THE ECOLOGICAL EFFECTS OF EXPERIMENTAL ACIDIFICATION UPON LITTORAL ALGAL ASSOCIATIONS OF LAKES IN THE BOREAL FOREST

by

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Abstract

This research evaluated the effects of acidification upon littoral algal associations in studies conducted at the Experimental Lakes Area in northwestern Ontario, Canada. The investigations included: experimental whole-lake sulfuric and nitric acidification, experimental whole-lake nutrient additions, and surveys of lakes varying in nutrient concentrations. Two principal littoral algal associations were studied: epilithon (association on rock surfaces), and metaphyton (algal community associated with, but unconstrained by, a surface).

Nutrient controls of littoral and planktonic algal photosynthesis differed greatly due largely to the diffusive resistance to benthic uptake of dissolved inorganic carbon (DIC). Eplithic net photosynthesis declined as a result as acidification altered the carbon cycle. With a parallel increase in epilithic respiration, the energy balance within epilithon became unfavourable (i.e. respiration as a fraction of 'gross' photosynthesis increased) causing decline of this association. This dysfunction serves as an early warning of metabolic imbalance in lakes, which are more sensitive to acidification than previously thought.

Filamentous green algae (FGA) of the Zygnematales proliferated in the littoral zone initially as periphyton, and later as metaphyton, as acidification progressed. FGA had high photosynthetic capacity, displaying an energy

balance similar to unacidified epilithon. Their growth was controlled negatively by density-dependent feedback, and positively by light intensity, DIC, water movement, and water temperature. FGA biomass varied seasonally, being at a minimum in spring, and reaching an annual maximum in early fall.

FGA blooms, sometimes reaching 30 cm in thickness, affected several aspects of the littoral zone both positively and negatively. Large intra- and interannual variability diminished their ability to compensate for acidification-induced oligotrophication seen in the littoral zone. The FGA were sometimes the largest epilimnetic phosphorus-containing compartment. Their nitrogen dynamics caused both acidification (spring and summer) and alkalinization (fall) of lakes. Blooms attenuated light available to other phytobenthos by as much as 90%. The FGA provided seasonal habitat for animals, but respiration- and decomposition-related oxygen depletion posed potential risks for inhabitants. FGA in acid lakes will likely proliferate further as human activities release the algae from several growth limitations by increasing nutrient availability (e.g. CO_2), by increasing water temperatures, and by extending their growing season.

Dedication

I dedicate this thesis to my grandfather, Dr. Bertrum Roy Jenkins, who died during my doctoral voyage. An earlier alumnus of the University of Manitoba (Jenkins 1991), Ga was always an example to me of 'youthful' inquisitiveness, even in his one hundredth (and last) year of discovery. Ga invariably displayed the courage that is needed to hold ideas that differ from the norm. I will miss his gentleness, enthusiasm and laughter, and cherish the memories of Ga that live on inside of me.

Miscellany

"That's the whole problem with science. You've got a bunch of empiricists trying to describe things of unimaginable wonder" (Calvin and Hobbes 1992).

"Scientists are vulnerable to a classical trap whose jaws are the scholars' greatest virtues: curiosity, objectivity, skepticism, experience, and a wholesome desire for simple order in nature and in human affairs. ... Trapped by a pedant's logic and a desire to appear objective and reasonable, [scientists may] tacitly accept the proposition that a tight causal proof is the only basis for instituting controls that might protect [our environment] from destruction by regional or global pollution.

"If such proofs are required, there is little that scientists can do to prevent the destruction of [our environment]. Tight causal proofs are elusive in ecology as in most of science" (Woodwell 1989).

Acknowledgments

I thank the people of Canada who, through the auspices of Fisheries and Oceans, Canada, have financially supported the Experimental Lakes Area (ELA) program during this protracted recession. This research would have been impossible without the ELA, the world's greatest natural aquatic laboratory.

Dr. Gordon Robinson was a fine example to me of a successful and dedicated scientist. He provided effective and kindly guidance during my scientific endeavours, and frequently helped me hone my experimental ideas and interpretations. Gordon also navigated me successfully among the bureaucratic paths of the doctoral program. He provided friendly yet forceful support throughout this exercise. His supervisory assistance pervades the thesis. Gordon and Bob (Dr. R. Hecky) confirmed that chivalrous qualities are an important ingredient of scientific leadership.

Dr. David Schindler was an example of scientific prioritization and dedication who remained a touchstone during this endeavour. David provided the initial freedom and challenge that persuaded me to pursue the doctorate. He taught me that an important component of leadership of a research team is to accept the heaviest load. It was with David that I had initial discussions about the character of a successful benthic research program in Lake 302S; this is largely reported in Chapter 2.

Dr. Robert Hecky, both as a member of my thesis committee and as my immediate supervisor within Fisheries and Oceans, Canada, provided further impetus for my doctorate program. Bob assured that I retained the scientific freedom and financial support to complete this research. His insightful comments during discussions and on drafts of my manuscripts were always helpful. His wise suggestions on nutrient dynamics during our discussions warranted his coauthorship in Chapter 3.

Dr. Brenda Hann provided a zoological perspective throughout my thesis research, supplementing my 'phytocentricity'. Brenda participated (perservered) in the planning and execution of the 1989 mesocosm experiment reported in Chapter 5. She also made many useful comments on the thesis as a member of my thesis committee, and refereed Chapters 2 to 4 in their journal form for the Publications Review Committee of the Freshwater Institute.

Dr. David Rosenberg, as a member of my thesis committee and as a friend, made many constructive editorial suggestions that have tangibly improved the thesis and the journal papers. As a result of his criticisms and our discussions, I understand better the mechanics and 'art' of scientific writing.

Dr. Norman Kenkel, provided useful criticisms and comments on my research plans as a member of my thesis committee.

Dr. E. Todd Howell provided critical, constructive and sometimes stubborn evaluation of my ideas. He provided an algal counterpoint to my more biogeochemical view of the world. Todd cooperated in the 1989 survey of

epilithic metabolism, and was involved in extensive discussions of the ideas in Chapter 3. Todd cooperated in the design and execution of the procedural experiments reported in Chapter 4. Most of all, Todd was a friend.

My summer research students provided enthusiasm, willingness to work long hours, and critical participation during their tenure. These students were: Leif Sigurdson from Queen's University (1988-9), Shawn Zettler from the University of Manitoba (1990-1), and Lisa Kirkendale from the University of Victoria (1992).

Bruce Townsend provided cold-water SCUBA assistance during the several years of epilithic and metaphytic sampling. In 1990, Bruce coordinated the efforts of the participants in his Research Diver Course (John Amaral, Stuart Cauvin, Dave Hamilton, Kathleen Hamilton, Dean Janzen, Karin Mathias, Randy Sigurdson, and Gina Bell) who collected much of that year's FGA biomass data reported in Chapter 5.

As an outgrowth of Bruce's course, John Amaral and I further investigated the potential for blooms of littoral algae to alter the sulfur cycle. The majority of this research is reported in his thesis and in Kelly et al. (1994); the role of FGA in modifying pH and oxygen concentrations is reported in Chapter 5.

Dr. John Brewster and Linda Neden, participated in the development of the designs of the procedural experiments reported in Chapter 4. John also critiqued the FGA biomass sampling program during 1989 and 1990.

Michael Jackson was invariably a proponent of the role of intuition in science. Michael performed the visual surveys of FGA distribution reported in Chapter 2.

Paul Campbell participated in the 1992 survey of epilithon in lakes at the ELA reported in Chapter 3. He was a reliable critic of my ideas, and reviewed several of the chapters in their journal form. Paul was a close friend throughout this endeavour, who reinstilled confidence in me when I sometimes tired along the way.

David Findlay analysed the algal taxonomy samples reported in Chapters 2 and 4, and enjoyed his role as sceptic. Ticia Lyng, Alison Broughton, Brian Hauser, Jack Boughen and Ron Schade performed most of the chemical analyses of particulates reported in the thesis. Eva Schindler provided the phytoplankton data in Chapter 3. Discussions with Susan Kasian were useful in resolving the issue of selecting an appropriate mass correction strategy for P_{gbm} considered in Chapter 4. Neil Strange provided technical assistance in both the field and laboratory and assisted in the data analysis of the epilithic metabolism. I also thank the numerous other members of the ELA who provided support (in)directly throughout this research.

Finally, but most importantly, my family (Alison, Bryan and Evelyn) gave me more love and support, patience and understanding, than I deserved. They loved me even when I was at the ELA or was writing, when I should really have been a husband and a father.

Preface

Chapters 2 to 5 have been prepared as contributions to a series to be published in the Canadian Journal of Fisheries and Aquatic Sciences in honour of the 25th anniversary of the ELA. The journal versions of Chapters 2 to 5 are cited in the list of references as Turner et al. 1994d, 1994b, 1994a, and 1994c, respectively. For the reasons described in the acknowledgments, several individuals appear as coauthors with me in these submissions. The authorship is: Chapter 2 (M. A. Turner, D. W. Schindler, D. L. Findlay, M. B. Jackson, and G. G. C. Robinson), Chapter 3 (M. A. Turner, E. T. Howell, G. C. C. Robinson, P. Campbell, R. E. Hecky, and E. U. Schindler), Chapter 4 (M. A. Turner, E. T. Howell, G. G. C. Robinson, J. F. Brewster, L. J. Sigurdson, and D. L. Findlay), and Chapter 5 (M. A. Turner, G. G. C. Robinson, B. J. Hann, B. E. Townsend, and J. A. Amaral).

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Chapter 1. General Introduction

"When stress is detectable at the ecosystem level, there is real cause for alarm, for it may signal a breakdown in homeostasis" (Odum 1985). This thesis presents evidence that breakdowns as a result of acidification can occur at higher pH than expected in aquatic ecosystems. This insight was gained as a result of developing the techniques necessary to ask questions that differed from those that had been asked before, and by dispensing with some of my most cherished hypotheses after they proved untenable.

The Littoral Zone

The study was conducted at the Experimental Lakes Area (ELA), a natural laboratory situated in northwestern Ontario, Canada. The research focuses on the complex part of lakes called the littoral zone. Unlike the relatively homogeneous open-water or pelagic zone, the littoral zone is by comparison a heterogeneous aggregate of individual but interconnected communities. Furthermore, it is a region of interfaces: between the terrestrial component of the watershed and the pelagial region; between the lake bottom and overlying water; between the water surface and atmosphere. As a result, littoral investigations require carefully crafted questions, with the ensuing research having to focus on particular elements. Choosing the appropriate components and questions is critical to success - more so perhaps than in

other subecosystems of lakes.

As a result of the difficulty of littoral research (Wetzel 1983), this zone has frequently been ignored. For example, little littoral algal information was derived from the Lake 223 (Schindler et al. 1985) and Little Rock Lake, Wisconsin (Brezonik et al. 1993) whole-lake studies. Consequently, understanding of the impacts of various perturbations, and of acidification in particular, on the littoral zone have been slower to unfold (Stokes 1986). Compounding the problem is the inevitable consequence that conclusions based on pelagic observations have often been generalized to the littoral zone, causing erroneous conclusions on occasion. This phenomenon has hindered our understanding of the impact of acidification (see Chapters 2 and 3).

Acidification - An Overview

In spite of Canada's Green Plan conclusion that "Canadian and U.S. acid rain control programs will solve Canada's acid rain problem" (Anonymous 1990, p. 120), Canadians will likely be struggling with acidified aquatic ecosystems for quite some time. It is unclear whether proposed regulations on sulfur dioxide emissions will be sufficient to prevent additional acidification, let alone to initiate recovery (Galloway 1989). It is also uncertain that the political will exists to withstand the economic pressures that call for the lessening or abandonment of these measures. There are currently no limits on the emissions of nitrogen oxides, in spite of both their increased release in North America and Europe

(Galloway 1989), and the demonstration that nitric acid is a surprisingly efficient acidifier of lakes (Rudd et al. 1990). Even if emissions of sulfur dioxide in Europe and North America remained stable as a result of legislation, acidification in these regions will continue, and in some cases will worsen, due to lags in ecosystem responses (Galloway 1989).

The global situation is far less optimistic. Major increases in emissions of both sulfur dioxide and nitrogen oxides are expected to occur in Asia, Africa and South America during the next several decades as per capita energy consumption increases coincident with continued population growth (Galloway 1989, Rodhe 1989). Hence, while acidification research may be politically inexpedient, in reality such studies are much more than a theoretical exercise.

Several recent articles summarize the published state of knowledge of acidification effects. Gorham (1989) reviewed historical developments in the scientific understanding of acidification of ecosystems. Stokes' (1986) review of the impacts of acidification upon primary producers in aquatic ecosystems revealed that knowledge of the effects on phytobenthos was limited. This situation has since improved only marginally as evidenced by the more recent reviews of Stokes et al. (1989), Muniz (1991) and Schindler et al. (1991). The principal objective of this thesis (Chapters 2 and 4 in particular) was to address these perceived shortcomings. Chapter 3 reevaluates what controls epilithic growth in low alkalinity lakes; a reevaluation was necessary to overcome misconceptions that hindered theoretical developments. The reviews provided

less information on the consequences of acidification of phytobenthos to other components of the ecosystem; this is the principal issue of Chapter 5.

The Lake 302S Experimental Study

Much of the thesis research was undertaken in experimental ecosystem Lake 302S at the Experimental Lakes Area (ELA, Johnson and Vallentyne 1971). A multiphase experiment was undertaken in the southern, upstream basin of double-basin Lake 302; the two basins were separated in 1981 by installation of an artificial curtain. Controlled acidification was accomplished by additions of acid to the epilimnion to achieve or maintain target pH levels (Turner et al. 1987, 1991).

Phase I (1982-1986) of the experiment was designed partly to determine the relative efficiencies of sulfuric acid (Lake 302S) and nitric acid (Lake 302N) as acidifying agents in lake ecosystems (Rudd et al. 1990). The experimental plan was to lower the pH of Lake 302S in fixed steps to pH 5.1 from its original value of about 6.6. Chapter 2 includes data from this period principally to establish the trajectory of changes brought about by acidification upon the normally dominant periphyton.

The pH was reduced further to 4.5-4.6 by 1988 in Phase II of the experiment (1987-1991). Lake 302S was maintained at pH 4.5: (a) to examine the effects of more extreme acidification than was possible in the earlier Lake 223 study; and (b) to assess the ecosystem's ability to reestablish homeostatic

control over the various structures and functions that appeared to have been disturbed by acidification below pH 5. It is this second phase during which the majority of investigations reported in this thesis have taken place.

Chapter Previews

Chapter 2 provides an overview of the disruption that has occurred within the littoral zones of two experimental lakes, one acidified with sulfuric acid (Lake 302S), and another acidified with nitric acid (Lake 302N). The research tracks the demise of the normally dominant epilithon, and their replacement with a new algal association dominated by filamentous green algae. It builds upon the earlier findings reported in Turner et al. (1987, 1991).

Chapter 3 reconsiders the understanding of nutrient controls on the growth of epilithon. The previously dominant idea that phosphorus is the principal controller of periphytic growth has hindered learning about acidification effects in the littoral zone. This revision of ideas is important to understanding the impact of acidification, and it is argued, to interpreting and predicting the impact of other disturbances.

Chapter 4 investigates the growth characteristics of the new algal association, the filamentous green algae, which seasonally dominates acidified littoral zones. This research is an outgrowth and extension of the pilot research reported in Howell et al. (1990).

Chapter 5 evaluates the consequences of blooms of filamentous green

algae in the littoral zone. The results are surprising and occasionally startling in that the impact of the algal blooms was often pervasive and substantial.

Finally, the general discussion integrates and summarizes the findings of the thesis research. It provides a consolidated view of the consequences of acidification upon the littoral zone, one of the most visible but least understood areas of inland lakes.

Chapter 2. Disruption of Littoral Algal Communities Caused by Experimental Lake Acidification

Abstract

The effects of acidification upon littoral algal communities were examined in two experimentally acidified lakes of the Experimental Lakes Area located in the boreal forest of northwestern Ontario. As Lake 302S was acidified experimentally with sulfuric acid from pH 6.7 to 4.5, net photosynthesis of the previously dominant periphyton declined due partly to increased carbon limitation. The ratio of respiration to photosynthesis, possibly the most important of all ecosystem functions, increased (worsened) in epilithon (periphyton on rock surfaces) as acidification progressed. There were major changes in algal taxonomic composition of the previously dominant epilithon; both biomass and taxonomic richness declined, especially as the pH dropped below 5. Although filamentous green algae (FGA) appeared at pH >6, they bloomed as metaphyton (no longer actually attached to the substratum) once pH declined to 5.5 and below. *Zygogonium*, the most common taxon in acid lakes of southcentral Ontario, became the dominant metaphytic FGA. The metaphytic FGA displayed a ratio of respiration to photosynthesis that was similar to unacidified epilithon. Annual growths of metaphytic FGA sometimes covered nearly the entire littoral bottom, affecting the biological, chemical and physical properties of the littoral zone. Changes in Lake 302N, acidified less

severely for a shorter time with nitric acid, corroborated the effects seen in Lake 302S. The functional changes in littoral algal communities resulting from acidification, even at pH >6, are among the most sensitive ones known in aquatic ecosystems.

Introduction

Studies of communities in the littoral zone of acidified lakes have sometimes provided conflicting information about the effects of acidification on the metabolism of littoral algal communities. Almer et al. (1978) proposed that the production of benthic algae in acid lakes was large. Müller (1980) reported that photosynthesis of periphyton on artificial substrata was unchanged by experimental acidification of mesocosms located in oligotrophic Lake 223 at the Experimental Lakes Area (ELA). Lazarek (1982a) reported high rates of photosynthesis by benthic blue-greens in an acidified oligotrophic lake in Sweden. However, both Müller's (1980) and Lazarek's (1982a) conclusions were probably artifacts of the methods used (Turner et al. 1987). In contrast, both Hendrey et al. (1976) and Hall et al. (1980) reported that chlorophyll-specific photosynthesis declined in periphyton of acidified streams. During the experimental acidification of oligotrophic Lake 302S at the ELA, net photosynthesis of naturally occurring epilithon declined in parallel with the acid-induced decline in dissolved inorganic carbon (DIC) (Turner et al. 1987). The importance of DIC in controlling the rate of growth of acidified periphyton was

substantiated in studies of communities on artificial substrata (Fairchild and Sherman 1990, 1992), and of naturally occurring communities (Turner et al. 1991, Chapter 3).

There is less dispute about the effects of acidification upon the compositional character of littoral algal communities. Müller (1980) reported that acidification lowered species richness in periphyton on artificial substrata in experimental mesocosms. Filamentous blue-greens, a previously stable codominant of epilithic algae under neutral conditions, began to decline in importance as the pH of Lake 302S was decreased to 5 (Turner et al. 1991). Filamentous green algae (FGA) bloomed frequently in the littoral zones of acid lakes in Scandinavia (Hendrey et al. 1976, Almer et al. 1978, Hendrey 1982) and North America (Stokes 1986, Wei et al. 1989, Howell et al. 1990, France et al. 1992). These blooms have also been seen in whole-lake acidification experiments (Müller 1980, Schindler and Turner 1982, Schindler et al. 1985, Howell et al. 1990, Webster et al. 1992). FGA were successful at obtaining DIC at low concentrations, allowing them to overcome (at least partly) the carbon limitation found in acidified lakes (Turner et al. 1991). During the progressive acidification of Lake 302S, the character and composition of FGA growths changed. FGA appeared initially both as a shoreline band of epilithon and as epiphyton at pH >6 (Turner et al. 1987), and changed to a metaphytic growth form (no longer truly attached to the substratum) as the pH declined to 5.5 and below (Howell et al. 1990; Chapters 4 and 5).

Here, the effects of continued acidification on littoral algal communities in two experimental lakes (302S and 302N) were studied in ongoing experiments (Turner et al. 1987, 1991; Howell et al. 1990). The changes in metabolism and composition of naturally occurring communities in the acidified lakes were compared with those in unperturbed reference lakes. The decline of the normally dominant periphyton, the emergence of the acidification-induced FGA, and the accompanying consequences for food webs and biogeochemical cycles in the littoral zone are described.

Methods and Materials

Study Lakes

The studies were conducted in small oligotrophic lakes at the ELA, a natural laboratory located in the boreal forest of the Canadian Shield in northwestern Ontario. Turner et al. (1987, 1991), Rudd et al. (1990) and Schindler et al. (1991) described the early experimental histories of Lakes 302S and 302N. The southern basin was separated from its northern downstream basin using a vinyl curtain. From 1981 to 1986, equivalent amounts of sulfuric and nitric acid (in μeq/L) were added to the S and N basins, respectively, to test the relative acidification efficiences of the two acids (Rudd et al. 1990). The techniques for adding sulfuric and nitric acids to the epilimnia were equivalent to those described for Lake 223 (Schindler et al. 1985). The pH was decreased in Lake 302S from 6.5-6.8 in 1980-81 to ~ 4.5 by 1988, and remained at this pH

through 1991 (Fig. 2.1). Lake 302N pH declined less than in Lake 302S (Fig. 2.1) because of the greater efficiency of lakes in neutralizing nitric acid (Rudd et al. 1990). Lakes 239 and 382, nearby circumneutral lakes, were used as reference lakes for studies of epilithon and FGA. Circumneutral Lake 226S was used as another reference lake for the distribution of metaphytic FGA. Morphometric and chemical features of the study lakes are characterized by Turner et al. (1987) and in Chapter 3.

Chemical conditions arising from the acidification of Lake 302S and 302N have been described elsewhere (Turner et al. 1987, Rudd et al. 1990, Schindler et al. 1991). Epilimnetic concentrations of hydrogen ion, sulfate, nitrate (Lake 302N only), ammonium, and total dissolved manganese increased. Dissolved organic carbon, DIC and nitrate (Lake 302S only) declined. Phosphorus concentrations were unchanged.

Metabolism, Biomass and Composition of Epilithon

Both epilithon and benthic growths of FGA were studied. The bottom of the littoral zone of the study lakes is largely rock, so SCUBA-based techniques were developed (Turner et al. 1983, 1987) to measure the metabolism and composition of epilithon. Naturally occurring communities were studied because periphytic productivity is better examined using natural communities rather than those that develop on artificial substrata (Aloi 1990). Epilithon on rock surfaces of low slope ($< 10^{o}$) was sampled at unshaded locations with

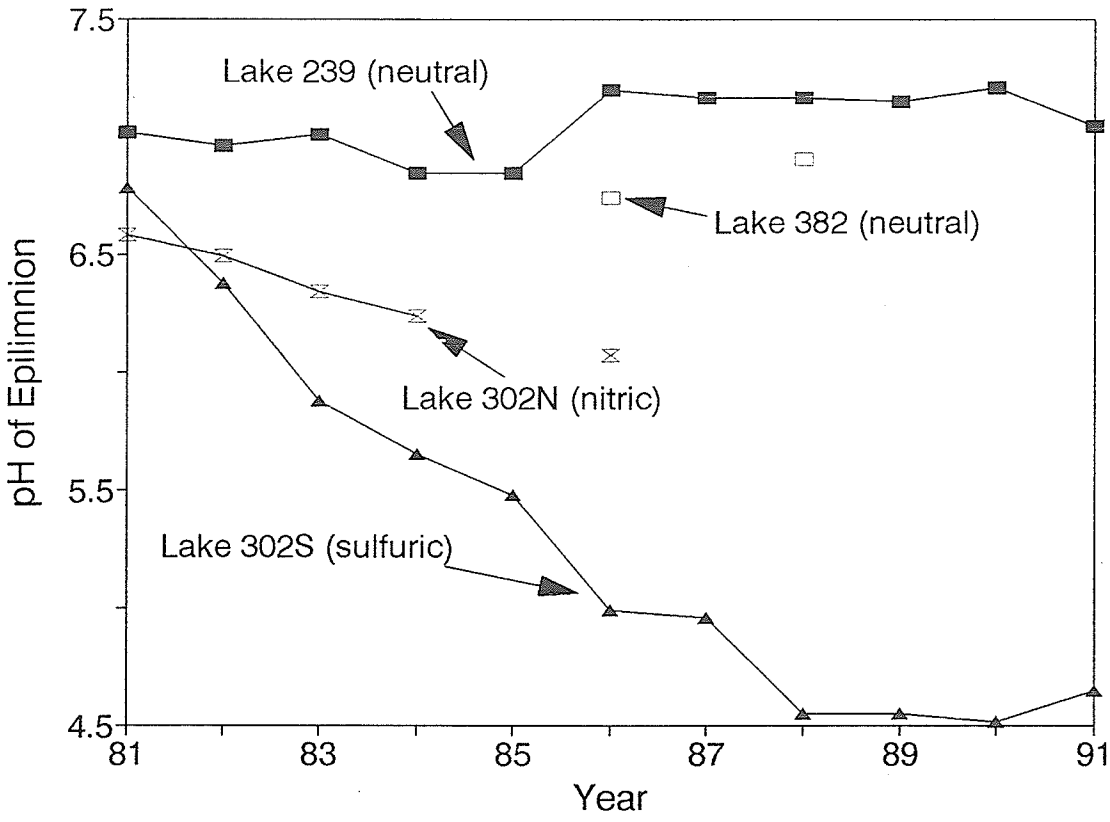

Fig. 2.1. Mean pH in the epilimnia of the acidified lakes (302S and 302N) and reference lakes (239 and 382) during the open-water periods of the study. Acidification of Lakes 302S (sulfuric) and 302N (nitric) began in July of 1982.

exposures to the south. Sampling was conducted in the middle littoral zone, typically between 1 and 2 m of water depth.

Rates of photosynthesis and respiration were measured *in situ* by monitoring directly the changes in DIC that occurred in the water overlying enclosed epilithon. Samples were isolated by sealing chambers, which transmitted varying amounts of light, to rock surfaces. Each light condition was sampled in three different locations. DIC concentrations in these low DIC lakes were analysed using an infrared gas analyzer (Turner et al. 1987).

The maximum rate of net photosynthesis during each sampling period was estimated as the mean areal rate of DIC uptake by three or more samples incubated at ambient DIC and exposed to 100% of available irradiance. Turner et al. (1987) determined that such samples were light saturated. Respiration was similarly measured as the mean areal rate of DIC release by three samples incubated in the dark. Values of respiration less than zero were assumed to be due to measurement error; in these cases, respiration was assumed to be 0.1 $\mu molC \cdot m^{-2} \cdot h^{-1}$. Lakes were sampled typically every four weeks, i.e. six to seven times during the ice-free season (except in 1981 when sampling started in late July, and in 1982 and 1983 when sampling was more frequent). On several occasions in 1982, supplementary DIC was added to the water prior to incubation; these estimates of photosynthesis have been excluded from the analysis of naturally occurring rates. Annual mean rates were then computed as the simple average of the estimates derived from each sampling period.

Seasonal patterns of epilithic photosynthesis were examined by computing the rate of photosynthesis at each sampling period as a percentage of its corresponding annual maximum. The average percentage for each month was then calculated for years in which there were six or more sampling periods: 1982 to 1991 in Lakes 239 and 302S; 1983, 1984 and 1986 in Lake 302N; 1984 and 1986 in Lake 382.

The ratio of respiration to gross photosynthesis was calculated to examine the energy balance within algal communities. Gross photosynthesis was calculated by summing rates of net photosynthesis and dark respiration. This procedure overestimates actual gross photosynthesis because epilithic respiration in the light was less than in the dark (Graham and Turner 1987). Because the bias was especially large in acidified epilithon, in which respiration was large (see below), the effect of acidification on gross photosynthesis is unknown. However, the bias has little effect on the calculated ratio because respiration is included in both its numerator and denominator.

Epilithon for taxonomic and carbon content analyses was collected using a diver-borne syringe scraper (Turner et al. 1991). Collections prior to 1986 were made with a non-quantitative sampler (Stockner and Armstrong 1971) precluding estimation of areal concentrations. Subsequent modifications improved the efficiency of collection, reduced lateral contamination, and allowed estimation of areal concentrations of particulate carbon (Turner et al. 1991).

Samples of epilithon of 5 cm^2 were collected in duplicate at each of

three sampling sites; two composite samples were then created in the laboratory by pooling one replicate from each site. Sample suspensions were then filtered (Turner et al. 1987), frozen, and analysed for particulate carbon (Stainton et al. 1977). Aliquots of these composite samples were also preserved for taxonomic analysis by adding equal quantities of acid Lugol's solution and FAA (formaldehyde, acetic acid and alcohol) to achieve 4% final volume. The relative frequencies of algal taxa were determined using the methods described in Turner et al. (1991).

Metabolism, Biomass and Composition of FGA

Methods for assaying the metabolism of FGA (Chapter 4) involved measuring changes in DIC in samples collected from several locations in Lake 302S. Aliquots of these samples were then incubated in gradients of light, algal density, and available DIC. The details of FGA metabolism measured during 1988 to 1991 are described in Chapter 4. The energy balance of the FGA (as computed for the epilithon), obtained by calculating ratios of mean annual rates of respiration to gross photosynthesis, is reported here.

In August or September of each year from 1982 to 1988, the entire perimeters of Lakes 302S, 239, 226S (1988 only) and 382 (1983 and 1984 only) were surveyed for occurrences of metaphytic FGA. Thickness and percentage shoreline coverage were determined visually (Turner et al. 1987). A substantially different technique of transect sampling (Chapter 5) was also used

in 1988 to measure FGA biomass in Lake 302S.

Algal composition of the FGA was analysed until 1988 using collections made during the shoreline surveys (Turner et al. 1987). Thereafter, subsamples of collections made for metabolic measurements were analyzed (Chapter 4).

Results

Metabolism of Epilithon

Mean rates of net photosynthesis in epilithon during the open-water period declined as acidification progressed (Table 2.1, Fig. 2.2). The rapidity of decline was similar in both the sulfuric and nitric acid lakes. Preacidification rates in epilithon of both basins of Lake 302 were lower than in the neutral lakes, likely reflecting the lower epilimnetic DIC in Lake 302 prior to manipulation (Chapter 3). Much of the decline in the annual rates observed in Lake 302S occurred between pH ~ 7 and 5.5.

The seasonal pattern of net photosynthesis in epilithon was much different between neutral and acidified lakes (Fig. 2.3). The communities in circumneutral Lakes 239 and 382 displayed maximum rates of photosynthesis during July and August. In contrast, epilithon in acidified Lakes 302S and 302N had spring and fall maxima, and exhibited minimum photosynthesis in July and August. The degree of this change was greater in epilithon of the more acid Lake 302S. In addition, although the absolute variability in acidified and neutral

Table 2.1. Open-water summaries of epilithic metabolism and particulate carbon in four lakes at the Experimental Lakes Area during 1981 to 1991. DIC is dissolved inorganic carbon. Two values of "N" (number of sampling periods) are given where they differed for respiration and net photosynthesis. Including an outlier increased the carbon in 302N during 1986 to 2.02 $\pm$ 0.35 $M \cdot m^{-2}$.

Lake	Year	N	DIC	Dark Respiration		Net Photosynthesis		Carbon	
			(µM)	($\mu molC \cdot m^{-2} \cdot h^{-1}$)		($\mu molC \cdot m^{-2} \cdot h^{-1}$)		($molC \cdot m^{-2}$)	
				Mean	SE	Mean	SE	Mean	SE
239	81	6	156	-105	34	315	33		
239	82	12	139	-111	22	346	18		
239	83	12	144	-126	31	396	39		
239	84	7	176	-76	34	488	77		
239	85	7	146	-57	26	358	16		
239	86	6	148	-54	8	378	48	1.82	0.17
239	87	7	143	-64	22	342	53	1.85	0.10
239	88	7	146	-138	43	343	45	2.12	0.26
239	89	6	153	-84	31	431	53	2.01	0.32
239	90	7	169	-80	27	459	36	1.88	0.20
239	91	7	173	-9	6	481	35	1.98	0.26
382	84	7	105	100	35	284	27		
382	86	6	86	72	18	316	25	2.03	0.16
302S	81	4	75	-74	26	231	26		
302S	82	12,8	62	-121	17	221	33		
302S	83	9	32	-191	15	176	23		
302S	84	7	31	-181	38	98	42		
302S	85	7	29	-222	30	88	24		
302S	86	6	17	-366	46	58	11	1.63	0.27
302S	87	7	32	-371	72	133	25	2.08	0.29
302S	88	7	28	-333	61	46	26	1.60	0.25
302S	89	6	26	-403	70	45	47	1.16	0.10
302S	90	7	21	-444	76	-44	43	0.74	0.09
302S	91	7	27	-262	53	113	30	0.61	0.21
302N	81	3	80	62	35	256	51		
302N	82	7,3	53	110	15	218	7		
302N	83	6	46	154	39	164	44		
302N	84	7	51	144	47	136	32		
302N	86	6	20	174	23	74	15	1.68	0.09

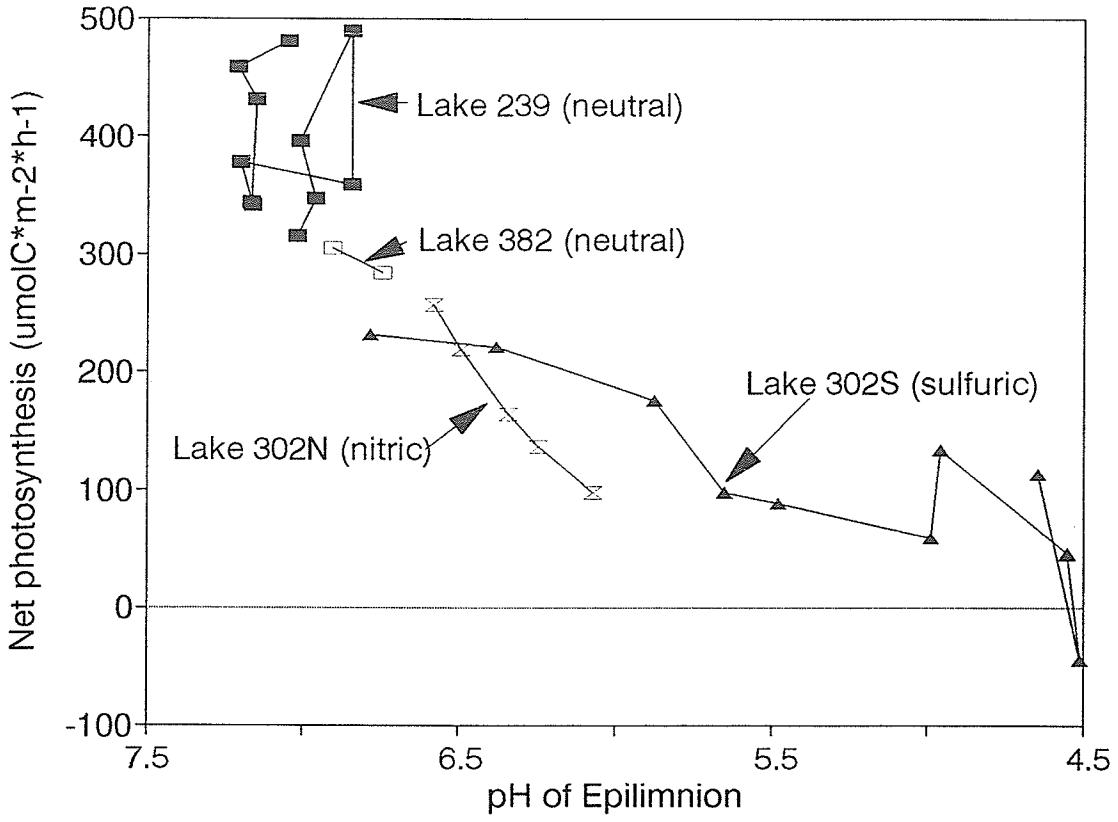

Fig. 2.2. Means of the maximum rates of net photosynthesis in epilithon during the open-water period. Each value shown represents the mean of three to 12 seasonal samplings (typically six or seven) during the open-water period, each comprised of three or more estimates of the maximum rate of net photosynthesis.

seasonal patterns was similar, the relative variability was greater in the acidified communities. For example, the average % standard error of the monthly means was 7% and 4% in neutral Lakes 239 and 382, respectively, whereas the corresponding values in acidified Lakes 302S and 302N were 15% and 29%, respectively.

