.

Vitt, D. H. 2006. Function characteristics and indicators of boreal peatlands. p. 9–24. *In* R. K. Wieder and D. H. Vitt (eds.) Boreal Peatland Ecosystems. Springer, New York, USA.

Weishaar, J. L., G. R. Aiken, B. A. Bergamaschi, M. S. Fram, R. Fujii, and K. Mopper. 2003. Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. Environmental Science and Technology 37: 4702–4708.

Wetzel, R.G. and G. E. Likens. 2000. Limnological Analyses, 3rd edition. Springer-Verlag, New York, USA.

Wickland, K. P., J. C. Neff, and G. R. Aiken. 2007. Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems 10: 1323–1340.

Wicks, R. J., M. A. Moran, L. J. Pittman, and R. E. Hodson. 1991. Carbohydrates signatures of macrophytes and their dissolved degradation products as determined by a sensitive high-performed ion chromatography method. Applied and Environmental Microbiology 57: 3135–3143.

Wieder, R. K. 2006. Primary production in boreal peatlands. p. 145-164. *In* R. K. Wieder and D. H. Vitt (eds.) Boreal Peatland Ecosystems. Springer, New York, USA.

Wright, R. T. 1988. Methods for evaluating the interaction of substrate and grazing as factors controlling planktonic bacteria. Archiv für Hydrobiologie – Beiheft Ergebnisse der Limnologie 31: 229–242.

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.

Yoshikawa, K. and L. D. Hinzman 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. Permafrost and Periglacial Processes 14: 151–160.

CHAPTER 5

CONCLUSION

Aquatic ecosystems in northern boreal regions are often characterized by low energy, low temperatures and a short growing season with low primary productivity (Duff et al. 1999). Many areas of the boreal biome, such as western North America have undergone rapid climate warming in recent years and climate models predict that temperatures will continue to increase with human activity (Serreze et al. 2000). In response to recent climatic change, the surface area of open water bodies within some wetland-rich landscapes of Alaska is expanding, likely due to permafrost thaw and increased runoff from surrounding uplands (Osterkamp et al. 2000). In other areas of Alaska, the surface area of open water is declining, likely due to increased summer moisture deficits and drainage related to permafrost thaw (Oechel et al. 2000, Yoshikawa and Hinzman 2003, Hinzman et al. 2005, Riordan et al. 2006). Increases in the extent of seasonal ice thaw and drought are predicted to increase microbial decomposition, which will probably promote nitrogen (N) and phosphorus (P) mineralization in the expanded active soil layer (Bridgham et al. 1995), as well as chemical weathering of parent rock material (Rouse et al. 1997). In addition to disturbance associated with climate change (i.e., Rouse et al. 1997, Osterkamp et al. 2000, Hinzman et al. 2005), increasing human activities such as mining, peat excavation and fossil fuel combustion (i.e., Walker et al. 1987, Charman 2002, Hinzman et al. 2006) may significantly affect aquatic systems in boreal regions (Schindler 1998). In the interior region of Alaska, 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). In a cool, wet climate, much of the anthropogenic emissions of sulfur oxides deposited by precipitation is reduced and stored as sulfur in the anoxic soils of wetland ecosystems (Schindler 1998). In future warmer, dryer conditions where wetland sediments are exposed to atmospheric oxygen, the stored sulfur is likely to reoxidize and result in the acidification of aquatic ecosystems in boreal regions (Schindler 1998). The goal of this dissertation was to evaluate the response of wetland algae to changes in nutrients, pH and hydrology that are expected for boreal regions with future climate change, and to relate changes in algal parameters to potential ecosystem functions associated with carbon (C) cycling.

I manipulated water column concentrations of N, P and silica (Si) in a completely crossed experimental design using mesocosms in an Alaskan marsh to test the hypothesis that nutrients are an important factor limiting algal biomass and constraining community structure in northern boreal wetlands, and that increases in algal biomass would be driven by taxa requiring high nutrient conditions. Additionally, since algae can release significant amounts of C fixed during photosynthesis into the water column (Myklestad, 1995), I hypothesized that water column dissolved organic C (DOC) concentrations would increase with algal biomass following nutrient enrichment. I found that algal growth was not stimulated following enrichment with N, P or Si alone or with P and Si together, but algal accrual increased significantly with the addition of N in any combination with P and Si. Additionally, I found that water column DOC concentrations increased in step with algal biomass. There was a significant shift in community composition in response to nutrient enrichment, especially in N-combination treatments, reflecting the interaction between nutrient limitation and resource competition. Taken together, these results provide several lines of evidence for nutrient co-limitation and the central importance of N limitation for regulating algal production and taxonomic composition in the wetlands of interior Alaska.

