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The effects of water level fluctuations on algal communities of freshwater marshes

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THE EFFECTS OF WATER LEVEL FLUCTUATIONS ON ALGAL COMMUNITIES OF FRESHWATER MARSHES

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The effects of water level fluctuations on algal communities of freshwater marshes

by

Syed Mohammad Hosseini

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TABLE OF CONTENTS

GENERAL INTRODUCTION

Freshwater marshes with dense growths of emergent and submergent macrophytes have extensive epiphytic communities. Several studies have indicated that epiphytes growing on macrophytes are a major source of primary productivity in shallow water habitats (Allen 1971; Cattaneo and Kalff 1980; Kairesalo 1980), and, therefore, epiphyton productivity is potentially a major component of overall wetland primary productivity. Cattaneo and Kalff (1980) showed that the epiphytic contribution to the total production of Lake Memphremagog macrophyte beds changes in a predictable fashion with the season, the morphology of the macrophytes, the depth of the bed, and the trophy of the water. They also demonstrated that in the mesotrophic portion of the lake, epiphytes fixed more carbon than did the macrophytes only at the beginning and end of the growing season, whereas under more eutrophic conditions they did so even during the summer.

Few studies have addressed the contribution of phytoplankton to the overall primary production of shallow water systems dominated by macrophytes (Brandle et al. 1970; Brown 1972; Goulder 1969; Hickman and Jenkerson 1978; Kairesalo 1980; Kalff and Knoechel 1978). In these systems, macrophyte production passes primarily through the detritus food web, whereas algal production forms the energetic base of the grazing food web (Cattaneo and Kalff 1980; Smirnov 1958; Sozska 1975).

Among the investigators who have studied the biomass and primary productivity of algal communities, particularly of epiphyton, in

littoral zones of shallow lakes and freshwater marshes are Allen (1971), Brown (1972), Cattaneo and Kalff (1980), Hickman (1971), Kairesalo (1980), and Wetzel (1964, 1983a,b). In prairie marshes, Hooper and Robinson (1976) and Hooper-Reid and Robinson (1978a) have investigated the primary production and standing crop of epiphytic algae in Crescent Pond, Delta Marsh, Manitoba. I have found no other studies of algal production in prairie wetlands.

Investigations of the effect of water-level fluctuations on plants of inland marshes have concentrated mainly on the vascular plants (Harris and Marshall 1963; Kadlec 1962; Meeks 1969; van der Valk 1981, 1985, 1986; van der Valk and Davis 1980; Walker 1965). Ollason (1977) has shown, however, that algal communities in fluctuating environments also undergo large-scale changes. Despite numerous studies concerning the productivity, biomass and ecology of algae in freshwater marshes, no study of the impact of water level fluctuation, which is a characteristic of prairie marshes, on the productivity and biomass of algae has been completed.

The specific objectives of this study are:

1. To investigate the effect of prolonged flooding on productivity of epiphyton and phytoplankton in freshwater marshes.
2. To investigate changes in the biomass of phytoplankton and epiphyton due to flooding in a freshwater marsh.
3. To investigate spatial and temporal heterogeneity of epiphyton and phytoplankton in wetlands.

4. To correlate physico-chemical parameters with estimates of phytoplankton and epiphyton productivity and biomass.
5. To estimate the total annual productivity of epiphyton and phytoplankton algae in a wetland under different environmental conditions.

The overall contribution of algal communities to marsh production during prolonged flooding will be emphasized. The algal productivity under such environmental conditions has not been investigated. The investigation of the above objectives would contribute valuable knowledge to the field of phycology in general and the ecology of freshwater marshes in particular.

Explanation of Dissertation Format

This dissertation is divided into three sections, each in a format for publication in a technical journal. References cited in the general introduction and literature review are at the end of the dissertation. References cited within a section are at the end of that section.

The first section of the dissertation deals with the response of epiphyton and phytoplankton algae to flooding. The experimental design is three treatments of unflooded marshes (natural), marshes flooded one year in 1982, and marshes flooded continuously for two years in 1981 and 1982 (Pederson 1983). The second section discusses the response of filamentous algae in the same treatments. The third section discusses the algal response to flooding in two treatments (marshes flooded two years continuously in 1982 and 1983 and

unflooded, natural marshes). Also in this section the temporal and spatial heterogeneity of epiphyton and phytoplankton of freshwater marshes are discussed. The appendix presents tables not discussed in the text.

LITERATURE REVIEW

Phytoplankton primary productivity in freshwater marshes, ponds and littoral zones of lakes has been investigated by Brown (1972), Dokulil (1973), Goulder (1969), Hickman and Jenkerson (1978), Hutchinson (1975), Round (1981), Sand-Jensen and Sondergaard (1981), Straskraba and Pieczynska (1970), and Wetzel (1983a). Many investigators have also studied the primary productivity of epiphytic algae in such habitats (Allen 1971; Brock 1970; Cattaneo and Kalff 1978, 1979, 1980; Goldsborough and Robinson 1983; Hickman 1971; Hooper and Robinson 1976; Hooper-Reid and Robinson 1978a,b; Howard-Williams and Allanson 1981; Hutchinson 1975; Jones 1984; Jones and Adams 1982; Kairesalo 1980; Komarkova and Marvan 1978; Kowalczewski 1975; Lazarek 1982; Mason and Bryant 1975; Moss 1976; Riber et al. 1984; Round 1981; Straskraba and Pieczynska 1970; Wetzel 1964, 1983a,b). However, few studies have addressed the relative contributions of epiphyton, phytoplankton, and macrophytes to productivity of freshwater marshes and littoral zones of lakes (Cattaneo and Kalff 1980; Goulder 1969; Kairesalo 1980; Round 1981; Wetzel 1964, 1983a,b). Recently, Crumpton (1986) has reviewed the productivity of epiphyton and phytoplankton in prairie glacial marshes.

The use of $^{14}C\text{-}CO_2$ uptake is a standard method in aquatic habitats (see Peterson 1980). In spite of many challenges and an ever increasing number of modifications of the original method, the $^{14}C\text{-}CO_2$ uptake remains the standard against which all other methods are

compared (Peterson 1980). Robinson (1983) has reviewed the modifications and applicability of this method in freshwater marshes.

Because it is often difficult to remove epiphyton from the surface of macrophytes, artificial substratas of various shapes and materials have been used in experimental investigations of productivity (Hosseini 1979; Robinson 1983; Sladeckova 1962). According to the literature, the most commonly used materials are wood, celluloid, paraffined-coated substratas, polyvinyl chloride, styrofoam, acrylic rods and plates, plexiglass and glass (Hosseini 1979; Robinson 1983). However, comparisons between epiphyton productivity and biomass on artificial and natural substratas have given conflicting results (see Allen 1971; Cattaneo 1978; Cattaneo and Kalff 1978, 1979; Flint et al. 1977; Goldsborough and Robinson 1983; Gough and Gough 1981; Hooper and Robinson 1976; Hosseini 1979; Wetzel 1983a,b). Acrylic rods have proven to be a suitable substrata and have come to be used increasingly by many investigators (Goldsborough and Robinson 1983; Robinson 1983). Extensive reviews of the use of artificial substratas in aquatic systems have been done by Hosseini (1979), Robinson (1983) and Sladeckova (1962). Robinson (1983) has reviewed specifically the applicability of artificial substrata in freshwater marshes.

Measurements of chlorophylls, carbon, nitrogen and ash-free dry weight long have been used as estimates of algal biomass (APHA 1980; Bowen 1979; Carignan and Kalff 1982; Cattaneo and Kalff 1978, 1979, 1980; Goldsborough and Robinson 1983; Gons 1982; Hickman 1971; Hickman

and Jenkerson 1978; Holm-Hansen and Riemann 1978; Marker 1972; Moss 1968; Nichols 1973; Pieczynska 1971; Robinson 1983; Round 1981; Stainton et al. 1977; Strickland and Parsons 1972; Vollenweider 1974; Wetzel 1983a,b). Recently, investigators have used high pressure liquid chromatography methods for better, more accurate estimates of chlorophylls (Abaychi and Riley 1979; Bidigare et al. 1985; Falkowski and Sucher 1981; Jacobsen 1978; Mantoura and Llewellyn 1983).

The interactions among epiphyton, phytoplankton and macrophytes in littoral zones of lakes and marshes (including shading effect, host specifity, nutrient exchange, algal blooms, etc.) have been extensively investigated (Allanson 1973; Allen 1971; Barica et al. 1980; Brandle et al. 1970; Brock 1970; Brown 1973a,b; Brown and Austin 1973; Carignan and Kalff 1982; Cattaneo 1978; Cattaneo and Kalff 1979; Dokulil 1973; Eminson and Moss 1980; Eminson and Phillips 1978; Fitzgerald 1969; Gons 1982; Goulder 1969; Hickman 1971; Hooper and Robinson 1976; Hooper-Reid and Robinson 1978a,b; Howard-Williams and Allanson 1981; Jansson 1980; Jenkerson and Hickman 1983; Jones et al. 1983; Kalff and Knoechel 1978; Komarkova and Marvan 1978; Kowalczeski 1975; Landers 1982; Lazarek 1982; Marvan et al. 1978; Moore 1980; Morin and Kimball 1983; Moss 1976; Moss 1981; Nicholls 1973; Nicholls 1976; Phillips et al. 1978; Prowse 1959; Riber et al. 1984; Roos 1981; Sand-Jensen and Sondergaard 1981; Shamess et al. 1985; Sozska 1975; Straskraba and Pieczynska 1970; Wetzel 1983a,b).