Epilithic respiration increased strongly with acidification in both the nitric and sulfuric acid lakes (Fig. 2.4). As a result, the energy balance of epilithon, expressed as the percentage of gross photosynthesis used for respiration, increased (worsened) with acidification in both Lakes 302S and 302N; i.e. the ratio of respiration to photosynthesis increased as acidification progressed (Fig. 2.5). Respiration as a fraction of gross photosynthesis in Lake 302S averaged 90% $\pm$ 8% ($\pm$ SE, n = 4 y) during the four years at pH 4.5. In contrast, the ratio in epilithon of reference Lakes 239 and 382 was only 17% $\pm$ 2% (n = 11 y) and 23% $\pm$ 3% (n = 2 y), respectively.

Algal Taxonomic Composition and Biomass of Epilithon

The major taxonomic groups of the epilithon changed markedly with acidification (Fig. 2.6). Taxonomic composition, which had been stable until pH 5.6, became variable as the pH declined to 5 and below, when filamentous blue-greens declined to 0%. Filamentous blue-green algae (principally *Lyngbya* and *Anabaena*) remained the annually dominant taxa until the pH dropped below 5. Thereafter, coccoidal blue-greens (first *Merismopedia minutissima* and

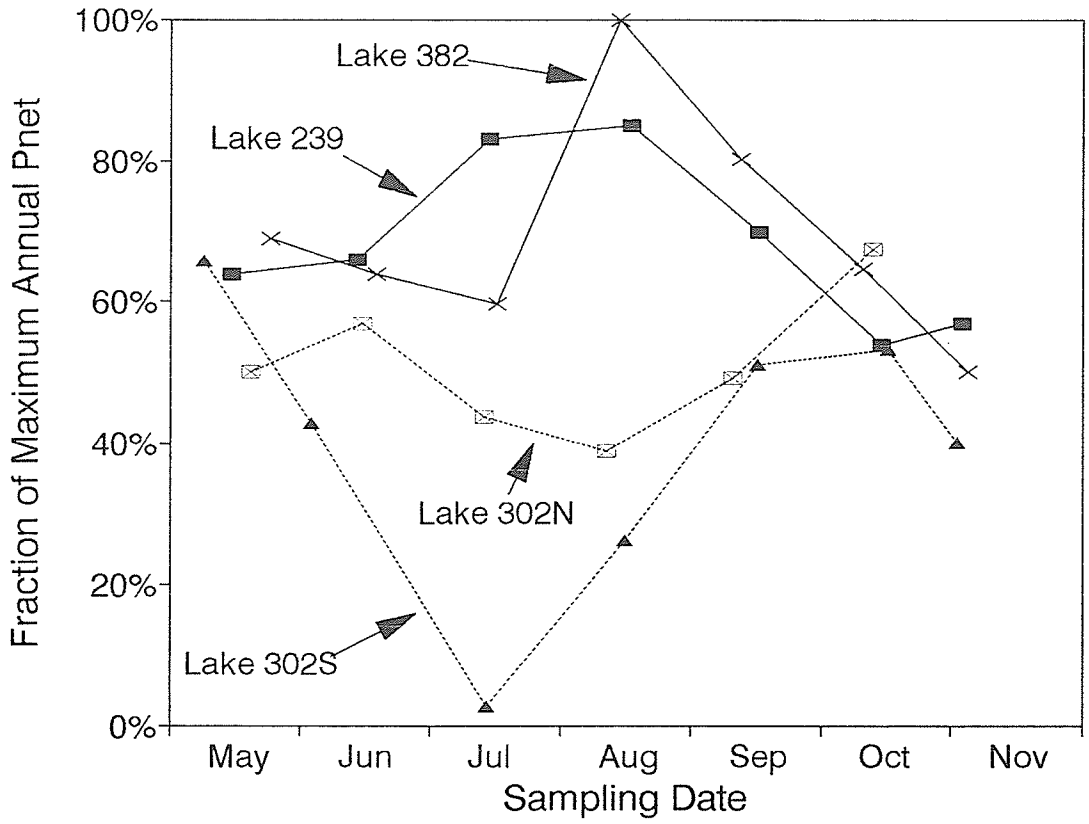

Fig. 2.3. The monthly pattern of epilithic photosynthesis in the acidified lakes (302S and 302N) and that occurring in the reference lakes (239 and 382). Daily estimates of the maximum rate of photosynthesis were standardized as a percentage of the annual maximum rate in each lake. Monthly means (shown) were then computed for the years described in the text.

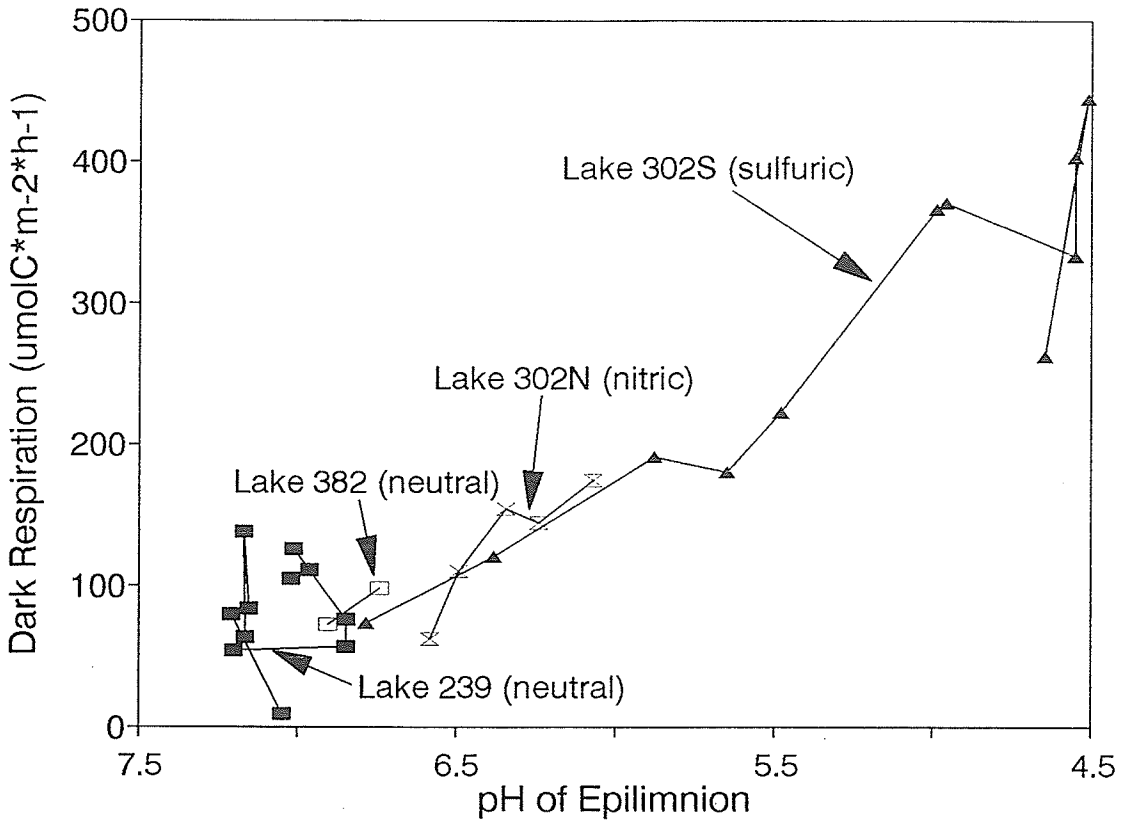

Fig. 2.4. Mean rates of respiration in epilithon during the open-water period. Sampling frequency paralleled that of photosynthesis (Fig. 2.2), except that the estimate obtained on each sampling occasion was typically the mean of three observations.

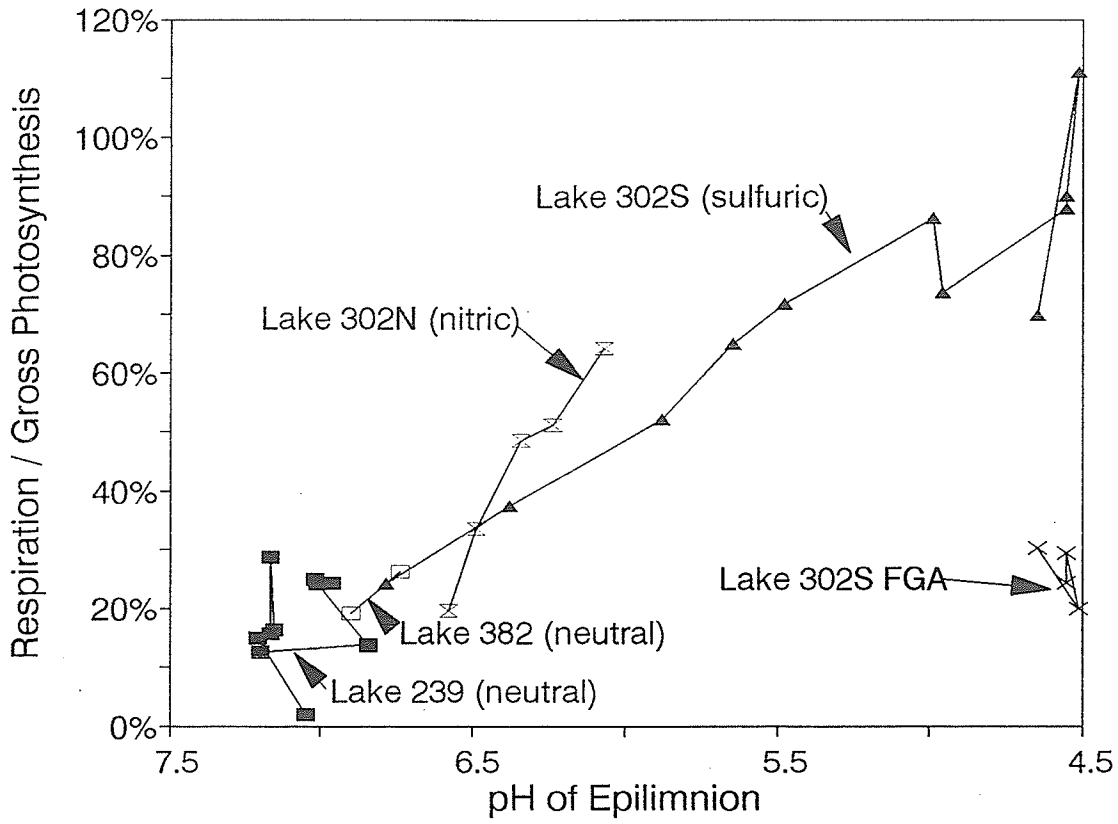

Fig. 2.5. Mean rates of respiration as a proportion of calculated rates of gross photosynthesis in epilithon of the study lakes and in FGA of Lake 302S (see below) during the open-water period.

then *Chroococcus minutus*) or diatoms (e.g. *Eunotia pectinales* and *Anomoeoneis serians* var. brachysira) dominated. In contrast, filamentous blue-greens and diatoms remained stable codominants in Lake 239 throughout the study, contributing 52% ± 3% (± SE, n = 11 yr) and 39% ± 3% of cells and filaments, respectively.

Particulate carbon of epilithon in Lake 302S declined as the pH decreased below 5 (Table 2.1). Mean annual values of particulate carbon reached a minimum of 0.61 molC/m^2 in 1991 at pH 4.5. The decline in epilithic carbon in Lake 302S during 1991 mirrored that in photosynthesis, reaching an August low of 0.04 molC·m^{-2}. In comparison, epilithic carbon in Lake 239 was surprisingly stable during 1986-1991, with a mean of 1.94 molC·m^{-2} ± 0.05 (± SE, n = 6 yr). Similar values (2.03 molC·m^{-2}) were observed in Lake 382 during 1986. The decline seen in epilithon of Lake 302S was accentuated by the visual impression of more epilithon in Lake 302S in its preacidification state than there was in Lake 239. A possible decline of carbon at higher pH in Lake 302S is uncertain because of non-quantitative sampling prior to 1986.

Metabolism of Filamentous Green Algae

The mean annual ratio of respiration to calculated gross photosynthesis averaged 26% (± 3%, ± SE) in FGA during the four years that the pH of Lake 302S was ~ 4.5 (Fig. 2.5). This value differed sharply from the 90% (see above) seen in the epilithon of Lake 302S during the corresponding period of time. In

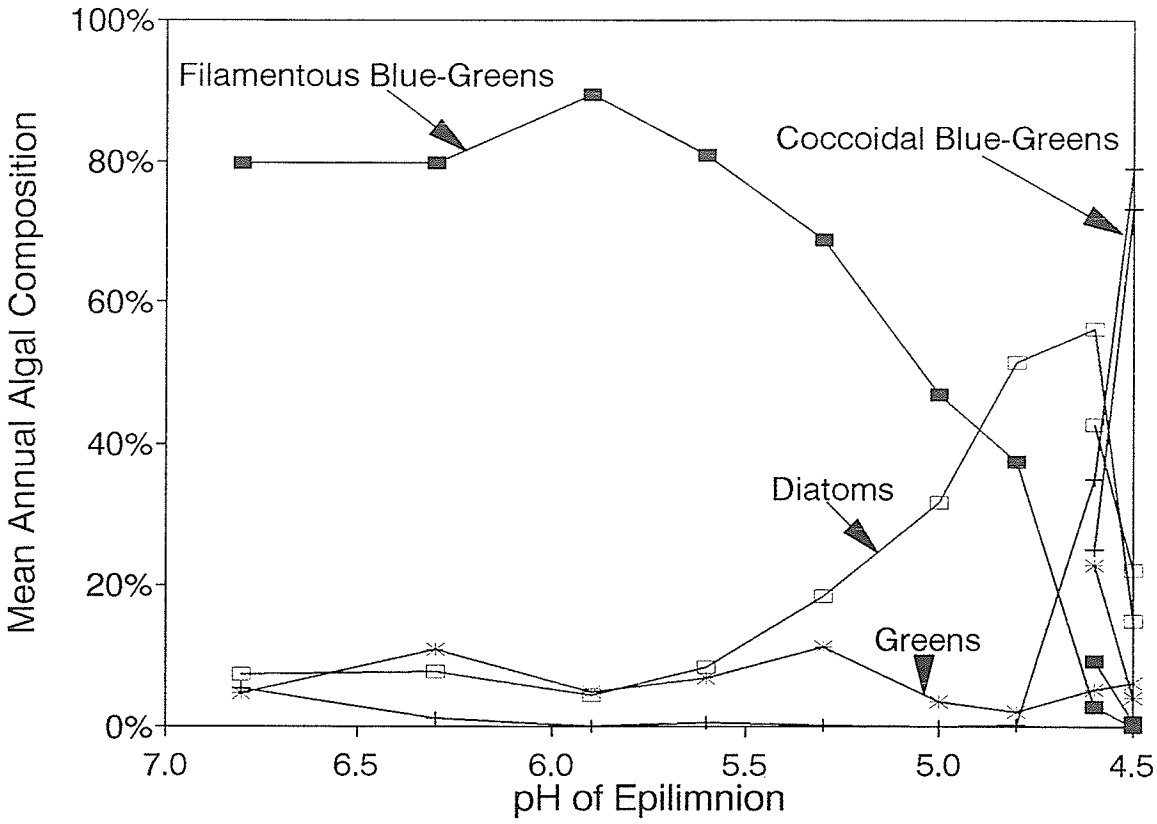

Fig. 2.6. Algal taxonomic composition of epilithon in Lake 302S. Values shown are the mean annual proportions that each major taxon contributed to the cell or filament frequency in the epilithon.

contrast, the ratio in FGA was more similar to the value of 15% (± 6%) seen in the epilithon of neutral Lake 239 during these years.

Taxonomic Composition and Biomass of Filamentous Green Algae

Taxonomic composition of the metaphytic FGA, measured as the annual mean fraction of FGA biovolume, changed as acidification progressed (Fig. 2.7). *Spirogyra* dominated the metaphytic FGA in 1985, but was in low abundance by 1987. *Mougeotia* dominated during 1986 and 1987 at a pH ~ 5, but declined in abundance as the pH decreased to 4.5. *Zygogonium* was consistently the most abundant metaphytic FGA at the lowest pH values.

Appreciable metaphytic FGA was first noted in Lake 302S during 1985 as the epilimnetic pH declined to about 5.5 (Fig. 2.8). Both the extent of metaphytic coverage and the thickness of growths increased with further acidification. In the first year of acidification to pH 4.5, most of the shoreline was affected by metaphyton of almost 30 cm median thickness. In contrast, during annual surveys in neutral Lakes 239 (1982 to 1988) and 382 (1983 and 1984), no detectable amounts of metaphytic FGA were found. Similarly, no metaphytic FGA were found in nearby circumneutral Lake 226S during 1988.

The results of the transect survey corroborated those of the visual survey technique; 83% of the littoral bottom from 0 to 4 m was covered by FGA to a mean thickness of 22 cm (Chapter 5).

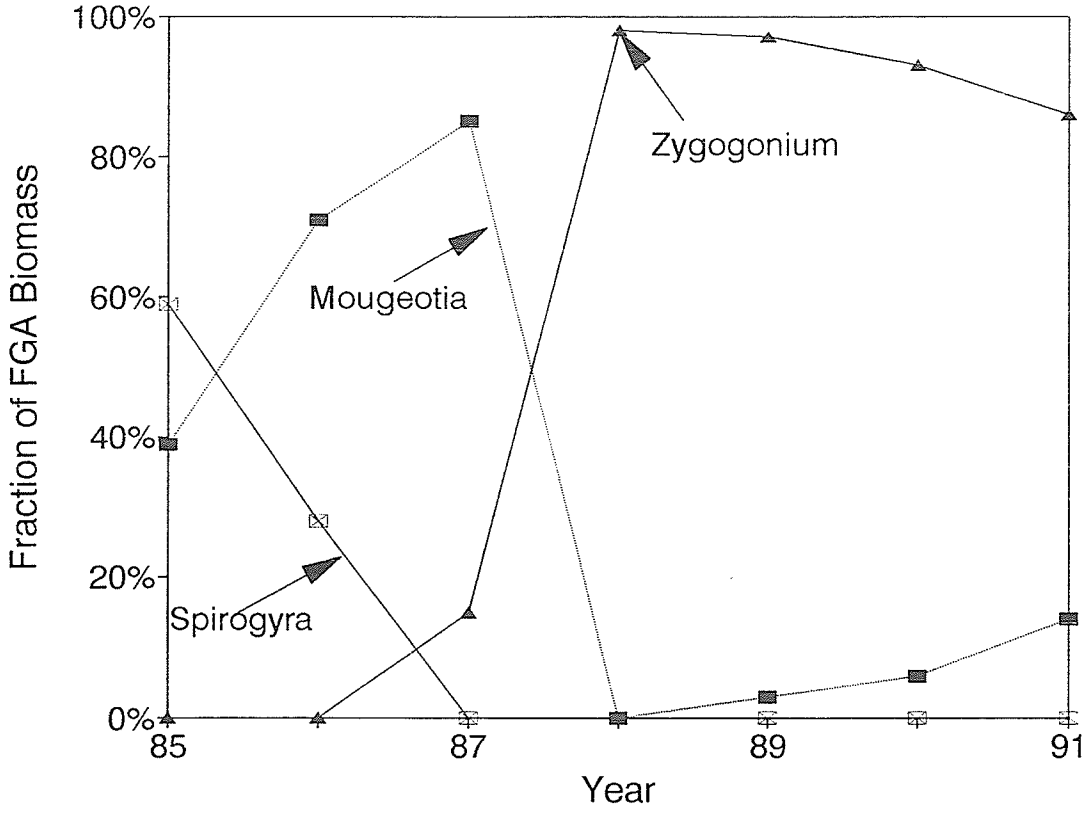

Fig. 2.7. Taxonomic composition of metaphytic filamentous green algal blooms during the acidification of Lake 302S. Values for 1989 to 1991 were derived from (Chapter 4).

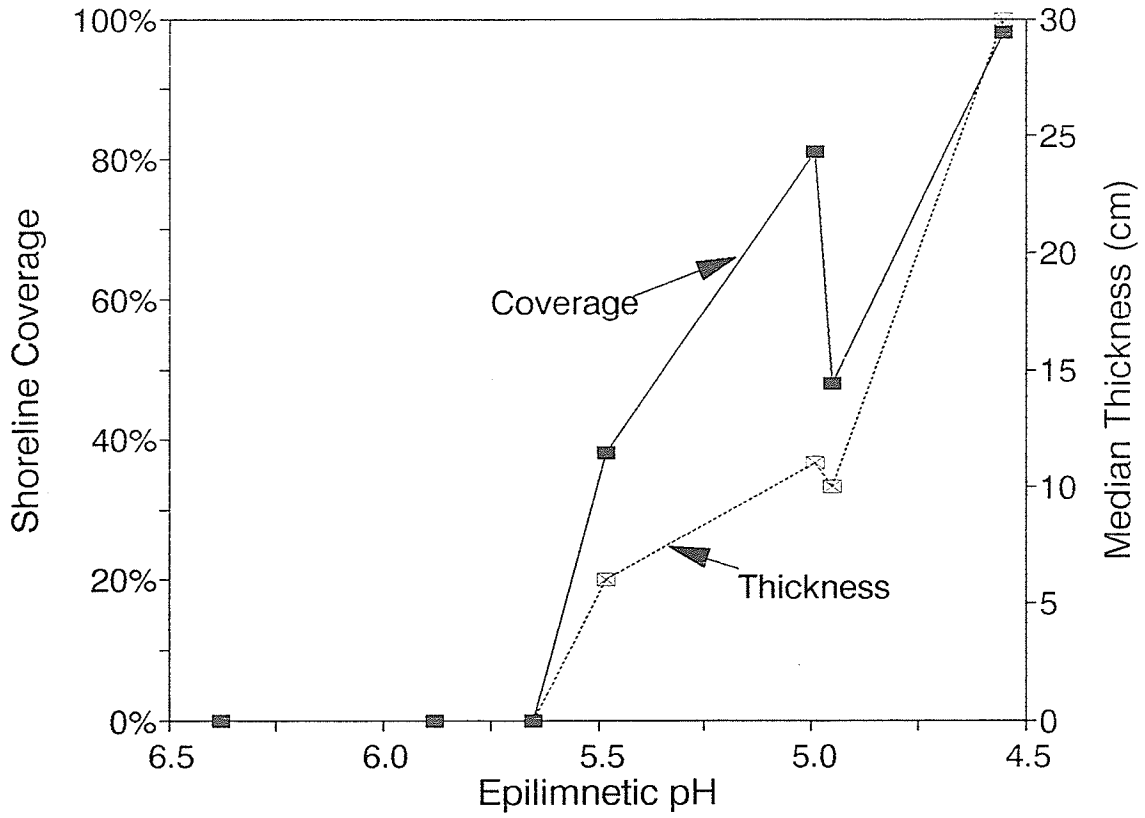

Fig. 2.8. Coverage of the bottom of Lake 302S by unattached growths of filamentous green algae as the pH declined.

Discussion

Effects of Acidification on Production and Respiration

A decline in net photosynthesis (Fig. 2.2) was the first detected functional response of epilithon to acidification. The decline in photosynthesis of epilithon occurred in response to acidification by either sulfuric or nitric acid, even at pH >6 (Fig. 2.2, Turner et al. 1987). As a result, epilithic energy flow (photosynthesis and respiration) was the lake function most sensitive to acidification (Schindler 1990). Other lake functions such as nitrification, nitrogen fixation, and internal alkalinity generation, were affected at much lower pH values (Schindler 1990, Schindler et al. 1991).

The decrease in epilithic photosynthesis occurred because of carbon limitation as acidification depleted the DIC available by eliminating the bicarbonate pool (Turner et al. 1987, Chapter 3). Turner et al. (1987, 1991) described the early phase of the decline in response to decreased concentrations of DIC, and the stimulation of photosynthesis by increased DIC. Similar responses were seen in epiphyton on the common macrophyte *Eriocaulon septangulare* (Turner et al. 1991). These findings diverged from the expectation that photosynthesis of all benthic algal associations would increase with acidification, based upon anecdotal reports of massive increases in benthic biomass resulting from acidification (e.g. Almer et al. 1978).

The seasonal pattern of epilithic photosynthesis in acidified lakes also changed with acidification (Fig. 2.3). Maximum epilithic photosynthesis in acidic

Lake 302S occurred in the spring and fall, when water temperatures were low, solubility of CO_2 was high, and DIC concentrations were at their open-water maximum. Minimum photosynthesis occurred during midsummer when water temperatures were high, solubility of CO_2 was low, and DIC concentrations were at their open-water minimum. This pattern was opposite to that seen in the circumneutral lakes (Fig. 2.3). In circumneutral epilithon, it appears that the temperature enhancement of photosynthetic rates (Turner et al. 1987) exceeded the seasonal reduction in CO_2, probably because bicarbonate was available to counteract the reduced solubility of CO_2 in the warmer water temperatures of summer.

The effect of acidification upon epilithic photosynthesis was in marked contrast to the apparent lack of effect on phytoplankton photosynthesis (Chapter 3), which is measured using the ^{14}C uptake technique (Shearer et al. 1985), and therefore does not account for respiration. This measure of phytoplankton photosynthesis was sustained or even increased as the lakes acidified (Shearer and DeBruyn 1986; Shearer et al. 1987; Schindler 1988, 1990). Turner et al. (1991) hypothesized that the diffusive boundary layer around phytoplankton is thinner than that adjacent to many benthic algae because of the circulation of planktonic algae within the epilimnion; the probable limits to this generalization are considered in Chapter 3. Because the rate of nutrient uptake is inversely related to boundary layer thickness (Riber and Wetzel 1987), phytoplankton are less likely than periphyton to be limited by the

acidification-caused depletion of DIC. For example, photosynthesis of phytoplankton in experimentally acidified Lake 223 was never enhanced by DIC enrichment (Shearer et al. 1987). This distinction between benthic and open-water communities leads to a better understanding of the potential consequences of lake perturbations that affect the carbon cycle (Chapter 3).

Periphytic respiration increased as the lakes acidified (Fig. 2.4, Turner et al. 1991). However, respiration was expected to decline, partly explaining the accumulation of organic detritus seen previously in littoral zones of acidified Scandinavian lakes (Hendrey 1976, Almer et al. 1978, Traaen 1980). Increased epilithic respiration also appeared inconsistent with the conclusion that winter decomposition was reduced by acidification to pH $\leq$ 5 (Kelly et al. 1984, Schindler 1990). This disparity may be due to differences in: catabolism of 'new carbon' versus 'old' and refractory carbon; the time of year of the observations; or metabolism of periphyton versus that of the whole lake (Chapter 6).

The cause(s) of increased periphytic respiration remain uncertain (Turner et al. 1991), but the increase occurred in parallel with increased concentrations of inorganic nitrogen in the acidified lakes (Chapter 3). This relationship is being studied to determine whether ammonia is a cause (by enhancing the ratio of nitrogen to carbon), or a result (a metabolic byproduct) of increased respiration.

Respiration accounted for much of epilithic gross photosynthesis during

the four years at pH 4.5 (Fig. 2.5). The ratio of respiration to (gross) photosynthesis is considered by Odum (1971) as possibly the most important of all ecosystem functions. From the increase in this ratio, it can be deduced that acidified periphyton would eventually be unable to support a (classical) littoral food web. This hypothesis is consistent with the decline seen in epilithic carbon (Table 1), although other factors (e.g. herbivory) are likely involved in the biomass decline. In contrast, the ratio of respiration to photosynthesis in the more successful metaphytic FGA was similar to that seen in neutral periphyton (Fig. 2.5), which is consistent with the ability of FGA to bloom under acid conditions (Fig. 2.8).

Effects of Acidification on Species Composition and Community Structure

Major structural changes in the algal composition of epilithon accompanied acidification and the resulting decline in net production (Fig. 2.6). Mucilaginous coccoidal blue-greens and acidophilic diatoms replaced filamentous blue-greens as the pH declined below 5. With the loss of heterocystous blue-greens, the nitrogen-fixing capacity of the community would also have been lost. However, this loss should have been unimportant as carbon became more limiting to periphyton and as epilimnetic ammonium concentrations increased. Blue-greens also disappeared from the plankton of Little Rock Lake, Wisconsin, as it acidified (Schindler et al. 1991). Such declines are inconsistent with predictions that filamentous blue-greens should

be important in acidified benthos (Lazarek 1982a).

Structural changes in periphyton also included a decrease in algal taxonomic richness, with numbers of green and blue-green taxa declining (M. A. Turner and D. L. Findlay, unpublished data), confirming the experimental mesocosm observations of Müller (1980). In contrast, the composition of periphyton at neutral pH was stable (Turner et al. 1987).

Epilithic biomass (as inferred from concentrations of carbon) declined dramatically at pH 4.5 (Table 1). This was especially noticeable during midsummer when rocks appeared almost bare; e.g. in midsummer of 1991, epilithic carbon decreased to only 2% of values in the reference lakes. The character of sedimentary areas in the littoral zone also changed in a parallel manner. The depth of sediment appeared to decrease over the several years of acidification, exposing previously buried Fe-Mn encrustations in some regions (M. A. Turner, unpublished observations). Possible effects of such sediment consumption include relocation of the site of sedimentary-based oxidation-reduction reactions, followed potentially by the reduction of internal alkalinity generation (Kelly et al. 1994).

In contrast to what occurred in the epilithon, FGA proliferated with acidification. FGA had first developed at pH >6.0 attached both to rocks in the wave zone and to macrophytes in the shallows (Turner et al. 1987). FGA then developed annual blooms of unattached forms, or metaphyton, as the pH declined to about 5.5 and below (Fig. 2.8, Howell et al. 1990), spreading over

additional bottom types, and growing deeper. Similarly, extensive benthic growths of FGA were first seen at pH 5.6 during the experimental acidification of Little Rock Lake (Webster et al. 1992). In contrast, no metaphytic FGA were seen in the ELA reference lakes.

The dominant taxa of the metaphytic FGA changed with progressive acidification: *Spirogyra* was replaced by *Mougeotia* and finally by *Zygogonium* (Fig. 2.7). *Zygogonium* remained the dominant FGA during the four years that Lake 302S was held near pH 4.5. This taxon is the most common of the bloom-forming FGA in the littoral zone of acidic lakes in southcentral Ontario (Wei et al. 1990, France et al. 1992). These FGA proliferated because of their ability to adapt to low concentrations of DIC (Turner et al. 1991, Chapter 4), and their obvious tolerance of high H^+ concentrations. Similarly, Robinson et al. (1994) found that *Zygogonium* in Lake 302S had high affinity for CO_2. The loss of large potential grazers such as *Hyalella* (Grapentine and Rosenberg 1992) and *Orconectes* (Davies 1989) may also have contributed to their buildup (Hendrey 1976).

Effects of Changed Littoral Algal Communities on Other Ecosystem Processes

The fundamental character of energy flow within the littoral food web was altered by acidification. Net photosynthesis decreased in the normally dominant epilithon (Fig. 2.2) and in epiphyton (Turner et al. 1991), as respiration increased as a fraction of photosynthesis (Fig. 2.5), and as compensation

irradiances increased (Turner et al. 1991). As well, the seasonality of the remaining epilithic photosynthesis became the opposite of that seen in reference communities (Fig. 2.3). The edibility of the remaining epilithic algal taxa (dominated by mucilaginous blue-greens, Fig. 2.6) likely was diminished, but this was not examined.

In contrast to the decline of the normally dominant periphyton, FGA proliferated in response to acidification (Fig. 2.8), displaying a ratio of respiration to photosynthesis more similar to periphyton in neutral lakes (Fig. 2.5). Given that FGA can be used as food (Fulton 1988), one might conclude that FGA could compensate for the declining role of periphyton. However, much of the FGA blooms remained ungrazed in early fall (Chapter 4) despite the associated proliferation of several groups of littoral Cladocera (e.g. chydorids and macrothricids) (Hann and Turner 1994). With the decomposition of these blooms in late fall and in winter, the overall pattern of energy flow in the littoral zone would have been altered beyond that resulting from dysfunction of periphytic metabolism. Furthermore, the seasonal pattern of FGA photosynthesis was not fully complementary to that of the residual epilithic photosynthesis (Chapter 4). As well, if food was limiting the consumer community, FGA would have been an unstable base for a food web because of particularly large intra- and interannual variations in biomass (Chapter 5). For example, FGA biomass varied by two orders of magnitude during 1991 (Chapter 4), and the size of FGA blooms varied by more than an order of

magnitude during the four years Lake 302S was held at pH 4.5 (Chapter 5). Variability in herbivory, which is unknown, may overshadow this interpretation. Interannual variation in chronically acidified lakes may also be lower than in Lake 302S, but this remains unstudied.

The acid-induced blooms of FGA radically altered the littoral zone of Lake 302S in other ways. Wave energy and light reaching the lake bottom were reduced (Chapter 5); e.g. other phytobenthos were shaded (up to 90%) in proportion to the amount of FGA. The FGA also affected major nutrient cycles (carbon, nitrogen and phosphorus), in part by the sequestering of nutrients (Chapter 5) as predicted by Hendrey (1982) and Stokes (1986). FGA also affected internal alkalinity generation, but this effect was both seasonal and bidirectional (Chapter 5). During growth, FGA took up ammonia from ammonium, leaving H^+, which further acidified the lake. During decomposition, FGA released ammonia, which sequestered H^+, resulting in the formation of ammonium and neutralizing the lake. Kelly et al. (1994) concluded that FGA also affected alkalinity generation via the sulfur cycle.

Conclusions

Lake acidification disrupted the metabolism and structure of littoral algal associations, causing dramatic changes both to the base of the littoral food web. Periphytic energy flow (photosynthesis and respiration) was more sensitive to acidification than any other aspects of lake metabolism or

biogeochemistry yet studied. Previous reviews, based largely on pelagic observations, and done before consequences for the littoral zone were fully known, predicted that ecosystem functions would be unaffected by acidification until relatively low pH values were reached (Schindler 1987, 1990). The importance of the new information will vary with the extent to which the littoral zone contributes to whole-lake metabolism. The importance of acid-induced shifts in the carbon cycle was similarly overlooked because the role of DIC in controlling growth of epilithon was incompletely understood (Chapter 3).

The experimentally acidified lakes have been allowed to recover, so it is unknown whether all the features that were observed will pertain to chronically acidified lakes. Some of the observed effects might have occurred at higher pH (suggesting even greater sensitivity) had the experimental acidifications progressed more slowly. However, the general description provided here is accurate based upon an earlier comparison of biota in experimentally and anthropogenically acidified lakes (Schindler et al. 1991).

Chapter 3. Roles of Nutrients in Controlling Growth of Epilithon in Oligotrophic Lakes of Low Alkalinity.

Abstract

The ability of nutrients to control photosynthesis was compared in epilithon (the complex associated with rock surfaces in the littoral zone) and phytoplankton of thirteen low alkalinity lakes in the Experimental Lakes Area of northwestern Ontario. The study included surveys of lakes varying in nutrient concentrations; experimental lake additions of carbon and nitrogen, with or without phosphorus; and experimental sulfuric and nitric acidification of lakes. Nutrient controls of epilithic and planktonic algal photosynthesis were consistently different. Inorganic carbon limited epilithic growth in both perturbed and unperturbed lakes because diffusive resistance kept the effective supply of inorganic carbon below the level needed for optimal growth. When disturbances reduced the concentration of dissolved inorganic carbon, epilithic photosynthesis was further lowered. Although epilithon displayed nitrogen and phosphorus deficiencies based upon particulate nutrient ratios, rates of epilithic photosynthesis were unrelated to phosphorus availability or to nitrogen supplies. Increased concentrations of inorganic nitrogen were correlated with increased rates of benthic respiration. Improved understanding of the role of inorganic carbon has implications for the predicted impact of atmospheric increases in carbon dioxide on aquatic food webs.

Introduction

Phosphorus limits growth of phytoplankton in most inland lakes (Goldman et al. 1974, Schindler 1974) and of stream periphyton (Traaen 1978, Bothwell 1988 and 1989). However, the role of phosphorus in controlling growth of periphyton in lakes is less clear. For example, phosphorus in lake water was correlated with benthic algal biomass on artificial substrata (Shortreed et al. 1984) and was shown to regulate growth of benthic filamentous green algae in the Great Lakes (Auer et al. 1983). In contrast, Fairchild and Sherman (1992) concluded that phosphorus was not the primary limiter of biomass developing on artificial substrata in twelve lakes ranging in total phosphorus from 0.2 to 1.3 μM. In other studies, development of periphytic biomass on artificial substrata in lakes was uncorrelated with ambient phosphorus levels (Stockner and Armstrong 1971, Evans and Stockner 1972, Ennis 1975), or correlated less well than did phytoplankton biomass (Cattaneo 1987); there is, however, some disagreement about this interpretation (e.g. see Ennis 1975, and Shortreed et al. 1984).

