Primary Productivity and Biomass of Periphyton and Phytoplankton in Flooded Freshwater Marshes*

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Abstract: Periphyton and phytoplankton productivities, chlorophyll *a*, carbon and nitrogen concentrations in experimental marshes flooded 1 m above normal level for 1 year and 2 years were compared to values for unflooded control marshes. Primary productivity was estimated from uptake of ^{14}C-bicarbonate. Periphyton productivity was measured on artificial substrata that had been placed in the marshes. Phytoplankton productivity was estimated using samples of marsh water incubated in 60-ml glass bottles. All productivity measurements were made in the laboratory at 19°C and 15 μE m^{-2} sec^{-1} of PAR, a low level of irradiance compared to field levels. Mean phytoplankton primary productivity, chlorophyll *a*, total suspended carbon, and total suspended nitrogen in control marshes were significantly higher than in flooded marshes. Mean periphytic primary productivity per unit area of artificial substrata was significantly higher in marshes flooded for 1 year than in control marshes; however, there was no significant difference between periphytic primary productivity of marshes flooded for 2 years and control marshes. There were no significant differences between control and flooded marshes in the amounts of periphytic chlorophyll *a*, particulate carbon, or nitrogen per unit area of artificial substrata. Flooding increased periphytic productivity and two of three measures of biomass, while phytoplankton productivity and biomass were reduced. Because the bulk of the nutrients were sequestered by the periphyton and metaphyton, we hypothesize that the increases in periphytic and metaphyton production associated with flooding were responsible for the decrease in phytoplankton production.

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INTRODUCTION

Few studies have addressed the contribution of phytoplankton or periphyton to the overall primary productivity of shallow water systems or wetlands dominated by macrophytes (Brandle et al., 1970; Brown, 1972; Dokulil, 1973; Goulder, 1969; Hickman and Jenkerson, 1978; Wetzel, 1983). Periphyton growing on macrophytes in the littoral zones of shallow freshwater lakes and ponds, however, are known to be important components of overall aquatic primary productivity (Allen, 1971; Hooper and Robinson, 1976; Wetzel, 1964, 1983). Freshwater marshes with their often dense stands of emergent and submersed macrophytes provide extensive surface areas for colonization by periphytic algae.

There appear to be no investigations of the impact of water-level changes, characteristic of many prairie wetlands, on the primary productivity of either their periphyton 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; Meeks, 1969; van der Valk, 1981, 1985; van der Valk and Davis, 1978, 1980; Walker, 1965). Ollason (1977) indicated that algal communities in fluctuating environments may undergo large-scale changes.

The objective of this study was to investigate the impact of abnormally high water level on periphytic and phytoplankton primary productivities and biomass in a freshwater wetland. The responses of phytoplankton and periphyton to flooding duration were measured in an experimental marsh complex where three flooding treatments were present in 1982 (unflooded control marshes, marshes flooding in 1982, and marshes flooding in 1981).

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 control marshes. The initial vegetation in the experimental marshes was similar to that in the main Delta marsh and consisted of zones of emergent vegetation (bands dominated by *Scolochloa festucacea, Phragmites australis, Typha glauca,* or *Scirpus lacustris* var. *acutus*) interspersed with areas free of emergents, locally called bays (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 dams. Thus the "normal" water level of the Delta marsh for over 20 years 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 occurred before lake level regulation began. Two additional marshes were flooded to 248.5 m in 1982. Most of the emergent vegetation was killed in flooded marshes and, consequently, there was much standing litter, particularly dead *Phragmites* and *Typha* shoots. In marshes flooded for 2 years, only that portion of the dead shoots below water remained standing.

Field Sampling

Each of the 12 marshes was divided from north to south into 10 zones, and in each marsh 4 of these were randomly selected. Four sites within each zone were randomly chosen as periphyton sampling sites, for a total of 16 periphyton sites per marsh. Two sites within each zone were randomly selected for phytoplankton sampling. Extruded clear acrylic rods of 0.63 cm diameter were used as artificial substrata for periphyton (Goldsborough and Robinson, 1983; Robinson, 1983). Each acrylic rod was notched at 2 cm intervals prior to placement in the field (Goldsborough and Robinson, 1983). Rods were positioned vertically at all sites in May 1982. Samples were collected at 4-week intervals from June through September. Phytoplankton samples were collected from 20 cm below water surface at the same times that periphyton samples were collected.