Seasonal patterns of productivity and biomass, site variations and spatial heterogeneity of algae in littoral zones of lakes and

freshwater marshes have been investigated extensively (Allen 1971; Barica 1975; Barica et al. 1980; Brown 1972; Brown 1973a,b; Brown and Austin 1973; Cattaneo and Kalff 1978; Coulombe and Robinson 1981; Emison and Moss 1980; Gons 1982; Hickman and Jenkerson 1978; Hillebrand 1983; Hooper and Robinson 1976; Hooper-Reid and Robinson 1978a,b; Hosseini 1979; Hutchison 1975; Jenkerson and Hickman 1983; Jones and Adams 1982; Kairesalo 1980; Kalff and Knoechel 1978; Marvan et al. 1978; Moss 1981; Pieczynska 1971; Pip and Robinson 1982a,b; Round 1971, 1972, 1981; Sand-Jensen and Sondergaard 1981; Shamess et al. 1985; Wetzel 1983a,b). Crumpton (1986) has reviewed the seasonal patterns of algal productivity in prairie glacial marshes.

Finally, researchers have investigated various aspects of grazing on productivity, community structure and population dynamics of periphyton and phytoplankton (Cattaneo 1983; Crumpton 1986; Cuker 1983; Higashi et al. 1981; Mason and Bryant 1975; Moss 1976; Round 1981; Smirnov 1958; Sozska 1975; Sumner and McIntyre 1982; Timms and Moss 1984; and Wetzel 1983a,b).

SECTION I. THE PRIMARY PRODUCTIVITY AND BIOMASS OF EPIPHYTON AND PHYTOPLANKTON IN FLOODED FRESHWATER MARSHES

The primary productivity and biomass of epiphyton and phytoplankton in flooded freshwater marshes

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Running head: The response of algae to flooding

ABSTRACT

Epiphyton and phytoplankton productivity, chlorophyll-a content, and carbon and nitrogen concentrations in experimental marshes flooded 1 m above normal level for one year and two years were compared to values for unflooded marshes. Primary productivity was estimated using the ^{14}C method. Epiphyton productivity was measured using artificial substratas in the marshes. Phytoplankton productivity was estimated using marsh water incubated in 60-ml glass bottles. All productivity measurements were made at 19°C±1 and 15 $\mu E/m^2/sec.$ of PAR in the laboratory.

Mean phytoplankton primary productivity, chlorophyll-a, total suspended carbon and total suspended nitrogen in unflooded marshes were significantly higher than in marshes flooded for one or two years. Mean epiphytic primary productivity per unit area of artificial substrata was significantly higher in marshes flooded for one year than in unflooded marshes. There was no significant difference between mean epiphyton primary productivity of marshes flooded for two years and unflooded marshes. There were no significant differences between unflooded and flooded marshes in the amounts of chlorophyll-a, particulate carbon or nitrogen per unit area of artificial substrata.

INTRODUCTION

Freshwater marshes with their often dense stands of emergent and submersed macrophytes have extensive surface areas that can be colonized by epiphytic algae. Epiphytes growing on macrophytes in the littoral zones of shallow freshwater lakes and ponds are known to be an important component of overall aquatic primary productivity (Allen 1971; Hooper and Robinson 1976; Wetzel 1964, 1983). Few studies have addressed the contribution of phytoplankton (including metaphyton) to the overall primary productivity of these shallow water systems dominated by macrophytes (Brandle et al. 1970; Brown 1972; Goulder 1969; Hickman and Jenkerson 1978; Wetzel 1983).

Ollason (1977) indicated that algal communities in fluctuating environments may undergo large-scale changes. However, there appear to be no investigations of the impact of water-level cycles, such as those that characterize many prairie wetlands, on the primary productivity of either their epiphyton or phytoplankton. Previous investigations of the impact of water level fluctuations on marshes have concentrated on the responses of the vascular plants (Harris and Marshall 1963; Kadlec 1962; Meek 1969; van der Valk 1981, 1985; van der Valk and Davis 1978,1980; Walker 1965).

The objective of this study was to investigate the impact of abnormally high water level on epiphyton and phytoplankton primary productivity and biomass in a freshwater wetland. In an experimental marsh complex where three flooding treatments were present in 1982 (unflooded marshes, marshes flooded for one year in 1982, and marshes

flooded for two years continuously in 1981 and 1982), the responses of phytoplankton and epiphyton to flooding duration were measured using ^{14}C uptake to estimate primary productivity and chlorophyll-*a*, particulate carbon and nitrogen to estimate algal biomass.

MATERIALS AND METHODS

Study site

This study was conducted during the summer of 1982 in the experimental marsh complex of the Marsh Ecology Research Program (MERP) at the Delta Waterfowl and Wetlands Research Station in south central Manitoba, Canada (50 11'N, 98 19'W). Ten experimental marshes (approximately 5 ha each) were constructed with dikes along the northern edge of Delta Marsh (Batt et al. 1983; Murkin et al. 1985; Murkin and Kadlec 1986). Two sections of natural marsh, of about equal size, at each end of experimental complex were selected as unflooded marshes. The initial vegetation within the experimental marshes was similar to that in the main Delta marsh (Murkin and Kadlec 1986; Pederson 1981).

The MERP complex is being used to study the impact of water level changes on a lacustrine wetland. Since 1962, the water level of lake Manitoba has been regulated using a dam. Thus the "normal" water level of the Delta marsh for over 20 year has been 247.5 m AMSL. Before the water levels were regulated, lake level fluctuated by more than 1.5 m. In 1981, water levels in 8 of the 10 MERP marshes were raised 1 m above normal to 248.5 m AMSL to simulate high water conditions that occured before lake level regulation began. Two additional marshes were flooded to 248.5 m in 1982. High water levles in both sets of marshes were maintained for two years (Batt et al. 1983; Murkin et al. 1985; Murkin and Kadlec 1986). Most of the emergent vegetation was killed in flooded marshes and, as a

consequence, there was a great deal of standing litter, particularly dead Phragmites and Typha shoots. In marshes flooded for two years in 1982, only that portion of the dead shoots below water remained standing.

Field sampling

Each of the twelve marshes was divided from north to south into 10 zones, and four of these were randomly selected. Four sites within each zone were randomly selected as epiphyton sampling sites for a total of 16 epiphyton sites per marsh. For phytoplankton sampling, two sites within each zone were randomly selected for a total of eight phytoplankton sampling sites per marsh. Extruded clear acrylic rods with 0.63 cm diameter were used as an artificial substrata for epiphyton (Goldsborough and Robinson 1983; Robinson 1983). Each acrylic rod was notched at 2 cm intervals prior to incubation in the field (Goldsborough and Robinson 1983). Rods were positioned vertically at all sites in May of 1982. Samples were collected at four week intervals from June through September. Phytoplankton samples were collected from 20 cm below water surface in 1-liter bottles at the same periods.

Primary productivity measurements

The primary productivity of epiphyton and phytoplankton algae was estimated using a ^{14}C method (Goldsborough and Robinson 1983; Peterson 1980). A two centimeter length of acrylic rod colonized by epiphytic algae was clipped off and placed in a 30-ml glass bottle filled with

filtered marsh water (Goldsborough and Robinson 1983). A phytoplankton sample consisted of a 60-ml glass bottle filled with marsh water. A known amounts of standardized $NaH^{14}CO3$ with known activity was added to each algal sample, which was then incubated in the laboratory for four hours at a constant low irradiance of 15 $\mu E/m^2/sec.$ of PAR and temperature of 19°C ±1. The algae incubated were not saturated at this irradiance (unpublished data). After incubation epiphyton attached to the rod and phytoplankton samples were filtered through 0.45 µm cellulose acetate filters, acid-fumed with concentrated HCl and placed in a vial containing 10 ml of scintillation cocktail (Goldsborough and Robinson 1983). Within 24 hours both rod and filter dissolved in the vial. Incorporated radioactivity was determined with a Picker Liquimat 220 scintillation counter (Goldsborough and Robinson 1983). The inorganic carbon level in the marsh water was determined from measurements of alkalinity, pH and temperature (APHA 1980; Goldsborough and Robinson 1983; Strickland and Parsons 1972). Total inorganic carbon assimilated in laboratory conditions per unit of artificial substrata for epiphyton and per unit volume of marsh water for phytoplankton was calculated using standard equations (APHA 1980; Goldsborough and Robinson 1983; Peterson 1980; Vollenweider 1974). The mean of sixteen measurements for epiphyton and eight measurements for phytoplankton for each marsh per period were used in all analyses.

Chlorophyll-a, carbon and nitrogen measurements

One piece of colonized acrylic rod from each of the 16 sites within each marsh was scraped with the dull edge of a scalpel to remove all epiphyton. This composite sample in a known volume of distilled water was mixed and divided into three equal subsamples.

One of the subsamples was filtered through GFC Whatman filters, frozen in the dark, and later extracted in 95% methanol (Holm-Hansen and Riemann 1978) for measurement of chlorophyll-a by the fluorometric method (APHA 1980; Marker 1972; Stainton et al. 1977). Another subsample was filtered onto pre-ashed GFC filters and its particulate N and C content determined with an autoanalyzer at the Freshwater Institute of Winnipeg (Stainton et al. 1977).

For phytoplankton, water samples from the eight phytoplankton sites of each marsh were mixed into a composited sample. Five hundred ml of this composite sample were filtered through GFC Whatman filters and the sample frozen. The chlorophyll-a of the algae frozen on the filter was extracted in 95% methanol and measured fluorometrically (APHA 1980; Marker 1972; Stainton et al. 1977). Another 500 ml of the composite sample were filtered through pre-ashed GFC filter and the total suspended carbon and nitrogen of the sample measured using an autoanalyzer (Stainton et al. 1977). Macroinvertebrates were removed from the filters with a pair of fine forceps prior to all analyses.

Water depth, temperature, pH, alkalinity (APHA 1980) and specific conductance were measured whenever a sample was collected. Ammonia, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP)

also were measured according to the methods described by Stainton et al. (1977) for three flooded and two unflooded marshes. These data were used to examine correlations between algal productivity and biomass and water chemistry.

Statistical tests

All productivity and biomass estimates were analyzed using an ANOVA (using the GLM procedure) in which the classification variables were marsh, flooding treatments, months and their interactions. Statistical Analysis System (SAS 1982) was used for all calculations of summary statistics, tests of significance (LSDs at the 0.05 level), and correlations between different environmental parameters and algal productivity and biomass.