There is little known about the role of nitrogen in controlling the growth of epilithon in lakes. Nitrogen was claimed to limit benthic algal photosynthesis when concentrations were very low (Reuter et al. 1983). This view was supported by the frequent occurrence of heterocystous blue-greens in benthic assemblages (Reuter et al. ibid., Turner et al. 1987). Fairchild and Sherman (1992) concluded that nitrogen limitation was likely when the lake water ratio of

dissolved inorganic carbon to nitrogen exceeded the Redfield (1958) atomic ratio of 6.6:1. This value is equivalent to the ratio of algal carbon to nitrogen that Healey and Hendzel (1979) determined was the threshold for nitrogen deficiency.

Few lake studies have evaluated the ability of inorganic carbon to limit epilithic growth. The view "that inorganic carbon is not the major nutrient controlling algal growth in natural waters" (Goldman et al. 1974, p. 572) has been extended implicitly to benthic algal associations. However, recent studies have indicated that dissolved inorganic carbon (DIC) can be important to benthic photosynthesis in acid lakes (Turner et al. 1987, 1991; Fairchild et al. 1989; Fairchild and Sherman 1990, 1992). Photosynthesis of epilithon and epiphyton in acidified lakes declined partly as a result of the reduced supply of inorganic carbon caused by acidification-induced loss of bicarbonate (Turner et al. 1987). In contrast, there was no lessening in rates of phytoplankton photosynthesis (Shearer and DeBruyn 1986, Shearer et al. 1987).

There have been few studies concluding that inorganic carbon limits benthic algal productivity in unperturbed lakes. Sheldon and Boylen (1975) argued that low-productivity epiphyton removed from *Potamogeton* in an oligotrophic lake was carbon limited. Turner et al. (1991) showed that photosynthesis of both epiphyton of *Eriocaulon* and epilithon in a low alkalinity lake was stimulated by additions of DIC. Fairchild and Sherman (1992) also concluded that photosynthesis of epilithon developing on artificial substrata in

low alkalinity lakes was limited by DIC.

The objective of this study was to reexamine the abilities of carbon, nitrogen, and phosphorus to regulate growth of epilithon compared with phytoplankton. Photosynthesis and respiration of natural communities of epilithon were studied in experimental (acidified and eutrophied) and unperturbed lakes in the Experimental Lakes Area (ELA) in northwestern Ontario.

Methods

Study Area

The regional geology of the ELA ($93^{o}30'$-$94^{o}00'$ and $49^{o}30'$-$49^{o}45'$) was described by Brunskill and Schindler (1971) and by McCullough and Campbell (1993). The basic morphometric characteristics, experimental status, and years of seasonal monitoring of epilithic photosynthesis in the study lakes are described in Table 3.1. Water residence times exceeded 0.5 y for all lakes except for Lake 938 (annual mean value = 0.07 y). Pertinent epilimnetic chemistry (methods according to Stainton et al. 1977) of the study lakes is summarized in Tables 3.2 and 3.3.

Algal Associations Studied

Undisturbed epilithon on natural substrata were studied *in situ*, as described below, for most of the experiments. Unshaded communities on rock

Table 3.1. Basic morphometric characteristics and experimental status of the study lakes during the investigation. The years are given for which epilithic photosynthesis was monitored. The sources of the morphometric data are: (1) McCullough and Campbell (1993); (2) Beaty and Lyng (1989); (3) D. Cruikshank (Fisheries and Oceans, Canada, pers. comm.).

Lake	Surface Area (ha)	Mean Depth (m)	Experimental Status	Epilithic Monitoring	Source
149	26.9	2.0	Reference		1
226N	8.3	5.7	+ C, + N, + P		2
226S	7.8	5.7	+ C, + N		2
226S			Reference		2
228	1677	55.4	Reference		3
239	54.3	10.5	Reference	1981-1991	2
302N	12.8	5.7	+ HNO_3	1981-1984,	2
302S	10.9	5.1	+ H_2SO_4	1981-1991	2
305	52.0	15.1	Reference		3
373	27.3	11.0	Reference		1
375	18.7	11.6	Reference		3
377	26.9	9.2	Reference		1
382	36.9	5.8	Reference	1984, 1986	2
442	16.0	9.0	Reference		1
938	19.2	2.0	Reference		1

surfaces of slope $\leq 10^{o}$ were sampled at depths of 1 to 2 m (Turner et al. 1987). However, epilithon that developed on artificial substrata (acrylic and granite) in the Lake 226 whole-lake nutrient enrichment experiment (Turner 1981) also were used. These substrata, which had been placed *in situ* the year prior to sampling, were transferred by SCUBA diver from the lake bottom to an incubation chamber.

Metabolic Measurements

Photosynthesis, rather than accrual of biomass, was measured as a surrogate for growth in this study because changes in availability of a limiting nutrient could modify algal growth rates without altering final yields (O'Brien 1972), and changes in epilithic biomass provide little information about nutrient limitation of growth (Fairchild and Sherman 1992). For a variety of reasons, a direct relationship between yield and periphytic algal growth is almost impossible to establish.

Analysis of epilithic metabolism mainly involved measurement of the change in DIC concentration in water overlying enclosed samples. Community dark respiration (R_d) was estimated by measuring efflux of DIC in samples enclosed in the dark. By manipulating the amount of light available to other samples *in situ*, photosynthesis-irradiance responses were generated. From these, the maximum rate of net photosynthesis (P_{max}) could be estimated as described by Turner et al. (1991). Photosynthesis was also estimated by

measuring changes in DI^{14}C in water overlying epilithic samples during the Lake 226 study. For the purposes of this study, ^{14}C uptake by epilithon or phytoplankton at saturating irradiances was interpreted as being equivalent to P_{max}. Estimation of gross photosynthesis by adjusting P_{max} for R_d was avoided because this frequently used technique is biased (Graham and Turner 1987), especially when R_d is large relative to P_{max}.

The dependence of P_{max} on DIC (see below) was not an artifact of lowered DIC concentrations during the incubation assays. Photosynthesis of Lake 239 epilithon at saturating irradiances was linear for at least 4 h (Turner et al. 1983, 1987). In spite of these findings, incubation times were shortened to 1.5 to 2 h to reduce further any chance of artificial limitation. It is interesting to note that the highest rate of epilithic photosynthesis measured in Lake 239 preceded this change.

The investigation of epilithon in Lake 938 was a special case because the water in this riverine lake was flowing even at depths of ~ 2 m during sampling. Turner et al. (1991) demonstrated that static incubations were inappropriate for epilithon in the shallows (< 1 m) where boundary layers were much thinner than those found in static chambers. Similarly, the naturally occurring boundary layer in Lake 938 would have been thin because of water flow, so static incubations would cause unnaturally thick layers around Lake 938 epilithon and actual *in situ* rates would be underestimated (Turner et al. 1991).

Phytoplankton sampling techniques were described by Shearer (1978). The laboratory procedures for measurement of phytoplankton photosynthesis prior to 1986 (^{14}C uptake) were described in detail by Shearer et al. (1985). Laboratory procedures from 1986 to 1992 differed only in that a single addition of ^{14}C was mixed into the phytoplankton sample, which was then subsampled, and that a different type of incubator was used in 1992.

Lake 226 Nutrient Enrichment Experiment

The Lake 226 whole-lake experiment was designed to test the role of phosphorus in controlling algal growth when carbon and nitrogen were also supplied. The north and south basins of the lake were separated and enriched with carbon (as sucrose) and nitrogen (as nitrate) at an annual rate of 4 gC/m^2 and 2 gN/m^2 (Schindler 1974, Cruikshank 1984). Phosphoric acid was added to Lake 226N at a rate of 0.3 gP/m^2. The comparison of planktonic and epilithic photosynthesis took place from May to October of 1976; the ratio of maximum rates of photosynthesis in Lake 226N to those in Lake 226S was used to simplify comparison of epilithic and planktonic results. The mean epilimnetic concentrations (μM) of DIC, DIN (ammonia plus nitrate, excluding nitrite which is negligible) and total phosphorus were 130, 7.5, and 0.26 in Lake 226S, and 116, 2.2, and 0.68 in Lake 226N. Total phosphorus is used as the measure of available phosphorus in the absence of any other more suitable measure of available phosphorus in these lakes (Schindler 1973b).

Normal incubation procedures were modified for Lake 226N samples. In spite of the carbon added to Lake 226N, epilimnetic DIC fluctuated markedly, declining to a minimum of 17 µM in July. Because the important role of inorganic carbon to benthic photosynthesis was not recognized at the time, Lake 226N samples were occasionally supplemented with sodium bicarbonate to achieve DIC levels similar to those in Lake 226S. As a result, epilithic rates measured in Lake 226N samples potentially overestimated *in situ* rates.

Time Series and Midsummer Surveys of Algal Metabolism

Seasonal rates of epilithic photosynthesis were monitored in several lakes (details provided in Table 3.2).

The epilithon of four lakes (224, 226S, 239, and 305), representing a gradient of phosphorus concentrations, was examined during late July and early August of 1989. Algal composition at this time represented the annually dominant assemblage (Turner et al. 1991), and rates of photosynthesis and respiration of natural epilithon would be near their annual maxima (Chapter 4). In contrast, rates of photosynthesis of acidified epilithon (Lake 302S) would be at their annual minimum in July and August.

A second survey of epilithic metabolism was conducted during July and early August of 1992 with a larger suite of lakes (149, 228, 239, 302S, 373, 375, 377, 442 and 938) that extended the range of epilimnetic chemistry conditions examined. DIC ranged from 12 to 480 µM, DIN from 0.2 to 17 µM,

Table 3.2. Open-water means of epilimnetic chemistry and metabolism of epilithon and phytoplankton in several Experimental Lakes Area lakes. Units of measurement are: pH for H^+; µM for dissolved inorganic carbon (DIC), NH_3, NO_3 and dissolved inorganic nitrogen (DIN); $\mu molC \cdot m^{-2} \cdot h^{-1}$ for epilithic maximum net photosynthesis (P_{max}) and respiration (R_d); and $\mu molC \cdot m^{-3} \cdot h^{-1}$ for optimum phytoplankton photosynthesis (P_{opt}).

Lake	Year	H^+	DIC	NH_3	NO_3	DIN	P_{max}	R_d	P_{opt}
239	81	7.0	156	0.5	0.3	0.9	315	105	498
239	82	7.0	139	0.7	1.0	1.6	346	111	309
239	83	7.0	144	1.4	1.0	2.4	396	126	309
239	84	6.8	176	0.7	0.6	1.3	488	76	300
239	85	6.8	146	3.6	0.9	4.4	358	57	446
239	86	7.2	148	1.0	0.6	1.6	378	54	252
239	87	7.2	143	1.2	0.4	1.6	342	64	289
239	88	7.2	146	0.9	0.2	1.1	343	138	367
239	89	7.2	153	0.4	0.5	0.9	431	84	330
239	90	7.2	169	0.7	0.4	1.1	459	80	242
239	91	7.1	173	0.4	0.6	1.1	481	9	235
382	84	6.7	105	0.7	0.2	0.9	276	98	568
382	86	6.9	86	2.1	0.4	2.5	305	72	336
302N	81	6.6	80	0.4	0.1	0.6	256	62	731
302N	82	6.5	53	1.1	17.1	18.3	218	110	811
302N	83	6.3	46	2.4	23.0	25.6	164	154	550
302N	84	6.2	51	2.1	43.3	44.0	196	144	792
302N	86	6.1	20	3.4	49.8	53.5	97	174	634
302S	81	6.8	75	0.5	0.1	0.6	231	74	637
302S	82	6.4	62	0.8	0.6	1.4	214	121	436
302S	83	5.9	32	1.9	1.8	3.7	176	191	424
302S	84	5.7	31	2.5	0.7	3.3	98	181	621
302S	85	5.5	29	4.0	1.7	5.8	88	222	575
302S	86	5.0	17	4.4	1.0	5.4	58	366	362
302S	87	5.0	32	4.6	1.0	5.6	133	371	748
302S	88	4.6	28	13.3	1.1	14.3	46	333	504
302S	89	4.6	26	21.8	1.6	23.5	45	403	732
302S	90	4.5	21	29.1	2.5	31.6	-44	444	579
302S	91	4.7	27	22.9	3.3	26.2	113	262	384

and total phosphorus from 0.06 to 0.32 μM (Table 3.3). All lakes were unperturbed except for Lake 302S (Table 3.1). Lakes 239 and 302S were sampled twice during this period.

Results

Lake 226 Nutrient Enrichment Experiment

The responses of the two algal associations in Lake 226 to phosphorus enrichment differed markedly (Fig. 3.1). Phytoplankton photosynthesis was increased by the addition of phosphorus to Lake 226N on 13 of 14 occasions. The mean ratio of rates in Lake 226N : Lake 226S was 3.1 $\pm$ 2.5 (SD), with a maximum of 9.7 in midsummer. In contrast, epilithic P_{max} was similar in magnitude in the two basins; the mean ratio of epilithic rates was 1.0 $\pm$ 0.2 ($\pm$ SD). However, the supplementation of Lake 226N epilithic samples with DIC prior to incubations raised measured rates; hence, the ratio of *in situ* rates would have been lower.

The irradiance parameter (α) of epilithon, derived using Smith's (1936) photosynthesis-irradiance relationship, was also independent of phosphorus levels. The mean values of α for 17 May to 7 July were similar between lakes (N:S = 1.1 $\pm$ 0.4, $\pm$ SD, n = 5). Therefore, potential shading effects by phytoplankton did not cause a large systematic change in α of epilithon.

Epilithic respiration also was unaffected by phosphorus addition. Dark respiration of epilithon in the phosphorus-enriched and the unenriched basins

Table 3.3. Epilimnetic characteristics of Experimental Lakes Area lakes surveyed in 1989 and 1992. Units of measurement are: ^{o}C for water temperature; pH for H^{+}; µM for dissolved inorganic carbon (DIC), dissolved inorganic nitrogen (DIN) and total phosphorus (P).

Lake	Year	Day	Temp.	H^{+}	DIC	DIN	P	Notes
224	1989	214	24	7.2	79			
226S	1989	221	25	7.2	86			
239	1989	219	23	7.2	138			
305	1989	212	22	7.5	115			
149	1992	202	24	7.2	171	9.9	0.29	
228	1992	223	19	7.4	128	9.7	0.06	
239a	1992	189	17	7.2	147	0.6	0.16	
239b	1992	217	19	7.3	149	1.0	0.16	
302a	1992	191	18	4.8	23	16.6	0.29	1
302b	1992	219	20	4.8	17	10.2	0.32	1
373	1992	197	20	7.4	178	0.2	0.16	3
375	1992	199	19	7.5	479	0.5	0.16	
377	1992	195	19	7.0	126	0.2	0.26	
442	1992	196	20	7.0	126	0.2	0.27	3
938	1992	203	19	7.1	203	0.2	0.23	2

Notes: (1) experimentally acidified lake; (2) riverine in character; (3) based upon profile information.

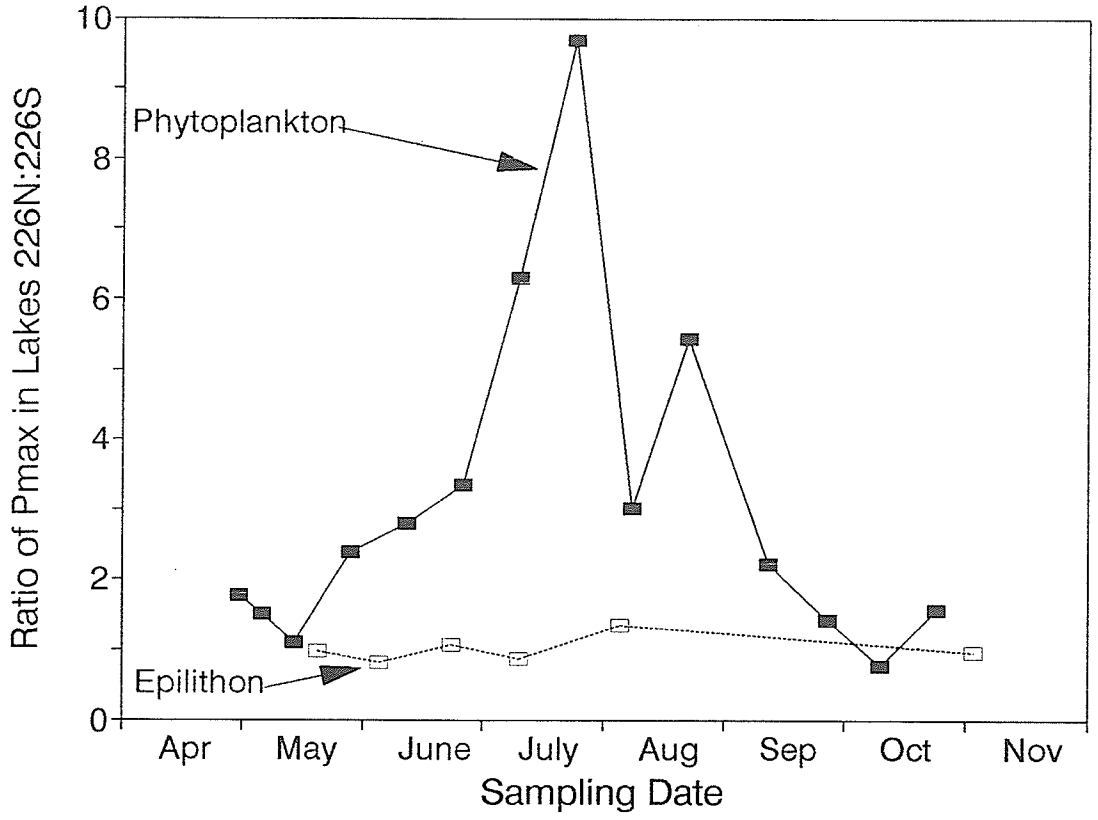

Fig. 3.1. The ratio of maximum rates of photosynthesis (P_{max}) in Lake 226N : Lake 226S of phytoplankton and epilithon during 1976.

was similar. Mean respiration rates for the period 17 May to 7 July were 200 ± 41 (± SE, n = 5 means) and 180 ± 24 $\mu molC \cdot m^{-2} \cdot h^{-1}$ for Lakes 226N and 226S, respectively.

It was impossible to confirm that epilithon in Lake 226N was phosphorus enriched in the absence of information on phosphorus concentrations in epilithon during the experiment. However, Stockner and Armstrong (1971) observed that average concentrations of phosphorus per unit of organic matter were higher in the epilithon of phosphorus-fertilized Lake 227 than in that of nearby unfertilized lakes (239, 240 and 305), although they also found that areal concentrations of phosphorus were unrelated to water column concentrations.

Time Series in Acidified and Reference Lakes

Annual mean rates of epilithic and planktonic photosynthesis were negatively related in the four study lakes (Table 3.2, Fig. 3.2; r = -0.62, n = 29, $P << 0.01$). When the lakes were separated according to acidity, the relationship remained negative in circumneutral Lakes 239 and 382 (r = - 0.69, n = 13, $P < 0.01$). Photosynthesis in the communities of the acidified Lakes 302N and 302S was unrelated (r = 0.27, n = 16); this analysis is, however, confounded by the declines in pH that occurred in these lakes.

Epilithic photosynthesis correlated positively with pH (i.e. declined with acidification) in these four lakes (Table 3.2; r = 0.89, n = 29, $P << 0.01$). DIC

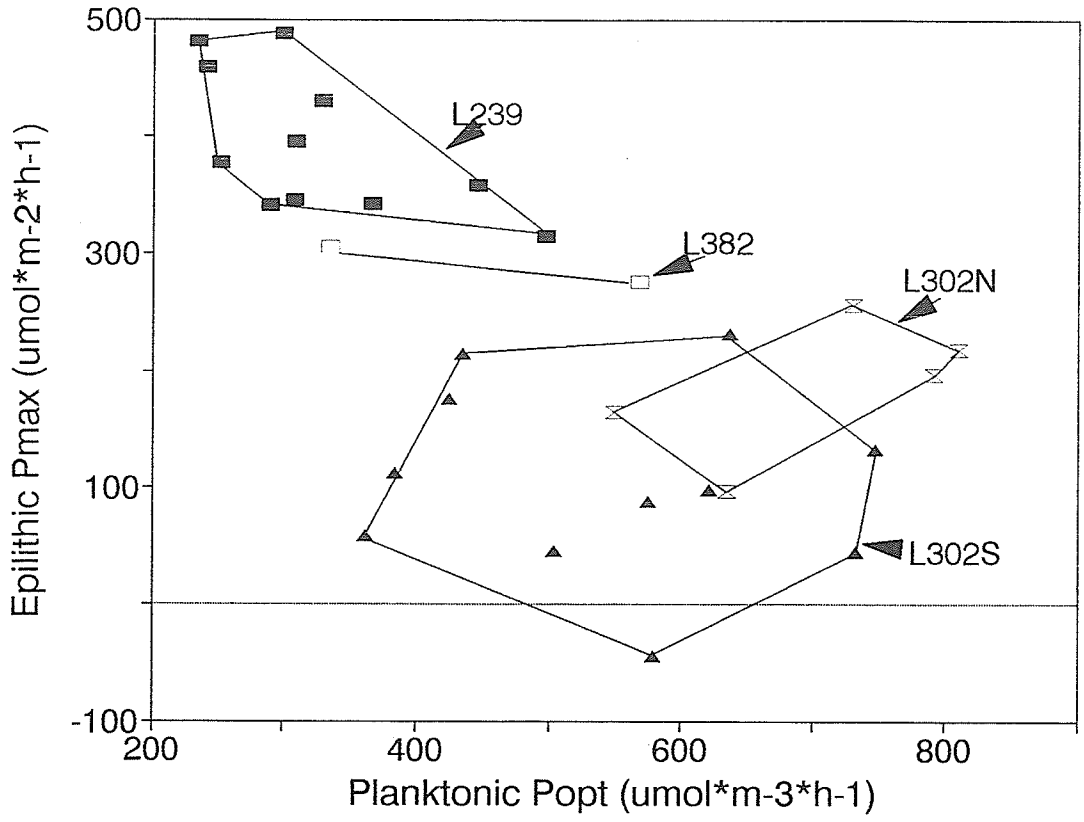

Fig. 3.2. The relationship between epilithic and planktonic photosynthesis. Open-water mean rates in four study lakes are shown for the periods described in Table 3.1. Means for specific lakes are enclosed within envelopes.

concentrations declined strongly in Lakes 302N and 302S during their acidification (Fig. 3.3); the major decline occurred as pH decreased from 7 to 6, as bicarbonate was lost. As a result, rates of epilithic photosynthesis were positively related to ambient DIC (Fig. 3.4; $r = 0.95$, $n = 29$, $P << 0.01$), and declined with acidification. In contrast, decreasing DIC was correlated with increasing planktonic photosynthesis ($r = -0.65$, $n = 29$, $P << 0.01$).

Rates of epilithic respiration correlated negatively to pH (i.e. increased with acidification) during the acidification studies (Table 3.2; $r = -0.93$, $n = 29$, $P << 0.01$). In contrast, respiration correlated positively with ammonia (Table 3.2; $r = 0.77$, $n = 29$, $P << 0.01$) and with the logarithm of ammonia concentrations (Fig. 3.5).

Midsummer Surveys of Algal Metabolism

The relationship of DIC concentrations with rates of photosynthesis differed between algal communities during the midsummer surveys (Table 3.4). Maximum rates of phytoplankton photosynthesis were unrelated to DIC in both 1989 ($r = 0.11$, $n = 4$) and 1992 ($r = 0.07$, $n = 11$). In contrast, epilithic photosynthesis was related linearly to DIC in both surveys. In 1989, the maximum *in situ* rates of epilithic photosynthesis in several circumneutral lakes (239, 226S, 224, and 305) were related linearly to DIC (Fig. 3.6). However, the relationship was not statistically significant because of the low number of observations ($r = 0.90$, $n = 4$, $P \sim 0.1$). In 1992, photosynthesis was related

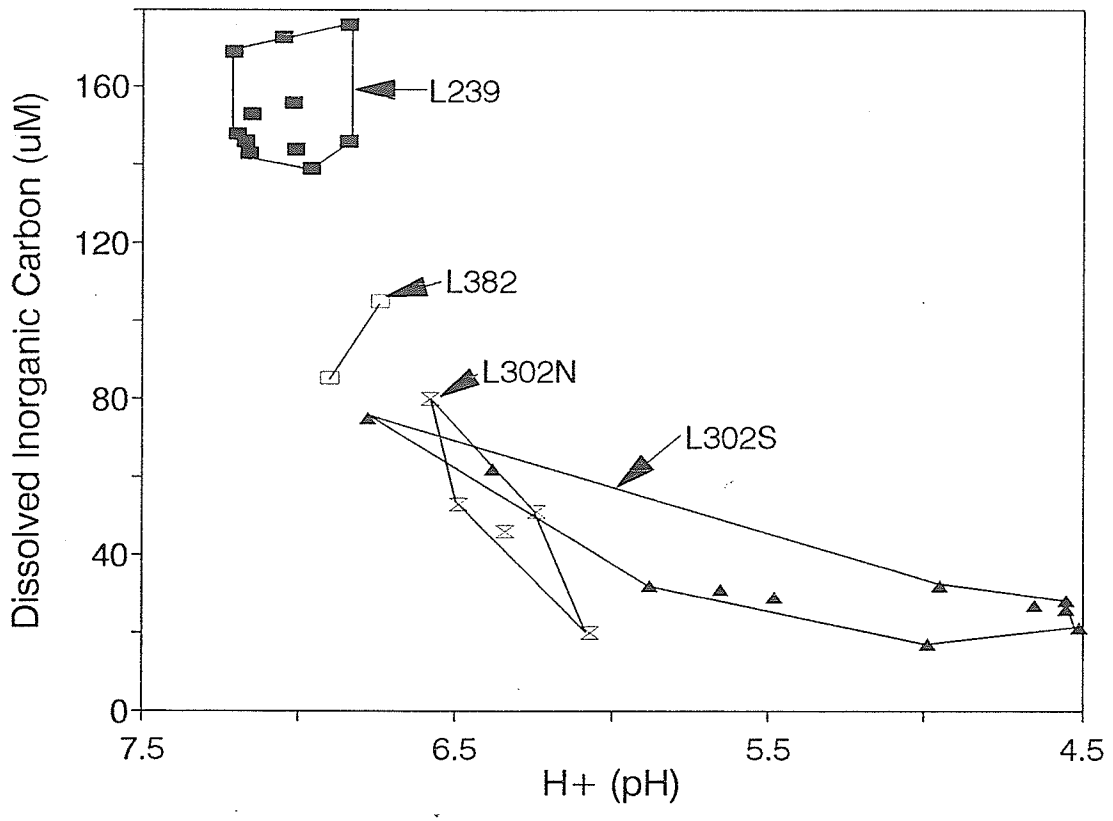

Fig. 3.3. The relationship between epilimnetic DIC and pH. Open-water means of epilimnetic DIC are shown for four study lakes for the periods described in Table 3.1. Means for specific lakes are enclosed within envelopes.

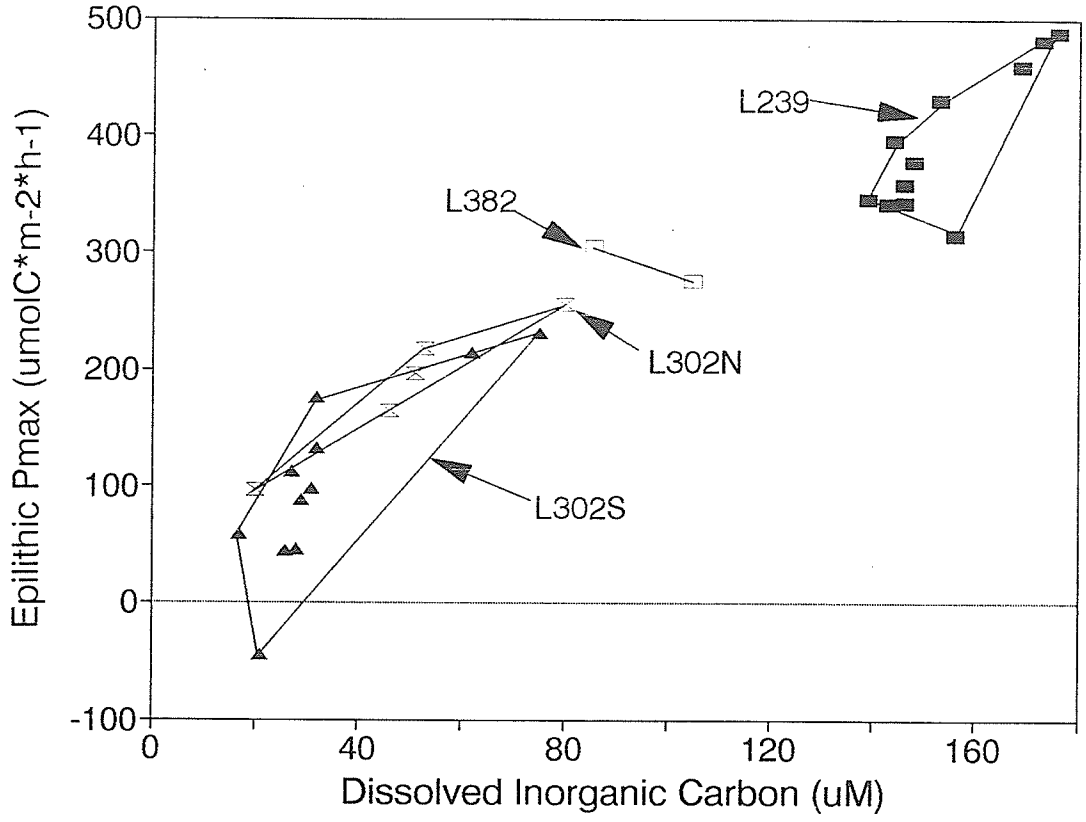

Fig. 3.4. Mean annual maximum rates of net photosynthesis in epilithon as a function of epilimnetic DIC. Means for specific lakes are enclosed within envelopes.

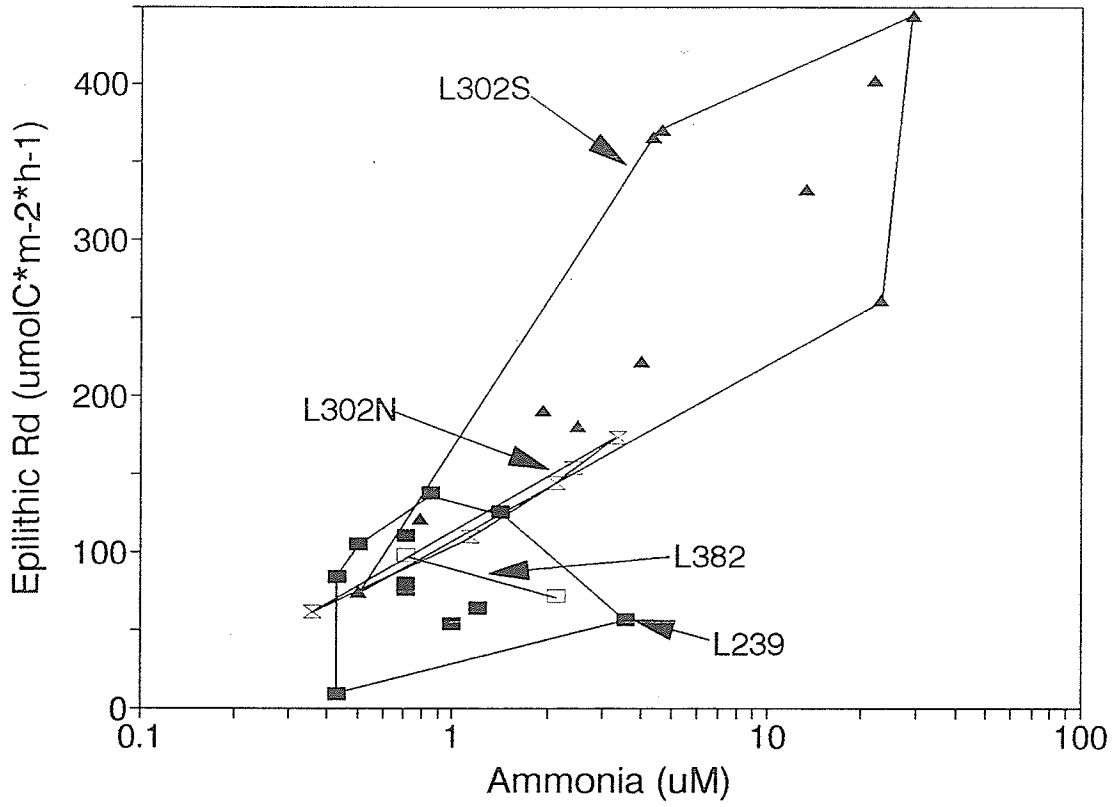

Fig. 3.5. Mean open-water values of epilithic respiration as a function of epilimnetic mean concentrations of ammonia in four study lakes (see Fig. 3.3 for details). Means for specific lakes are enclosed within envelopes.

Table 3.4. Survey of metabolism of phytoplankton and epilithon in several Experimental Lakes Area lakes during 1989 (*) and 1992. Phytoplankton were also sampled at other times as noted. Units of the measurements are: $\mu molC \cdot m^{-3} \cdot h^{-1}$ for phytoplankton optimum photosynthesis (P_{opt}); $\mu molC \cdot m^{-2} \cdot h^{-1}$ for epilithic maximum net photosynthesis (P_{max}) and respiration (R_d); and $\mu mol/cm^2$ for epilithic C, N and P.

Lake	P_{opt}	P_{max}	R_d	C	N	P	Notes
224*	237	418	233	484	36	0.47	5
226S*	390	439	188	221	17	0.25	6
239*	300	564	116	293	20	0.35	7
305*	174	585	146	233		0.28	8
149	1214	740	310	259	23	0.25	1
228	108	459	221	219	19	0.19	
239a	327	436	-24	390	26	0.51	2a
239b	308	493	-9	331	22	0.42	2b
302a	704	21	367	167	14	0.31	
302b	424	38	352	141	12	0.31	
373	164	875	76	258	18	0.28	
375	300	1662	-65	209	13	0.21	
377	296	550	24	226	15	0.23	
442	327	423	46	125	9	0.13	
938	380	521	5	149	11	0.28	3

Notes: Phytoplankton P_{opt} was determined as the average of several samplings: (1) 14 and 28 July; (2a) 29 June and 13 July; (2b) 27 July and 10 August; (3) 14 and 21 July; (5) 11 July and 8 August; (6) 19 July and 17 August; (7) 24 and 31 July, 3 and 10 August 1989; (8) 27 July and 8 August 1982, 10 July, 7 and 29 August 1984; 15 July and 12 August 1985; 30 July and 25 August 1986.