Primary Productivity Measurements

Periphyton and phytoplankton productivities were estimated using a ^{14}C-bicarbonate uptake method (Goldsborough and Robinson, 1983; Peterson, 1980). A 2-cm length of acrylic rod colonized by periphytic algae was clipped off and placed in a 30-ml glass bottle filled with marsh water passed through a GFC Whatman filter (Goldsborough and Robinson, 1983). A phytoplankton sample consisted of a 60-ml glass bottle filled with marsh water. Known amounts (0.5 to 2 ml) of standardized $NaH^{14}CO_3$ with known activities (4,500,000 dpm ml^{-1}) were added to each algal sample, which was then incubated in the laboratory for 4 hours at a constant low irradiance of 15 μE m^{-2} sec^{-1} of PAR and temperature of 19 $\pm$ 1°C. All productivity estimates were made under very low irradiance levels and represent only 10 to 13% of the productivity found under light-saturated conditions. Subsequent unpublished studies under low-light conditions indicate that about 25% and 50% of the uptake for periphyton and phytoplankton, respectively, are dark uptake. No correction for the dark uptake is made in the data presented.

After incubation, periphyton samples still attached to the acrylic rods and phytoplankton samples that had been filtered onto 0.45 μm cellulose acetate filters were acid-fumed with concentrated hydrochloric acid and placed in a vial containing 10 ml of Bray's scintillation cocktail (Goldsborough and Robinson, 1983). Within 24 hours both rods and filters 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 per unit of artificial substratum for periphyton 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 means of 16 measurements for periphyton and 8 measurements for phytoplankton for each marsh per period were used in all analyses.

Chlorophyll *a*, Carbon, and Nitrogen

One piece of colonized acrylic rod from each of the 16 periphyton sites within each marsh was scraped with the dull edge of a scalpel into a composite periphyton sample; all macroinvertebrates were removed at the same time. This composite sample in a known volume of distilled water was mixed carefully to produce a homogeneous mixture. One third of this sample was filtered, frozen and maintained in the dark, and extracted in 95% methanol (Holm-Hansen and Riemann, 1978) for measurement of chlorophyll *a* by a fluorometric method (APHA, 1980; Marker, 1972; Stainton et al., 1977). Another third was filtered onto a pre-ashed GFC Whatman filter and its particulate nitrogen and carbon content determined at the Freshwater Institute, University of Manitoba, Winnipeg, Canada, using methods described in Stainton et al. (1977). The other third was preserved to determine its species composition.

For phytoplankton, water samples from the eight sampling sites in each marsh were mixed into a composite sample. Five hundred ml of this composite sample was filtered through GFC Whatman filters and frozen. The chlorophyll *a* of the frozen algae 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 was filtered through a precombusted GFC filter, and particulate carbon and nitrogen of the sample were measured using the methods described in 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. Water samples to determine ammonia, total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) also were collected during the same period in all marshes (Kadlec, 1986) and analyzed according to the methods described by Stainton et al. (1977). 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 SAS 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

Periphyton

Periphyton productivity per unit area of substratum was significantly higher (6.31 mg C m^{-2} h^{-1}) in marshes flooded 1 year than in control marshes (3.52 mg C m^{-2} h^{-1}); in marshes flooded 2 years (4.58 mg C m^{-2} h^{-1}), it was not significantly different from either the control or 1-year flooded marshes (Fig. 1). Productivities were lowest in June and highest in September in all treatments; i.e., there was no shift in seasonal productivity patterns because of flooding (Fig. 2).

Periphyton chlorophyll *a*, carbon, and nitrogen were not significantly different among treatments (Fig. 1). Carbon and nitrogen reached their maxima in unflooded marshes during August, whereas marshes flooded 2 years had their maxima during September. There was an increase in carbon and nitrogen from July to August in both unflooded and 2-year flooded marshes, whereas marshes flooded 1 year gradually increased from June through September (Fig. 2). Mean chlorophyll *a* increased from July to August in all treatments and then stayed constant (Fig. 2).

The primary productivity of periphyton was poorly correlated with chlorophyll *a* concentrations ($r = 0.51$, $P < .01$), but the correlation between productivity and particulate carbon ($r = 0.73$, $P < .01$) was fairly strong. There also was a low correlation ($r = 0.52$, $P < .01$) between carbon and chlorophyll *a*. No significant correlation was observed between periphyton productivity or biomass and any physicochemical parameter.