RESULTS

Epiphyton

Marshes flooded one year had significantly higher mean productivity (6.31 mg C/m^2 substrata/h) than the unflooded marshes (3.52 mg C/m^2 substrata/h); the productivity of marshes flooded two years (4.58 mg C/m^2 substrata/h) was not significantly different from either the unflooded or one-year flooded marshes (Table 1). All treatments had lowest productivities in June and highest in September; i.e., there was no shift in seasonal productivity patterns because of flooding (Table 1).

Epiphytic biomass, as estimated by chlorophyll-*a*, carbon, and nitrogen, showed no statistically significant differences among different treatments (Table 1). Carbon and nitrogen peaked in unflooded marshes in August, whereas marshes flooded two years had their highest values in September. There was an increase in carbon and nitrogen from July to August in both unflooded and two-year flooded marshes, whereas marshes flooded one year gradually increased from June through September (Table 1). Mean chlorophll-a increased from July to August in all treatments and then stayed constant (Table 1).

The primary productivity of epiphyton was poorly correlated ($r = 0.51$, $p<0.01$) with chlorophyll-*a*, while the correlation between productivity and carbon ($r = 0.73$, $p<0.01$) was fairly strong. There also was a poor correlation ($r = 0.52$, $p<0.01$) between carbon and

Table 1. Average epiphyton primary productivity and biomass in unflooded, one-year (N=2 per month) and two-year (N=8 per month) flooded marshes in 1982

Treatments	June	July	August	September	Mean ±1 SE
	Carbon-14 (mg C/m^2 substrata/h)				
Unflooded	2.30	2.95	3.55	5.30	3.53 ± 0.82[a]
One-year flooded	4.80	5.90	6.25	8.30	6.31 ± 0.71
Two-year flooded	1.54	3.71	6.49	6.60	4.58 ± 0.46
Mean	2.21	3.95	5.96	6.67	
±1 SE (N=12)	0.41	0.53	0.63	0.62	
	Chlorophyll-a (mg/m^2 substrata)				
Unflooded	4.9	7.5	63.3	59.4	33.7 ± 12.4
One-year flooded	4.5	18.6	34.4	35.4	23.2 ± 6.8
Two-year flooded	1.6	7.7	29.1	29.1	16.9 ± 3.2
Mean	2.62	9.50	35.7	35.2	
±1 SE (N=12)	0.81	2.03	7.3	6.0	
	Carbon (mg/m^2 substrata)				
Unflooded	636	535	1756	1032	990 ± 234
One-year flooded	932	1473	1508	1612	1381 ± 275
Two-year flooded	649	958	1796	2847	1593 ± 235
Mean	698	978	1723	2292	
±1 SE (N=12)	111	190	257	364	
	Nitrogen (mg/m^2 substrata)				
Unflooded	94	58	210	135	124 ± 25
One-year flooded	119	175	234	262	197 ± 50
Two-year flooded	67	125	318	439	236 ± 36
Mean	81	122	286	351	
±1 SE (N=12)	14	22	38	71	

[a]LSD $p<0.05$ between unflooded and one-year flooded only.

chlorophyll-a. No significant correlation was observed between epiphyton productivity or biomass and any physico-chemical parameters.

Phytoplankton

Phytoplankton primary productivity, as well as all biomass estimates, was significantly higher in unflooded (38.8 mg $C/m^3/h$) than in both flooded treatments (2 to 3 mg $C/m^3/h$) (Table 2). There was no significant difference between one-year and two-year flooded marshes (Table 2). The two unflooded marshes were very different in their mean annual phytoplankton primary productivity, with values of 67 and 11 mg $C/m^3/h$, respectively, for marshes 11 and 12. There was less heterogeneity, however, in primary productivity estimates (2 to 5 mg $C/m^3/h$) in two-year flooded marshes, while the two marshes flooded for one year had very similar values (2 to 3 mg $C/m^3/h$). Productivity of phytoplankton in unflooded marshes peaked in September, whereas in marshes flooded one year and two years it peaked in August and July, respectively (Table 2). Chlorophyll-a in unflooded marshes peaked in August, whereas in marshes flooded one year and two years it peaked in June and July, respectively (Table 2). Suspended carbon and nitrogen increased from July to August in unflooded marshes, whereas they decreased in flooded marshes from June to July and then remained constant (Table 2).

Suspended carbon and chlorophyll-a both had very high correlations with primary productivity ($r = 0.91$ and $r = 0.87$, respectively $p<0.01$) and with each other ($r = 0.98$ $p<0.01$).

Primary productivity also was correlated with both TDP ($r = 0.72$ $p < 0.01$) and TDN ($r = 0.61$ $p < 0.01$).

Table 2. Mean phytoplankton primary productivity and biomass in unflooded, one-year (N=2 per month) and two-year (N=8 per month) flooded marshes in 1982

Treatments	June	July	August	September	Mean ±1 SE
			Carbon-14 (mg C/m^3/h)		
Unflooded	17.8	27.9	37.5	45.0	38.8 ± 14.2[a]
One-year flooded	2.7	2.5	4.4	1.9	2.9 ± 0.5
Two-year flooded	1.9	5.1	2.0	1.6	2.6 ± 0.4
Mean	4.6	8.4	8.3	13.4	
±1 SE (N=12)	2.5	3.5	5.2	10.2	
			Chlorophyll-a (mg/m^3)		
Unflooded	19.0	26.0	97.0	98.5	65.0 ± 21.7[a]
One-year flooded	5.5	3.0	2.5	4.5	3.9 ± 0.7
Two-year flooded	5.6	7.6	4.1	4.1	5.4 ± 0.7
Mean	7.8	8.5	19.3	19.9	
±1 SE (N=12)	2.2	2.3	13.1	11.1	
			Suspended Carbon (mg/m^3)		
Unflooded	2840	2764	6314	7860	4944 ± 1160[a]
One-year flooded	937	476	444	667	633 ± 93
Two-year flooded	917	834	487	509	687 ± 75
Mean	1241	1096	1451	1762	
±1 SE (N=12)	282	286	776	867	
			Suspended Nitrogen (mg/m^3)		
Unflooded	519	578	1519	1793	1102 ± 281[a]
One-year flooded	152	74	102	98	107 ± 21
Two-year flooded	146	171	88	83	122 ± 16
Mean	209	223	329	395	
±1 SE (N=12)	55	66	185	220	

[a]LSD $p<0.05$ between unflooded and both one-year and two-year flooded marshes.

Table 3. Mean values of chemical parameters measured in unflooded, one-year and two-year flooded marshes in 1982

	Treatments		
Measurements	Unflooded	One-year	Two-year
pH	7.96	8.05	8.30
Alkalinity (mg/L as $CaCO_3$)	539	620	543
Conductance (mhos/cm)	2521	2831	2501
Ammonia (NH_4-N) (g/L)	296	159	110
Total Dissolved Nitrogen (TDN) (g/L)	5733	3986	3815
Total Dissolved Phosphorus (TDP) (g/L)	778	208	183

DISCUSSION

All productivity estimates were made under very low irradiance in the laboratory and represent only 10-13% of the productivity found under light saturated conditions. Dark uptake under laboratory conditions was about 25% and 50% of the light uptake for epiphyton and phytoplankton, respectively. No correction for the dark uptake is made in the data presented.

Epiphyton

Epiphyton productivity in marshes flooded one year was significantly higher than in unflooded marshes. One reason for this higher productivity in one-year flooded marshes could be increased irradiance below the surface due to macrophyte death. Murkin and Kadlec (1986) reported that during the first year of flooding only dead standing litter remained. Hooper and Robinson (1976) and Straskraba and Pieczynska (1970) found that low productivity of epiphytic algae within *Phragmites* and dense *Typha* sites was related to low light intensity. Why then was epiphyton productivity in marshes flooded for two years not significantly different than in the unflooded marshes? One possible reason for this was the large masses of floating filamentous algae found in two-year flooded marshes. These shaded the epiphyton resulting in a light regime similar to that found in unflooded marshes. Hosseini and van der Valk (1986) found that mean ash-free dry weight of filamentous algae in marshes flooded for two years (66 g/m^2) was significantly higher than both marshes flooded for one year (20 g/m^2) and unflooded marshes (2.6 g/m^2).

One might also expect higher productivity in flooded marshes because increased nutrients in the water column that are released by the dead macrophytes. In fact, mean TDN and TDP were lower in flooded marshes, compared to unflooded marshes (Table 3); and no significant correlation was found between these chemical parameters and epiphyton productivity. However, this does not mean that changes in nutrient levels have had no effect on epiphyton productivity, since it is not possible to determine what amount of available N and P were present in the three treatments. Epiphyton productivity and biomass were calculated per unit area of artificial substrata. However, in flooded marshes, total available surface area for epiphyton increased four to five times over unflooded marshes (mean water depth of 0.20 m for unflooded and 1.0 m for flooded marshes) and, therefore, the total annual productivity and biomass per unit marsh area was significantly higher in flooded than in unflooded marshes.

Epiphyton productivity increased in all treatments throughout the season, with a fall maximum. This is similar to seasonal patterns in other temperate aquatic systems such as Lawrence Lake (Allen 1971) and Crescent Pond, Delta Marsh (Hooper and Robinson 1976).

Phytoplankton

The productivity and biomass of phytoplankton were significantly higher in unflooded marshes than in flooded ones. As with epiphyton, reduced irradiance within stands of emergent macrophytes seems to be a factor limiting planktonic productivity in wetlands (Dokulil 1973; Straskraba and Pieczynska 1970; Wetzel 1983). The death of emergent

macrophytes in flooded marshes should have resulted in increased irradiance, but there was no corresponding increase in planktonic productivity. Therefore, the low phytoplankton productivity and biomass in flooded marshes is not due to light limitation. Lower nutrient levels in flooded than in unflooded marshes may be one important reason (Table 3). The primary productivity of phytoplankton is positively correlated with TDN and TDP concentrations. Perhaps another reason for low phytoplankton productivity of flooded marshes is heavy grazing by zooplankton. Murkin (1983) reported very high densities of cladocerans, which are primarily planktivores, in the water column of flooded marshes. Timms and Moss (1984) have also reported a reduction in phytoplankton population due to grazing.