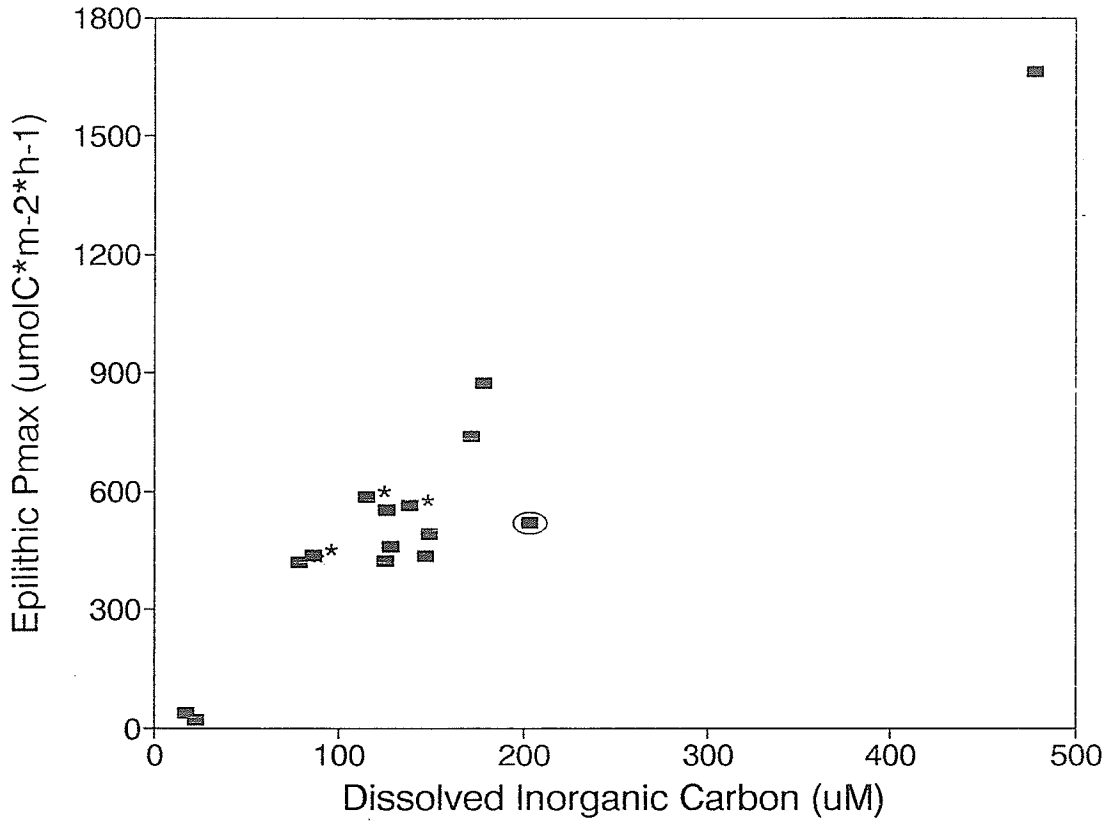

Fig. 3.6. The maximum rate of net photosynthesis of epilithon (P_{max}) in lakes as a function of DIC during surveys (see Table 3.3) in July and August of 1989 (denoted by *) and 1992. Measurements in riverine Lake 938 (circled) were probably biased low as described in the text.

linearly to ambient DIC (Fig. 3.6; r = 0.96, n = 11, P << 0.01). The relationship between epilithic photosynthesis and DIC may have become nonlinear at higher DIC concentrations; additional observations are needed to confirm this point. Measured rates of photosynthesis in riverine Lake 938 were slower than those in lakes of similar DIC (Fig. 3.6), as expected (see methods).

Epilithic P_{max} was unrelated to epilimnetic total phosphorus concentrations. Lake 305 epilithic rates were the highest seen in the 1989 survey. Yet Lake 305 is ultraoligotrophic with planktonic chlorophyll levels typically < 1 µg/L. Epilithic photosynthesis was also unrelated to epilimnetic phosphorus (r = -0.41, n = 11, P >0.05) in 1992. Similarly, epilithic rates were unrelated to the concentration of phosphorus in epilithon (r = -0.24, n = 15, P >0.05; combining 1989 and 1992 observations) or to the ratio of nitrogen:phosphorus (r = 0.26, n = 14, P >0.05). Unlike epilithic photosynthesis, phytoplankton photosynthesis was positively related to prevailing epilimnetic concentrations of phosphorus (r = 0.61, n = 11, P <0.05).

Epilithic respiration was related positively to ambient levels of DIN (Fig. 3.7; r = 0.94, n = 11, P <0.01). Although respiration was most rapid in acidified Lake 302S, surprisingly high rates also were measured in circumneutral Lakes 149 and 228. DIN was dominated by ammonia in shallow mesotrophic Lake 149, and by nitrate in deep ultraoligotrophic Lake 228. The relationship between phytoplankton respiration and DIN is unknown.

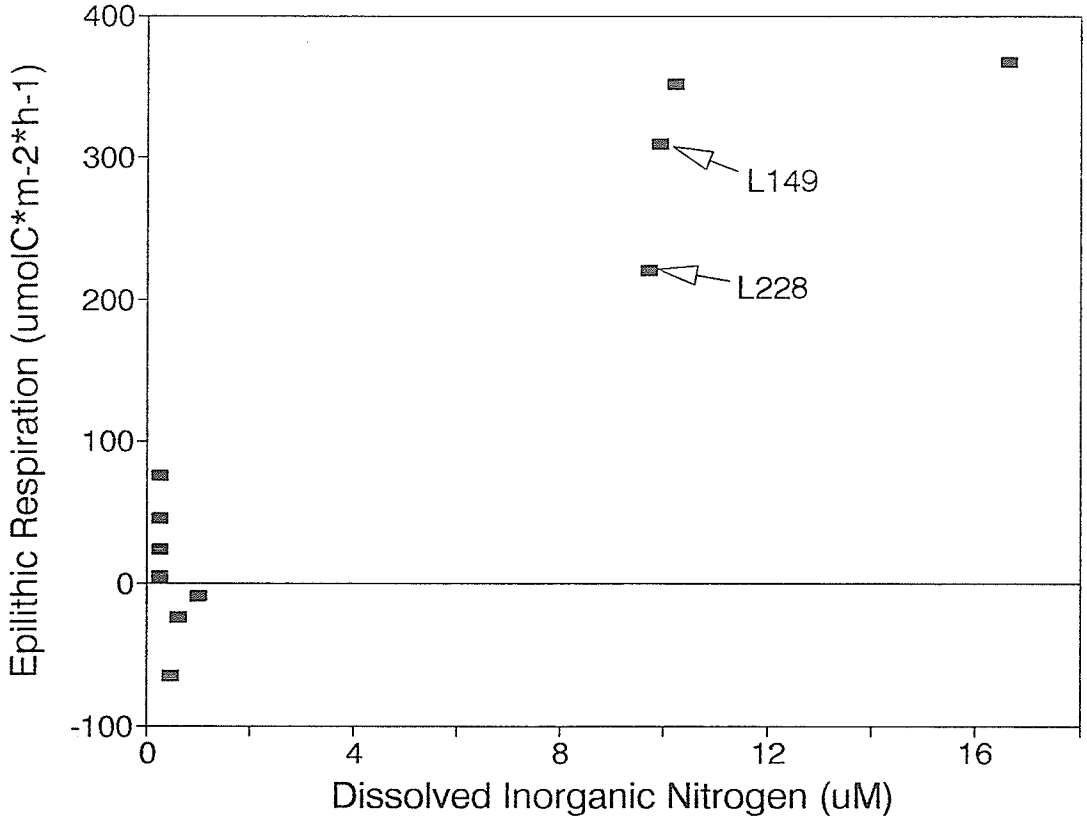

Fig. 3.7. The relationship between rates of dark respiration in epilithon and epilimnetic concentrations of dissolved inorganic nitrogen in several lakes during July and August 1992 (see Fig. 3.6 for details).

Discussion

Each of the three investigations confirmed that the roles of nutrients in controlling photosynthesis of epilithon and phytoplankton were different. However, the role that physical factors play in epilithic nutrient uptake must be understood prior to discussing nutrient control of epilithic growth.

Physical Controls of Epilithic Nutrient Uptake

Water movement affects nutrient limitation in several ways. First, increased water movement thins boundary layers overlying epilithic biofilms, potentially increasing rates of nutrient uptake (Turner et al. 1991). When water movement is sufficient to erode the biofilms, as can occur in streams and the shallows of lakes, both the degree of diffusive resistance and the incidence of density-dependent effects will be reduced. Here, only non-erosional, natural conditions will be discussed.

Second, the geometry of benthic biofilms can also affect nutrient limitation (Fairchild and Sherman 1992). Although nutrients are accessible from within the epilithic matrix, epilithon also obtain nutrients from the overlying water column across a largely two-dimensional surface. Thus, density-dependent effects can occur that are related to diffusion of CO_2 or other nutrients, especially as epilithic thickness increases (Stevenson et al. 1991). A major factor controlling inorganic carbon uptake in phytoplankton is the physical mass transport bottleneck within the photosynthetic process itself (Goldman and

Graham 1981). For epilithon, the bottleneck is the liquid-solid interface, where the liquid is the overlying water phase and the solid is the epilithic matrix.

Third, surface roughness of benthic biofilms also affects nutrient dynamics. Turner et al. (1991) estimated that boundary layer thicknesses at depths ≥ 1 m in ELA lakes were ca. 0.5 mm, a scale larger than most algae. Hence, only those algae that form filamentous chains, or are stalked, will usually escape the laminar flow conditions (and resulting slower nutrient uptake) associated with the surface of epilithic biofilms.

Fourth, orientation of substrata will also be a factor in benthic nutrient limitation. For example, vertically orientated samplers would tend to have low accumulation of materials (decaying algae or otherwise), and little recycling of phosphorus or other nutrients that would occur normally on surfaces of low slope. The result would be more similar to plankton, epiphyton on vertical surfaces, and epilithon on steep slopes where erosional forces are large. A corollary of the above arguments is that compared to plankton, there will be slower losses of nutrients from epilithon where water movement is nonerosional and the slope of the substratum is low.

Inorganic Carbon Limitation

Rates of photosynthesis in epilithon were limited by concentrations of inorganic carbon in the overlying water in both experimental and unperturbed communities. Photosynthesis of epilithon declined (Fig. 3.4) as DIC decreased

with acidification (Fig. 3.3), and was most rapid in lakes with high DIC (Fig. 3.6). These observations are consistent with the stimulation of photosynthesis of both epilithon and epiphyton by experimental additions of DIC in circumneutral lakes with DIC < 200 μM (Turner et al. 1987, 1991). The occurrence of much higher rates of periphytic photosynthesis in high DIC lakes (e.g. in Borax Lake, California, Wetzel 1964) than seen in the low-DIC ELA lakes reinforces the importance of DIC.

Different types of carbon limitation occur in the benthic associations. For example, carbon limitation in acidic lakes may be attributable simply to concentrations of DIC that are below the DIC compensation point of many algae (Birmingham and Colman 1981, cited by Williams and Turpin 1987). Because phytoplankton photosynthesis is unaffected by acidification, the degree of planktonic limitation must be insufficient to affect those planktonic taxa capable of efficient use at low concentrations. In contrast, the degree of epilithic limitation is sufficiently intense that even the most efficient DIC users are limited. Limitation in this study occurred both in acidified epilithon (Fig. 3.4), where the number of algal taxa declined with acidification (Chapter 2), and in unperturbed associations.

Diffusive resistance keeps the effective supply of DIC below the level observed to limit growth even in lakes where concentrations would otherwise exceed the threshold level of individual taxa. The deduction that carbon supply to periphyton is restricted by boundary layers was substantiated by isotopic

fractionation of ^{13}C in both epilithon and epiphyton compared to phytoplankton (R. H. Hesslein, Fisheries and Oceans, Canada, and M. A. Turner, unpubl. data).

If DIC directly affects rates of epilithic photosynthesis, then seasonal changes in DIC should cause corresponding changes in photosynthesis. This was seen in acidic lakes but not in circumneutral lakes at ELA with more bicarbonate (Chapter 5). The effects of temporal changes of DIC in circumneutral lakes were dampened by temperature effects (Chapter 2). Thus, relatively small changes in DIC concentrations were uncorrelated, or were negatively correlated, with changes in photosynthesis. Several compensatory processes may have increased with higher temperatures, including active algal uptake, passive diffusion of CO_2, and the efficiency of the photosynthetic process itself.

Phosphorus is Generally in Sufficient Supply for Epilithon

Although the majority of the ELA study lakes were oligotrophic, rates of epilithic photosynthesis were unrelated to either epilimnetic or epilithic concentrations of phosphorus (Tables 2 and 3). This was true even in ultraoligotrophic Lake 228. In contrast, phytoplankton photosynthesis was related directly to epilimnetic phosphorus. A similar dichotomy between phytoplankton and periphyton was observed in response to additions of sewage to Lake Mikolajskie, Poland (Chróst and Sikorska 1976) and nutrients to

subarctic lakes in Sweden (Persson et al. 1977).

The notion of phosphorus sufficiency in epilithic habitats of low slope is consistent with several related concepts. Both Confer (1972) and Jackson and Jackson (1972) concluded that periphyton can have greater phosphorus trapping ability than an equivalent biomass of phytoplankton. The littoral zone (or lake bottom) is also a site of accumulation and degradation of materials (Castenholz 1960). That is, decomposing cells in the epilithic matrix provide phosphorus for growth by viable cells, making the effective residence time of phosphorus (and other nutrients) much longer in the littoral than in the pelagic zone.

The hypothesis of phosphorus sufficiency in epilithon of oligotrophic lakes cannot be generalized to all epilithon. For example, phosphorus limitation in epilithon of streams has been well documented (Traaen 1978, Bothwell 1988 and 1989), and is caused by several factors. First, erosional forces of water movement thin the epilithic matrix, reducing the effective residence time of phosphorus there. Second, water movement also reduces diffusive resistance to CO_2 uptake and enhances the uptake potential for all nutrients. These considerations apply to both lacustrine epiphyton and epilithon developing on vertical surfaces in regions, especially where water movement is high.

Phosphorus limitation of epilithic growth in lakes can also occur when DIC is high. For example, phosphorus controls the growth of the filamentous green algae, *Cladophora* and *Ulothrix*, in the high DIC environment of the Great

Lakes (Auer et al. 1983). High DIC effectively diminishes the resistance to diffusion of DIC into epilithon, enhancing the relative importance of other nutrients. In addition, for *Ulothrix* growing in the shallows, the considerations described for streams will apply.

The Roles of Nitrogen

Nitrogen, like phosphorus, played a lesser role than carbon as a limiter of epilithic photosynthesis. Photosynthesis in Lake 302N declined despite increasing nitrate concentrations caused by nitric acid additions (Table 3.2). Similarly, photosynthetic rates in Lake 302S declined during sulfuric acidification despite strongly elevated concentrations of ammonium (Table 3.2). Rates in Lakes 149 and 228, which had high DIN (Table 3.3), were consistent with values expected based on the dependency of P_{max} on DIC (Fig. 3.6). Furthermore, despite the addition of nitrate to Lake 226S, rates of epilithic photosynthesis were similar to those seen in lakes of much lower DIN. For example, the 1976 July mean value for P_{max} in Lake 226S (~ 560 $\mu mol \cdot m^{-2} \cdot h^{-1}$ at ~ 125 µM DIC) coincides with the 1989- and 1992-derived relationships of P_{max} with DIC (Fig. 3.6).

Heterocystous blue-greens often are important components of epilithon (Persson et al. 1977; Loeb and Reuter 1981; Reuter et al. 1983; Turner et al. 1987, 1991), and as a result, nitrogen fixation by benthic blue-greens may allow epilithon to at least partly overcome nitrogen limitation (Schindler 1977, Reuter

et al. 1983). Furthermore, nitrogen fixation is inducible as a result of experimental phosphorus-only additions (Persson et al. 1977). This capacity will decline with acidification because heterocystous blue-greens are lost below pH 5 (Turner et al. 1991, Chapter 2); however, ammonium concentrations increase with acidification (Rudd et al. 1988, 1990), diminishing the need for supplemental nitrogen.

An unexpected role for nitrogen?

The association of high rates of epilithic respiration with high ambient concentrations of DIN may indicate an unexpected role for inorganic nitrogen in controlling benthic algal growth. Rates of epilithic respiration increased as concentrations of ammonium increased with acidification during the time-series studies of lakes 302N and 302S (Fig. 3.5). Although this correlation may have been caused by acidification (reviewed by Turner et al. 1991), the correlation was also found in circumneutral lakes 149 and 228, which had high rates of respiration (Fig. 3.7) and high concentrations of DIN (Table 3.3). Moreover, the dominant forms of DIN were different. Although it can be concluded that high ammonia in shallow Lake 149 is a result of respiration rather than a cause, this is difficult to argue when nitrate is the dominant form in deep Lake 228. Oxidation of ammonia may occur more rapidly in Lake 228; additional research is needed to resolve this matter. However, the relationship between DIN and epilithic respiration is consistent with the observation that increasing the ratio of nitrogen to carbon in terrestial materials stimulates rates of decomposition (e.g.

adding inorganic nitrogen to compost piles to accelerate decompositon).

Past and Future Aquatic Perturbations

Eutrophication

Epilithic photosynthesis was independent of phosphorus concentrations in both the Lake 226 experiment (Fig. 3.1), and in the lake surveys (Table 3.4). In contrast, planktonic photosynthesis was related positively to phosphorus as expected. As a result, eutrophication or increased phosphorus loading in low alkalinity lakes favours energy flow in the pelagic zone. A corollary is that the relative importance of epilithic photosynthesis in such lakes should increase as external phosphorus loading declines with the introduction of phosphorus control measures.

Epilithon should also decline in importance relative to phytoplankton as a lake is eutrophied because CO_2 utilization by phytoplankton will decrease available DIC. Shading by phytoplankton can also decrease benthic photosynthetic potential. For example, there was no change in effectiveness of epilithon at using irradiances at low intensities (i.e. α was unchanged) despite more severe attenuation of light in the epilimnion of the phosphorus-addition basin of Lake 226 than in the control (Fee et al. 1991).

Acidification

Carbon limitation increased in acidified epilithon and epiphyton of lakes (Turner et al. 1987, 1991; Fairchild and Sherman 1990; Fig. 3.2) and streams $\leq$

pH 6 (Mulholland et al. 1986). This is consistent with the major decline seen in DIC with acidification (Fig. 3.3). The absence of carbonate in acid lake water also eliminated any possibility of chemical enhancement of CO_2 transport across the atmosphere-epilimnion interface, such as occurs in eutrophic lakes (Schindler 1975).

Even bloom-forming, filamentous green algae (Zygnematales) can be CO_2 limited (Howell et al. 1990, Chapter 4). Although their success in acid lakes can be attributed partly to their ability to sequester CO_2 at the low concentrations characteristic of acid lakes (Turner et al. 1991, Robinson et al. 1994), concentrations can be low enough to limit their rate of CO_2 uptake (Chapter 4).

Unfortunately, the importance of inorganic carbon to benthic algal associations can also induce artifacts in experimental studies of stream acidification. Acidification of circumneutral stream water without equilibration with the atmosphere can cause unnaturally supersaturated CO_2 solutions (e.g. Parent et al. 1986, Planas et al. 1989). As a result, researchers may cause unusually high growth rates, and distort the algal composition of the experimental communities.

Increases in Atmospheric Carbon Dioxide

Aqueous CO_2 concentrations have already increased since the beginning of the industrial age (Hutchinson 1957). With further global change, CO_2 levels should increase further in the atmosphere and consequently in lake

epilimnia. Although anticipated increases in water temperature will lower CO_2 solubility, the expected increase in atmospheric CO_2 levels should overwhelm this effect (Fig. 3.8). Therefore, an increase in aqueous CO_2 will stimulate epilithic photosynthesis (Fig. 3.6), which is limited by current concentrations in low DIC lakes, without affecting phytoplankton photosynthesis, which is not limited by DIC.

The significance of increased aqueous CO_2 caused by increasing atmospheric CO_2 will also vary with pH (assuming the size of the bicarbonate pool remains unaffected; R. H. Hesslein, Fisheries and Oceans, Canada, pers. comm.) causing the proportion of CO_2 in the DIC pool to vary (Hutchinson 1957). For example, at 15°C, 96% of DIC is CO_2 at pH 5, 73% at pH 6, 21% at pH 7, and < 3% at pH 8. Rates of epilithic photosynthesis would increase by 92% of the increase in aqueous CO_2 if the linear regression of P_{max} versus DIC (Fig. 3.6) continued to hold. Therefore, rates of epilithic photosynthesis would increase by 88%, 67%, 19%, and 2% above current rates at pH 5, 6, 7 and 8, respectively; temperature effects will modify these increases.

The interaction between acidification and increased atmospheric CO_2 could have even greater biological consequences. Filamentous green algal associations already proliferate in acidic lakes in spite of demonstrated CO_2 limitation (Chapter 4). Their growth could be substantially increased with higher CO_2. Their further proliferation could reduce the value (aesthetic and recreational) of lakes, and lead to important changes in several physical,

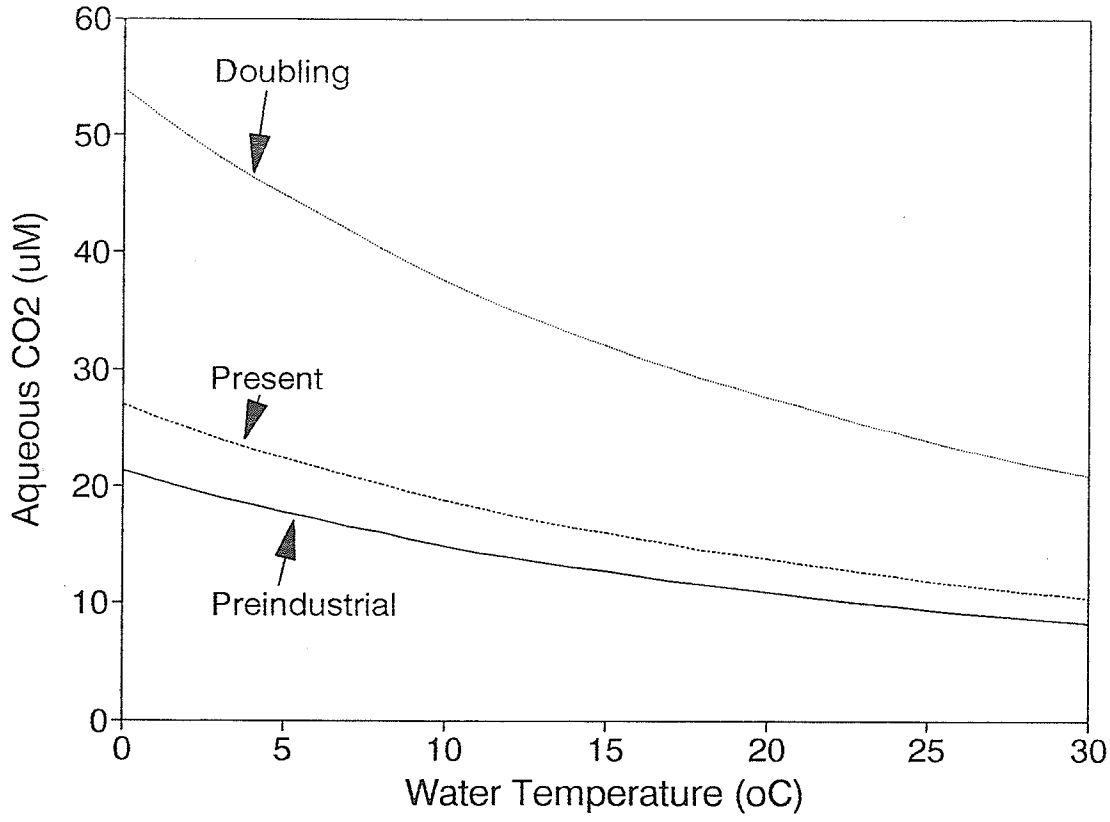

Fig. 3.8. The dependency of aqueous CO_2 concentrations upon water temperature (Stumm and Morgan 1970) is shown for several scenarios of atmospheric CO_2: preindustrial atmospheric concentration (280 ppmV), the current value (353 ppmV), and double current concentrations. Atmospheric concentrations are given by Hengeveld (1991).

chemical and biological properties of the acidified littoral zones (Chapter 5). It will be important to test the hypotheses that the importance of littoral productivity will increase relative to the pelagic zone as atmospheric CO_2 levels increase, and that acid systems will be most sensitive to this increase.

Chapter 4. Growth Characteristics of Bloom-Forming Filamentous Green Algae in the Littoral Zone of an Experimentally Acidified Lake.

Abstract

Filamentous green algae (FGA) bloom frequently in the littoral zone of acidified lakes. The growth characteristics of FGA were studied in experimentally acidified Lake 302S at the Experimental Lakes Area of northwestern Ontario. The major factors controlling photosynthesis of FGA (principally *Zygogonium*) included algal crowding, irradiance, dissolved inorganic carbon (DIC) and water movement. These factors operated without interaction, allowing straightforward interpretation of their roles. The FGA displayed high photosynthetic capacity in spite of the oligotrophic nature of this acidified system. Rates of photosynthesis were negatively dependent upon algal crowding, and highest growth rates were associated with minimum algal crowding. Light requirements for photosynthesis were higher than those of epilithon that were previously dominant. The dependence of photosynthesis on ambient concentrations of DIC was partly regulated by water temperature, so the development of FGA biomass was seasonal. FGA were present in low abundance as periphyton in spring, increased as metaphyton throughout summer, and reached a maximum in early fall. Anthropogenically caused releases from growth limitations (e.g. increases in the availability of limiting nutrients, increases in water temperature, and extension of the growing season)

may produce FGA proliferation in the future.

Introduction

The proliferation of filamentous green algae (FGA) is a major change in the phytobenthos of the littoral zone that is caused by acidification (Stokes 1986). Acid-induced growths of periphytic FGA occurred initially as epilithic, water-line bands and epiphytic accumulations at pH $\geq$6.0 in experimentally acidified Lake 302S (Turner et al. 1987). As lake acidification progressed, the FGA began to grow as metaphyton (Howell et al. 1990), i.e. as forms that were either unattached to any substratum, or were so large that their growth form was unrestricted by the surface on which the algae initially developed. Metaphyton bloomed annually as the epilimnetic pH declined to 5.5 and below in Lake 302S (Chapter 2), although this also occurred at pH ~ 6 in lakes located on the Canadian Shield in central Ontario (France and Welbourn 1992). Blooms of *Spirogyra* and *Mougeotia* at pH of 5.5 to 4.8 were followed by *Zygogonium* as the pH declined below 4.8 (Chapter 2). *Zygogonium* is the most abundant Zygnematacean alga that blooms metaphytically in acidified lakes of central Ontario (Wei et al. 1989, France et al. 1992).

Despite their status as nuisance algae (SPR Associates 1986), the ecology of FGA in acid lakes is little understood for a number of reasons. First, ecological studies of lake acidification have focused primarily on structure and function of the pelagic zone (Stokes 1986). Second, the littoral zone was

considered unimportant to energy flow in many lakes (Schindler et al. 1973a). Third, appropriate methods were unavailable to address littoral heterogeneity and the structural complexity of benthic algal communities (Howell et al. 1990). As a result, previous intensive whole-lake experiments, such as performed in Lake 223 (Schindler et al. 1985), have neglected the study of FGA.

Metabolism of metaphytic FGA appears to differ from that of acidified periphyton (Howell et al. 1990). For example, FGA required high light intensities for optimal photosynthesis, were capable of potentially high rates of photosynthesis, and demonstrated an inverse relationship between rates of biomass-normalized photosynthesis and algal biomass.

The principal objective of this study was to provide information for modelling the growth of FGA. This information would eventually be used to propose potential control strategies. Experimental and descriptive studies in Lake 302S were conducted as it was acidified to pH 4.5 from pH 5.0, factors that were important to the growth of FGA were determined, and their limits of variation were delineated.

Methods

Study Area

Lake 302S, located in the Experimental Lakes Area of northwestern Ontario (93^{o} 45' W, 49^{o} 40' N), was first described by Brunskill and Schindler (1971). It has a surface area of 10.9 ha, a mean depth of 5.1 m, a mean July

thermocline depth of 5 m, and a median Secchi depth of 4 m (Cruikshank 1988). The nutrient chemistry of this oligotrophic lake was characterized by Howell et al. (1990), Rudd et al. (1990) and Turner et al. (1991); the trace metal chemistry was documented by Cruikshank et al. (1988). The artificial separation of Lake 302S from the downstream northern basin and its subsequent experimental acidification with sulfuric acid were described by Turner et al. (1991). The lake's epilimnetic pH was lowered in annual stepwise increments beginning from about 6.7 in 1982 to about 4.5 in 1988, a level that was held through to 1991. The development of FGA during the progressive acidification of Lake 302S has been documented by Turner et al. (1987, Chapter 2) and Howell et al. (1990).

Measurement of FGA Photosynthesis

Collection of Algae

Metaphytic forms of FGA were collected near three shoreline stations known to regularly develop blooms. Metaphyton was usually unavailable during May and early June of each year so epiphytic samples were collected from macrophytes and submerged trees.

Duplicate samples of FGA were collected at each site (0 - 1 m water depth) using a 100-µm mesh sweep net, except in early 1991 when collections were made by a SCUBA diver. Algae were drained of most of their water as they were removed from the net, their volume was measured, and they were

returned rapidly to lake water in a 1-L polyethylene bottle. About 5 mL of FGA from each station were combined, yielding about 15 mL of $FGA \cdot L^{-1}$.

Lake water used for incubations was collected from the epilimnion at the midlake station. All samples were returned to the laboratory, and incubations were started within about 2 h of algal collection.

Description of Incubator

The incubator was a simple open basin (0.44 m x 1.20 m x 0.13 m, ID) constructed of grey opaque polyethylene (0.9 cm thick). Mirrors lined the bottom and walls of the interior. Clear acrylic replaced the grey polyethylene at one end where a single 150W.HPS sodium-vapour lamp (Sylvania type HPS-61-150-N) was placed. Water temperature within the incubator was maintained within 1-2 ^{o}C of epilimnetic temperature by addition of ice as needed. Locations within the incubator that yielded the needed light intensities were determined prior to the start of the experiments. Dark bottles used to measure dark respiration were prepared by dipping pyrex bottles in rubberized black paint; the joint between cap and bottle neck was sealed with black polyethylene tape during incubations.

Measurement Strategy

Algal suspensions were placed in the incubator at an irradiance of about 500 $\mu E \cdot m^{-2} \cdot s^{-1}$. Just prior to sample manipulation, the 1-L bulk samples were "grated" at the lowest available setting for 1 - 3 s in the blender, and returned to the incubator.

Aliquots of algae were removed using syringes with Tygon® tubing attached. Aliquots were added to 125-mL Pyrex reagent bottles filled with lake water. The bottles were closed and shaken for ~ 5 s. Two or three water samples for initial DIC were then withdrawn from each 125-mL suspension through a porous polyethylene frit (nominal pore size of 100-µm) connected to a 2.5 mL syringe by a 3-way valve and Tygon® tubing. Water removed for DIC analysis was replaced immediately with lake water of appropriate DIC concentration (see below). The sample bottle was then stoppered, and placed in the incubator (see below) at a preassigned location. The initial DIC samples were placed in a dark ice bath until analysis by an infrared gas technique (Turner et al. 1987). Final DIC samples were collected after an incubation of about 30 to 60 min. using procedures paralleling those used for initial DIC samples.

Dry weight of algal suspensions was determined by filtering each 125-mL sample suspension, usually within 6 - 8 h of sample collection, through preweighed 45- or 25-mm Whatman GF/C filters. Filters and blanks were dried at 60 ^{o}C to constant weight.

In samples specifically requiring water movement, procedures equivalent to those described by Turner et al. (1991) were used. Teflon stoppers adapted to accommodate two lengths of silicone tubing (inlet and outlet) were used for the 125-mL bottles. The inlet tube was sealed at one end, and perforated at several locations along the portion inside the bottle to permit water discharge

and algal movement. The outlet tube was fitted to ~ 1 cm length of porous polyethylene frit (nominally 100 μm). A Masterflex peristaltic pump was adjusted to create a water-renewal rate of about 10%·min.$^{-1}$.

Algal photosynthesis was calculated as the measured change in DIC adjusted for incubation time and the amount of algal material incubated. See App. I for a list of symbols, their meanings and units.

Evaluation of Procedures Used to Measure Photosynthesis

Estimating Collection Variance

The magnitude of variation between collections was assessed by comparing two sequential but separate collections of FGA made at each of the three designated sites in Lake 302S. Samples were incubated in triplicate at an irradiance of ~ 180 μE·m^{-2}·s^{-1} for < 0.5 h. The respective means ± SD of the two collections were 0.70 ± 0.06 and 0.68 ± 0.12 μmolC·mg^{-1}·h^{-1}. Hence, variation in the sample collections was deemed to be negligible.

Effect of Incubation and 'Holding' Times

Variability caused by duration of incubation and the delay between algal collection and incubation was examined to better understand the constraints of the incubation procedures. There were three treatment conditions: (a) samples were processed on arrival in the laboratory vs. a 45-min. delay; (b) samples were incubated for 0.2, 0.5 or 0.8 h; (c) samples were incubated under conditions of expected nonlinearity (i.e. high algal density: 53 ± 5 mgdw/L; low

DIC: 19 ± 0 μM; flowing water; and high irradiance: ~ 1000 $\mu E \cdot m^{-2} \cdot s^{-1}$) vs. conditions unlikely to cause nonlinearity (i.e. low algal density: 18 ± 3 mg/L; high DIC: 37 ± 1 μM; static water; and low irradiance: ~ 180 $\mu E \cdot m^{-2} \cdot s^{-1}$).

Holding time was unimportant. The mean ratio of rates of the initial and delayed collections paired among the six treatment conditions was 1.00 ± 0.14 (SD, n = 6).

The effect of incubation time varied with incubation conditions. Photosynthetic rates (± SD, n = 2) for the expected linear response varied from 0.67 (± 0.07) to 0.76 (± 0.04) to 0.43 (± 0.05) $\mu molC \cdot mg^{-1} \cdot h^{-1}$ for 0.2, 0.5 and 0.8 h, respectively. Photosynthetic rates for the expected nonlinear response were 0.80 (± 0.04), 0.57 (± 0.04), and 0.37 (± 0.04) $\mu molC \cdot mg^{-1} \cdot h^{-1}$. In this case, the algae had depleted DIC levels to 4 μM in less than 0.5 h and further depletion did not occur. Therefore, 4 μM was the threshold level for DIC utilization by *Zygogonium* under the incubation conditions of this experiment.

Incubation time was a critical experimental factor, so it was kept as short as possible given the sensitivity of the techniques used. In addition, incubation densities were adjusted downward to minimize the negative feedback of density dependence (see below); however, the low density condition of this experiment (~ 0.025 $g \cdot L^{-1}$) was substantially lower than those occurring *in situ* even when FGA densities were at their minimum (see below).

The Effect of Blending

Blending of algal samples was necessary to control the amounts of algal

material incubated because Howell et al. (1990) observed that rates of photosynthesis were negatively dependent upon the degree of algal crowding in samples. The possible effects of blending on photosynthesis were examined in a series of experiments.

A single collection of FGA, made 1 June 1988, was partitioned into two approximately equal amounts. One aliquot was blended for ~ 1 s; the second aliquot remained unblended. Three samples from each treatment were incubated, holding constant DIC, irradiance and incubation times. Equal volumes of algal suspension were added in each case, but the variability in mass of FGA actually added was substantially greater in the unblended sample (59% CV) than in the blended sample (11% CV). The distribution of FGA mass was also dissimilar between the two conditions. However, rates were similar between treatments when examined as a function of the amount of FGA incubated.

The above experiment was repeated on 10 August 1989. Once again, it was difficult to pair incubation densities; four of six unblended samples fell outside of the range of blended densities. Rates of biomass-normalized photosynthesis were similar, although rates of blended samples possibly were greater than those of unblended samples in the range of overlap.

FGA was collected on 30 September 1992 from Lake 302S to examine the possible effects of blending on algal structure. The samples were 96% FGA, of which *Zygogonium* was 86% and *Mougeotia* 14%. Subsamples for

algal taxonomic analysis were taken after 0, 3 and 10 s of blending. Blending ($\leq$ 3 s) produced no visible damage to the algal cells, and no effect on filament length of either *Zygogonium* or *Mougeotia*; at 10 s *Mougeotia* filaments were shortened by 27%. Thus, low-speed blending $\leq$ 3 s did not affect cellular structure.

Interactions Among the Main Factors Regulating Photosynthesis

Possible interactions among all main factors (irradiance, algal density, DIC, and water movement) were examined to determine whether it was possible to examine each factor individually. The general design of this experiment was factorial, with two levels (high and low) of each factor (irradiance, DIC and water movement) yielding 8 treatment combinations. Each combination was examined on each of two days, yielding two blocks with each block being either high or low algal density (the fourth main factor). Two 'covariate' samples were replicated in each block, however, there was a substantial shift in density between the 2 and 3 August 1988 runs, causing a significant block effect ($P < 0.01$) which was independent of all major factors ($P > 0.4$). Although sampling time declined from ~ 0.7 h to ~ 0.4 h with increasing sampling order within each block, biomass-normalized photosynthesis was independent of sampling time when the effects of the other factors were first removed ($P \sim 0.35$).

Each main factor was significant ($P < 0.01$). The relative importance of these factors was (in decreasing order of F values): density, DIC, irradiance

and water movement. The effects of water movement were not examined further. All interaction terms were unimportant ($P > 0.1$). Analysis of residuals confirmed that interaction terms were unimportant.