Phytoplankton

Mean phytoplankton productivity, as well as biomass, was significantly higher in control marshes (38.8 mg C m^{-3} h^{-1}) than in either of the flooded treatments (2 to 3 mg C m^{-3} h^{-1}) (Fig. 3). There were no significant differences between 1-year and 2-year flooded marshes (Fig. 3). The two control marshes differed significantly in mean annual phytoplankton productivity, 67 and 11 mg C m^{-3} h^{-1}). There was much less heterogeneity, however, in primary productivity in either the 2-year flooded marshes (2 to 5 mg C m^{-3} h^{-1}) or the two marshes flooded for 1 year (2 and 3 mg C m^{-3} h^{-1}). Productivity of phytoplankton in control marshes reached a maximum in September, whereas marshes flooded 1 year and 2 years reached maxima in July or August (Fig. 4).

Chlorophyll *a* in unflooded marshes peaked in August, whereas in marshes flooded 1 year and 2 years it peaked in June and July, respectively (Fig. 4). Suspended carbon and nitrogen increased from July to August in control marshes but decreased in flooded marshes from June to July and then remained constant (Fig. 4). Both suspended carbon and chlorophyll *a* had very high correlations with primary productivity ($r = 0.91$ and $r = 0.87$, respectively, $P < .01$) and with each other ($r = 0.98$, $P < .01$).

Primary productivity also was correlated with both TDP ($r = 0.72$, $P < .01$) and TDN ($r = 0.61$, $P < .01$).