Low phytoplankton productivity in flooded marshes could also be due to dilution. However, conversion of chlorophyll-a, suspended carbon and suspended nitrogen from mg C/m^3 to mg C/m^2 indicates that biomass of unflooded marshes is still two to three times higher than that of flooded ones. Unflooded marshes per unit area are about three times more productive than flooded ones (7.8 mg C/m^2 versus 2.8 mg C/m^2).

Chlorophyll-a of phytoplankton shows a high correlation with productivity, perhaps due to less chlorophyll-c and degradated pheophytin in phytoplankton communities than in epiphyton. Even though all components of organic carbon, such as algae, zooplankton, invertebrates, fungi, etc., were included in measurements of suspended C, the very high correlation with productivity suggests that this is perhaps a reliable estimate of algal biomass.

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SECTION II. THE IMPACT OF PROLONGED FLOODING ON FILAMENTOUS ALGAE IN A FRESHWATER MARSH

The impact of prolonged flooding on filamentous algae in a freshwater marsh

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Running head: Flooding impact on filamentous algae

ABSTRACT

The biomass of filamentous algae per unit area was estimated during the summer of 1982 in marshes flooded one year in 1982, marshes flooded continuously for two years in 1981 and 1982 and unflooded experimental marshes of the Marsh Ecology Research Project (MERP) in the Delta Marsh, Manitoba, Canada. The two-year flooded marshes had the highest filamentous algal biomass in June and July and gradually declined through September, with an annual mean of 66 g AFDW/m^2. In one-year flooded marshes, filamentous algal biomass was significantly lower than in two-year flooded marshes, but higher than unflooded marshes. In one-year flooded marshes, algal biomass was lowest in June and July, but gradually increased through September with an annual mean of 20 g AFDW/m^2. Unflooded marshes had consistently low filamentous algal biomass with an annual mean of only 2.6 g AFDW/m^2. Filamentous algal biomass in flooded marshes was not correlated with any chemical parameter measured.

INTRODUCTION

Filamentous algae, though an important component of fresh water marshes, have been generally overlooked by researchers. Although it is sometimes difficult to delineate this community from loosely associated epiphyton, it is not normally sampled when periphyton, phytoplankton or metaphyton are sampled. Nevertheless, filamentous algae may attain great densities and have a high annual primary productivity (Komarkova and Marvan 1978). In the Netherlands, floating masses of filamentous algae are used as fertilizer, and the Dutch language even has a common name for this group of algae, flab (Hillebrand 1983). In freshwater marshes, filamentous algae, however, differ from the free floating flab because they become entangled with standing litter and emergent vegetation.

Representatives from many genera of freshwater filamentous algae can be found as floating masses in aquatic systems, including species of Oedogonium, Cladophora, Rhizoclonium, Microspora, Ulothrix, Tribonema, Enteromorpha, and Vaucheria (Hillebrand 1983). The large number of species in this community suggests that all these species grow best under a similar set of environmental conditions that are conducive to flab formation (Hillebrand 1983).

Little is known about the impact of water level cycles, that are a characteristic of prairie wetlands, on filamentous algae of wetlands. Harris and Marshall (1963) have reported that green algae sometimes form thick mats in recently reflooded wetlands. Weller and Fredrickson (1974) found a sharp increase in abundance of Hydrodiction

spp. in Rush Lake because of flooding. van der Valk (1986) also reported them as dried litter inhibiting seedling germination in drawdown impoundments of Delta Marsh, Manitoba. Recently, many researchers have emphasized that significant changes in chemical and physical conditions occur in freshwater marshes when they are flooded above normal water levels (Hosseini and van der Valk 1986; Kadlec 1983; Murkin 1983; Murkin and Kadlec 1986). The only study of the impact of flooding on algae (Hosseini and van der Valk 1986) found that epiphyton and phytoplankton communities undergo distinct changes in marshes flooded one or two years.

The objective of this study was to investigate the impact of abnormally high water level on the biomass of filamentous algae in freshwater marshes in an experimental marsh complex. Three flooding treatments (unflooded, flooded for one year, and flooded for two years) occurred in this complex during the study period.

MATERIALS AND METHODS

Study site

This study was conducted in the experimental marsh complex of Marsh Ecology Research Program at the Delta Waterfowl and Wetlands Research Station in South Central Manitoba, Canada (50°11' N, 98°19' W). Ten experimental marshes (approximately 5 ha each) were constructed with dikes along the northern edge of Delta Marsh (Batt et al. 1983; Hosseini and van der Valk 1986; Murkin et al. 1985; Murkin and Kadlec 1986). Two sections of natural marsh of about equal size at each end of the experimental complex also were selected as unflooded marshes. The initial vegetation within the experimental marshes was similar to that in the main Delta Marsh (Murkin and Kadlec 1986; Pederson 1981). Of the ten experimental marshes, eight were flooded 1 m above normal continuously for two years in 1981 and 1982, and two for one year in 1982 (see Hosseini and van der Valk 1986).

Most of emergent vegetation was killed during the first year of flooding and, as a consequence, there was a great deal of standing litter, particularly dead Phragmites and Typha shoots in the flooded marshes (Hosseini and van der Valk 1986). In marshes flooded for two years, only the bases of the dead shoots below the water level remained (Hosseini and van der Valk 1986).

Field sampling

Each of the twelve marshes was divided from north to south into 10 zones, and four of these were randomly selected in each marsh.

Within each zone, four sampling sites were randomly selected for a total of 16 sites per marsh. Eight habitat types were identified in the marsh complex based on the vegetation or other features around a sampling site: open water (no emergent vegetation), submersed vegetation, living Phragmites, living Scirpus, living Typha, dead Phragmites, dead Scirpus and dead Typha.

An algal sampler was constructed (Figure 1). Adjacent to each sampling site the sampler was pushed down to the bottom of the marsh. It was then moved to the sampling site, pulled up and all the algae caught on the prongs removed. Macroinvertebrates, submersed plants and debris were separated by hand from filamentous algae. The cleaned sample from each site was placed in a pre-weighed aluminum pan, dried at 105 °C for 24 hours, weighed, ashed at 500 °C for a minimum of three hours, and then reweighed to estimate its ash-free dry weight (Vollenweider 1974). The mean of 16 sites per marsh per period was used in all analysis. Samples were collected at four-week intervals from June through September.

Water depth, water temperature, pH, alkalinity and specific conductance were measured whenever a sample was collected (Hosseini and van der Valk 1986). Ammonia, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were measured according to the methods described by Stainton et al. (1977) during these periods; the data were used to examine correlations between algal biomass and water chemistry.

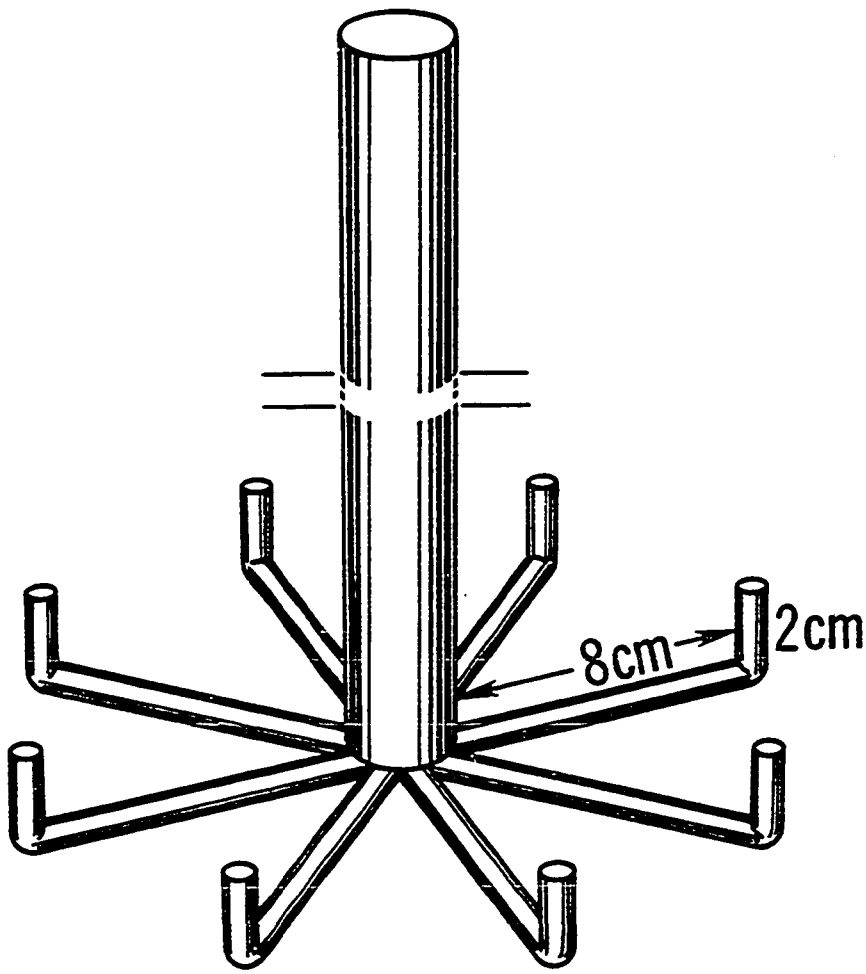

Figure 1. Filamentous algal sampler with collectable surface area of 200 cm^2.

Statistical tests

Biomass estimates were analyzed using an ANOVA (using GLM procedure) in which the classificiation variables were marsh, treatments, months and their interactions. Statistical Analysis System (SAS 1982) was used for all calculations and tests of significance (LSDs) at the 0.05 level. Simple correlations between different environmental parameters and algal biomass were also calculated using SAS (SAS 1982).