To examine the hypothesis that water column pH is an important regulator of algal biomass and community structure in boreal wetlands, I exposed an algal community to a wide range of experimental pH conditions, both increased and decreased from ambient levels in an Alaskan marsh. Specifically, I expected 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, I expected that alkaline conditions would result in an algal community comprising few acidophilic taxa. Also, I expected that some of the changes in community composition that commonly occurs 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). As predicted from survey data of other wetlands, changes in pH levels resulted in alterations in the wetland algal community. Contrary to my expectations, algal biomass did not increase following acidification. I did, however, observe a significant increase in algal accrual in the alkaline treatment, which may have been due, in part, to the increase in nutrient concentrations that occurred at pH 9. There were distinct shifts in community composition across the pH spectrum, including a significant increase of *Trachelomonas* and a significant decrease of *Euglena* (Euglenopyta) in the alkaline treatment 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 DIC.

Lastly, I monitored surface water chemistry and algal productivity following a spring flooding event at sites previously exposed to a four-year, ecosystem-scale water table manipulation to evaluate how changes in hydrology might affect C cycling and energy flow in boreal peatlands. Water column concentrations of soluble reactive P and dissolved inorganic N were significantly greater at sites previously exposed to drought (lowered water table treatment) compared to control or continuously flooded conditions (raised water table treatment). Algal productivity peaked immediately following the maxima in nutrient concentrations, and was consistently higher in the lowered water table treatment compared to the control or raised water table treatments throughout the summer growing season. Across treatment plots, water column DOC concentrations increased with algal productivity, and I calculated that algae released 18% of fixed carbon into the water column as DOC. Approximately 25% of the algal exudates were carbohydrates, which were extremely labile, and likely an important energy source for heterotrophic metabolism in the lowered water table treatment. While surface water conditions would only typically allow for continuous algal production at the raised water table treatment in previous years, the flooding event afforded a unique opportunity to examine the legacy effects of drought on surface water chemistry and algal production in an Alaskan fen. These findings suggest that algae may become increasingly important for energy flow in boreal peatlands if seasonal drying trends become more frequent with future climate change.

This study of Alaskan wetlands add to a growing pool of literature showing the effects of disturbance on algae in aquatic ecosystems globally, and contribute to a small number of empirical studies on algal community ecology in wetlands. Depending on regional factors such as landscape position, changes in climate will likely regulate local factors such as flood disturbance frequency, which may have important implications for water chemistry (especially pH and nutrient concentrations) in boreal wetlands. My studies show that changes in proximate factors such as water chemistry and pH will directly affect the ability of algal species to survive and thrive in boreal wetlands. Taken together, these results indicate that nutrients, particularly N and P are currently the strongest regulator of algal productivity and community composition in Alaskan wetlands. This finding follows trends for aquatic ecosystems globally and offers support for the hypothesis that nutrient enrichment will result in greater overall productivity in boreal wetlands (i.e., Rouse et al. 1997). The algal response to direct nutrient enrichment was also observed following increases in nutrient concentrations at sites exposed to seasonal drought and in alkaline conditions during the pH study. Thus, processes related to increased organic matter mineralization and/or weathering of parent rock material will probably increase algal productivity and alter their community structure in northern boreal wetlands. Further, decreases in surface water pH associated with fossil fuel emissions or drying at sites previously exposed to nitrate and sulfate deposition will likely reduce algal diversity in boreal wetlands. The resulting biomass, species, and chemical composition of algae will likely alter other aspects of wetland ecosystems such as food web structure and sediment formation. Since algae release a significant amount of photo-assimilated C into the overlying water column, they may become increasingly important for heterotrophic metabolism and C cycling with higher rates of productivity in boreal wetlands. These changes could alter current wetland function and have large-scale effects on ecosystem processes in Alaska, owing to the extensive coverage of wetland ecosystems on the landscape in this region.

References

Bridgham, S., D. Johnston, A. Carol, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience 45: 262–274.

Charman, D. 2002. Peatlands and environmental change. John Wiley, Sons, Inc., New York, USA.

Duff, K., T. E. Laing, J. P. Smol, and D. R. Lean. 1999. Limnological characteristics of lakes located across Arctic treeline in northern Russia. Hydrobiologia 391: 205–222.

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.

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. p. 39–61. *In* F.S. Chapin, M.W. Oswood, K. Van Cleve, L.A. Viereck, and D.L. Verbyla (eds.) Alaska's Changing Boreal Forest. Oxford University Press, New York, NY, USA.

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.

Myklestad, S. M. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. The Science of the Total Environment 165: 155–164.

Oechel. W. C, G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, D. Kane. 2000. Acclimation of ecosystem CO^2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406: 978–981.

Osterkamp, T. E., L. Viereck, Y. Shur, M. T. Jorgenson, C. Racine, A. Doyle, and R. D. Boone. 2000. Observations of thermokarst and its impact on boreal forests in Alaska, USA. Arctic Alpine Research 32:303–315.

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.

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. Rouet, 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.

Schindler, D. W. 1988. Effects of acid rain on aquatic ecosystems. Science 239:149–157.

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.

Walker, D. A., P. J. Webber, E. F. Binnian, K. R. Everett, N. D. Lederer, E. A. Nordstrand, and M. D. Walker. 1987. Cumulative impacts of oil fields on northern Alaskan landscapes. Science 238: 757–761.

Yoshikawa, K. and L. D. Hinzman. 2003. Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska. Permafrost Periglac Process 14: 151–160.