An all-inclusive model (all main factors, interaction terms and block effects = 17 terms, 24 df) yielded $r^2 = 0.96$ with 7 error df. The predictions from this model were unbiased. Therefore, the roles of the main factors in FGA photosynthesis could be studied without examining interactions. For example, in spite of the relationship between photosynthesis and incubation density, it was inappropriate to adjust photosynthetic parameters derived during other analyses for differences in algal masses incubated.

Preliminary Evaluation of Factors Regulating Photosynthesis

The relationship between algal crowding and photosynthesis was examined in detail on 26 August 1988. Five levels of density were duplicated in two complete randomized blocks, according to the time that the algal suspension was held prior to manipulation.

The relationship between photosynthesis and irradiance was examined on 30 August 1988 by incubating FGA at six intensities ranging from 0 to 1700 $\mu E \cdot m^{-2} \cdot s^{-1}$. Each irradiance was replicated three times using a randomized block design, where holding time was again the blocking factor.

Seasonal Variability in FGA Photosynthesis and Respiration

Lake 302S was sampled approximately once every four weeks during the open-water seasons of 1988-1991. At each sampling in 1988 photosynthesis was measured in triplicate at each of three different levels of algal crowding or density; on 26 August there were five levels. The mean algal density of the intermediate level was 47 $\pm$ 24 mgdw$\cdot L^{-1}$ ($\pm$ SD, n = 7). Four levels of density were sampled in duplicate on each sampling occasion during 1989 - 1991. The mean algal density at the second lowest level, the level at which variation in responses to DIC and irradiance were examined, was 24 $\pm$ 7 mgdw$\cdot L^{-1}$ ($\pm$ SD, n = 20).

The photosynthesis-irradiance relationship was measured during 1989-1991 using four levels of irradiance, each examined in duplicate. Nominal light intensities were: 0, 75, 500, and 1600 $\mu E \cdot m^{-2} \cdot s^{-1}$. Respiration was measured in duplicate during 1988 and 1989, and in triplicate during 1990 and 1991. These samples were inoculated with FGA at the same algal density as for DIC as described above.

FGA were incubated at three nominal levels of DIC (ambient, one-half of ambient, and twice ambient) during 1989 to 1991. Nitrogen gas was bubbled through a 1-L container of lake water for about 20 min. to obtain low DIC (one-half of ambient) concentration. One to 2 mL of saturated CO_2 solution were added to 1 L of lake water to obtain the high DIC (twice ambient) concentration.

Analysis of Algal Composition

Duplicate lake collections were combined and sampled for taxonomic analysis on each sampling occasion. These samples were then preserved in a final concentration of 4% acid Lugol's solution and FAA (formalin, ethanol and acetic acid). Turner et al. (1987 and 1991) described the procedures used for subsequent taxonomic analysis.

Measurement of Particulate Composition

Several nutrient ratios were measured to determine whether nitrogen and phosphorus were limiting FGA growth using the guidelines of Healey (1975) and Healey and Hendzel (1979), recognizing that both nonalgal material and algae in varying growth states could obscure the interpretation. Aliquots of FGA of known volume were filtered through preignited Whatman GF/C filters. Filters were then frozen and analysed subsequently for particulate carbon, nitrogen and phosphorus according to the procedures of Stainton et al. (1977).

Duplicate check samples were created during the first sampling period of 1990 to assess the degree of analytical variation over time. These samples were processed along with those generated during the remainder of the seasonal sampling program. The overall percent coefficients of variation for particulate carbon, nitrogen, and phosphorus were 11%, 16%, and 9%, respectively. Duration of freezing of the check samples was not responsible for this variation.

Measurement of FGA Biomass

Seasonal changes in *in situ* FGA biomass at 1 m were measured in 1991 to evaluate the accuracy of the studies of metabolism, and to establish the ecologically relevant bounds for the factors in the FGA productivity model. The shoreline of Lake 302S was marked every 20 m, and the total possible sampling sites were divided into 16 equal groups, the anticipated maximum sampling load. A single station was randomly selected from the first sampling group; the corresponding station was sampled in all other groups. Average slope of the lake bottom at these stations was 31% $\pm$ 19% ($\pm$ SD, n = 16; range 3% - 88%).

The diver used a 1-m x 1-m polyethylene square to sample three quadrats within the sampling zone at each station. Percent areal coverage and growth thickness were measured; typically three to nine measurements were made in each quadrat. A small sample of any FGA found was also taken, preserved and archived for taxonomic purposes.

Seasonal changes in density were measured by making collections adjacent to two stations (3 and 59) on each sampling occasion. The geometric shape of the sampled growth form was characterized (typically a box, sphere, or cylinder), and the pertinent dimensions were measured by the diver to allow calculation of the volume of the algal growth form. The entire growth form was then cleaned carefully of any attached or entangled debris, and collected into a polyethylene bag. The sample was dried and its weight was measured to

calculate algal crowding or density as $gdw \cdot L^{-1}$.

Depth variation (1, 2, 3, 4 and 5 m) was measured at eight stations during August 12 to 14. At each combination of station and depth, % coverage and growth thickness were measured in three adjacent 1-m x 1-m quadrats as described above. FGA were collected at stations 3 and 59 to measure depth variation in algal density.

Results

Photosynthesis as a Function of Algal Density

The rates of photosynthesis standardized for the amount of algal material incubated (P_b, App. I), were nonlinear decreasing functions of algal density. For example, a linear relationship accounted for only 51% of variance in the detailed 26 August 1988 experiment. In contrast, other relationships fit better: P_b = log(D), 64%; $(-1/P_b)$ = intercept + (slope x D), 84%; and $\log(P_b)$ = log(D), 91%.

Rates of photosynthesis normalized for respiration (P_g, App. I) were approximately linear functions of the amount of algal mass incubated (Table 4.1), i.e. P_g = slope x mass. The constant was assumed to be equal to zero because P_g = 0 by definition when I = 0. The slope of this linear relationship ranged from 0.02 to 0.46 (Table 4.1), varying seasonally with annual minima in spring and fall (Fig. 4.1); the fall of 1989 was an exception.

Table 4.1. The effect of algal mass on FGA photosynthesis. The linear model is P_g = Coefficient x Mass. P_g is defined in App. 1.

Year	Day	N	Coeff.	SE	% r^2
88	139	9	0.091	0.004	98.2
88	160	9	0.116	0.005	98.8
88	182	9	0.161	0.008	98.1
88	211	9	0.176	0.012	96.6
88	239	10	0.458	0.056	88.1
88	262	9	0.320	0.046	86.0
88	289	9	0.246	0.011	98.6
89	151	8	0.236	0.020	95.1
89	172	8	0.284	0.018	97.3
89	206	8	0.284	0.011	98.2
89	228	8	0.221	0.010	97.6
89	262	8	0.321	0.039	90.5
89	291	8	0.422	0.021	98.3
90	129	8	0.184	0.021	91.5
90	156	8	0.241	0.010	98.9
90	185	8	0.302	0.060	78.4
90	214	8	0.285	0.017	97.6
90	240	8	0.246	0.033	88.6
90	268	8	0.267	0.025	94.4
90	296	8	0.135	0.013	93.8
91	131	8	0.016	0.003	74.8
91	161	8	0.226	0.012	98.2
91	189	8	0.311	0.017	98.0
91	218	8	0.149	0.019	89.9
91	241	8	0.238	0.027	91.9
91	274	8	0.338	0.014	98.7
91	302	8	0.080	0.008	95.0
Mean			0.235	0.020	93.7
SD			0.101	0.015	6.3
N			27	27	27

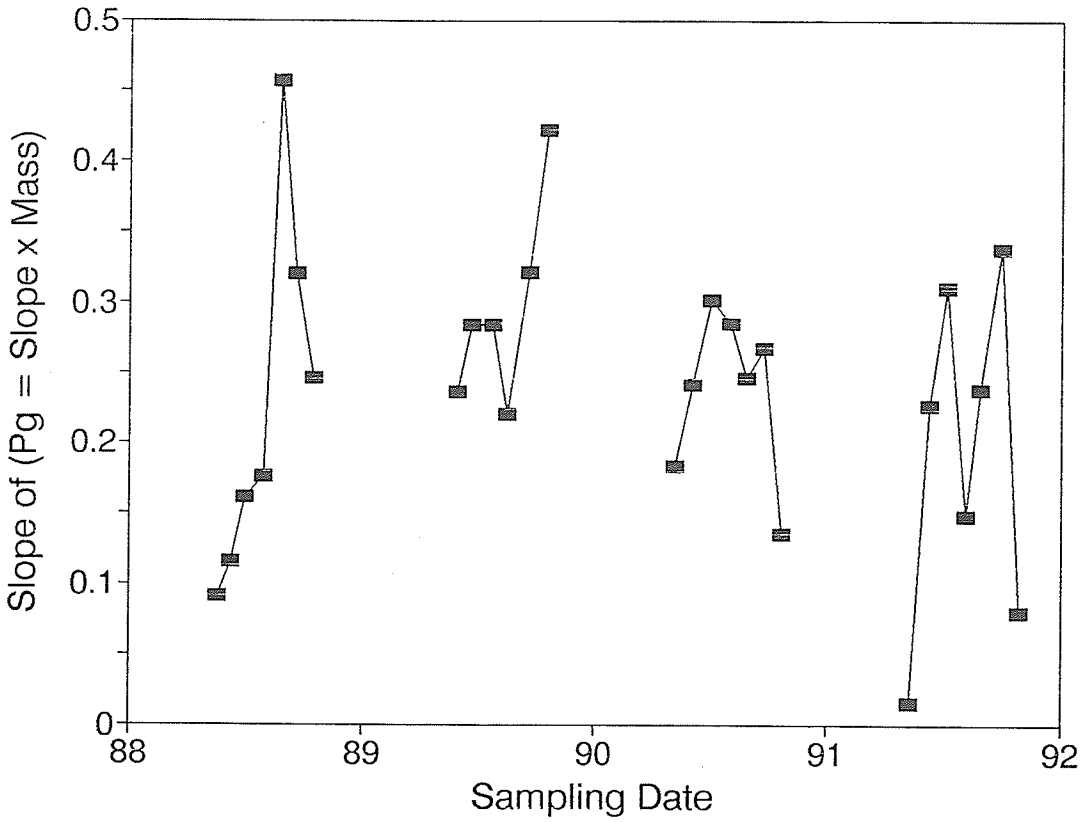

Fig. 4.1. Seasonal variation in the slope of the linear fit of rates of respiration-normalized photosynthesis versus incubated algal masses. Photosynthesis was modelled as P_g = slope x mass, where P_g was the measured rate of photosynthesis adjusted for respiration measured in the dark.

Although the linear model was a good descriptor of the relation between P_g and algal mass, it was biased. The mean r^2 of these linear fits was 94% $\pm$ 6%. However, the small residuals were significant because the linear relationship underestimated rates of photosynthesis when the masses of FGA incubated were very small. That is, measured rates of photosynthesis were higher than predicted when algal crowding was very low, which is consistent with the nonlinear decreasing relationship of P_b with algal crowding. However, these low densities were uncharacteristic of benthic FGA (see below), so the bias was deemed acceptable.

Photosynthesis as a Function of Irradiance

The overall mean ($\pm$ SE) rate of respiration for the 27 sets of seasonal observations was 0.098 ($\pm$ 0.013) $\mu molC \cdot mg^{-1} \cdot h^{-1}$. There was no general seasonal pattern observed. Correlational analysis indicated that respiration was independent of DIC, algal mass, and water temperature. The lack of relationship between respiration and temperature may have been due to insufficient sensitivity of the measurement techniques. For example, the mean % coefficient of variation in R_d was 61% (computed from Table 4.2).

The nonlinear dependency of biomass- and respiration-normalized photosynthesis (P_{gb}, App. 1) on irradiance was evaluated in more detail on 30 August 1988 than in the seasonal studies. Both Smith's (1936) and Jassby and Platt's (1976) own hyperbolic tangent function fitted equally well (~

Table 4.2. Irradiance parameters for Lake 302S FGA fit to Smith's (1936) equation. Abbreviations, symbols and their units are described in App. I. (1) means that the asymptotic standard error (ASE) was not computable.

Year	Day	N	R_d	SD	N	P_{gbm}	ASE	α	ASE	$\%r^2$
88	139	2	0.03	0.01						
88	160	2	0.08	0.02						
88	182	2	0.09	0.01						
88	211	2	0.06	0.01						
88	239	2	0.11	0.01						
88	262	2	0.07	0.02						
88	289	2	0.06	0.03						
89	151	2	0.06	0.11	8	0.29	0.03	9.0e-04	1.3e-04	95
89	172	2	0.14	0.05	8	0.35	0.02	1.8e-03	1.1e-04	98
89	206	2	0.11	0.02	8	0.27	0.02	2.0e-03	1.4e-04	98
89	228	2	0.06	0.03	8	0.34	0.04	1.3e-03	1.6e-04	94
89	262	2	0.11	0.03	8	1.04	0.17	2.0e-03	3.2e-04	93
89	291	2	0.31	0.17	8	0.53	0.09	3.5e-03	1.5e-03	90
90	129	3	0.12	0.08	9	0.18	0.06	1.3e-03	4.4e-04	60
90	156	3	0.16	0.12	9	0.29	0.05	1.1e-03	2.2e-04	86
90	185	3	0.10	0.08	8	0.41	0.09	1.8e-03	4.2e-04	82
90	214	3	0.16	0.07	9	0.45	0.06	3.5e-03	1.6e-03	91
90	240	3	0.07	0.16	9	0.86	0.18	2.1e-03	5.5e-04	83
90	268	3	0.04	0.02	9	0.50	0.04	2.2e-03	3.2e-04	96
90	296	3	0.07	0.08	9	0.15	(1)	5.8e-04	(1)	55
91	131	3	0.00	0.02	9	0.05	(1)	1.5e-04	(1)	69
91	159	3	0.08	0.04	9	0.28	0.02	1.8e-03	1.1e-04	97
91	189	3	0.21	0.05	9	0.51	0.04	3.3e-03	9.8e-04	96
91	218	3	0.06	0.03	9	0.55	0.27	4.2e-04	2.7e-04	96
91	241	3	0.04	0.03	9	1.16	0.51	5.7e-04	1.4e-04	95
91	274	3	0.21	0.10	9	0.39	0.04	6.0e-03	2.2e-03	95
91	302	3	0.05	0.02	8	0.09	0.01	1.6e-03	2.0e-04	93
Mean			0.11	0.07		0.44		1.9e-03		88
SD			0.07	0.05		0.29		1.4e-03		13
N			20	20		20		20		20

89%) using the "Marquardt" convergence procedure. Values of the maximum rate of biomass- and respiration-standardized photosynthesis (P_{gbm}, App. 1) predicted by the first two equations were within 1%. The initial slope of the photosynthesis-irradiance relationship (α, App. 1) predicted by Smith's equation was 34% greater than that derived from Jassby and Platt's. This reasonable agreement between formulations was expected (Geider and Osborne 1991). Smith's equation was chosen for use. Its degree of fit in the seasonal studies was generally good, averaging 88% ($\pm$ 13%, SD; Table 4.2). The degree of fit varied seasonally somewhat, being poorer in early spring and in late fall, possibly as a result of an inferior signal-to-noise ratio caused by the lower photosynthetic rates at these times.

The mean ($\pm$ S.D.) value of P_{gbm} ($\mu molC \cdot mg^{-1} \cdot h^{-1}$) was 0.44 ($\pm$ 0.29) for the 20 experimental cases during 1989 to 1991 (Table 4.2). The corresponding mean value for α ($\mu molC \cdot m^{-2} \cdot [3600 \mu E \cdot mg]^{-1}$) was 0.0019 ($\pm$ 0.0014).

The seasonal pattern of variation in P_{gbm} was generally unimodal with annual maxima occurring typically between late August and mid September (Fig. 4.2). P_{gbm} was correlated with water temperature ($r = 0.44$, $n = 20$, $P = 0.05$), but appeared to lag behind water temperature. Allowing temperature to lag by one sampling period improved the correlation ($r = 0.61$, $P < 0.01$).

The degree to which FGA were readily saturated by light varied seasonally. When the above mean values of P_{gbm} were incorporated in a

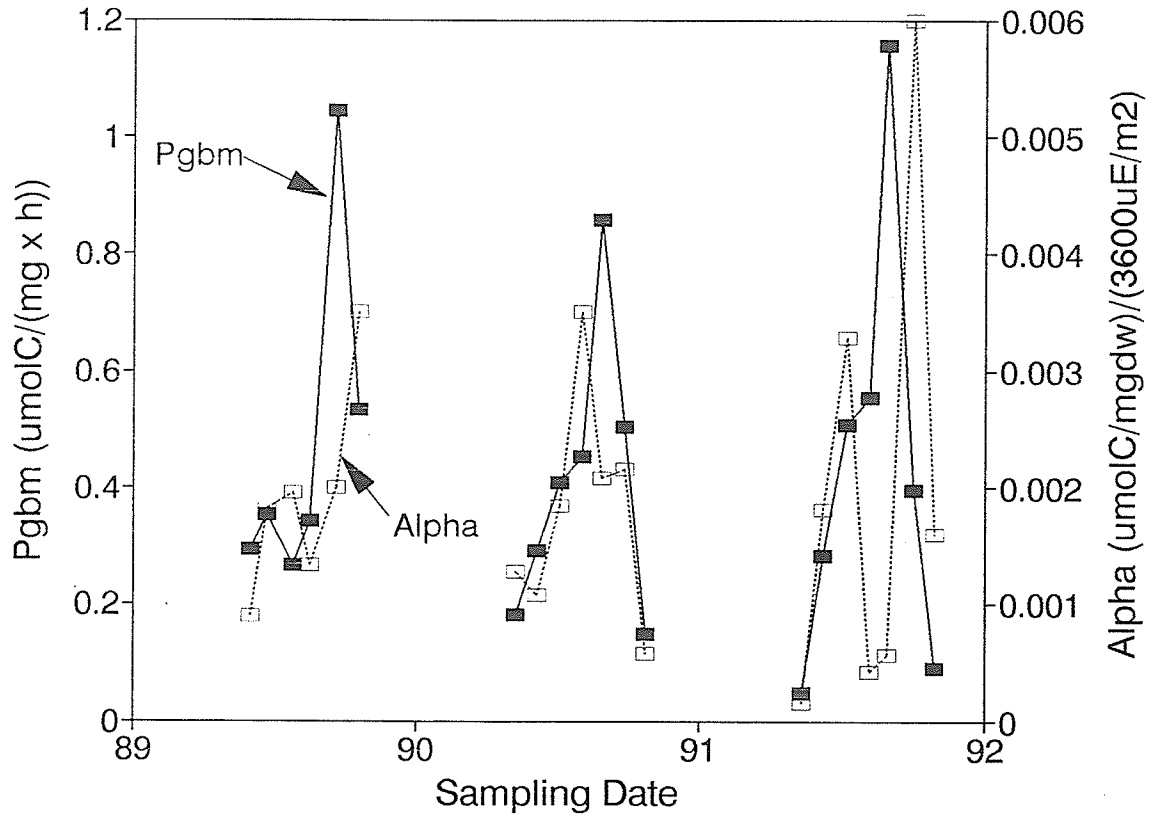

Fig. 4.2. Seasonal changes in the dependency of photosynthesis upon irradiance. The parameters, P_{gbm} and α (defined in App. I), were derived from fitting Smith's (1936) equation to the incubator-generated data.

photosyntheis-irradiance model, 90% of P_{gbm} was achieved at irradiances of 500 $\mu E.m^{-2}.s^{-1}$; this was similar to the average situation in spring. By late August, 90% of P_{gbm} was achieved on average at the much higher value of 1300 $\mu E \cdot m^{-2} \cdot s^{-1}$. In contrast, by late October, 90% was achieved below 300 $\mu E \cdot m^{-2} \cdot s^{-1}$.

There was no evidence of photoinhibition in these investigations, which was confirmed by observing that the residuals of the fit of Smith's equation were independent of irradiance. If photoinhibition had been important, residuals should have been large at high irradiances.

Photosynthesis as a Function of Inorganic Carbon

Photosynthetic rates were a linear function of DIC, i.e. P_{gb} = slope x DIC (Table 4.3) assuming the constant = 0 because P_{gb} = 0 when DIC = 0. The average r^2 was 82% $\pm$ 20% (SD, n = 20). Minima occurred in spring and fall, whereas annual maxima occurred during July and August (Fig. 4.3a).

The slope of P_{gb} as a linear function of DIC correlated positively with water temperature ($r = 0.69$, $n = 20$, $P \leq 0.001$; Fig. 4.3b), which is consistent with enzymatic control of the affinity for CO_2. The synchrony between the slope and P_{gbm} was also strong ($r = 0.59$, $n = 20$, $P \leq 0.01$), possibly due to linkage via water temperature.

The slope of P_{gb} as a linear function of DIC was negatively correlated with DIC as expected, but the correlation was weak ($r = -0.42$, $n = 20$, $P \sim 0.06$).

Table 4.3. Control of FGA photosynthesis by DIC. The model used was P_{gb} = slope x DIC, with the intercept = 0.

Abbreviations, symbols and their units are described in App. I.

Year	Day	DIC	Slope	SE	$\%r^2$
89	151	32	0.0069	0.0007	95
89	172	27	0.0109	0.0014	92
89	206	11	0.0181	0.0012	98
89	228	12	0.0165	0.0021	93
89	262	41	0.0147	0.0009	98
89	291	38	0.0113	0.0019	88
90	129	33	0.0055	0.0002	99
90	156	19	0.0082	0.0015	89
90	185	18	0.0147	0.0029	84
90	214	14	0.0153	0.0026	87
90	240	18	0.0231	0.0037	89
90	268	45	0.0081	0.0010	93
90	296	21	0.0074	0.0020	74
91	131	32	0.0047	0.0003	27
91	161	12	0.0085	0.0024	72
91	189	17	0.0141	0.0030	82
91	218	15	0.0094	0.0016	87
91	241	18	0.0132	0.0019	90
91	274	31	0.0131	0.0026	83
91	302	28	0.0014	0.0012	26
Mean		24	0.0112	0.0018	82
SD		10	0.0052	0.0009	20
N		20	20	20	20

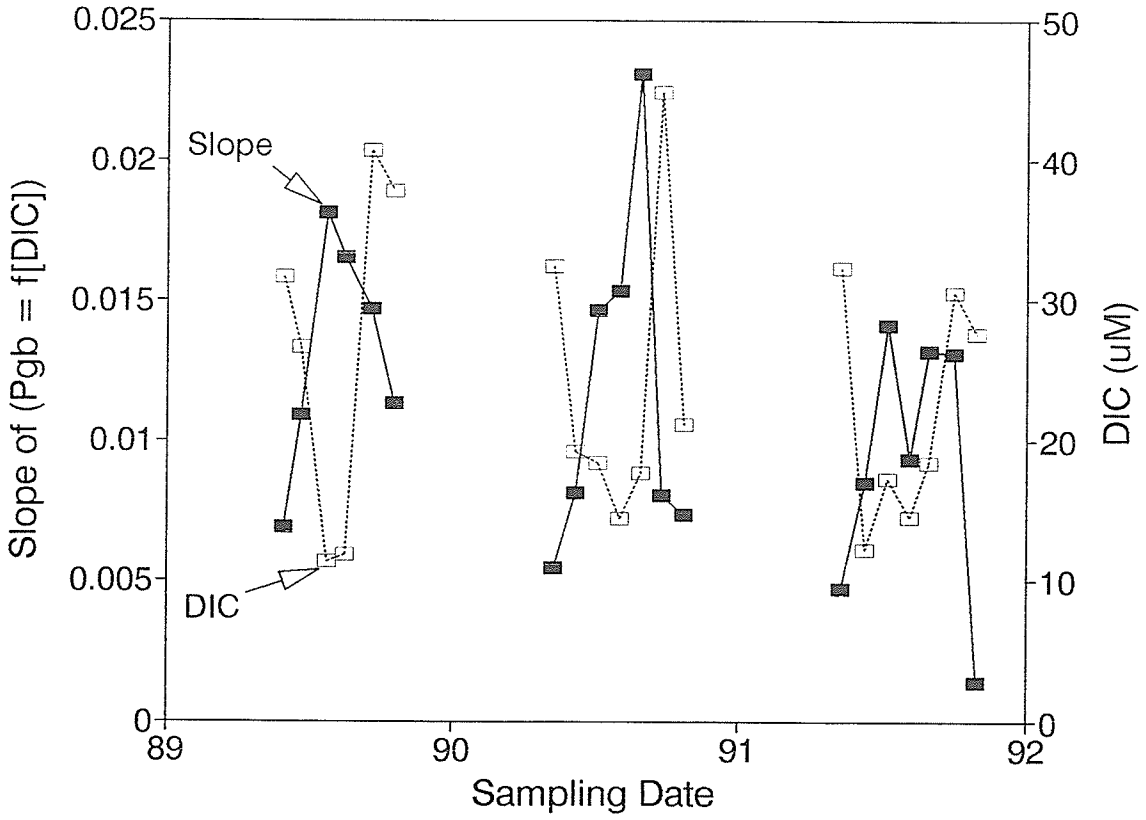

Fig. 4.3a. Seasonal variation in the slope of the linear dependence of photosynthesis on concentrations of dissolved inorganic carbon (DIC). Prevailing epilimnetic concentrations of DIC are shown also.

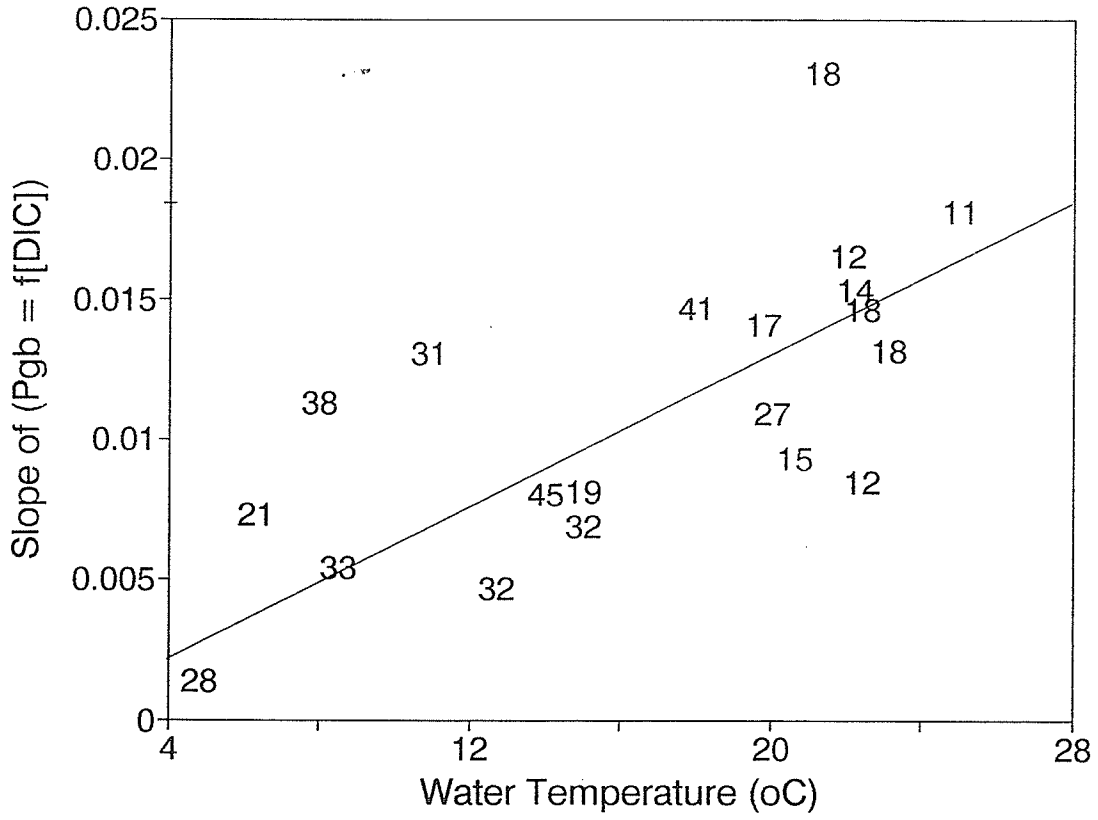

Fig. 4.3b. Variation in the slope of the linear dependence of photosynthesis on dissolved inorganic carbon (DIC) with water temperature. Individual concentrations of DIC are shown. The linearly fitted regression line of this relationship is also shown.

Although this preliminary result supports the idea that affinity for CO_2 is sensitive to its availability, a multiple regression of the slope with both temperature and DIC was performed. Inclusion of DIC provided no significant additional improvement ($P \sim 0.98$) over that contributed by temperature alone. Therefore, it was concluded that the negative relationship between the slope and DIC availability occurred indirectly through the generally negative relationship between DIC and water temperature.

Characteristics of Particulate Composition

The indicator of nitrogen deficiency, the mass ratio of nitrogen : carbon, averaged 0.11 ± 0.02 (SE, $n = 4$ y), and showed no regular seasonal trend during 1988 to 1991. Thus, the FGA on average were moderately nitrogen deficient ($0.10 < N:C < 0.13$) (Healey 1975).

The two indicators of phosphorus deficiency (1000 x P:C and N:P) yielded similar conclusions. The mass ratio of 1000 x P:C in combined samples of incubated FGA averaged 5.8 ± 0.6 (SE, $n = 3$ y), and remained below 10 during 1989 to 1991 with one exception, indicating extreme deficiency (Healey and Hendzel 1979). The ratio of N:P averaged 19 ± 1 (SE, $n = 3$ y), suggesting borderline deficiency (Healey 1975).

Characteristics of Biomass Development in 1991

Seasonal Changes in Biomass, Algal Density and Mass

Development of FGA varied substantially during 1991 (Table 4.4) as expected from the seasonal variation in the different metabolic parameters. The coverage by FGA of the lake bottom at 1-m depth increased from 6% in May to a maximum of 74% in early September, declining to 46% in late October. The pattern of seasonal variation in both algal and areal thickness (algal thickness adjusted for bottom coverage) was similar to that of bottom coverage (Fig. 4.4a). The minimum occurred in spring, the maximum in August, and a minimum in October. The maximum mean algal thickness was 16 cm ($\pm$ 2 cm, SE), with station means ranging from 7 to 30 cm.

Algal density, measured as the dried mass of FGA that occupied a volume of water, varied during the year as the inverse of the other biomass measures (Fig. 4.4b). The FGA reached a minimum of 0.1 $g \cdot L^{-1}$ in mid August, and maxima of 26 $g \cdot L^{-1}$ and 0.9 $g \cdot L^{-1}$ in spring and fall, respectively. The greater spring maximum corresponds with the FGA growing as periphyton rather than as metaphyton.

Seasonal variation in the areal mass of FGA was similar but not identical to other measures of FGA coverage (cf. Fig. 4.4b with 4.4a). Areal mass of algae was calculated by adjusting areal thickness for algal density. The maximum mass of algae at 1-m depth occurred in early October (Fig. 4.4b), whereas, the minimum surprisingly happened in June (rather than in May). Possibly, there was incomplete under-ice decomposition of FGA that had grown in 1990, but which then decomposed after exposure to the higher water

Table 4.4. Biomass of FGA at 1-m depth in Lake 302S during 1991. Stations refers to the number of sites sampled for algal cover and thickness.

		Sampling Day							
		May 15	Jun 11	Jul 10	Aug 12	Sep 3	Oct 2	Oct 28	Mean
Stations		4	16	16	16	16	16	5	
Bottom Coverage	Mean	6	8	11	57	74	68	46	39
(%)	SE	6	3	6	8	7	6	11	11
Algal Thickness	Mean	0.25	0.84	3.9	16.1	14.6	5.5	3.5	6.4
(cm)	SE	0.25	0.09	0.4	1.8	1.4	0.4	0.8	2.4
Areal Thickness (cm)		0.02	0.06	0.42	9.2	10.9	3.7	1.6	2.5
Algal Density (g/L)	Mean	26	0.54	0.21	0.10	0.21	0.87	0.87	4.1
	SE	9	0.13	0.07	0.02	0.12	0.63	0.25	3.6
Algal Mass (g/m2)	Mean	4.0	0.3	0.9	8.9	22.8	32.4	14.2	11.9

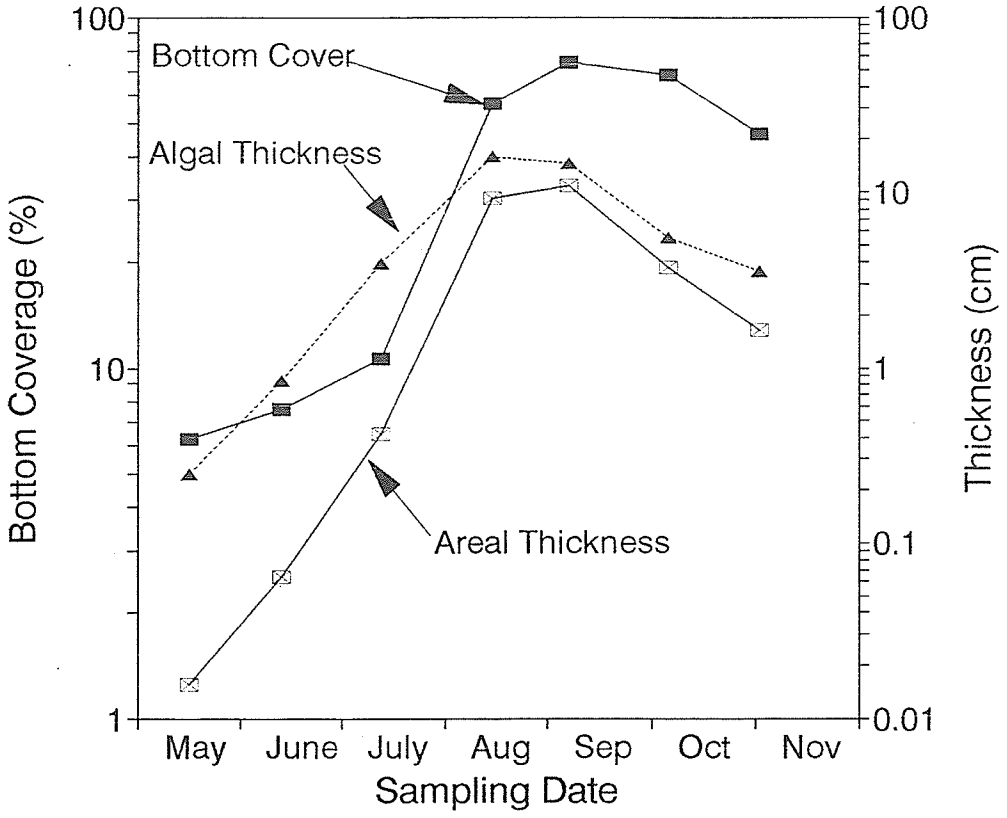

Fig. 4.4a. Features of the development of FGA biomass (% areal coverage, algal and areal thickness) at the 1-m sampling stations. Algal thickness (cm) is the median thickness of algal occurrences, whereas areal thickness (cm) is calculated as the thickness when the algae are dispersed evenly over the lake bottom.