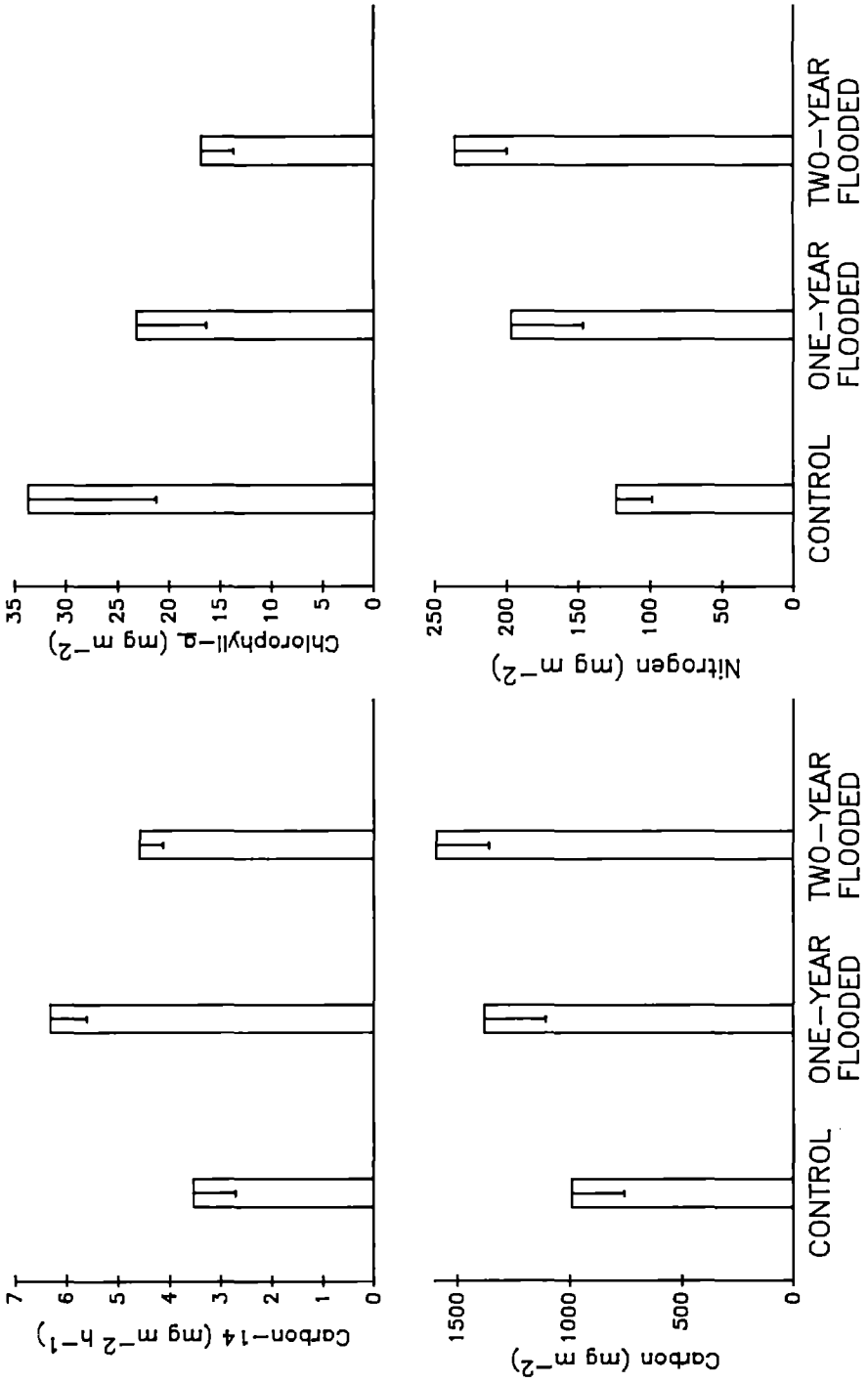

Fig. 1 Mean annual periphyton productivity (^{14}C-bicarbonate uptake) and chlorophyll *a*, suspended carbon, and suspended nitrogen per m^2 of substrata in control, 1-year, and 2-year flooded marshes. The bars represent standard errors.

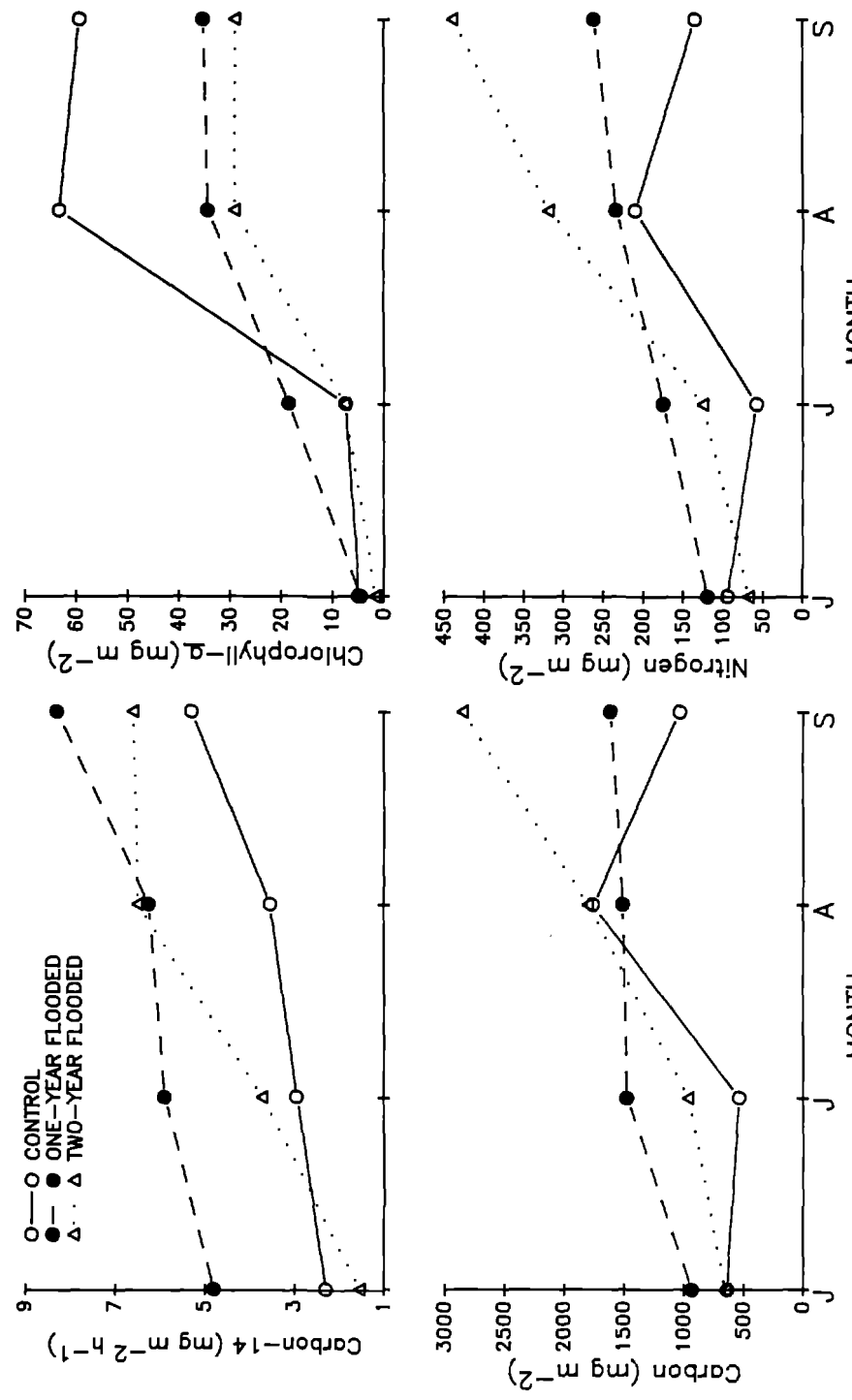

Fig. 2 Mean monthly periphyton productivity (^{14}C-bicarbonate uptake) and chlorophyll *a*, carbon, and nitrogen per m^2 of substrata in control, 1-year, and 2-year flooded marshes in 1982.