RESULTS

The average biomass (66.3 g/m^2) for filamentous algae in marshes flooded for two years was significantly higher than in both marshes flooded for one year (20.1 g/m^2) and unflooded marshes (2.6 g/m^2). On the other hand, the filamentous algal biomass of marshes flooded one year was not significantly different from biomass in unflooded marshes (Table 1). The annual mean biomass of filamentous algae for two-year flooded marshes had a range of 19.6 to 150.7 g/m^2. Four of the marshes flooded for two years had extensive areas covered with dead Phragmites and Typha shoots. These marshes had a mean algal biomass of 101 g/m^2, three times higher than the other four marshes (31.5 g/m^2). Marshes flooded one year had annual biomass mean of 13.4 and 26.7 g/m^2, while unflooded marshes had lowest annual mean of 0.4 and 4.8 g/m^2.

Filamentous algal biomass had a similar seasonal pattern in both unflooded and two years flooded marshes with a peak in June and a decline in biomass for the remainder of the season (Table 1). Marshes flooded for one year, however, had their lowest biomass in June, and it increased through September.

The highest average algal biomass in flooded marshes was among dead emergent macrophytes (Table 2), while in unflooded marshes open water areas had the highest biomass. In all other habitats in marshes flooded for two years, there was more biomass than in similar habitats in one year flooded and unflooded marshes (Table 2).

No significant correlation was found between physico-chemical parameters and filamentous algal biomass.

Table 1. Comparison of Ash Free Dry Weight (g/m^2) of filamentous algae between unflooded, one- and two-year flooded marshes in 1982

Periods	Treatments			
	Unflooded N=2	One-year Flooded N=2	Two-year Flooded N=8	Mean ± 1 SE N=12
June	5.2	9.8	84.3	58.7 ± 16.7
July	1.1	22.9	87.9	62.6 ± 19.4
Aug.	3.1	12.8	60.4	42.9 ± 15.5
Sept.	1.0	34.9	32.6	27.7 ± 6.5
Mean ±1 SE	2.6[a]±1.2	20.1[b]±6.1	66.3 ±9.9	

[a]LSD $P < .05$ between unflooded and two-year flooded.

[b]LSD $P < .05$ between one-year and two-year flooded.

Table 2. Ash Free Dry Weight (g/m^2) of filamentous algae in different habitats in Delta Marsh in 1982

Habitat	Treatments		
	Unflooded	One-year Flooded	Two-year Flooded
Dead *Phragmites*	--	40.5	163.5
Dead *Typha*	--	1.5	40.0
Submersed Vegetation	1.5	12.0	28.0
Emergent *Typha*	2.0	--	27.5
Open Water	7.0	0.5	19.5
Emergent *Phragmites*	--	--	19.0
Dead *Scirpus*	--	27.5	--
Emergent *Scirpus*	2.0	--	--
Mean	2.6	6.1	66.3

DISCUSSION

The efficiency of our sampler varied depending on the density of the mat. Our biomass estimates are underestimates at low density sites and overestimates at high density sites. The biomass values given in Tables 1 and 2 are only semi-quantitative estimates and adequate for making comparison among flooding treatments. They are not reliable estimates of the actual biomass present in the different treatments.

The death of emergent macrophytes in flooded marshes created favorable habitats that stimulated filamentous algal growth. Even within a flooded marsh, sites with dead standing Phragmites, Scirpus and Typha had a higher biomass than other habitats.

Open water sites in unflooded marshes had a higher biomass than shaded sites with emergent macrophytes. The gradual death of emergent macrophytes throughout the 1982 growing season in one year flooded marshes was inversely correlated with an increase in their filamentous algal biomass (Table 1). Such a seasonal pattern was not found in the other two treatments. These data suggest that an increase in light was one of the major factors causing the increase in filamentous algal biomass observed (Straskraba and Pieczynska 1970). Hillebrand (1983) also indicated that flab abundance was light dependent, and vertical ascent of filamentous algae was only possible when a sufficent amount of light reaches the bottom. The primary productivity of epiphytic

algae (Hooper and Robinson 1976; Hosseini and van der Valk 1986) was also stimulated by the death of the emergent canopy.

Irradiation, however, cannot be the only factor regulating filamentous algal productivity because open water areas in the one-year flooded marshes did not have high filamentous algal biomass (0.5 g/m^2). Other factors, such as differences in temperature, substrata (litter) abundance, water depth, and nutrient level between one- and two-year flooded and unflooded marshes, also must play a role.

Higher algal biomass in flooded marshes could be due to increased nutrients in water released from the dead macrophytes. This seems not to be a factor, since mean TDN and TDP concentrations actually were lower in flooded marshes (Hosseini and van der Valk 1986) compared to unflooded marshes; and there was no correlation between any physico-chemical parameters measured and filamentous algal biomass.

We have been unable to find any other studies except Hillebrand (1983) that quantify the biomass or productivity of filamentous algae in wetlands or other aquatic systems. This community, nevertheless, is potentially one of the most important primary producers in prairie wetlands during the high water or lake stage of their wet/dry cycles (see Weller and Fredrickson 1974), and additional studies of this unjustifiably ignored algal community are certainly in order.

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SECTION III. EPIPHYTON AND PHYTOPLANKTON PRODUCTIVITY AND BIOMASS IN FLOODED AND UNFLOODED FRESHWATER MARSHES

Epiphyton and phytoplankton productivity and biomass in flooded and unflooded freshwater marshes

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ABSTRACT

Epiphyton and phytoplankton productivity and biomass were compared in two marshes flooded continuously 1 m above normal for two years and five unflooded marshes. Primary productivity was estimated using a ^{14}C method. Epiphyton productivity was measured on artificial substrata previously incubated in the marshes. Phytoplankton productivity was estimated using marsh water incubated in 60-ml glass bottles. Productivity measurements were made both in the field and under standard conditions in the laboratory (temperature 19°C±1, and irradiance 175 $\mu E/m^2$/sec. of PAR). There was no significant difference between field and laboratory measurements of epiphyton and phytoplankton productivity. Total chlorophyll, chlorophyll-*a*, particulate carbon and nitrogen were measured as estimates of biomass.

Mean phytoplankton productivity (2290 mg C/m^3/day) and biomass in unflooded marshes were significantly higher than in marshes flooded two years (290 mg C/m^3/day). Mean epiphyton primary productivity per unit area of artificial substrata in marshes flooded two years (1000 mg C/m^2/day) was not significantly different than in unflooded marshes (670 mg C/m^2/day).

Seasonal patterns of epiphyton and phytoplankton productivity were affected by flooding, but algal efficiency measured by productivity:chlorophyll ratio remained the same in both flooded and unflooded marshes. Epiphyton productivity peaked in the fall in

flooded marshes, while unflooded marshes had maximum productivity in the spring. Phytoplankton productivity was highest during mid-summer in flooded marshes, whereas unflooded marshes had a fall maximum.

INTRODUCTION

Little is known about the role of epiphyton in freshwater wetlands, especially in prairie glacial marshes. Much of our knowledge about epiphyton productivity is derived from limited studies in littoral zones of lakes and ponds, which indicate that epiphyton are important contributors to overall primary productivity (Allen 1971; Brown 1973a,b; Brown and Austin 1973; Cattaneo and Kalff 1980; Hooper and Robinson 1976; Wetzel 1983a). Per area of lake surface, periphyton productivity may equal or exceed that of phytoplankton or macrophytes (Allen 1971; Cattaneo and Kalff 1980; Jones 1984; Kairesalo 1980; Kowalczewski 1975). Also, little is known about temporal and spatial patterns of epiphyton productivity in freshwater marshes (Crumpton 1986), especially on the scale relevant to microorganisms (Allanson 1973) because of methodological difficulties in dealing with these complex communities (Robinson 1983; Wetzel 1983a,b).

There have been few studies of the contribution of phytoplankton (including metaphyton) to the overall primary productivity of freshwater marshes (Brandle et al. 1970; Brown 1972; Dukolil 1973; Goulder 1969; Hickman and Jenkerson 1978; Kairesalo 1980; Kalff and Knoechel 1978). As with epiphyton, our knowledge of phytoplankton productivity, spatial and temporal distribution, and interactions with macrophytes or other algal communities is derived primarily from studies in littoral zones of lakes.

Algal communities in fluctuating environments undergo large-scale

changes (Ollason 1977). One type of environmental fluctuation that is common in prairie wetlands is changes in water levels caused by cyclical patterns in annual precipitation (van der Valk and Davis 1978). Periodically these wetlands have water levels so far above normal that their emergent vegetation may be almost totally killed. Hosseini and van der Valk (1986a,b) have investigated the impact of flooding on the epiphyton, phytoplankton and mass filamentous algae in freshwater wetlands flooded for one and two years above normal. They found a significant reduction in phytoplankton productivity, but an increase in epiphyton productivity and filamentous algal biomass in flooded marshes. Two natural marshes were used as unflooded (control) in their studies (Hosseini and van der Valk 1986a,b), but these marshes differed markedly in their mean productivity and biomass of both phytoplankton and epiphyton.

The objectives of this study were: 1) to investigate the impacts of two years of flooding on epiphyton and phytoplankton productivity and biomass in a freshwater wetland, 2) to investigate spatial and temporal responses of these algae to flooding, 3) to compare algal productivity under field conditions verses constant laboratory conditions, and 4) to correlate physico-chemical parameters with algal productivity and biomass. In an experimental marsh complex two flooding treatments (two marshes flooded continuously in 1982 and 1983 and five unflooded marshes) occurred during the study period.

MATERIALS AND METHODS

Study site

This study was conducted during the summer of 1983 in the experimental marsh complex of the Marsh Ecology Research Program (MERP) at the Delta Waterfowl and Wetlands Research Station in south central Manitoba, Canada (50 11' N, 98 19' W). This complex consists of 10 diked marshes constructed along the northern edge of Delta Marsh, each about 5 ha in area (Batt et al. 1983; Murkin et al. 1985). The vegetation of the Delta Marsh has been described by Anderson and Jones (1976) and Walker (1959, 1965). The initial vegetation within the experimental marshes was similar to that in the main marsh (Murkin and Kadlec 1986; Pederson 1981).