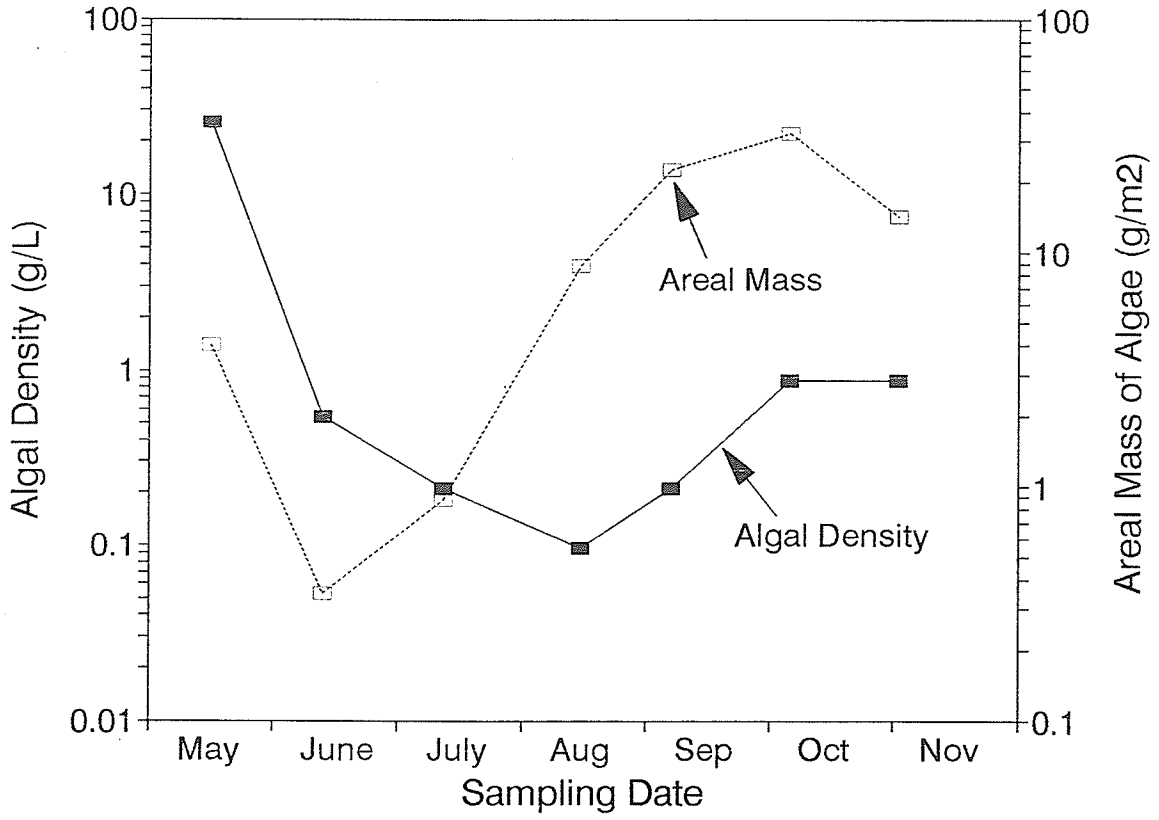

Fig. 4.4b. Mean seasonal density ($g \cdot L^{-1}$) of FGA observed at two of the 1-m sampling stations during 1991. Seasonal variation in algal mass ($g \cdot m^{-2}$) was calculated from measured algal density and calculated areal thickness.

temperatures of spring.

Variation with Depth and Slope

FGA biomass varied strongly with depth (Fig. 4.5a). Coverage by FGA of the lake bottom declined as water depth increased beyond 2 m. Algal thickness, and as a consequence, areal thickness, also declined progressively with depth. In contrast, algal density increased with water depth. This increase was insufficient to offset the decline in both algal coverage and thickness so that algal mass decreased with water depth. FGA mass decreased markedly between 2 and 3 m, as found for *Zygogonium* in Plastic Lake (Howell et al. 1990).

Slope of the lake bottom was important to development of FGA (Fig. 4.5b). The average proportion of the lake bottom covered by FGA during the open-water season decreased as slope increased ($r^2 = 0.44$, $n = 16$, $P < 0.01$). However, algal thickness was independent of slope ($r^2 = 0.09$).

Qualitative Observations of Seasonal Progression

Several qualitative observations of FGA development aided in understanding the seasonal effects of the main factors affecting FGA growth. FGA were epiphytic on submerged plants and branches, etc., in the shallows during spring; this growth form was sampled in spring for analysis. FGA were also found as highly compact, brownish mats on sediments and in some rock crevices. This brown phase, which was probably decomposing FGA, was frequently underlain by an easily disturbed black floc that had high

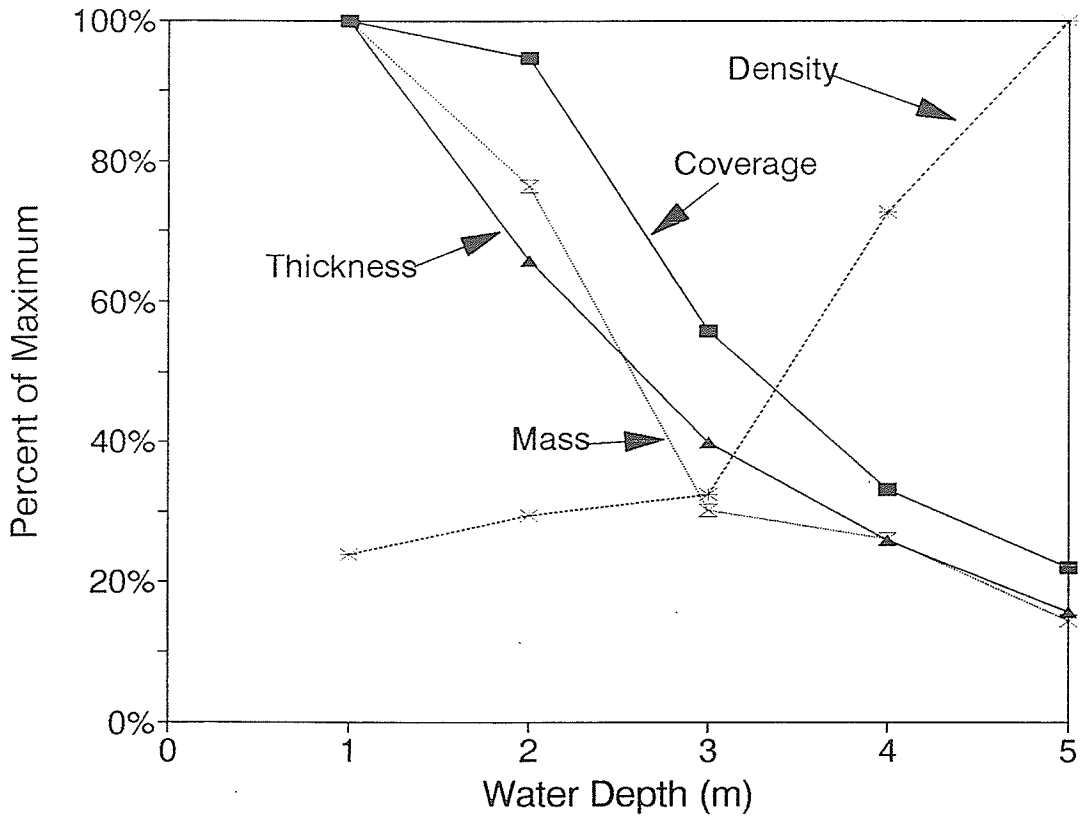

Fig. 4.5a. The percentage distribution of FGA at eight stations during 12 to 14 August 1991 expressed as a function of water depth in terms of bottom coverage, algal thickness, algal density (stations 3 and 59 only), and areal mass.

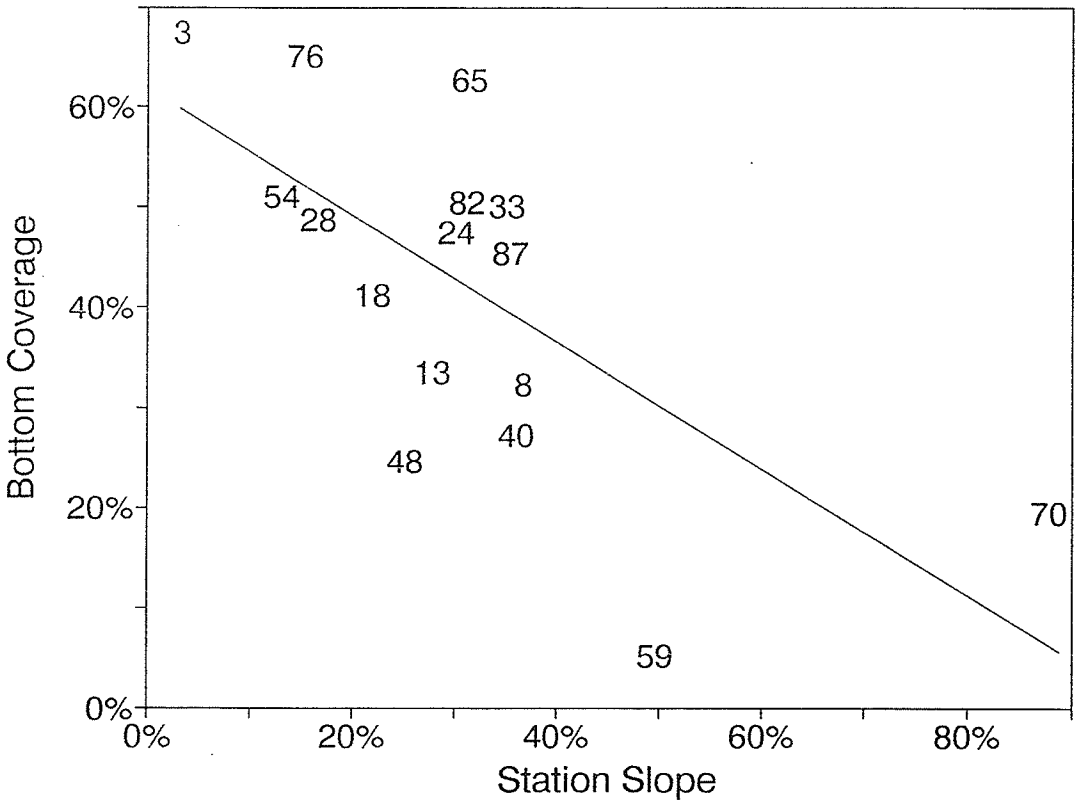

Fig. 4.5b. The role of slope of the lake bottom in the development of FGA biomass. Station numbers are indicated. The linearly fitted regression line is also shown.

concentrations of iron sulfide (Amaral 1991). In addition, the brown phase could be covered by an orange layer (presumably enriched with iron oxides).

In the early to mid summer, previously periphytic FGA broke away in some locations to form the 'tumbleweed' or ball stage. These amorphous masses then 'settled' in new areas, spreading and thickening with continued growth. In some cases, the FGA eventually blanketed large expanses of the littoral bottom.

In late summer or early fall, thick mats of FGA sometimes trapped quantities of gas bubbles, formed from underlying sediments and/or algal photosynthesis. This trapping of bubbles could sometimes cause the FGA to raft to the lake surface and again relocate. Alternatively, the FGA collapsed, usually in locations where patches of the otherwise green or grey mats had begun to darken, eventually forming the blackened sediment seen in spring.

Characteristics of Algal Composition

Apparently pure collections of FGA were sometimes rather diverse assemblages. Although green algae dominated collections from 1989 to 1991 (Fig. 4.6a), periphytic samples in spring sometimes contained a large proportion of diatoms, principally *Tabellaria quadriseptata*, *T. fenestrata* or *T. flocculosa*. The abundance of *Zygogonium* as periphyton varied among years (Fig. 4.6b). *Mougeotia* dominated the assemblage briefly in the early summers of 1990 and 1991, but *Zygogonium* was dominant by midsummer and remained so

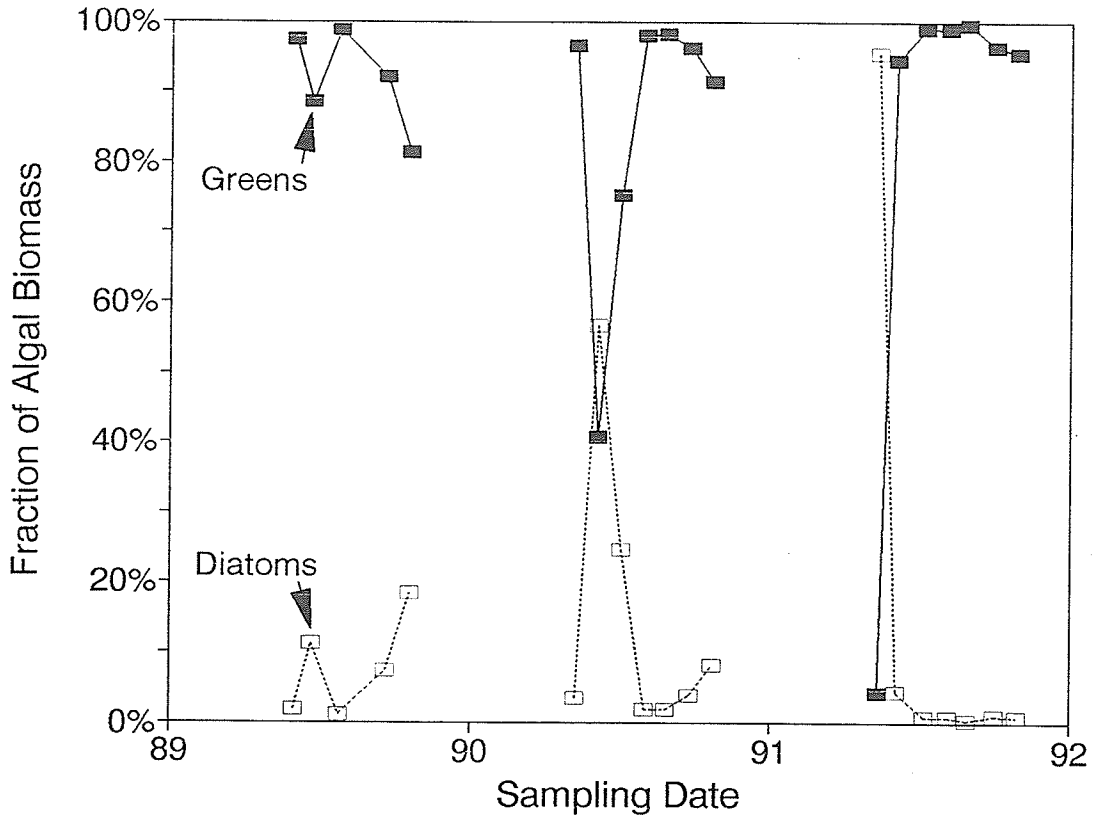

Fig. 4.6a. The percentage composition of algal biomass in FGA samples by greens and diatoms.

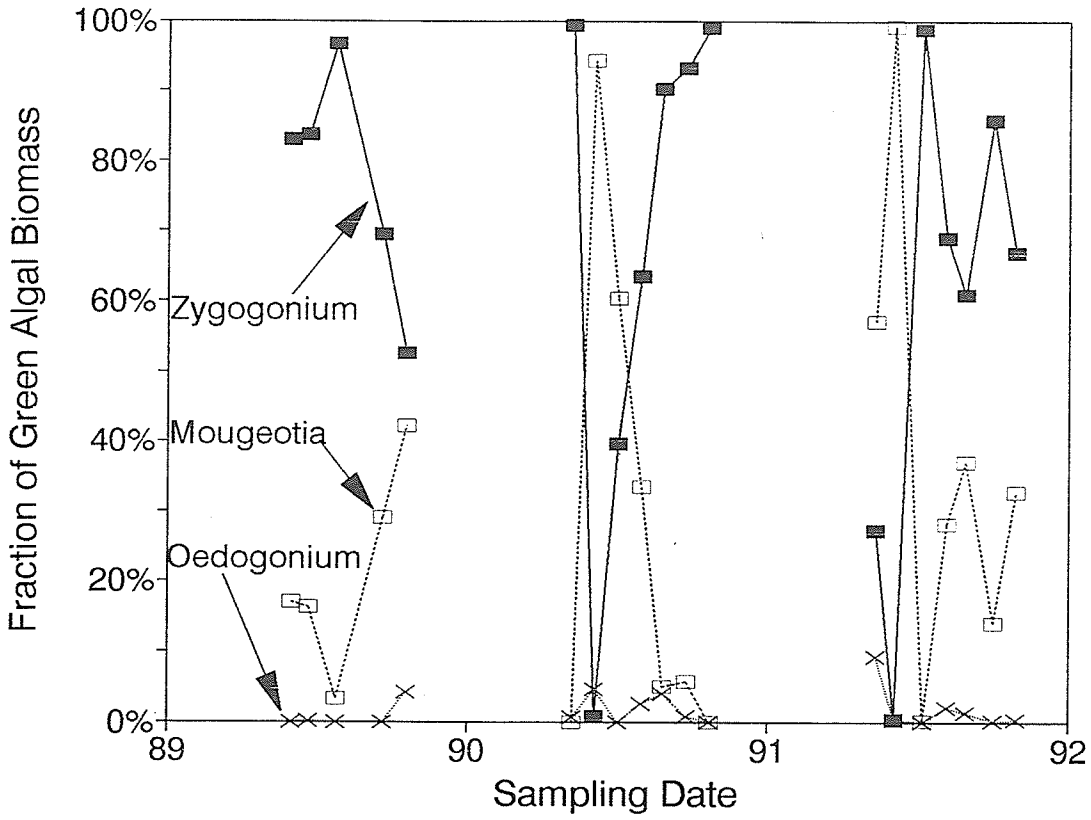

Fig. 4.6b. The percentage composition of green algal biomass in FGA samples by *Zygogonium*, *Mougeotia* and *Oedogonium*.

subsequently. *Oedogonium* was a small component and displayed no regular seasonal pattern.

Discussion

Photosynthesis of FGA in Lake 302S was a function of irradiance, DIC, water movement and algal density or crowding. The experimental findings apply principally to the FGA complex dominated in summer and fall by *Zygogonium*, and a heterogeneous spring-time complex (Fig. 4.6a and 4.6b). *Zygogonium*, the most common bloom-forming Zygnematacean alga in acid lakes of central Ontario (Wei et al. 1989, France et al. 1992), became the dominant member of the FGA with the further acidification of Lake 302S (Fig. 4.6b). It replaced *Mougeotia*, the subject of an earlier related study (Howell et al. 1990).

Photosynthesis - Algal Density

The density dependence of FGA photosynthesis observed in the laboratory (Fig. 4.1) helps in understanding some of the implications of the structural character of FGA growth forms. The lower rate of photosynthesis per unit of FGA at higher densities suggests that interior cells are unfavourably exposed to light and CO_2. In essence, this dependency represents a summation of the photosynthetic relationships with irradiance, DIC and water movement. That is, a large fraction of interior cells grows in less optimal

conditions as the FGA thicken because nutrient and physical limitations come into play. In contrast, when FGA densities are very low, their environment resembles that of a planktonic alga, which has relatively good access to nutrients, water movement and light. Clearly, FGA at the surface of the growth forms will have good access to light and waterborne nutrients.

The relationship between biomass-normalized photosynthesis (P_b) and biomass (B) was described mathematically by using the relationship P_b = slope/B + constant (Howell et al. 1990). However, a mathematical complication of this relationship is that P_b is undefined when B = 0, i.e. there is no y intercept. A further complication of any statistical analysis of P_b as a function of biomass is the potential for self-correlation, which could arise because biomass is also an element of the denominator of the dependent variable, P_b. Therefore, alternative descriptions of the relationship between photosynthesis and algal biomass were sought.

The effect of algal density on respiration-normalized photosynthesis (P_g), unadjusted for the amount of algal biomass incubated, was described well by the simple linear model, P_g = slope x biomass (Table 4.1), where the intercept is forced through zero. The residuals of these fits were small, but nonzero, although only when algal densities were very low. This nonlinearity followed from the fact that algae at very low levels of density were photosynthesizing more rapidly than at higher densities.

Seasonal Changes

Density dependence of FGA photosynthesis varied seasonally (Fig. 4.1). Seasonal variation in the slope of the photosynthesis - biomass relationship represented variability in the physiological ability of the FGA to overcome crowding, including changes in photosynthetic capacity. The blending technique effectively standardized any effect of *in situ* changes in structure of the FGA that may have occurred.

The linear coefficients of the photosynthesis-biomass relationship during spring were small (Fig. 4.1), consistent with the observation that FGA were then growing in the less effective form of periphyton, in which density feedback is high. The low springtime coefficients may also result from the more heterogeneous algal composition typical of this period (Fig. 4.6).

As the FGA progressed into metaphyton during summer, the linear coefficients increased (Fig. 4.1). This improvement coincided with the improved growth conditions of high light and temperature, although not necessarily with better nutrient availability (CO_2 declined). The coefficients declined in three of the four fall periods, consistent with qualitative observations of changes in the community (compression and darkening) and the decline in biomass seen (Fig. 4.4b). Alternatively, the density dependent factors controlling *Zygogonium* growth may have changed in the fall. For example, as the FGA aged, algal and detrital decay would result in increased internal DIC and other nutrients. In addition, grazing by numerous microcrustacea could lead to filament shortening and loss of community structure (B. Hann, University of Manitoba, and M.

Turner unpubl. obs.) which would result in mat compression. The resulting increased algal density would diminish photosynthetic capacity (Fig. 4.1).

Photosynthesis-Irradiance Relationship

The relatively low respiration rates in summer caused the ratio of respiration : photosynthesis to be much lower than that seen in acidified periphyton (Turner et al. 1987, 1991, Chapter 2). For example, respiratory losses in the FGA averaged 16% during August of 1989-1991 (Table 4.2). In contrast, average epilithic losses approached 100% during these periods (Chapter 2). That is, metaphytic *Zygogonium* was able to put a greater fraction of its photosynthesis into net growth during the warm periods of the open-water season than could the previously dominant epilithon. This FGA growth also exceeded any grazing losses, resulting in appreciable accumulation of biomass (Fig. 4.4b).

Characterization of the dependence of photosynthesis upon irradiance indicated that Smith's formulation (1936) of the relationship fit well (Table 4.2). Therefore, it was reasonable to evaluate the relationship in terms of both α and P_{gbm}. An important feature of the relationship between light and FGA photosynthesis was that photoinhibition was absent, which agrees with the laboratory studies of O'Grady (1987 for *Mougeotia*) and is also consistent with the initial development of the FGA in the shallows (Fig. 4.5a, Howell et al. 1990). As a result, additions of calcite that were intended to provide alkalinity

to acidified lakes, but which also reduced water clarity (Roberts and Boylen 1989), will likely impede FGA growth (reported by Jackson et al. 1990). The apparent lack of photoinhibition also simplifies estimation of P_{gbm} for those unable to measure photosynthesis over a range of irradiances. That is, simple *in situ* incubations of FGA in the shallows during sunny periods should suffice to characterize P_{gbm}.

The seasonal variation of P_{gbm} was regular from year to year (Fig. 4.2), and was similar to that seen in epilithon of circumneutral lakes (see fig. 5 of Turner et al. 1987). One distinction was that the FGA maximum occurred later in the open-water period than did the circumneutral epilithic maximum, exhibiting a lag in development. However, the FGA pattern was distinctly different from that of acidified epilithon; i.e. the FGA's pattern of a mid-year maximum with minima in spring and fall, contrasted sharply with the epilithic pattern of a mid-year minimum, and maxima in spring and fall.

There was greater uncertainty in estimating α (Table 4.2), so that its seasonal pattern was less clear than for P_{gbm} (Fig. 4.2). However, α increased regularly in value from its spring-time minimum in advance of the increase seen in P_{gbm}. Alpha was positively correlated with seasonal variation in the slope of the dependency of photosynthesis upon algal mass ($P \leq 0.01$). Although the significance of this correlation is unclear, it may reflect the dependency of both parameters, α and the slope of P=f(mass), on the physiological status of the community.

Nutrient Controls on Photosynthesis

Inorganic Carbon

DIC was an important controller of FGA photosynthesis (Table 4.3). This was also seen both in acidified epilithon and epiphyton (Turner et al. 1987, 1991, Chapter 3), and in FGA of different composition or in different lakes (Howell et al. 1990). Related in-mat observations that FGA photosynthesis draws DIC down to low levels (~ 4 μM) corroborates the conclusion that DIC can be limiting (Howell et al. 1990, Chapter 5). This limit was also seen in the laboratory experiment evaluating incubation conditions.

The strength of the dependence of FGA photosynthesis on DIC varied seasonally (Fig. 4.3a). The pattern of seasonal changes in DIC dependency supports the hypothesis that the maximum need (highest P_{gbm}) coincides with midyear lows in DIC. There is a simple explanation for lessened stimulation by DIC in spring and fall that is consistent with changes in the life cycle of the algae. Rates of FGA growth were relatively low during these periods (Fig. 4.2) so that there would be relatively less need for DIC. Cold water during these periods would be characterized by high levels of DIC due to increased solubility of CO_2.

Photosynthetic control appeared to shift from DIC to other factors at about 30 μM (Fig. 4.3a); self-shading and phosphorus limitation could be such factors. This low-level saturation by DIC is unlike that seen previously in other benthic algae (Turner et al. 1991, Chapter 3), but it has been seen in laboratory

algal cultures acclimated to very low DIC concentrations (Mayo et al. 1986).

FGA appear to have been more successful in overcoming limitation by low levels of DIC than have acidified periphyton. In part, FGA community architecture would increase water movement in the algal community, reducing the diffusive boundary layer thickness, and increasing the nutrient influx (Turner et al. 1991, Chapter 5). FGA mats can also be transient sources of DIC for photosynthesis given that night-time buildup of DIC can occur (Chapter 5). Similarly, high concentrations can also occur in the bottom region of FGA mats where decomposition is occurring; this would act as an internal source on a longer time scale. Alternatively, FGA may also be able to overcome low DIC by possessing an inducible carbon-concentrating mechanism (Robinson et al. 1994).

DIC may limit FGA photosynthesis in systems other than just acid lakes. For example, the pH in FGA mats can become high (e.g. from 7 to 12) in neutral systems, causing low CO_2 in the interior of cells (cited in Hoshaw and McCourt 1988).

Other Nutrients

The possibility that nitrogen and phosphorus were also limiting was evaluated to determine whether the factors that were identified in this research would suffice for future models of FGA growth. The ratios of nutrients in FGA were examined, remembering that (1) these ratios are insensitive to transient changes in nutritional status (Istvanovics et al. 1992), and (2) the collections

were impure because they included varying amounts of other algae and organisms. Although Hecky and Kilham (1988) believe the latter problem is overrated, at least in phytoplankton, these analyses are preliminary and need verification by more robust techniques.

Nitrogen limitation of the FGA appeared to be moderate, with $0.08 < N:C < 0.15$. Although epilimnetic concentrations of ammonium were high (Rudd et al. 1990), only a small proportion would have been available as ammonia at pH 4.5. Disruption of nitrification by acidification (Rudd et al. 1990) also limited the availability of nitrate. As a result, increased anthropogenic emissions of nitrogen oxides (Galloway 1989) may stimulate growth of FGA in situations where the nitrogen available to FGA is otherwise low.

FGA also were phosphorus limited using both the criteria established for N:P and 1000 x P:C by Healey (1975) and Healey and Hendzel (1979). Thus, the FGA complex may have been limited by phosphorus as well as by carbon and nitrogen. Phosphorus limitation was also demonstrated in *Oedogonium* in Lake Wingra, Wisconsin (McCracken et al. 1974), and both *Ulothrix zonata* and *Cladophora glomerata* in the Laurentian Great Lakes (Auer et al. 1983). If phosphorus availability limits growth of *Zygogonium*, then phosphorus control measures will be important in controlling FGA growth in some circumstances. For example, cottagers would worsen nuisance blooms of FGA metaphyton that already develop in acid lakes (SPR Associates 1986) by using inadequate septic systems.

Lake-Wide Distribution of Biomass

The progressive acidification of Lake 302S produced increased coverage (deepening and lateral extent) and thickening of metaphytic FGA (Howell et al. 1990, Chapter 2). The thickness of these FGA growths (Fig. 4.4a) was much greater than that of epilithon (typically measured in mm) in these oligotrophic lakes. During 1991, FGA reached a maximum coverage of about 30 $g \cdot m^{-2}$ at 1 m depth in Lake 302S, a much greater amount than the < 2 $g \cdot m^{-2}$ found in less acidic Plastic Lake (Howell et al. 1990), but similar to coverage by *Oedogonium* in circumneutral Lake Wingra (McCracken et al. 1974).

The occurrence of FGA varied both spatially (horizontally and vertically: Table 4.4 and Fig. 4.5a) and temporally (seasonally: Fig. 4.4; and annually: Chapter 5). Understanding this variability aids in evaluating the reliability of the information gathered for model formulation. For example, the seasonal pattern of biomass development generally corroborated the seasonal variation in P_{gbm} (cf. Fig. 4.2 and 4.4). The springtime decline in mass may have reflected the very low ratio of photosynthesis to respiration at this time.

The pattern of depth distribution (Fig. 4.5a) was similar to that found in Plastic Lake during August 1986 (Howell et al. 1990), with most growth at shallow depths. This depth distribution was similar to that for light intensity, except for the very shallow zone (not measured quantitatively in this study) where wave erosion and displacement likely were important factors. As well, the depth distribution was consistent with the observed stimulation of FGA

photosynthesis by water movement.

The increase in algal density with depth (Fig. 4.5a) may have been related to increasing water pressure with depth, which increases the solubility of oxygen and thereby reduces the formation of oxygen bubbles (Howell et al. 1990). Decreased light with increased depth contributed to lowered photosynthesis, again decreasing oxygen bubble formation, and lessening algal buoyancy. Lower rates of algal photosynthesis would be expected as a result of the increased algal density with increased water depth, based on the negative density dependent feedback seen.

The depth distribution also confirms that FGA growth was principally a littoral phenomenon. It is possible that the degree of depth penetration was a function of overall growth. That is, after the FGA grew and initially occupied optimal spaces, they then spread to other less favourable zones (lower light and higher pressure). This is consistent with the deepening of FGA development seen during the open-water period (M. A. Turner and B. E. Townsend, Fisheries and Oceans, Canada, unpubl. data).

Role of Temperature

Temperature was a factor examined only indirectly, but it appeared to be important to FGA growth. Both the unimodal variation in P_{gbm} and the seasonal development of FGA biomass lagged behind the variation in water temperature. The role of temperature appeared related to controls on

photosynthesis because respiration appeared unrelated to temperature. Temperature modified DIC concentrations, decreasing DIC levels with increased temperature as the solubility of CO_2 decreased. As a result, carbon limitation increased directly with temperature (Fig. 4.3b).

Algal density (Fig. 4.4b) was also inversely related to water temperature in part because oxygen solubility increased as temperature declined, reducing bubble formation. Algal density would increase as a result, yielding a self-perpetuating process: increased density caused decreased photosynthesis via negative density-dependent feedback (Howell et al. 1990); lowered rates of photosynthesis reduced the formation of bubbles, further increasing density; and so on. The eventual result would be a population collapse after a bloom, initiated by falling water temperatures. Such potential effects of temperature merit further study.

Prelude to Modelling

The controllers of FGA photosynthesis (DIC, irradiance, algal density and water movement) were independent of each other. If this is also true for nitrogen, phosphorus and temperature, then a model without interactive terms should serve to describe FGA photosynthesis. Thus, short-term, site-specific growth of *Zygogonium* can be described by an additive model that incorporates both photosynthesis (as a function of several variables) and respiration. Photosynthesis can be described as a nonlinear function of algal density or as

a linear function of algal mass; a nonlinear function of irradiance; and a linear function of DIC concentrations. Water movement was less important than the other main factors. In part, the role of water movement may have been subsumed by DIC, the nutrient most likely to limit photosynthesis in the short term, at least in these low DIC lakes. Hence, the photosynthetic description can be simplified by ignoring water movement, although the variation of water movement with depth may have to be retained in a more realistic model.

The development of appreciable mat thickness provides a further modelling complication because both DIC and irradiance are stratified with depth within the mat (Chapter 5). This vertical variation might be partly understood using the density-dependent relationship, although nutrient deficiencies may also vary with depth. Expansion of the model to lake-wide descriptions will also require incorporation of morphometric characteristics of the lake bottom such as slope (Fig. 4.5b).

Extension of a growth model beyond an instantaneous paradigm will be substantially more challenging. The interrelationship between FGA photosynthesis and its controlling factors varied seasonally, so that model parameters must be time-dependent functions. Information on rates of removal (herbivory or physical dispersal) must also be included in such an endeavour. Last, such long-term predictions may have to account for the roles of nitrogen and phosphorus in more detail than was considered in this study.

FGA in the Future

There are several indications that the growth of FGA, already a nuisance alga in some situations (SPR Associates 1986), will become more of a problem in the future. FGA growth is controlled by several factors that are now being altered by anthropogenic activities. It is clear that acidification increases FGA (Stokes 1986; Turner et al. 1987, Chapter 2; Howell et al. 1990). Global warming will increase the open-water period, principally in the spring when irradiances are also high (Schindler et al. 1990), potentially enhancing the ability of the FGA to overcome their lag in shifting from a periphytic to metaphytic growth form. Epiphytic FGA have increased in response to increased water temperatures in an unperturbed lake at the ELA (Schindler et al. 1990). Increased temperatures should also stimulate growth by improving the algal density-photosynthesis relationship by increasing the buoyancy of the FGA community. Increased concentrations of atmospheric CO_2 will also alleviate carbon limitation. Furthermore, any increase in ultraviolet radiation may destroy humic acids in lake water, increasing transparency, and increasing FGA growth as a result if the FGA are immune to the increased UV. Local releases of phosphorus as a result of human activities are likely to stimulate FGA growth. Finally, increased emissions of nitrogen oxides, aside from increasing rates of acidification (Rudd et al. 1990), may also remove nitrogen limitations.

Chapter 5. Ecological Effects of Blooms of Filamentous Green Algae in the Littoral Zone of an Acid Lake.

Abstract

The ecological effects of blooms of filamentous green algae (FGA) were studied in an oligotrophic lake acidified experimentally to pH 4.5 with sulfuric acid. Photosynthetic capacity of the FGA, dominated principally by *Zygogonium*, was greater than that of acidified epilithon, the normally dominant littoral algal community, partially offseting the acidification-induced oligotrophication seen in the littoral zone. However, the intra- and interannual variability of FGA growth was large, so that FGA were an unreliable energy source for the littoral food web. Nutrient uptake varied with the degree of FGA growth; FGA occasionally were the largest phosphorus pool in the epilimnion. FGA nitrogen dynamics varied seasonally causing acidification in spring and summer, and alkalinization in fall. The blooms also affected epilimnetic cycling of carbon dioxide. Peak blooms prevented up to 90% of the light from reaching the lake bottom. Local depletions of oxygen resulting from FGA decomposition posed potential risks for animals using the FGA as habitat. Blooms of FGA influenced chemical cycling, energy balance, physical features, and biological conditions in the littoral zone.

Introduction

Filamentous green algae (FGA) are widespread (Hoshaw and McCourt 1988), and can be especially prolific in acidified aquatic systems (SPR Associates, Inc. 1986; Howell et al. 1990). They may become a more widespread nuisance in future because of release from growth limitation by human activities (Chapter 4). There was little knowledge about the growth characteristics of FGA in acidified systems until recently (Howell et al. 1990, Chapter 4). Even less information is available about the ecological effects of FGA blooms, although Stokes (1986) speculated about the implications of FGA blooms for habitat modification.

The objectives of this study were to investigate the possible chemical, physical and biological effects of FGA blooms in a lake acidified experimentally to pH 4.5. These effects included: (1) alteration of nutrient cycles and internal alkalinity generation; (2) changes in light transmissivity, bottom temperatures, and water movement; (3) variation in energy flow among littoral algae, and (4) provision of habitat for animals. This study was designed to evaluate the scale of these effects rather than to quantify them precisely.

Methods

Turner et al. (1987, 1991, Chapter 4) and Howell et al. (1990) described the physical and chemical characteristics, and recent experimental history of oligotrophic Lake 302S. During the period of this study (1988-1991), Lake

302S was held at pH 4.5 by additions of sulfuric acid.

Measurement of Algal Metabolism and Biomass

Algal photosynthesis and nutrient concentrations

The techniques for measuring rates of FGA photosynthesis and concentrations of FGA macronutrients were described in Chapter 4. Areal productivity of FGA was determined using the metabolic information also in Chapter 4. In brief, seasonal changes in maximum rates of biomass-normalized photosynthesis were determined from measurements of photosynthesis-irradiance relationships. These maxima were then multiplied by the scalar coefficients derived from the corresponding measurement of the density dependence of FGA photosynthesis. Areal rates were derived by multiplying the adjusted maxima by the average areal amount of FGA seen at the corresponding sampling period.

Turner et al. (1991) described the *in situ* techniques used to measure rates of photosynthesis in epilithon (community on rock surfaces). Particulate samples of epilithon were collected using a scraping device (Turner et al. 1991), and analysed for concentrations of particulate carbon, nitrogen and phosphorus (Stainton et al. 1977).

Lake-wide biomass of FGA

Lake-wide mass of FGA was measured using a depth-stratified transect method (Howell et al. 1990, Chapter 4). Variations in these procedures over

the four years of the study are described below; in part, sampling strategies were modified to compensate for year-to-year variations in FGA biomass.

The procedures in 1988 and 1989 followed Howell et al. (1990). FGA was sampled from 8 to 26 August 1988 and 30 July to 1 August 1989. In 1988, four transects (selected randomly from 91 equally spaced locations around the lake perimeter) were sampled, whereas in 1989, 10 were sampled. Fifteen sampling sites, ranging in depth from 0.25 m to 4.0 m, were selected randomly along each transect in 1988, and in 1989, 10 sampling sites (0.1 m to 5 m depth) were used. The deepest collection depth was increased in 1989 after recognizing that 4 m was too shallow to include the vertical extent of FGA.

A SCUBA diver measured the % coverage by FGA of each plot area (0.5 m X 0.5 m), and the median thickness of FGA growing there. The entire mass of FGA in each plot was then collected by vacuum and screened through a 102-μm mesh net by an assistant. The FGA was retrieved from the net, cleaned of any visible debris and stored temporarily in polyethylene bags. The samples were then volumetrically measured, weighed wet, and dried at 60^{o}C until a stable weight was achieved.

In 1990, FGA were sampled along eight transects during six periods from 10 June to 29 October. The stations were selected randomly as before. Fixed sampling depths of 0.5, 1.0, 1.5, 2.0, 3.0, 4.0, and 5.0 m were established along each transect, and locations for later sampling periods were predefined and marked along each depth contour to avoid disturbance by the SCUBA

divers. The procedures followed were otherwise equivalent to those described for 1988.

The 1991 sampling program was described in Chapter 4. In brief, seasonal sampling was repetitive and nondestructive to enhance detection of time-related trends, and focussed on the 1-m depth contour to maximize effort spent in the growing zone. The quadrat area was increased to 1 m x 1 m because of patchy growth of FGA during spring and early summer. Measurements were also made in three adjacent quadrats, increasing the area sampled 12-fold at a single site in comparison with previous years. The number of sites sampled at 1 m was also increased to 16. Algal coverage and growth thickness were measured in the sample plots as before. Algal density was measured in separate collections made next to established transects. Algal density was calculated as the dry mass of an FGA sample divided by its growth volume measured by the SCUBA diver. Algal mass was then calculated as % bottom coverage x algal thickness x algal density. The vertical distribution of the FGA over 1 to 5 m also was evaluated along eight of the 16 transects from August 10 to 12.

Calculating whole-lake estimates

Mean masses found at each depth contour were multiplied by the corresponding area of lake bottom to scale the observations up to the whole lake. The whole-lake masses for sampling periods in 1991 were estimated using the assumption that the vertical distribution seen during August 10-12

applied throughout the open-water season. FGA developed first in the shallows and later at deeper depths (M. A. Turner, unpublished observations), so this assumption would likely overestimate lake-wide masses prior to mid-August and underestimate masses at subsequent periods.

Chemical Properties

Variation of CO_2 within mats of FGA

A well-developed mat of ~ 0.4 m thickness, located in ~ 0.9 m of water, was sampled for dissolved inorganic carbon (DIC) using a probe, the end of which was 100-µm porous polyethylene. Rigid acrylic tubing was inserted into this polyethylene, connecting it to Tygon® tubing that ended with a sampling syringe assembly at the lake surface. This assembly was composed of a 3-way valve connecting the Tygon® tubing to a 50-mL syringe and DIC sampling syringes. DIC samples were collected at each depth after flushing the sampling line at least three times with about 45 mL of water. This flushing procedure increased the sampling zone from a point source to a sphere of 2- to 3-cm radius.

The probe was held in place using a clamp held in the middle of a 1-m x 1-m frame with adjustable legs at the corners. The probe was moved manually and fixed vertically in position using a clamp. Depth of penetration into the FGA was determined from markings on the acrylic tubing, and by noting the point of entry into the mat. The bottom underlying the mat was rock and was

easily discerned when the probe contacted it.

Ammonia flux in FGA

Release or uptake of ammonia by FGA was determined four times in 1991. Samples were incubated for 1 d in darkness on 13 August. Samples were incubated for 4 h in darkness or in light (>650 $\mu E \cdot m^{-2} \cdot s^{-1}$) in September and October. The density of FGA incubated ranged from 8 to 15 mg dw in each 125-mL bottle. The ammonium concentration in the water phase was measured (using the methods of Stainton et al. 1977) prior to, and just after, incubation. The rate of change in concentration was expressed as a biomass-normalized flux.

Sequestering of phosphorus by FGA

A simple model was used to estimate sequestering by FGA of phosphorus in the epilimnion. The epilimnion was assumed to be 5 m deep, yielding an epilimnetic volume of 4.30×10^8 L; the corresponding epilimnetic bottom area was 4.7 ha. The amount of FGA was varied over the approximate range of coverage seen from 1988 to 1991 (Table 5.1). Phosphorus in FGA was calculated using the mean ratio of phosphorus : dry weight measured in 1991. The model assumed that both plankton and epilithon compartments were constant in size, and characterized by their average particulate phosphorus composition measured (using the procedures of Stainton et al. 1977) during the open-water period of 1991. It was assumed that the littoral bottom was covered entirely by epilithon; this assumption overestimates the roles of epilithon, but

Table 5.1. Approximate maximum amounts of FGA biomass found on the lake bottom in the littoral zone (0 to ~ 5 m) of Lake 302S from 1988 to 1991. Biases associated with particular years are noted in the text.

Sampling Information

Year	Date	Number of Samples	Total Sample Area (m^2)	Water Depth (m)		Bottom Slope (%)		Notes
				Mean	SD	Mean	SD	
88	230	55	14	2.0	1.1	16	18	
89	212	92	23	2.5	1.4	29	23	
90	275	56	14	2.4	1.6	36	21	
91	275	120	120	3.0	1.6	36	21	5

Algal Information

Year	Bottom Coverage (%)		Algal Thickness (cm)		Algal Density (g/L)		Mass (g/m^2)	Notes
	Mean	SD	Mean	SD	Mean	SD		
88	83	28	22	15	0.4	0.9	75	1, 2
89	5	15	7	6	0.6	0.6	2	2
90	33	19	4	3			22	6
91	41	33	3	4	1.6	1.3	18	3,4

(1) Areal mass was calculated as: % coverage x algal thickness x algal density.

(2) The seasonal maxima likely occurred after this sampling period.

(3) 1991 SD values are those measured on day 225 adjusted for the ratio of 1-m values between days 275 and 225.

(4) The maximum mass was seen on day 275 at 1-m sites; these data are adjusted for the vertical distribution seen on day 225.

(5) The sampling stations used to measure vertical distribution in 1991 were the same as those used in 1990.

(6) The corresponding algal density information from 1991 was used in the mass calculation for 1990.

likely accounts for the unmeasured compartments of epiphyton and macrophytes which are excluded from the model. The role of sedimentary phosphorus was ignored because littoral sedimentary phosphorus efflux was unlikely to be important (Levine and Schindler 1992).

Oxygen profiles in FGA mats

Changes in oxygen concentration were measured in several different masses of FGA overlying sediment. An oxygen-needle probe (Flett Research Ltd., Winnipeg, MB) was connected using waterproof cable to an oxygen meter operated by an assistant. The probe was marked in 1-cm increments permitting measurement of the depth of penetration into the FGA. The probe, secured in a micromanipulator arm situated on the lake bottom, was moved by the SCUBA diver. The FGA thickness was determined after completion of a profile.

Modification of pH by FGA mats

Porewater samplers (Hesslein 1976) were inserted by a SCUBA diver into the sediment. One sampler was inserted through a well developed FGA mat, while the other was placed in a location where there was no FGA. The sampler and its polycarbonate membranes (0.2 μm pore size) had been washed in distilled water. They were then soaked overnight in deionized water bubbled with nitrogen to deoxygenate the sampler (Kelly et al. 1984).

The samplers were retrieved 20 and 21 days later by the SCUBA diver. Locations of algal-water and sediment-algal interfaces were noted by the diver.

Samples for pH were removed immediately by a surface attendant by carefully extracting the contents of the sampler cells into glass syringes. Care was taken to avoid pH changes due to sample equilibration with the atmosphere (Kelly et al. 1984). These samples were analysed within hours using an Orion pH meter (Model 811) and an electrode using two-point calibration. The pH recorded was the first reading (to 0.01 units) that was obtained without change for 30 s.

Chemical Properties - Mesocosm Studies

Two sets of mesocosm experiments were conducted. The 1989 set was intended to evaluate the effect of varying grazing pressure upon FGA; only the nutrient chemistry information is reported here. The 1990 experiment was designed to evaluate changes in water chemistry accompanying FGA decomposition. The cylindrical mesocosm designs used in both years (1-m diam., ~ 1-m depth) had polyethylene walls and bottoms.

The 1989 experiment consisted of two blocks of three mesocosms each: low, medium and high grazing pressure. FGA were collected in bulk from an island station, to minimize the inclusion of shoreline detritus. Macroinvertebrates were removed for subsequent use. Approximately 9 L of FGA were added to each mesocosm. The herbivorous invertebrates were then added to the mesocosms as follows: one third to the medium treatments, and two thirds to the high treatments. Predaceous invertebrates were allocated equally to all three treatments. Substantial but unmeasured amounts of FGA

were transferred along with the invertebrates, and this yielded low, medium and high FGA densities. Water chemistry samples were collected 29 August and 9 September 1989, using an acrylic tube submerged ~ 0.8 m into the middle of each mesocosm from one block. The tube was sealed at the top, removed from the water and then drained into a sample bottle.

The 1990 decomposition experiment was designed to have better control of FGA densities, with two blocks of three levels of FGA in each block: none, low and high. FGA were collected as in 1989, except that invertebrate densities were not manipulated. Prior to algal addition, each mesocosm was filled with water pumped through a 102-μm screen. Treatments were assigned randomly to the mesocosms within each block. Additions of 57 and 570 mL of FGA were added to each low and high mesocosm, respectively. Using a conversion to dry weight of 6% (M. A. Turner unpubl. obs.), average areal densities of FGA in the low and high mesocosms were 4 and 40 gdw/m^2. Duplicate samples for water chemistry were collected 5 October, one day after the algal additions, and 24 October, 1990.

Physical Properties

Attenuation of irradiance by FGA

To evaluate the rate of attenuation of light within FGA mats, *Zygogonium* was collected on 31 August 1988, and handled as in photosynthetic experiments, with a suspension created after blending. Transmittance of

photosynthetically available radiation (400 to 700 nm) was measured using a flat cosine LiCor Inc. LI-192SA quantum sensor. The sensor was enclosed in a black shroud (except its uppermost surface) and mounted beneath a beaker of lake water exposed to natural light (~ 1000 $\mu E \cdot m^{-2} \cdot s^{-1}$) and connected to a LI-1000-32 data logger. Aliquots of algal suspension were added to the beaker, and measurements made repeatedly after each of four replicate additions. The effect of increasing the amount of FGA on the light transmitted was examined using the Beer-Lambert Law (Turner et al. 1983) and deriving the contribution of FGA to the attenuation coefficient.

The attenuation of light by FGA was confirmed *in situ* on the sunny afternoon of 29 August 1990. Photosynthetically available radiation was measured by a SCUBA diver using a spherical LiCor Inc. LI-193SA quantum sensor connected to the data logger operated by an assistant. The sensor was placed next to the FGA to measure the ambient irradiance, and then carefully placed underneath the FGA to measure the transmitted irradiance. The approximate water depth and vertical thickness of the FGA were measured.

Boundary layer thickness in FGA mats

Attenuation of water movement by FGA was determined using the techniques for measuring boundary layer thickness described by Turner et al. (1991). On 2 September 1988, preweighed chips of calcium sulphate were suspended at varying depths both outside and inside an algal mat. The rate of dissolution of the calcium sulphate over the 4- to 5-h sampling period was

determined by the rate of weight loss of the chips.

The ability of FGA to attenuate water movement was evaluated again on 29 August 1990. Chips were placed on the lake bottom by a SCUBA diver, either with or without FGA overlying the chips. Water depth and FGA thickness were recorded. Chips were retrieved after ~ 1 h, dried and reweighed.

Modification of water temperature

The influence of FGA on water temperature was measured on three occasions during August 1990. Because the SCUBA diver used a total-immersion thermometer (Fisher 15-043A), measured temperature differences applied to large volumes rather than to specific points within the mats.

Results

Algal Metabolism and Biomass

Algal Photosynthesis

The seasonal patterns of maximum rates of net photosynthesis in FGA and epilithon of Lake 302S were dissimilar during the period 1989 to 1991 (Fig. 5.1). Acidified epilithon exhibited relatively high rates in spring and early fall; annual minima occurred in midsummer. In contrast, the FGA pattern of biomass-normalized photosynthesis was unimodal, characterized by minima in the spring and fall and by a maximum in late summer; this pattern was similar to that seen in epilithon of circumneutral Lake 239 (Fig. 5.1). Calculated rates of FGA areal photosynthesis remained low until August when they were

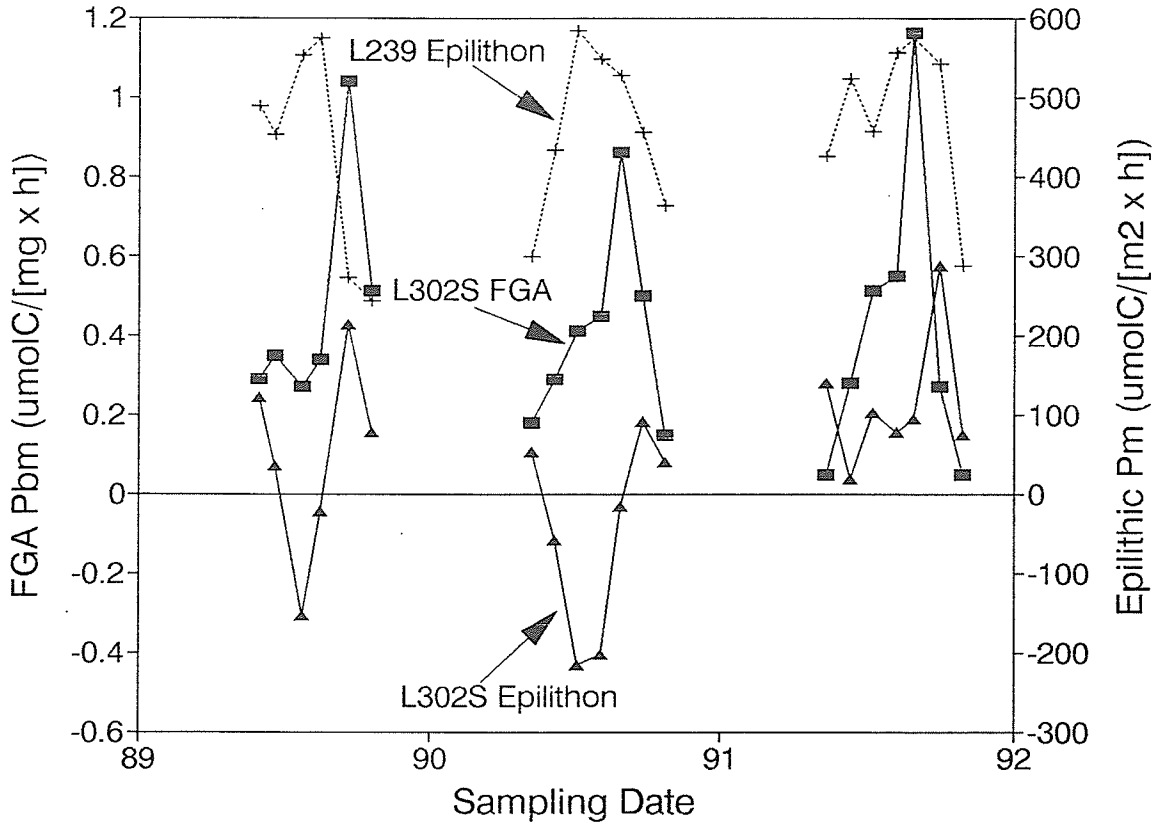

Fig. 5.1. Maximum rates of net photosynthesis in the epilithon of lakes 239 and 302S and in the FGA of Lake 302S from 1989 to 1991.

equivalent to those measured in circumneutral epilithon during 1991 (Fig. 5.2). FGA areal rates were much greater than those measured in epilithon in either the acidified or circumneutral lake during August and September of 1991 (Fig. 5.2).

Algal biomass

The seasonal distributions of biomass of acidified epilithon and FGA were almost mirror images in 1991 (Fig. 5.3). The maximum biomass of FGA at 1 m occurred in early October. Although both areal coverage and algal thickness had begun to decline at this time, algal density (quantity of algae per unit of growth volume) was high. In contrast, epilithic biomass in Lake 302S was at its maximum in the spring and fall, and was low from July to September. This epilithic pattern was different from that in circumneutral Lake 239. In spite of the substantial FGA areal photosynthesis, the 1991 sum of FGA and epilithic biomasses in Lake 302S was less than that of circumneutral epilithon (Fig. 5.3). This may not have been true in all years (e.g. 1988: see below).

The maximum biomass of FGA distributed over the entire littoral bottom fluctuated markedly from 1988 to 1991 (Table 5.1). Maximum annual amounts varied from 2 to 75 gdw/m^2. Variation in procedures among years may have contributed to the differences seen. The average bottom slope at sampling sites exceeded the average slope of 11% for the 0 - 5 m zone calculated from Brunskill and Schindler (1971), causing underestimates of FGA mass (Chapter 4). Second, the maximum mass was unlikely to have been measured in all

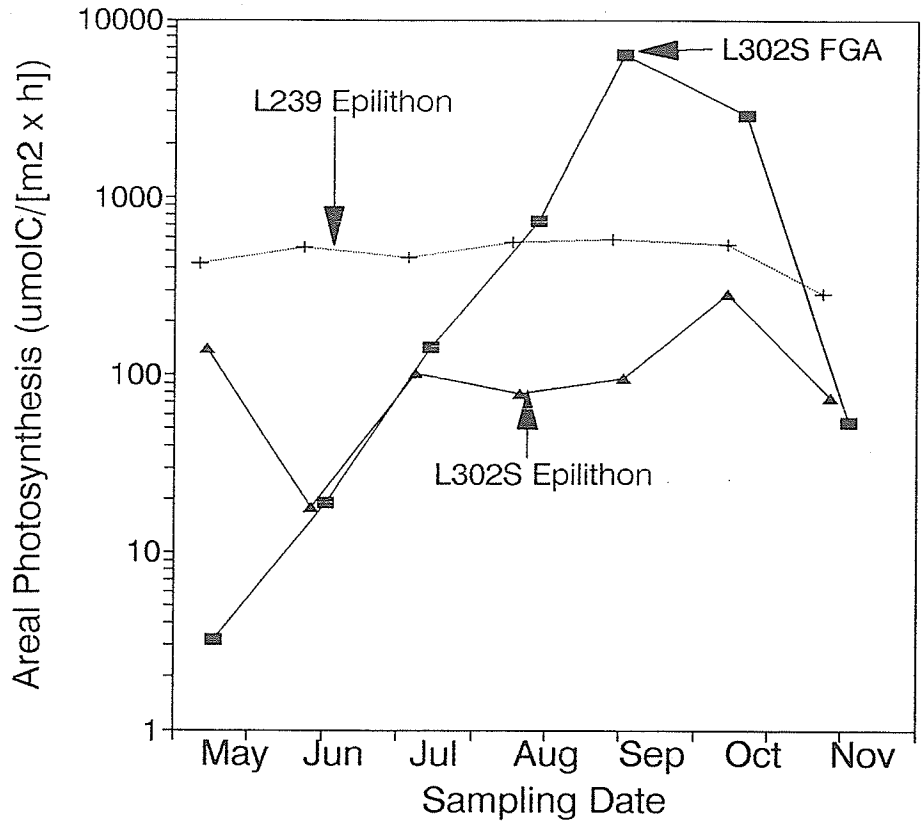

Fig. 5.2. Rates of net areal photosynthesis in two algal communities of Lake 302S and in epilithon of Lake 239 in 1991. FGA rates are expressed per unit of occupied lake area; epilithic rates are normalized per unit of sampled lake area.

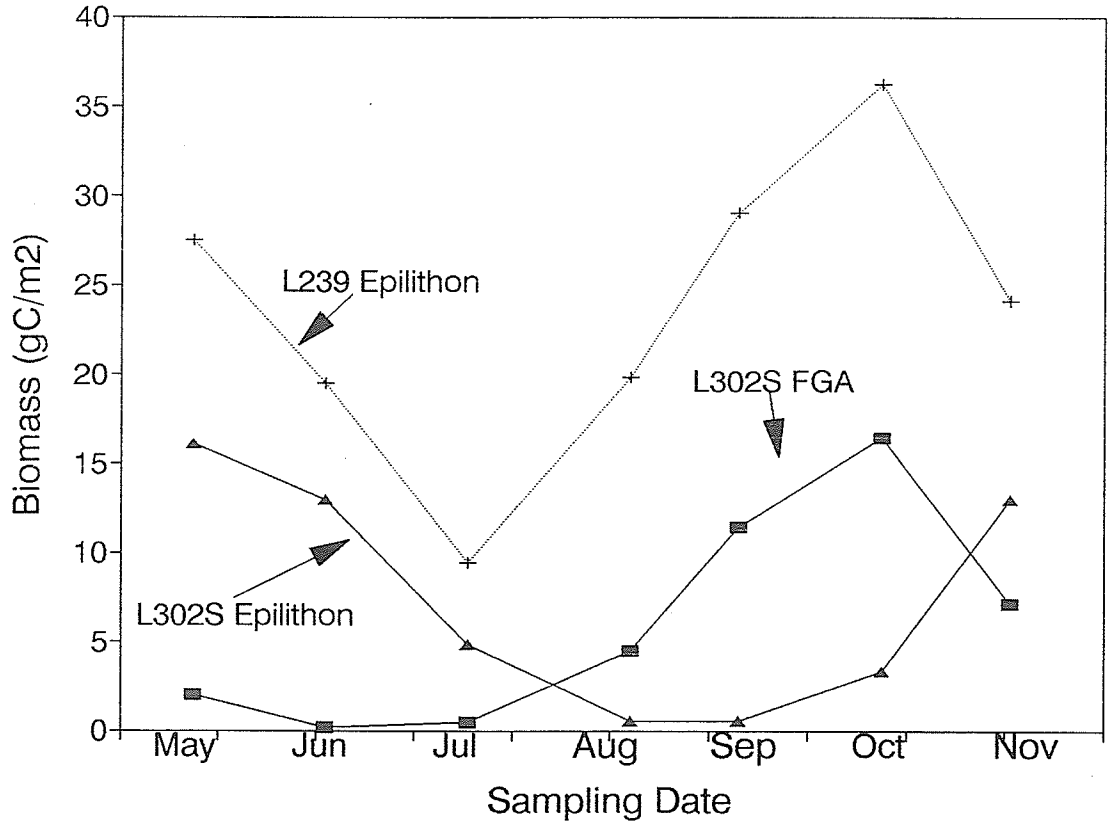

Fig. 5.3. Masses of epilithon and FGA at 1 m in Lake 302S, and of epilithon in nearby neutral Lake 239, during the open-water period of 1991. FGA masses are expressed per unit of occupied lake area; epilithic masses are normalized per unit of sampled lake area.

years. FGA maxima were seen in late September or early October during 1990 (M. Turner unpublished data) and 1991 (Fig. 5.3), so biomass measured during synoptic sampling in 1988, and especially 1989, was likely less than the annual maximum. The major conclusion, however, that FGA biomass varied substantially among years remains valid because the scale of the measurement errors appeared to be much smaller than the degree of interannual variation.

Chemical Properties

Variation of CO_2 within mats of FGA

Concentrations of CO_2 varied appreciably both with depth within an FGA mat and with the time of day (Fig. 5.4). Concentrations within the FGA were below those in the overlying water in the evening except at the very bottom of the mat, so FGA were a sink for CO_2 in the day-time. In contrast, early the next morning concentrations increased strongly with mat depth compared to those in the overlying water, so FGA were a source of CO_2 in the night. This was especially the case near the bottom where some FGA may have been decomposing, or there may have been abundant animal activity.

It is important to note that concentrations in the overlying water paralleled those in the upper portions of the FGA mat (Fig. 5.4). Change in DIC in the water overlying the FGA was corroborated by more frequent sampling in the epilimnion overlying the deepest point of the lake.

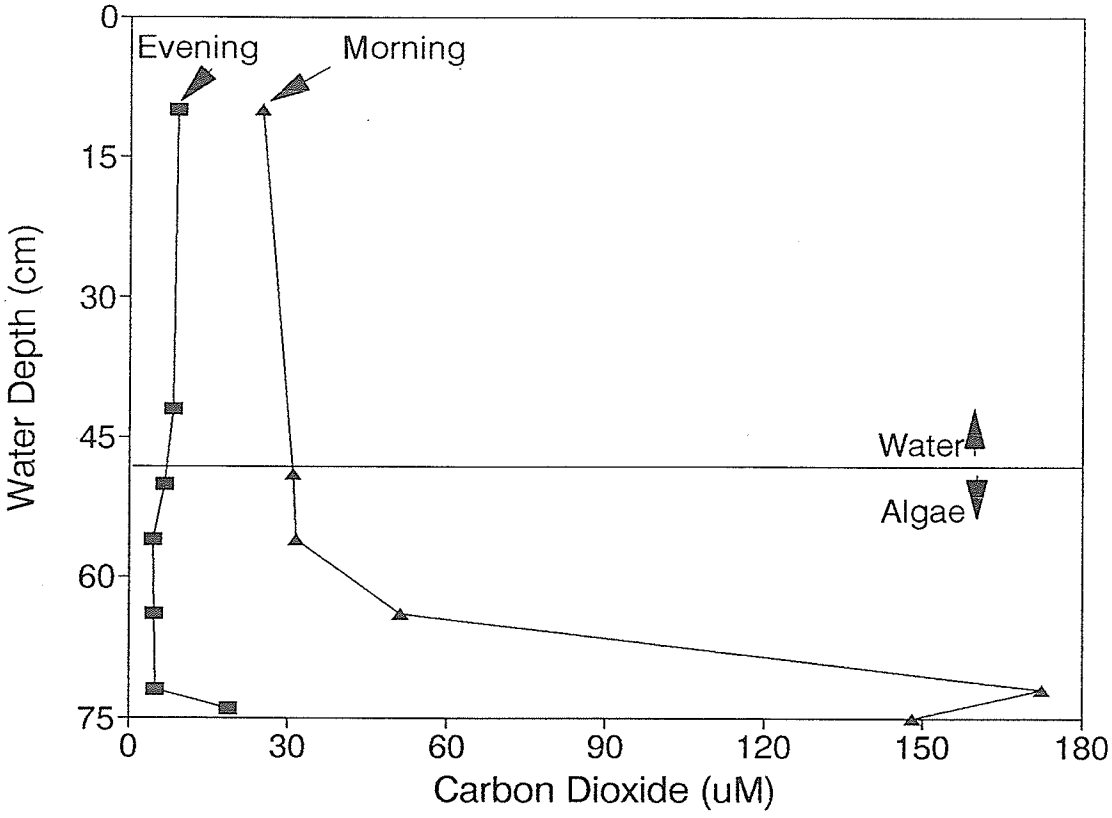

Fig. 5.4. Profiles of CO_2 measured during the evening of sunny 2 September 1988, and following morning, in a mat of FGA overlying rock in water depth of 75 cm in Lake 302S. Absolute concentrations are shown for the water phase overlying the FGA, and within the mat itself.

Ammonia flux in FGA

Ammonia flux in FGA was bidirectional depending on when bottle bioassays were conducted. Ammonia influx occurred in mid August at a rate of 0.037 $\pm$ 0.005 $\mu gN \cdot mgdw^{-1} \cdot h^{-1}$) ($\pm$ SD, n = 3). From 5 September to 29 October, there was net release of ammonia at a mean rate of 0.060 $\pm$ 0.013 $\mu gN \cdot mgdw^{-1} \cdot h^{-1}$ ($\pm$ SE, n = 3 means of 4 samples each). There was no effect on ammonia flux of exposing FGA to light; the average ratio of irradiated to dark rates was 96% $\pm$ 7% (SE, n = 3 means). Therefore, rates in the dark and light are included in the above estimate

The whole-lake flux of ammonia from FGA can be estimated for the fall of 1991 using the mean overall efflux of ammonia from September to October of 0.06 $\mu gN \cdot mgdw^{-1} \cdot h^{-1}$. Given the average mass of FGA in the 0- to 5-m zone during these months was 440 kg dw (calculated from Chapter 4), the resulting daily efflux of ammonium from FGA would be 0.63 kgN/d. When diluted into the whole lake (5.5×10^8 L), this would yield a daily increase of about 1 µgN/L, an amount equal to one-third to one-half of the total increase seen in the epilimnion during the fall (M. P. Stainton, Freshwater Institute, Winnipeg, MB, unpubl. data).

Sequestering of phosphorus

The calculated phosphorus content of FGA in the three-compartment epilimnetic model increased as FGA coverage increased (Fig. 5.5). The FGA reached the approximate importance of the periphyton and plankton at ~ 35

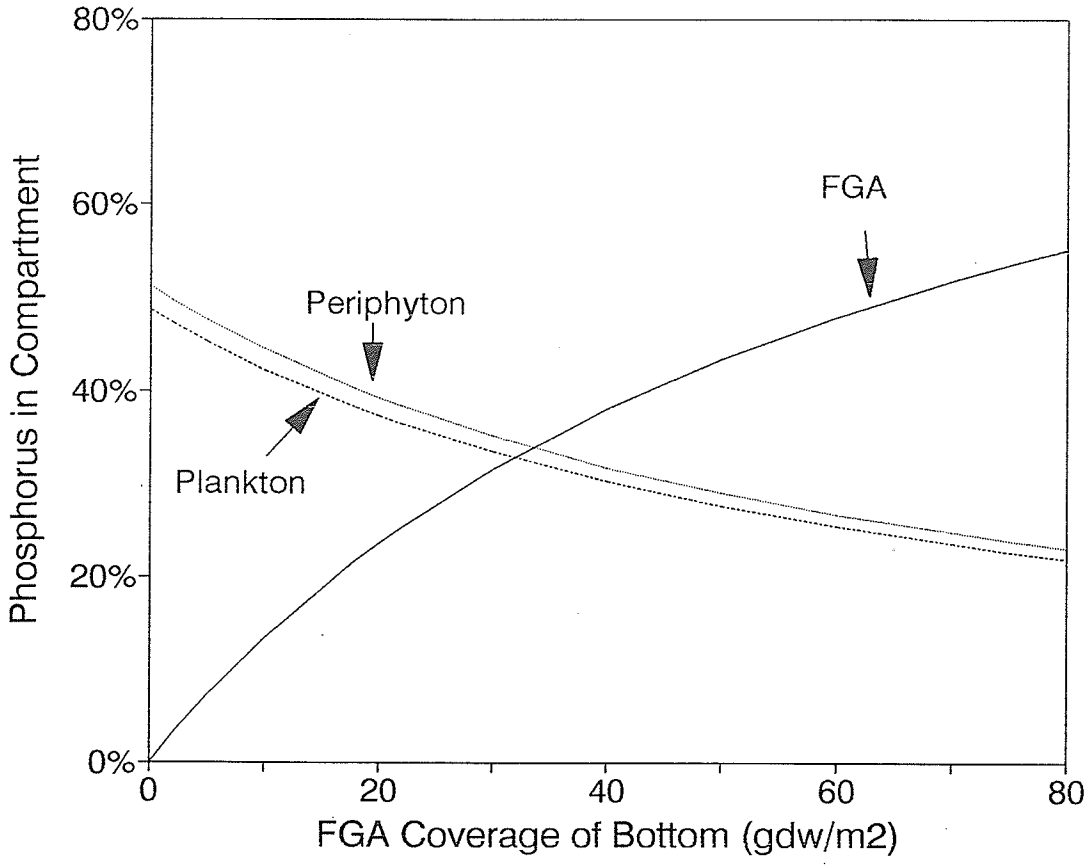

Fig. 5.5. The potential of FGA in Lake 302S to sequester epilimnetic phosphorus compared to periphyton and epilimnetic plankton.

gdw/m^2. At the1988 level of coverage (~ 75 gdw/m^2, Table 5.1), FGA would have sequestered ~ 54% of particulate phosphorus in the epilimnion. In contrast, FGA would have been unimportant (~ 3%) at the 1989 level of coverage (~ 2 gdw/m^2).

Changes in oxygen concentration

Profiles of oxygen concentration were measured during the cloudy morning of 29 September 1990, when the water temperature was 13.5 ^{o}C. In a sample profile measured in a mass of decaying FGA, oxygen concentrations declined rapidly in the lower half of the mat, reaching less than 20% of ambient values near the base (Fig. 5.6). This pattern was also seen in a second senescing mat.

When FGA were still healthy (i.e. green or gray rather than brown) oxygen concentrations were similar to ambient values. In one case, however, oxygen concentrations were as much as 80% greater at the bottom than in the overlying water.

Modification of pH by FGA mats

The presence of FGA increased the pH in water overlying the sediments as measured using the porewater samplers installed at two locations in 2 m of water depth on 4 October 1990 (Fig. 5.7). The pH increased almost 2 units in the established FGA mat that had diminished in thickness from 11 to 6 cm during the 20 d of equilibration. A smaller amount of FGA had developed around the non FGA sampler during the equilibration period. The increase in

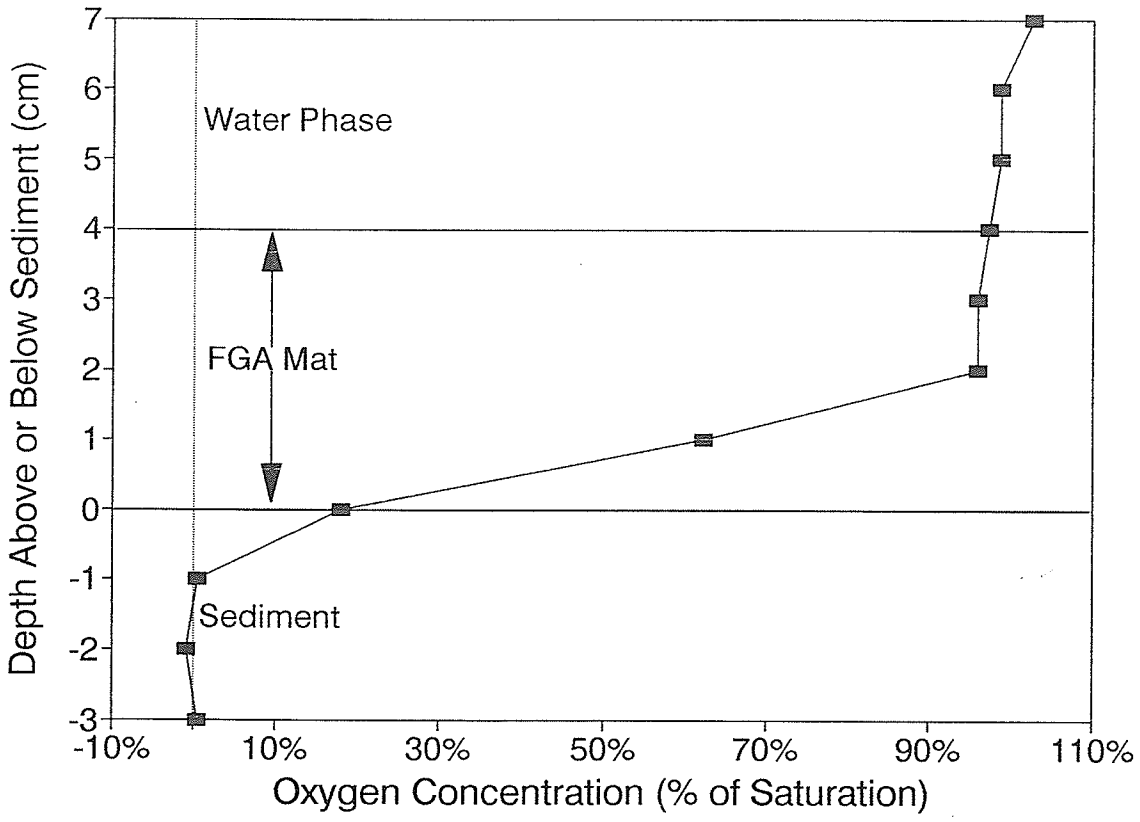

Fig. 5.6. An oxygen profile measured in a mat of FGA in Lake 302S on 29 September 1990. The FGA was beginning to decay. Relative oxygen concentrations are shown for water overlying the FGA, the algae themselves, and the underlying sediment.