The MERP complex is being used to study the impact of water level changes on a lacustrine wetland. Since 1962, the water level of Lake Manitoba has been regulated using a dam. Thus the "normal" water level of the Delta marsh for over 20 year has been 247.5 m AMSL. Before the water levels were regulated, lake level fluctuated by more than 1.5 m. In 1981, water levels in 8 of the MERP marshes were raised 1 m above normal to 248.5 m AMSL to simulate high water conditions that occurred before lake level regulation began. Two additional marshes were flooded to 248.5 m in 1982. High water levels in both sets of marshes were maintained for two years (Batt et al. 1983; Murkin et al. 1985). In 1983, only two marshes flooded for two years were sampled. Most of the emergent vegetation in these flooded

marshes was dead, and below water standing dead shoots, particularly of Phragmites, Typha and Scirpus, were common.

In the main marsh, five unflooded areas near the experimental marsh complex were monitored: one small pond (Clines Lake pond, approximately 2 ha); one large pond (McKenzie pond, approximately 10 ha), which was connected to open bay through emergent vegetation; open bay 22; and two sections of natural marsh of about 5 ha each (marshes 11 and 12) at each end of the experimental complex.

Field sampling

Five sites in open water areas within each flooded or unflooded marsh were randomly selected for epiphyton, and three open water sites were selected for phytoplankton sampling. Extruded clear acrylic rods with 0.63 cm diameter were used as artificial substrata for epiphyton (Goldsborough and Robinson 1983; Hosseini and van der Valk 1986a; Robinson 1983). Each rod was notched at 2 cm intervals prior to incubation in the field (Goldsborough and Robinson 1983; Hosseini and van der Valk 1986a). Rods were positioned vertically at all sites in May of 1983 and remained standing throughout the season. Epiphyton samples were collected 5 to 20 cm below the water surface at four week intervals from June through September. Phytoplankton samples were collected 20 cm below the water surface at each site in one liter bottles at four-week intervals from May through September.

Primary productivity measurements

Epiphyton and phytoplankton productivity were estimated using a ^{14}C method (Goldsborough and Robinson 1983; Hosseini and van der Valk

1986a; Peterson 1980; Robinson 1983). An epiphyton sample consisted of a two-centimeter length of acrylic rod colonized by epiphyton that was clipped off and placed in a 30-ml glass bottle filled with filtered marsh water. A phytoplankton sample consisted of a 60-ml glass bottle filled with marsh water. A known amount of $NaH^{14}CO3$ was added to each bottle (Goldsborough and Robinson 1983; Hosseini and van der Valk 1986a). Five light and three dark bottles for epiphyton and three light and three dark bottles for phytoplankton from each flooded marsh or unflooded marsh site were incubated for four hours in the laboratory at 175 $\mu E/m^2/sec.$ of PAR and 19°C ± 1. At the same time, three light and three dark bottles for both phytoplankton and epiphyton were incubated for four hours during mid-day in the field and returned to the laboratory immediately in a black box.

After incubation, epiphyton attached to the rod and phytoplankton samples were filtered through 0.45 µm cellulose acetate filters, acid-fumed for five minutes with concentrated HCL to remove residual inorganic ^{14}C and placed into scintillation vials containing 10 ml Bray's solution (Goldsborough and Robinson 1983; Hosseini and van der Valk 1986a). Within 24 hours, both the filter and acrylic rod dissolved completely in this solution. Radioactivity of a sample was determined by scintillation counting with a Picker Liquimat 220 counter and corrected for color quenching using the channels ratio (Goldsborough and Robinson 1983; Hosseini and van der Valk 1986a). The inorganic carbon level in the marsh water was determined from measurements of water alkalinity, pH and temperature (APHA 1980;

Strickland and Parsons 1972). Carbon assimilation rates were calculated using standard equations (Goldsborough and Robinson 1983; Peterson 1980; Vollenweider 1974). Mean dark uptakes were deducted from mean light uptakes for both laboratory and field samples of epiphyton and phytoplankton. Net primary productivity was expressed per unit of rod surface area for epiphyton and volume of marsh water for phytoplankton. The mean of five epiphyton and three phytoplankton samples for the laboratory and three epiphyton and three phytoplankton samples for the field were used for each marsh per period in all analyses. Our calculations of total annual production uses the mean laboratory productivity over the growing season from all sites in a treatment multiplied by 12 hours of daylight per day and 150 day growing season. No adjustments for daily temperature or irradiance were made.

Chlorophyll, carbon and nitrogen measurements

For each marsh one piece of colonized acrylic rod from each site was scraped with the dull edge of a scalpel to remove all epiphyton. The scrapings were then combined in a known volume of distilled water and thoroughly mixed. One subsample was filtered through GFC Whatman filters, kept frozen in the dark, and its chlorophyll extracted in 95% methanol (Holm-Hansen and Riemann 1978; Hosseini and van der Valk 1986a). Chlorophyll a,b and c were measured by High Performance Liquid Chromatography (Abaychi and Riley 1979; Bidigare et al. 1985; Falkowski and Sucher 1981; Jacobsen 1978; Mantoura and Llewellyn 1983). A second subsample was filtered onto pre-ashed GFC filters and

its particulate N and C content determined with an autoanalyzer at the Freshwater Institute of Winnipeg (Stainton et al. 1977).

For phytoplankton, water samples from the three sites of each marsh were mixed into a composite sample. Five hundred ml water of this composite sample were filtered through GFC filters and the chlorophyll a,b and c content was determined as described for epiphyton. Another 500 ml of the composite sample was filtered through a pre-ashed GFC filter and its suspended carbon and nitrogen measured using an autoanalyzer (Stainton et al. 1977). Macroinvertebrates were removed from the filters with a pair of fine forceps prior to all analyses.

Environmental measurements

Temperature, pH, alkalinity and specific conductance were measured whenever a sample was collected, (APHA 1980; Vollenweider 1974). Ammonia, total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) were also measured during these periods according to the methods described by Stainton et al. (1977).

Statistical tests

All productivity and biomass estimates were analyzed using ANOVA in which the classification variables were marshes, water level treatments, month and their interactions. Statistical Analysis Systems (SAS 1982) was used to calculate tests of significance between means at the 0.05 level and correlations between different environmental parameters and algal productivity and biomass.

RESULTS

Epiphyton

Mean productivity of epiphyton under laboratory conditions was not significantly different than field estimates. No significant difference was found between the mean primary productivity of two-year flooded (79 mg C/m^2 substrata/h) and unflooded marshes (56 mg C/m^2 substrata/h) (Table 1). Primary productivity of unflooded marshes was as low as 20 mg C/m^2 substrata/h in bay 22 and small pond and as high as 96 mg C/m^2 substrata/h in large pond (Table 1). Total chlorophyll, chlorophyll-*a*, carbon and nitrogen were not statistically different in flooded and unflooded marshes.

Total chlorophyll (and chlorophyll-*a*) varied in amount from a low of 8 mg/m^2 substrata (7 mg/m^2 substrata) in bay 22 to a high of 56 mg/m^2 substrata (43 mg/m^2 substrata) in marsh 11. Total chlorophyll and chlorophyll-*a* in flooded marshes had a means of 36.8 and 66.8 mg/m^2 substrata in marsh 3 and 29.3 and 52.5 mg/m^2 substrata in marsh 7 (Table 1). Chlorophyll-*a* was 74% of total chlorophyll in the unflooded marshes and 79% of total chlorophyll in two-year flooded marshes. In the areas of unflooded marshes, carbon ranged from 1100 mg/m^2 substrata in small pond to 3600 mg/m^2 substrata in large pond, while flooded marshes had annual means of 4490 and 3760 in marshes 3 and 7, respectively (Table 1). On the other hand, nitrogen fluctuated the most, from as low as 87 mg/m^2 substrata in small pond to 531 mg/m^2 substrata in large pond of unflooded marshes, while flooded marshes 3

and 7 had very similar annual means of 565 and 522 mg/m^2 substrata, respectively (Table 1).

Seasonal patterns of epiphyton productivity differed in different marshes. Both flooded marshes had fall maxima (Table 2). Marsh 11 and large pond had their peaks in June (127.4 and 266.0 mg C/m^2 substrata/h, respectively), bay 22 had its peak in July (38.6 mg C/m^2 substrata/h), while marsh 12 and small pond had their peaks in September (110.5 and 49.7 mg C/m^2 substrata/h, respectively) (Table 2). Total chlorophyll, chlorophyll-a and nitrogen had seasonal patterns similar to those for primary productivity (Table 3). Carbon, on the other hand, had a gradual increase throughout the season with a fall maximum of 4587 mg/m^2 substrata (Table 3).

The laboratory and field primary productivity estimates were highly correlated ($r = 0.97$ $p<0.01$). They were also highly correlated with total chlorophyll estimates ($r = 0.93$, $r = 0.92$ $p<0.01$, respectively).

Phytoplankton

Phytoplankton productivity under laboratory conditions was not significantly different than field estimates. The mean phytoplankton productivity was significantly lower in marshes flooded for two years than in the five unflooded marshes (Table 4).