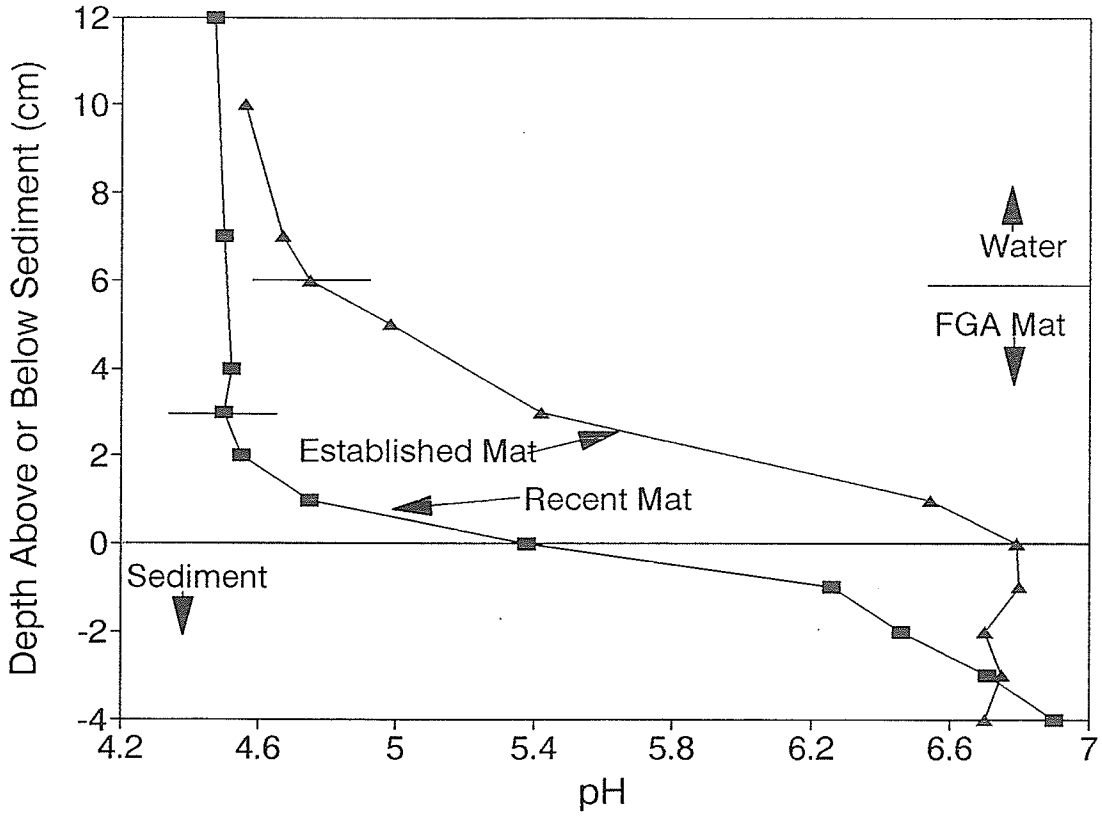

Fig. 5.7. Profiles of pH in Lake 302S water, FGA and underlying sediment on 24 October 1990. Horizontal lines denote the locations of the algal-water interfaces in the profiles.

pH was less than 1 unit in this recent FGA mat. In both cases, the increase occurred gradually with depth in the FGA.

Chemical Properties - Mesocosm Studies

1989

The appearance of the FGA varied markedly among the mesocosms, providing information on the growth status of the enclosed algae. FGA were yellow-green and remained dispersed in the low treatment mesocosms on 10 October. In contrast, FGA were clumped and brown to black in the high treatment mesocosms. The FGA in the medium treatment mesocosms were intermediate in these characteristics.

Changes in major nutrient chemistry were sensitive to the amount of algal material and/or numbers of herbivores (Table 5.2). The pattern of changes in carbon, nitrogen and phosphorus further supported the interpretation that FGA in the low mesocosm were growing (sequestering C, N and P). In contrast, FGA in the high treatment mesocosm were decomposing (releasing N and P). Note the large increase in total nitrogen in this mesocosm, caused almost entirely by an increase in ammonium.

1990

FGA concentrations in the low and high treatment mesocosms resembled concentrations in the lake (4 and 40 gdw/m^2, respectively). The high density FGA were likely in decline given the density-dependent negative

Table 5.2. Nutrient chemistry in the water phase of the 1989 mesocosm experiments. Changes in concentration are reported as a % of the initial values.

Mesocosm	Total C (μM)	Total N (μM)	Total P (μM)	Total C (%)	Total N (%)	Total P (%)
Low	-39	-2	-0.65	-16%	-6%	-20%
Medium	-11	3	0.00	-5%	11%	0%
High	-1	30	0.03	0%	35%	11%

feedback seen for FGA growth at that time of year (Howell et al. 1990, Chapter 4). Furthermore, the 1990 experiment was conducted in October as the water temperatures declined from 11 to 6^{o}C, when the FGA collapsed and coalesced into small clumps.

Water depth declined from 0.78 $\pm$ 0.01 m (SD, n = 6) to 0.71 $\pm$ 0.01 m during the experiment, so water chemistry in the algal mesocosms was compared with the mean of that in the water-only mesocosms to factor out the effect of evaporation (Table 5.3). The major increase in ammonium seen in 1989 (~ 7 $\mu gN \cdot L^{-1} \cdot d^{-1}$) was repeated in the high FGA enclosure in 1990 (Table 5.3a). The average daily increase was ~ 6 $\mu gN \cdot L^{-1} \cdot d^{-1}$ between FGA collection and initial mesocosm sampling, followed by a slower rate of ~ 3 $\mu gN \cdot L^{-1} \cdot d^{-1}$. The rates may have been slower than in 1989 either because a lower amount of FGA was added or because water temperatures were cooler. Both pH and alkalinity increased in the high FGA treatment compared to the water-only treatment (Table 5.3b), as would be expected from the observed increase in ammonium, a base cation. Sulphate also increased, possibly reflecting oxidation of organic sulphur in the FGA. Oxidation of reduced sulphur would be accompanied by release of hydrogen ion, decreasing pH, and would counteract the ammonia-induced pH increase. Total dissolved iron declined in the high FGA mesocosm, in contrast to the other cations which increased or were unchanged.

Table 5.3a. Nutrient chemistry of the 1990 mesocosms. Reported values are the mean difference in concentration relative to the mean concentration of the water-only mesocosms.

Chemical	Units	Water Only		Low FGA		High FGA	
		Mean	SD	Mean	SD	Mean	SD
Total C	µM	0	15	5	15	125	21
Total N	µM	0.0	0.7	-1.7	0.5	9.1	1.5
Total P	µM	0.00	0.07	-0.04	0.01	0.16	0.01
DIC	µM	0	7	-5	0	-5	0
DOC	µM	0	7	10	14	110	21
Susp C	µM	0	1	0	1	20	0
Nitrate	µgN/L	0	0	-1	0	-7	0
Ammonia	µgN/L	0	7	-20	7	98	18
Susp N	µgN/L	0	3	-3	0	36	2
TdP	µgP/L	0.0	2.1	-1.3	0.4	0.5	0.0
Susp P	µgP/L	0.0	0.1	-0.2	0.0	4.7	0.4

Table 5.3b. Ionic chemistry of the 1990 mesocosms. Reported values are the mean difference in concentration relative to the mean concentration of the water-only mesocosms. Total dissolved iron (TdFe) is assumed to have a valence of +3.

Chemical	Units	Water Only		Low FGA		High FGA	
		Mean	SD	Mean	SD	Mean	SD
H^+	µeq/L	0.0	0.6	0.0	0.2	8.3	1.0
Alkalinity	µeq/L	0	1	0	1	10	1
Sulfate	µeq/L	0.0	1.0	0.0	0.2	8.3	1.0
Chloride	µeq/L	0.0	0.0	0.4	0.0	6.1	0.0
Sodium	µeq/L	0.0	0.0	0.1	0.0	0.2	0.0
Calcium	µeq/L	0.0	0.0	0.0	0.0	0.0	0.0
Magnesium	µeq/L	0.0	0.9	0.6	0.0	6.6	0.3
TdFe	µeq/L	0.0	0.0	-1.3	0.0	-3.5	1.5

Physical Properties

Attenuation of irradiance by FGA

The transmittance of natural light through lake water was reduced from 91.4% to 72.9% ± 2.7% (SE, n = 4) by the experimental additions of FGA (2.63 gdw/m^2). Standard deviations of measurements without FGA averaged < 0.5%. Attenuation of light by FGA was calculated to exceed 90% when FGA was 40 gdw/m^2.

In situ measurements corroborated the substantial rate of attenuation of light by FGA. Seventy-two % to 81% of the light was intercepted by growths of FGA ranging in thickness from 5 to 25 cm (Table 5.4). The surprisingly high attenuation even at low thicknesses may have been caused by high algal densities.

Attenuation of water movement

The rate of weight loss in the chips, i.e. water movement, declined with water depth both within and outside of a 15-cm thick mat, on 2 September 1988. However, the rate of weight loss within the mat was ~ 10 mg/h less than that occurring at corresponding depths outside the mat.

Rates of weight loss in chips placed beneath mats of FGA on 29 August 1990 (Table 5.5) were 43% (± 11%, SD, n = 5) of rates at corresponding depths outside the mats. Rates of loss also appeared to vary inversely with FGA thickness.

Temperature changes

Table 5.4. *In situ* evaluation of the attenuation of irradiance by FGA in Lake 302S on 29 August, 1990.

Water Depth (m)	~ FGA Thickness (cm)	Irradiance Outside ($\mu E \cdot m^{-2} \cdot s^{-1}$)	Irradiance Inside ($\mu E \cdot m^{-2} \cdot s^{-1}$)	Attenuation (%)
1.3	5	915	260	72%
1.3	10	873	210	76%
1.3	15	957	209	78%
1.3	25	942	182	81%

Table 5.5. Attenuation of water movement by FGA as determined by measuring rates of weight loss of calcium sulphate chips.

FGA Thickness (cm)	Water Depth (m)	Weight Loss (mg/h)	Attenuation (%)
0	1.60	12.33	
0	1.15	11.05	
0	1.15	12.90	
0	1.50	9.57	
0	1.50	11.81	
10	1.60	7.67	38%
15	1.15	7.83	29%
15	1.15	7.83	39%
20	1.50	4.51	53%
20	1.50	5.16	56%

Measurements of water temperature made within clouds of FGA in 0.5 to 1 m of water on the overcast morning of 10 August 1990, revealed that the interior temperatures were 0.4 ^{o}C ($\pm$ 0.1 ^{o}C, SD, n = 7) higher than the ambient temperature of 22.3 ^{o}C. The temperature increase was independent of the size of the FGA (volumes ranged from about 1 to 100 L). The increase in temperature within growths of FGA during the cloudy afternoon of 15 August 1990 was 0.2 ^{o}C ($\pm$ 0.1 ^{o}C, SD, n = 14). Neither water depth (0.6 to 2.5 m) nor thickness of FGA (10 to 40 cm) influenced the degree of increase. Similar results were obtained on the sunny afternoon of 29 August 1990.

Discussion

Blooms of FGA transformed many biological, chemical and physical characteristics of the littoral zone. There were both negative and positive aspects (depending on the context) to these changes.

Impact of FGA Blooms on Energy Flow

FGA affected littoral productivity in several ways. First, FGA helped alleviate the oligotrophication (i.e. diminished productivity of algal communities) that occurs in the littoral zone of acidified lakes (Turner et al. 1987, 1991, Chapter 4), because the magnitude of FGA productivity was sometimes large enough to compensate for reduced epilithic productivity (Fig. 5.2). Peak areal productivity of FGA (Fig. 5.2) was even similar to the maximum rate (7.5

mmolC·m^{-2}·h^{-1}) measured in FGA (an *Oedogonium* mat) in productive Lake Wingra (McCracken et al. 1974), and FGA biomass was similar in magnitude (Table 5.1, 1988) to the maximum measured in Lake Wingra (90 gdw/m^2).

Second, the seasonal pattern of FGA photosynthetic rates resembled that of epilithon in circumneutral Lake 239, and counterbalanced that of acidified epilithon in Lake 302S (Fig. 5.1). Because appreciable FGA photosynthesis usually coincided with that of Lake 239 epilithon during midsummer (but when the acidified epilithon was near its minimum), the FGA reestablished some seasonal normality of productivity (Fig. 5.1) and biomass (Fig. 5.3) occurring within the acidified littoral zone.

Third, as a base for the littoral food web, the annual biomass of FGA was highly variable (Table 5.1) in contrast to epilithon in neutral lakes (Chapter 2). Maximum annual FGA biomass ranged from ~ 2 to 75 gdw/m^2 (Table 5.1), although pH remained at 4.5 over the four years of the study (Chapter 4). The lowest annual mass of FGA (1989) was similar to the small amounts of *Zygogonium* that developed in the oligotrophic, anthropogenically acidified Plastic Lake, Ontario (summer pH of 5.5 to 5.8) (Howell et al. 1990), whereas the highest (in 1988) resembled that in Lake Wingra (McCracken et al. 1974). The seasonal variability of energy flow was correspondingly large (Figs. 5.1, 5.2) unlike that observed for circumneutral epilithon (Figs. 5.1, 5.2; Chapter 2). Thus, the acidified littoral zone shifted from stability provided by reliable production of epilithon (Chapter 2), to instability caused by irregular production

of FGA. Such variability would favour herbivores with flexible life histories and adaptable feeding strategies.

Interannual variability of FGA biomass appeared to depend upon climatic conditions. Maximum development occurred during 1988 when epilimnetic temperatures reached 22 ^{o}C by the end of May. In contrast, end of May temperatures were 15, 17, and 19 ^{o}C for 1989 to 1991, respectively. Given that maximum masses of FGA occurred late in the year, the late ice-out in 1989 (11 days later than in any of the other years) also may have contributed to reduced productivity. FGA able to start growing early in the season (as will occur with global warming) will be exposed to a beneficial combination of favourable water temperatures and high spring irradiances (Chapter 4).

Influence of FGA on Chemical Properties

Effect of FGA on nutrient cycles

The effect of FGA upon CO_2 dynamics was seasonal. Carbon dioxide limits benthic algal photosynthesis in low DIC lakes (Chapter 4), especially in acidified systems (Turner et al. 1987, 1991; Fairchild and Sherman 1992), so consumption of CO_2 by FGA (Fig. 5.4) may slow growth in other benthic algae. In contrast, CO_2 released during FGA decomposition (Fig. 5.4), may contribute to increased epilimnetic concentrations and possibly enhance photosynthesis in other benthic algae.

Decomposing FGA also release dissolved organic carbon (DOC) during

their decomposition (Tables 5.2 and 5.3a). Given that levels of DOC can become especially low in acidified lakes (Schindler et al. 1992), production by FGA could be relatively large, feeding the microbial loop. FGA may also serve as a source of readily usable organic material for contaminant binding, metal chelation, and microbially mediated processes such as sulfate reduction.

FGA affected the nitrogen cycle principally through the flux of ammonia (Table 5.3a). The effect was bidirectional (Tables 5.2 and 5.3a) depending on the growth status of the community, with uptake of ammonium during summer growth, and efflux during decomposition in autumn and winter. This influence on nitrogen dynamics affects internal generation of alkalinity and acidity (see below).

Phosphorus sequestration was related to FGA growth (Fig. 5.5), and consequently to both time of year (Chapter 4) and pH (Chapter 3). There have been occasions in Lake 302S when FGA were the largest phosphorus-containing compartment in the epilimnion (excluding the sediments) (Fig. 5.5). Sequestering of phosphorus is especially important, because phosphorus has no alternative reservoir in the atmosphere as exists for carbon.

Additional research is needed to determine whether phosphorus in the FGA was liberated by the physical-chemical conditions created by FGA overlying littoral sediments, or was removed from other compartments. As FGA were increasing during 1991, epilithic phosphorus declined (paralleling the decline in particulate carbon seen in Fig. 5.3), as did planktonic phosphorus (M.

P. Stainton unpubl. data). In contrast, 1988 planktonic phosphorus concentrations, when FGA were extremely abundant (Table 5.1), were similar to those in other years.

The FGA can also exert other effects upon nutrient cycling. FGA can change redox conditions at the sediment-water interface because of changes in oxygen concentration during decomposition (Fig. 5.6) and photosynthesis, and affecting sediment-water exchanges of chemicals (see below). These processes produce markedly different results (e.g. the sedimentary efflux of phosphorus by epipelic algae; see Carlton and Wetzel 1988).

FGA blooms also produced oil-like films on the Lake 302S water surface. Similar results were obtained when FGA decomposed in the mesocosm experiments and in small containers of lake water held in the laboratory. These films may have been caused by lipid production by the FGA, and may have altered temporarily the air-water exchange of CO_2, thereby further affecting the carbon cycle.

Effects on internal alkalinity generation and acidification

FGA affected lake alkalinity in several ways. FGA can be expected to acidify the lake because of ammonium uptake during their growth phase, i.e. from spring to early fall. Conversely, FGA produce alkalinity during decomposition in fall and winter, enhancing the fall entrainment of hypolimnion-generated alkalinity into the epilimnion of acid lakes. Because the annual growths of FGA decompose each winter, their nitrogen-related long-term net

effect on alkalinity is probably negligible.

FGA can disrupt the sulphur cycle (Amaral 1991), and thereby further alter alkalinity generation (Kelly et al. 1994). FGA can shift the depth in sediments of oxidation-reduction reactions (Fig. 5.6). The site of sulphur reduction under the mats becomes shallower in summer, making reduced sulphur compounds more vulnerable to reoxidation when the FGA deteriorate in fall and winter, reducing the long-term in-lake generation of alkalinity.

Effects of FGA Growth on Physical Properties

Light attenuation by FGA was sufficient to impair the growth of other phytobenthos (Table 5.4), especially those that are normally light limited. The degree of attenuation was dependent upon the extent of FGA coverage, and so the impact would be seasonal. Given that photosynthesis in acidified epilithon displayed maxima in spring and fall (Fig. 5.1), the greatest effect on epilithon would occur in the fall, for surface irradiances then are lower (and FGA blooms are larger) than in spring. There is also the potential for decline of macrophytes because of attenuation of light by FGA. For example, the loss of isoetids reported by Roelofs (1983) may have been caused partly by attenuation of light by FGA.

The increase in bottom temperatures by FGA was small in scale, i.e. about one-half degree or less. Increased temperatures also would likely be transient, varying daily with light availability.

The FGA also diminished the amount of water movement reaching the littoral bottom (Table 5.5). This effect would diminish chemical transport at the sediment surface. The presence of FGA overlying the bottom could also reduce the degree of erosion, slowing translocation of materials from the littoral to the profundal zone.

Other Biological Consequences of FGA Growth

Biological consequences of the proliferation of FGA for some zoobenthos included (1) provision of a temporary refuge from the low pH of the overlying lake water (Fig. 5.7), and (2) risks associated with oxygen depletion that could occur in decaying mats (Fig. 5.6). However, these consequences would vary spatially and temporally with different states of decomposition, and with the availability of light, which would affect rates of photosynthesis and oxygen production.

The FGA also may provide a new habitat for some organisms. For example, some littoral Cladocera inhabit the FGA in enormous numbers (Hann and Turner 1994). Similarly, a littoral cladoceran and a trichopteran were associated with FGA growths in experimentally acidified Little Rock Lake (Webster et al. 1992). The FGA may provide a source of food for other taxa (Fulton 1988), and material for net spinning Trichoptera and substratum for chironomids. For some taxa, the FGA may provide a refuge (Webster et al. 1992). A detrimental effect is that FGA may make spawning sites unsuitable

(Mills and Schindler 1986).

Conclusion

Understanding the ecological effects of blooms of FGA was important to understanding the metabolism of acidified Lake 302S. FGA blooms replaced the acidification-induced loss of primary production by epilithon, but only partially. This positive benefit may have been offset by the potential for several negative consequences as high biomasses of FGA transformed the chemical, physical and biological properties of the littoral zone. Further research is needed to discover whether some of the apparent negative effects were in fact beneficial (e.g. sequestering of phosphorus by FGA may have been due partly to liberation of sedimentary phosphorus caused by changed conditions created by FGA blooms) because global warming may enhance FGA growth (Chapter 4).

Chapter 6. General Discussion

"...It is the relationship between the total rate of production and the rate of decomposition ... that is of overall importance in the biosphere as a whole. ... It is fortunate for man and his great oxygen-consuming machines that production has tended to exceed decomposition. But man now 'taketh more than he giveth back' to an extent that threatens vital balances" (Odum 1971, p.28).

Although it has been argued that "ecosystem-level production and respiration were the most resistant properties to acid stress" (Schindler 1990), this study argues otherwise; it demonstrates that the balance between photosynthesis and respiration was disturbed in littoral communities of acidified lakes (Chapter 2). The disruption occurred at much higher pH than previously anticipated partly because of the earlier understanding that "no other nutrient cycles [than nitrogen] appeared to be disrupted" by acidification (Schindler 1990). In fact, the disruption of the carbon cycle caused by acidification, which had profound consequences for normally dominant littoral algal communities (Chapters 2 and 3), was likely overlooked because of the belief that phosphorus was the growth limiting substance for all algae in these acidifying lakes.

Summary of Chapters

Chapter 2

The impact of acidification in the littoral zone was clearly different than in the pelagic zone. Acidification radically affected the energy flow within, and the composition of, epilithon, especially as pH declined below 5. As a result, the demise of normally dominant epilithon was observed. The ratio of respiration to photosynthesis was a sensitive and early indicator of stress upon this community. Epilithic respiration increased for as yet unconfirmed reasons, whereas photosynthesis declined in part due to carbon limitation as acidification decreased the amount of inorganic carbon available. Algal composition of periphyton changed markedly, and eventually, periphytic biomass declined to very low levels. In contrast, the altogether different community of FGA prospered. FGA first appeared as periphyton in restricted modes of growth at pH $\geq$6, but as the pH declined $\leq$5.5, they occupied a new niche as metaphyton, i.e. as benthic algae that were no longer constrained by the surfaces to which they were first attached.

Chapter 3

Carbon, rather unexpectedly, was the principal growth limiting nutrient for periphyton in low-DIC oligotrophic lakes. This limitation was the cause of major H^+-related changes in the function of littoral algae as opposed to the stability seen in phytoplankton photosynthesis. The diffusive boundary layer of algal matrices overlying surfaces appeared to be a bottleneck in the mass transport of inorganic carbon to benthic algal photosynthesis. Underestimation of the importance of disruption of the carbon cycle by acidification caused incorrect

interpretations of littoral phenonmena and incorrect predictions of effects of acidification (see below). The significance of inorganic carbon also explained why littoral communities have been especially sensitive to the impact of acidification. There are also ramifications for other perturbations (e.g. see Chapter 3).

Chapter 4

The growth characteristics of the FGA that proliferated in acidified lakes were described by temporal changes in their biomass distribution, their photosynthetic parameters and the factors controlling them. The major feature of FGA growth was that they were a productive algal community unlike acidified epilithon, but akin to circumneutral epilithon. Their rate of growth was dependent upon irradiance levels, DIC concentrations, algal crowding (negative, density-dependent feedback), and water temperature. The particulars of these relationships are discussed as a prelude to modelling their growth.

Chapter 5

The growth of FGA as metaphyton in the acidified littoral zone reestablished some of the energy flow lost as a result of the stress of acidification. The H^+-related changes that occurred in benthic algal communities, however, changed the acidified littoral zone from its original state. The development of metaphytic FGA blooms had consequences for the biological, chemical and physical conditions of the littoral zone. Further, because the coverage and thickness of metaphytic FGA varied both seasonally

and among years, conditions in the littoral zone were highly variable.

Challenges to Dogma

This thesis challenges several ideas that have become entrenched in the literature. For example, Baker and Christensen (1991, p. 105) concluded that "key ecosystem level attributes such as nutrient levels, decomposition rates, and primary production rates seem relatively insensitive to acidic conditions". Also, "overall standing crops at various trophic levels do not, however, seem to be reduced [by acidification]" (p. 105). Such ideas are pervasive in the literature, but require revision at least in regards to the littoral zone.

The opportunity to investigate these ideas directly arose from the development of experimental techniques for use in the littoral zone of ELA lakes. Techniques developed for the investigation of epilithic and epiphytic metabolism were based upon the direct measurement of DIC (Turner et al. 1983, 1987, 1991). This approach was then extended to the metaphyton (Howell et al. 1990, Chapter 4). With the opportunity to measure DIC directly rather than relying on radioisotope techniques, it was possible to look at carbon flux both as photosynthesis and respiration, without the complications and restrictions that can arise from the use of radioisotopes. The confinement of littoral algal communities to surfaces also provided the opportunity to experimentally adjust the ratio of algae : water to accommodate the sensitivity of the DIC analytical techniques available. The resulting sensitivity enabled the

asking of questions that were impossible to examine in planktonic communities.

Another problem in the literature was the confusion between periphytic and metaphytic responses to acidification. For example, Baker and Christensen (1991) confused the distinct and separate responses of these two algal communities in their review; epilithon declined while the metaphyton increased with acidification (Chapter 2). Interpretation of the impact of acidification was obscured as a result.

An important nutrient cycle was disturbed early by acidification

Early interference with a major nutrient cycle (carbon) by acidification has been recognized infrequently. It was known that the nitrogen cycle is interfered with by acidification (Rudd et al. 1988, 1990); at low pH (beginning at 5.4 to 5.7) the rate of nitrification is diminished resulting in lower concentrations of nitrate but increasing levels of ammonium. Caraco et al. (1989) have hypothesized that acidification increases epilimnetic phosphorus concentrations caused by changes in the sulfur cycle. This was not seen in Lake 302S (M. Turner unpubl. data). However, the carbon cycle was clearly disrupted at pH >6 (Fig. 3.3) as bicarbonate was removed from the inorganic carbon system, causing DIC concentrations to decline dramatically.

The neglect of changes to the carbon cycle has probably arisen because of the general belief that phosphorus is the principal nutrient limiting algal growth. However, inorganic carbon can limit rates of photosynthesis in benthic algal communities (Chapter 3) akin to the situation for macrophytes (Wetzel et

al. 1984, 1985). This phenomenon arises largely because of the generally large resistance to inorganic carbon uptake that results from the thick diffusive boundary layers associated with benthic algal associations. The importance of carbon as a growth-limiting substance may also apply to planktonic algae in the ocean (Raven 1993).

Respiration is affected by acidification

Prior to this study, there was no suitable direct measurement of *in situ* respiration in acidified, algal-based associations; this remains true for phytoplankton associations. Therefore, there was a misconception "that the accumulation of benthic algal biomass observed in the littoral of the lake is not a result of their high net production, but rather is an effect of ... reduced rates of decomposition" (Lazarek 1983, p. 73). Clearly this hypothesis needs revision because epilithic respiration (including decomposition) increased strongly with acidification (Chapter 2, e.g. Fig. 2.4). Respiration of epiphyton was also increased by acidification (Turner et al. 1991). However, H^+-induced growths of metaphytic FGA displayed ratios of respiration:photosynthesis that were similar to those of circumneutral periphyton (Chapter 2) because FGA respiration rates were much lower than those of acidified periphyton (Chapters 2 and 4, Fig. 2.5). This observation partly explains the success of FGA in acid lakes. As a result, the overall balance of respiration in the littoral zone probably varies substantially because of the seasonality of FGA growths (Chapter 4) and the large interannual variability in their development (Chapter 5).

Several reasons for increased periphytic respiration were suggested (Turner et al. 1991) including: (1) increased costs of acquisition of carbon dioxide; (2) stress associated with elevated H^+ concentrations; (3) increasing heterotrophic utilization of dissolved organics; or (4) an increase in the ratio of aerobic to anaerobic respiration. The possibility that the elevated inorganic nitrogen concentrations associated with acidification stimulate respiration (Chapter 3) can be added to this list.

The generally accepted conclusion that acidification reduces rates of microbial decomposition (Almer et al. 1978, Traaen 1980, Kelly et al. 1984, Schindler 1990) also may be opten to re-examination. This conclusion was made largely indirectly. Litter bag experiments appeared to support the conclusion (Traaen 1980), but their interpretation could have been confounded by the H^+-related decline of organisms capable of physically breaking down macroscopic detrital matter. Similar experiments in aquaria (McKinley and Vestal 1982) are equivocal, especially considering the complications arising from the uncontrolled large-scale changes in pH that occurred even after two days. The conclusion was substantiated indirectly by measurement of declines in rates of winter respiration (Schindler 1990); however, winter respiration represents only a small amount of annual lake decomposition (Schindler 1990), and it is probably sensitive to the rate of supply of organic materials. Direct tests of the conclusion using sediment-containing laboratory reactors (Kelly et al. 1984) may have been complicated by the lack of adaptation of experimental

microbial populations to severe changes in pH. However, the Kelly et al. (1984) experiments confirmed the importance of the supply of organic materials to rates of decomposition.

The inconsistency between direct measurements of increased periphytic respiration and both the winter and relatively short-term laboratory observations is intriguing. Supply of organics is an important controller of microbial activity (McKinley and Vestal 1982, Kelly et al. 1984, and Palumbo et al. 1987). Although H^+-induced losses of macroinvertebrates could delay microbial utilization of large pieces of terrestial litter, this would be less likely for littoral, algal-based associations. A further difference arises from the larger H^+-neutralization capacity in sediments relative to overlying water (Kelly et al. 1984) and relatively thin periphytic matrices (Palumbo et al. 1987). As a result, periphyton would be the more sensitive indicator of acidification stress as seen in stream epilithon (Palumbo et al. 1987).

The discrepancy in effects of acidification between sediment communities and periphyton may also partly be caused by differences in the time scales of measurements. For example, periphytic measurements may represent metabolism that is of shorter time scale than the sediment-based observations. As well, slower rates of winter decomposition could be observed if the supply of available carbon from summer epilimnetic activities was already depleted by rapid decomposition in summer.

Production is affected by acidification

Another misunderstanding that had prevailed until recently was that benthic algal productivity was increased or unaffected by acidification. This appears to be the situation in phytoplankton in spite of substantial changes in taxonomic composition (reviewed in Chapter 2). However, periphytic productivity was clearly diminished by acidification (Fig. 2.2), because of both carbon limitation (Turner et al. 1987, 1991; Chapter 3) and increased rates of respiration (Turner et al. 1991, Chapter 2). The important role of carbon for periphyton in acid lakes has been confirmed independently by Fairchild and Sherman (1990, 1992); in contrast it has been dismissed as a limiting factor in epiphytic productivity in acidified Lake Gårdsjön, Sweden (Lazarek 1982b). There still remains the issue of whether the rates of respiration are offset by higher rates of gross photosynthesis (unmeasured) or by the use of stored carbon.

Ecosystem metabolism or function is sensitive to stress

Another prevailing idea is that variables that reflect ecosystem function are poor indicators of ecosystem stress (Schindler 1987). The ability to measure both photosynthesis and respiration in the same algal community provided a unique opportunity to test this hypothesis directly by evaluating the ratio of respiration to photosynthesis, perhaps the most important of ecosystem functions (Odum 1971). A quite different picture emerged (Fig. 2.5) than would have been predicted based upon the prevailing idea. Although the situation for acidified planktonic communities remains unresolved because of insufficiency of

direct evidence (i.e. measurement of respiration rates), the prevailing idea must exclude benthic algal communities, which exist in more constrained circumstances than do phytoplankton, and appear sensitive to disruptions in the availability of inorganic carbon. Importantly, periphyton can be used as early warning detectors of some types of ecosystem stress such as acidification.

Future Research

The research described in the previous four chapters answered several important questions. However, a number of major issues remain unresolved, and inevitably, the research raised new queries. Some of these flowed logically from the work, whereas others arose as a result of perceived inconsistencies.

The effect of acidification upon interactions between littoral animals and algae remains little understood and continues to be a promising earea of research having consequences for other perturbations. For example, based upon the information in Chapter 4, grazing pressure could potentially control FGA development if it occurred early in the year before the FGA became well established. Unpublished mesocosm work (Howell, Hann, and Turner unpubl. data) supports this proposition, as do the herbivorous minnow experiments of Power et al. (1985, 1988) and the field surveys of France et al. (1991) and France and Welbourn (1992). As well, to what extent has acidification released them from grazing pressure (Hendrey 1976, Turner et al. 1987) and enhanced their competitive ability? Although FGA are present in unacidified systems, they

bloom in relatively few of these situations (shallow prairie ponds are an exception).

The differentiation between increased respiration and carbon limitation as contributors to reduced photosynthesis remains an intriguing question. However, if respiration is increased due to the extra costs of acquiring CO_2 in a low DIC environment, these factors are equivalent.

The apparently different conclusions of increased respiration in acidified periphyton vs. decreased decomposition (see above) should also be studied. It is intriguing that there are instances of acidified lakes (pH ~ 4.5) with high concentrations of CO_2. For example, Lazarek (1982a, 1982b) reported average DIC concentrations of 100 µM in Lake Gårdsjön, Sweden; Heselgrave (1992) reported similar concentrations in First Beaver Lake in Nova Scotia. Analytical complications may have been the source of these particular observations (see comments by Turner et al. 1987). However, CO_2 concentrations were also elevated in some Dutch surface waters (Leuven et al. 1992) and in the interstitial waters of acidified sediments (Roelofs 1983). Although Roelofs suggested that this increase may have been due to acidification of sedimentary carbonates (presumably an effect of limited duration in a chronically acidified lake), increased microbial activity cannot be discounted. The qualitative observations of declining sediment depth in Lake 302S (Chapter 2) further support the possibility of accelerated decomposition caused by acidification (see above). Is it possible that previous conclusions of suppressed decomposition

have reflected indirectly a decline in supply of organics, rather than of a direct suppression by H^+? Furthermore, the effects of acidification on communities could differ whether organic inputs were dominated by allochthonous or autochthonous sources.

The role of algal communities in altering littoral biogeochemistry was barely considered in Chapter 5, and is a rich area for research. For example, it remains to be determined whether sequestration of phosphorus by FGA reflects successful competition for existing epilimnetic phosphorus, and/or enhanced release from epilimnetic sediments. In addition, to what extent have the blooms of FGA affected macrophytes? For example, a decrease in CO_2 has been implicated in the decline of isoetid macrophytes in acid lakes (Roelofs 1983, Roelofs et al. 1984), but it may be that severe attenuation of light by FGA blooms accelerates their demise (Chapter 5).

Why does *Sphagnum* invade acidified systems of Europe, but only occur infrequently in acidified North American lakes (Stokes 1986)? Is this distinction a reflection of the longer period of acidification in European systems, and of the time lag required for such plant invasions? Several of the many consequences of FGA blooms (Chapter 5) could also occur as a result of *Sphagnum* invasions (Nyman 1990), although the severity of the latter may be greater due to their permanency. Could the differences in opinion of whether oligotrophication is caused by acidification (cf. Grahn et al. 1974 and Schindler 1980) result from the presence or absence of *Sphagnum* invasions?

The possibility of unexpected consequences of high nitrogen concentrations upon community metabolism (Chapter 3) warrants further study. Are high rates of respiration (including decomposition) the result or the cause of high levels of nitrogen? The ramifications of the former possibility are substantial.

The potential for interactions between acidification and various aspects of global change is another area of important research. A number of aspects of global change could interact with acidification: (1) expectations of increased water temperatures, (2) extended growing seasons, (3) increased availability of carbon dioxide, and (4) increased availability of light due to the possible destruction of organics by increased UV radiation. All of these aspects will affect littoral algal communities (Chapters 2 to 5), especially FGA, although not necessarily in well known ways given the potential for higher-order interactions.

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Appendix I. List of Abbreviations and Symbols, Their Meanings and Units.

Symbol	Meaning	Units
α	initial slope of P=f(I)	$\mu molC \cdot mgdw^{-1} \cdot (3600 \mu E \cdot m^{-2})\text{-}1$
B	areal concentration of biomass	$g \cdot m^{-2}$
DIC	dissolved inorganic carbon	µM
FGA	filamentous green algae	
I	irradiance or light intensity	$\mu E \cdot m^{-2} \cdot s^{-1}$
P_b	biomass-normalized photosynthesis	$\mu molC \cdot mgdw^{-1} \cdot h^{-1}$
P_g	respiration-normalized photosynthesis	$\mu molC \cdot (125\ mL)^{-1} \cdot h^{-1}$
P_{gb}	respiration- and biomass-normalized photosynthesis	$\mu molC \cdot mgdw^{-1} \cdot h^{-1}$
P_{gbm}	maximum rate of P_{gb}	$\mu molC \cdot mgdw^{-1} \cdot h^{-1}$
R_d	biomass-normalized respiration	$\mu molC \cdot mgdw^{-1} \cdot h^{-1}$