Total chlorophyll, chlorophyll-a, suspended carbon and suspended nitrogen also were significantly lower in marshes flooded for two years than in the unflooded marshes (Table 4). In unflooded marshes total chlorophyll had a range of 21 to 48 mg/m^3, while flooded marshes

Table 1. Annual mean epiphyton primary productivity and biomass for unflooded and two-year flooded marshes in 1983

Measurements	Unflooded						Two-year Flooded		
	Bay 22	Large Pond	Small Pond	Marsh 11	Marsh 12	Mean (±1SE) N = 20	Marsh 3	Marsh 7	Mean (±1SE) N = 8
PRIMARY PRODUCTIVITY (mg C/m^2 substrata/h)									
Laboratory	19.6	96.3	20.6	63.7	56.9	51.4 (12.9)	64.4	98.2	81.3 (10.6)
Field	25.3	99.6	24.1	69.1	61.9	56.0 (13.3)	74.0	84.1	79.0 (6.3)
BIOMASS (mg/m^2 substrata)									
Total Chlorophyll	8.0	50.5	10.0	55.5	40.8	33.0 (8.7)	36.8	66.8	51.8 (8.5)
Chlorophyll-a	7.0	32.5	8.8	42.8	31.5	24.5 (5.5)	29.3	52.5	40.9 (7.5)
Carbon	2416	3652	1127	2101	3446	2548 (403)	4486	3760	4071 (782)
Nitrogen	151	531	87	215	382	273 (59)	565	522	540 (131)

Table 2. Seasonal fluctuations of epiphyton primary productivity (mg C/m^2 substrata/h) in the field for unflooded and two-year flooded marshes in 1983

Treatments	Marsh	Periods				
		June	July	August	September	Mean (±1SE)
Two-year flooded marshes	3	79.9	72.0	57.1	86.8	74.0 (6.4)
	7	78.5	69.0	71.3	117.2	84.1 (11.2)
	Mean	79.2	70.7	64.2	102.0	79.0 (16.3)
Unflooded marshes	11	127.4	85.1	21.3[a]	42.4	69.1 (23.5)
	12	68.0	26.8[a]	42.3	110.5[a]	61.9 (18.3)
	Bay 22	26.5	38.6	31.7	4.2[a]	25.3 (7.4)
	Large Pond	266.0	38.0[a]	77.4	17.2[a]	99.6 (56.9)
	Small Pond	9.0	17.6[a]	20.1	49.7[a]	24.1 (8.9)
	Mean	99.4	41.2	38.6	44.8	56.0 (14.6)

[a]F test significant ($p<0.05$) with the previous month.

Table 3. Seasonal fluctuation of mean epiphyton primary productivity and biomass for unflooded and two-year flooded marshes in 1983

Measurements	Periods			
	June	July	August	Sept.
	PRIMARY PRODUCTIVITY (mg C/m^2 substrata/h)			
Laboratory	95.0	42.5	43.0	61.1
Field	93.6	49.6	45.9	55.8
	BIOMASS (mg/m^2 substrata)			
Total Chlorophyll	57.1	29.1	24.4	42.6
Chlorophyll-*a*	37.7	22.1	20.0	36.9
Carbon	2179	2233	2746	4587[a]
Nitrogen	385	186	223	558[a]

[a] F test significant ($p<0.05$) with the previous month.

had a mean of 4.2 and 3.4 mg/m^3 (Table 4). Chlorophyll-a was 87% and 89% of total chlorophyll in the unflooded and flooded marshes, respectively. Except for bay 22, suspended carbon and suspended nitrogen estimates were similar in unflooded marshes with an annual mean of 3796 and 584 mg/m^3, respectively (Table 4). Flooded marshes, had an average of 657 and 95 mg/m^3 for suspended carbon and suspended nitrogen, respectively (Table 4).

A mid-summer peak in phytoplankton productivity occurred in flooded marshes, whereas the unflooded marshes had a maximum in autumn, although these peaks were not significantly different than previous month. Different areas in the unflooded marshes, however, had different seasonal patterns (Table 5). In all marshes, mean biomass (suspended carbon, suspended nitrogen, total chlorophyll and chlorophyll-a) had a spring high in May and June and a fall maximum in September (Table 6).

Field and laboratory primary productivity had a very high correlation with each other ($r = 0.95$; $p<0.01$). They were also highly correlated with total chlorophyll ($r = 0.85$, $r = 0.83$; $p<0.01$). Suspended carbon had a moderate correlation with both field ($r = 0.70$, $p<0.01$) and laboratory ($r = 0.71$, $p<0.01$) primary productivity. No significant correlation was found between phytoplankton primary productivity and biomass and chemical parameters.

Table 4. Annual mean phytoplankton primary productivity and biomass for unflooded and two-flooded marshes in 1983

Measurements	Unflooded						Two-year Flooded		
	Bay 22	Large Pond	Small Pond	Marsh 11	Marsh 12	Mean (±1SE) N = 25	Marsh 3	Marsh 7	Mean (±1SE) N = 10
				PRIMARY PRODUCTIVITY (mg C/m^3/h)					
Laboratory	157.4	107.7	238.6	283.1	129.8	183.3 (26.3)	22.4	23.9	23.2 (6.2)[a]
Field	148.7	142.8	221.8	227.5	163.1	180.8 (22.3)	13.1	13.5	13.3 (2.5)[a]
				BIOMASS (mg/m^3)					
Total Chlorophyll	26.3	20.7	46.1	47.9	33.8	34.9 (5.8)	4.2	3.4	3.8 (0.5)[a]
Chlorophyll-a	23.5	18.4	38.7	40.6	30.0	30.2 (5.0)	3.8	3.0	3.4 (0.4)[a]
Suspended Carbon	5340	3140	3964	3197	3338	3796 (436)	754	561	657 (70)[a]
Suspended Nitrogen	651	511	629	605	527	584 (61)	112	78	95 (14)[a]

[a]F test significant ($p<0.05$) between unflooded and two-year flooded marshes.

Table 5. Seasonal fluctuations of phytoplankton primary productivity (mg C/m^3/h) in the field for unflooded and two-year flooded marshes in 1983

Treatments	Marsh	Periods					
		May	June	July	August	September	Mean (±1SE)
Two-year flooded marshes	3	2.2	12.0[a]	17.4[a]	27.5[a]	6.4[a]	13.1 (4.4)
	7	6.6	12.9[a]	15.0[a]	23.4[a]	9.7[a]	13.5 (2.9)
	Mean	4.4	12.5[a]	16.2[a]	25.5[a]	8.1[a]	13.3 (2.5)
Unflooded marshes	11	159.4	407.7[a]	184.8[a]	248.4	137.1[a]	227.5 (48.5)
	12	102.3	113.6[a]	209.8[a]	139.3[a]	250.7[a]	163.1 (28.8)
	Bay 22	105.9	131.7[a]	189.8	147.7	168.3	148.7 (14.5)
	Large Pond	16.9	22.2	152.2[a]	234.0[a]	288.7[a]	142.8 (54.8)
	Small Pond	2.6	113.8[a]	188.0	326.6[a]	477.7[a]	221.8 (82.9)
	Mean	77.4	157.8	184.9	219.2	264.5	180.8 (22.3)

[a]F test significant ($p<0.05$) with the previous month.

Table 6. Seasonal fluctuation of average phytoplankton primary productivity and biomass in unflooded and two-year flooded marshes in 1983

Measurements	Periods				
	May	June	July	Aug.	Sept.
	PRIMARY PRODUCTIVITY (mg C/m^3/h)				
Laboratory	71.7	107.1	121.7	187.2	200.2
Field	56.6	116.3	136.7	163.9	191.2
	BIOMASS (mg/m^3)				
Total Chlorophyll	---	22.3	14.0	20.2	47.7[a]
Chlorophyll-*a*	---	18.8	12.0	17.1	42.4[a]
Suspended Carbon	2659	1797	2288	3610	4141
Suspended Nitrogen	358	268	398	532	667

[a] F test significant ($p<0.05$) with the previous month.

DISCUSSION

Epiphyton

Prolonged flooding did not significantly increase epiphyton net productivity per unit area of artificial substrata. However, in flooded marshes, total surface area available for epiphyton increased three to four times over the area of unflooded ones and, therefore, the total annual production and biomass per unit marsh area was significantly higher in flooded marshes than in the unflooded marshes. The average annual net productivity of epiphyton in open areas of flooded marshes was estimated to be 1000 mg C/day/m^2 or 150 g C/year/m^2 (based on 12 hours a day and 150 days a year) of artificial substrata. This estimate is similar to epiphyton productivity measurements in the littoral zones of several freshwater lakes reported by Wetzel (1983a).

In this study all sampling sites were in open water areas free of emergents, and epiphytic algae were collected from 5 to 20 cm below water surface. Therefore, there was no difference in irradiation between the flooded and unflooded marshes. Several investigators have reported that irradiance is the major factor reducing productivity in freshwater marshes (Hooper and Robinson 1976; Hosseini and van der Valk 1986a; Straskraba and Pieczynska 1970). With regard to the study of algal response to flooding, Hosseini and van der Valk (1986a,b) suggested that lower productivity in marshes flooded for two years seems to be due to filamentous algae shading epiphyton. Although no significant changes in nutrient levels occurred in flooded marshes

compared to unflooded ones (Table 7), one should not rule out the possibility that an interaction between epiphyton productivity and nutrient levels occured because it is not known how much available N and P were present in the treatments. Hosseini and van der Valk (1986a) also found that increased epiphyton productivity in flooded marshes was not correlated with nutrient concentrations.

A spring peak with a fall maximum of epiphyton productivity in flooded marshes resembles seasonal patterns in shallow ponds and littoral zones of freshwater lakes but differs from that in unflooded marshes (Allen 1971; Cattaneo and Kalff 1978; Hooper-Reid and Robinson 1978; Round 1981). Although in the unflooded marshes productivity of each marsh peaked at a different time for reasons that are unknown, the unflooded marshes had a higher maximum mean productivity in spring with a decline over the rest of the season.

The average annual net productivity of epiphyton in open water areas of unflooded marshes was estimated at 670 mg C/day/m^2 or 100 g C/year/m^2 (based on 12 hours a day and 150 days a year) of artificial substrata (however, there was a lot of variation from site to site in both productivity and biomass of epiphyton (see Table 1)). This annual estimate is higher than both the value for Crescent Pond (86 mg C/day/m^2 macrophyte surface area) reported by Hooper and Robinson (1976) and the value for the littoral zone of Lawrence Lake (336 mg C/day/m^2) investigated by Allen (1971), but is nevertheless in close agreement with the value reported by Hickman (1971) for shallow, eutrophic Priddy Pool, England (63.9 mg C/m^2/h).

Table 7. Annual mean measurements of chemical parameters for unflooded and two-year flooded marshes in 1983

Chemical measurement	Unflooded						Two-year flooded		
	Bay 22	Large Pond	Small Pond	Marsh 11	Marsh 12	Mean	Marsh 3	Marsh 7	Mean
pH	9.08	8.58	8.28	8.38	8.28	8.52	8.44	8.34	8.39
Alkalinity (mg/L as $CaCO_3$)	387	489	521	686	425	502	544	576	560
Conductance (μmhos/cm)	1960	2516	2663	2620	2000	2339	2350	2224	2287
Ammonia (μg/L)	48	112	103	113	65	87.0	85	343	214
Total dissolved nitrogen (TDN) (μg/L)	2805	3860	4175	4933	3063	3693	3628	4518	4073
Total dissolved Phosphorus (TDP) (μg/L)	57	396	164	991	79	290	88.5	423	256

Phytoplankton

The mean annual net phytoplankton productivity under constant laboratory conditions (2290 mg C/m^3/day or 345 g C/m^3/year based on 12 hours a day and 150 days a year) for unflooded marshes was higher than those reported for littoral zones of freshwater lakes (Wetzel 1983a). The mean annual net primary productivity for flooded marshes was estimated as 166 mg C/m^3/day or 25 g/m^3/year based on 12 hours a day and 150 days a year) which is in close agreement with the productivity of littoral zones of several lakes reported by Wetzel (1983a). As with epiphyton, reduced irradiance within stands of emergent macrophytes seems to be a factor limiting planktonic productivity in littoral zones of freshwater lakes and wetlands (Brandle et al. 1970; Dokulil 1973; Goulder 1969; Straskraba and Pieczynska 1970; Wetzel 1983a). The extremely low phytoplankton productivity in flooded marshes is not due to light limitation because the sampling sites in this study were in open water areas with no light reduction. Lower nutrient levels in flooded marshes have been suggested as one reason for lower productivity (Hosseini and van der Valk 1986a), although no major changes were noticed in the water chemistry of flooded marshes as compared to unflooded ones (Table 7). Perhaps one reason for low phytoplankton productivity and biomass in flooded marshes was heavy grazing by zooplankton. Murkin (1983) reported very high densities of cladocerans, which are primarily planktivors, in the water column of flooded marshes. Timms and Moss

(1984) also have reported reductions in phytoplankton population due to grazing in a shallow wetland.

On a per unit marsh area basis, phytoplankton in unflooded marshes are about twice as productive as in flooded marshes (58 mg $C/m^2/h$ versus 25 mg $C/m^2/h$). Hosseini and van der Valk (1986a) also found phytoplankton productivity per unit area of marsh higher in unflooded marshes than flooded ones. Total chlorophyll, chlorophyll-a, suspended carbon and suspended nitrogen per unit area of marsh indicate that the unflooded marshes have twice the algal biomass of the flooded marshes (Hosseini and van der Valk 1986a), although ratios such as carbon:nitrogen and total chlorophyll:chlorophyll-a were not affected by flooding. An increase in carbon:productivity ratio from 21 in unflooded to 28 in flooded marshes suggests that perhaps there was more non-algal carbon in flooded marshes (i.e. zooplankton, invertebrates, fungi, etc.).

Flooding also affected the seasonal pattern of phytoplankton productivity. Areas within the unflooded marshes had different seasonal peaks (Table 5). There was a gradual increase in mean productivity over the growing season, a pattern different from that reported for littoral zones of some lakes (Kalff and Knoechel 1978; Wetzel 1983a). Both flooded marshes, on the other hand, had similar seasonal patterns with a mid-summer maximum.

For reasons unknown to us, unflooded marshes were extremely heterogeneous in their algal primary productivity, total chlorophyll and chlorophyll-a (see Table 5). This heterogeneity is an inherent

part of prairie marshes (Crumpton 1986), which are a mosaic of different aquatic habitats. This needs to be considered when studying algal communities of these wetlands.

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SUMMARY DISCUSSION

Epiphyton

In both 1982 and 1983, prolonged flooding did not significantly increase epiphyton net productivity and biomass per unit area of artificial substrata. However, available surface area for epiphyton increased three to four times in flooded marshes compared to unflooded ones, and, therefore, annual productivity and biomass per unit marsh area was significantly higher in flooded marshes than in unflooded marshes. For 1983, the mean annual net productivity of epiphyton for flooded and unflooded marshes was estimated as 1000 mg C/day/m^2 of artificial substrata (150 g C/m^2/year based on 150 days) and 670 mg C/m^2/day (1000 g C/m^2/year based on 150 days) respectively. These values are closer to measurements reported for littoral zones of freshwater lakes (Wetzel 1983a) and higher than similar marshes reported before (Hooper and Robinson 1976).

In 1982, epiphyton primary productivity per unit area of artificial substrata in marshes flooded one year was significantly higher perhaps because of increased irradiance in flooded marshes which were largely free of emergent macrophytes. Nutrients, on the other hand, seem not to be a factor for higher productivity in marshes flooded one year. Primary productivity in marshes flooded two years was not significantly different than in unflooded marshes. One likely reason is reduced irradiance for epiphyton caused by masses of floating filamentous algae in marshes flooded two years. Efficiency

of algae as indicated by productivity:chlorophyll or carbon:nitrogen ratios remained the same in both flooded and unflooded marshes.

Flooding also affected the seasonal pattern of epiphyton productivity. Unflooded marshes had a spring maximum in mean productivity and declined thereafter, whereas flooded marshes had a fall maximum, which resembles the seasonal patterns of epiphyton in littoral zones of lakes (Allen 1971; Cattaneo and Kalff 1978; Round 1981).

Total productivity:chlorophylly and productivity:chlorophyll-a did not change throughout the season in these freshwater marshes, while carbon:productivity ratio increased later in the season perhaps due to accumulation of dead algal cells and other non-algal components (Hooper and Robinson 1976).

Phytoplankton

For 1983, the mean annual net primary productivity of phytoplankton was estimated as 190 mg C/m^3/day (43.5 g C/m^3/year based on 150 days) for flooded marshes versus 2290 mg C/m^3/day (345 g C/m^3/year based on 150 days) for unflooded ones. Flooded marshes in spite of higher irradiance than unflooded, still had lower primary productivity and biomass. The death of emergent macrophytes in flooded marshes did not result in an increase in phytoplankton productivity. The reduction in phytoplankton productivity was not due to dilution, since per unit area unflooded marshes were about two times more productive than flooded ones (58 mg C/m^2/h versus 25 mg C/m^2/h, respectively). Lower nutrient levels and heavy zooplankton

grazing are suggested to be the reasons for the differences in productivity and biomass of phytoplankton in flooded and unflooded marshes.

Flooding affected neither the efficiency of phytoplankton shown by productivity:chlorophyll ratios nor the carbon:nitrogen or chlorophyll-a:total chlorophyll ratios. Carbon:productivity ratios increased in flooded marshes suggesting that there was more non-algal carbon suspended in flooded than in unflooded marshes. Flooding also affected the seasonal pattern of phytoplankton productivity. Unflooded marshes, on the average, had increasing productivity with a fall maximum, while flooded marshes had a mid-summer maximum.

The efficiency (productivity:chlorophyll ratios) of phytoplankton algae decreased in mid-summer in these freshwater marshes. However, suspended carbon:nitrogen ratios did not change seasonally, except in May because of more suspension of non-algal components after ice melting.

Filamentous algae

Increased irradiance, due to macrophyte death, apparently created favorable conditions for extremely high algal biomass in marshes flooded two years compared to unflooded ones. However, other factors, such as differences in temperature, substrata (litter) abundance, and water depth, may also play a role. Nutrients seem not to be a factor for higher algal biomass in flooded marshes since no correlation between chemical parameters and algal biomass was noticed.

No other study quantifying the biomass or productivity of filamentous algae in wetlands seems to have been done. This community is, nevertheless, one of the most important primary producers in prairie wetlands during the high water or lake stage of their wet/dry cycles.

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APPENDIX

Table A1. Epiphyton and phytoplankton annual mean primary production in three flooding treatments in 1982. Epiphyton N = 16 sits per marsh per period Phytoplankton N = 8 sites per marsh per periods = 4.

	Epiphyton (mg C/m^2/h)		Phytoplankton (mg C/m^3/h)	
Marsh	Mean	SE	Mean	SE
		TWO YEAR-FLOODED		
1	6.10	1.67	2.15	0.81
2	5.57	1.38	3.10	1.57
4	3.13	0.61	1.88	0.50
5	4.95	1.37	2.18	0.71
6	4.90	1.80	2.55	0.37
8	4.60	1.79	2.95	0.89
9	3.40	1.28	1.55	0.41
10	4.03	0.39	4.60	2.27
		ONE YEAR-FLOODED		
3	5.45	0.72	2.48	0.46
7	7.18	1.14	3.23	1.05
		UNFLOODED		
11	4.85	1.38	66.70	20.34
12	2.20	0.25	10.80	3.33

Table A2. Annual mean of ash-free dry weight (g/m^2) filamentous algae at three flooding treatments in 1982. 16 sites per marsh per period. Periods = 4. N = 64.

Marsh	Mean	SE
	TWO YEAR-FLOODED	
1	29.4	5.1
2	50.3	4.5
4	150.7	24.5
5	38.9	6.4
6	91.2	31.1
8	38.2	9.9
9	112.0	35.1
10	19.6	8.3
	ONE YEAR-FLOODED	
3	26.7	6.7
7	13.4	9.9
	UNFLOODED	
11	0.4	0.2
12	4.8	2.0

Table A3. Pearson correlation coefficients ($P<0.01$) for different measurements of phytoplankton algae in the experimental marsh complex of Delta Marsh, Manitoba in 1982.

Measurements	Suspended Carbon	Chlorophll-*a*	TDP	TDN
Primary Production[a]	.91	.87	.72	.61
Suspended Carbon		.97	.46	--
Total Dissolved Phosphorus (TDP)				.96

[a]Laboratory

Table A4. Percent dark $^{14}CO_2$ uptake measured for epiphyton and phytoplankton in 1983.

	% dark uptake			
	Epiphyton		Phytoplankton	
Treatments	Laboratory	Field	Laboratory	Field
Natural marsh areas	1.8	1.7	2.3	2.7
Two-year flooded marshes	1.1	0.9	6.1	8.8