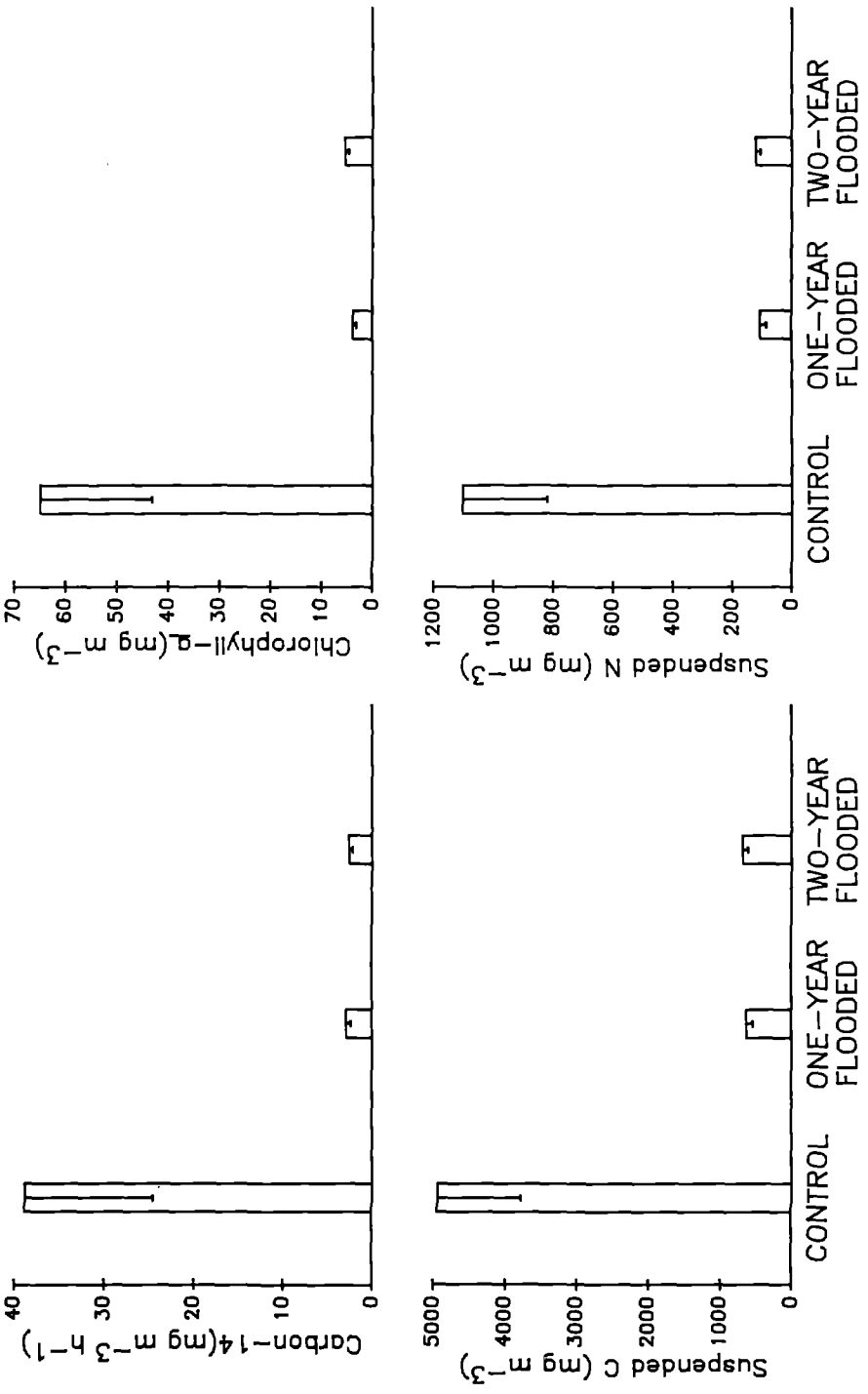

Fig. 3 Mean annual phytoplankton productivity (^{14}C-bicarbonate uptake) and chlorophyll *a*, suspended carbon, and suspended nitrogen per m^3 in control, 1-year, and 2-year flooded marshes. The bars represent standard errors.

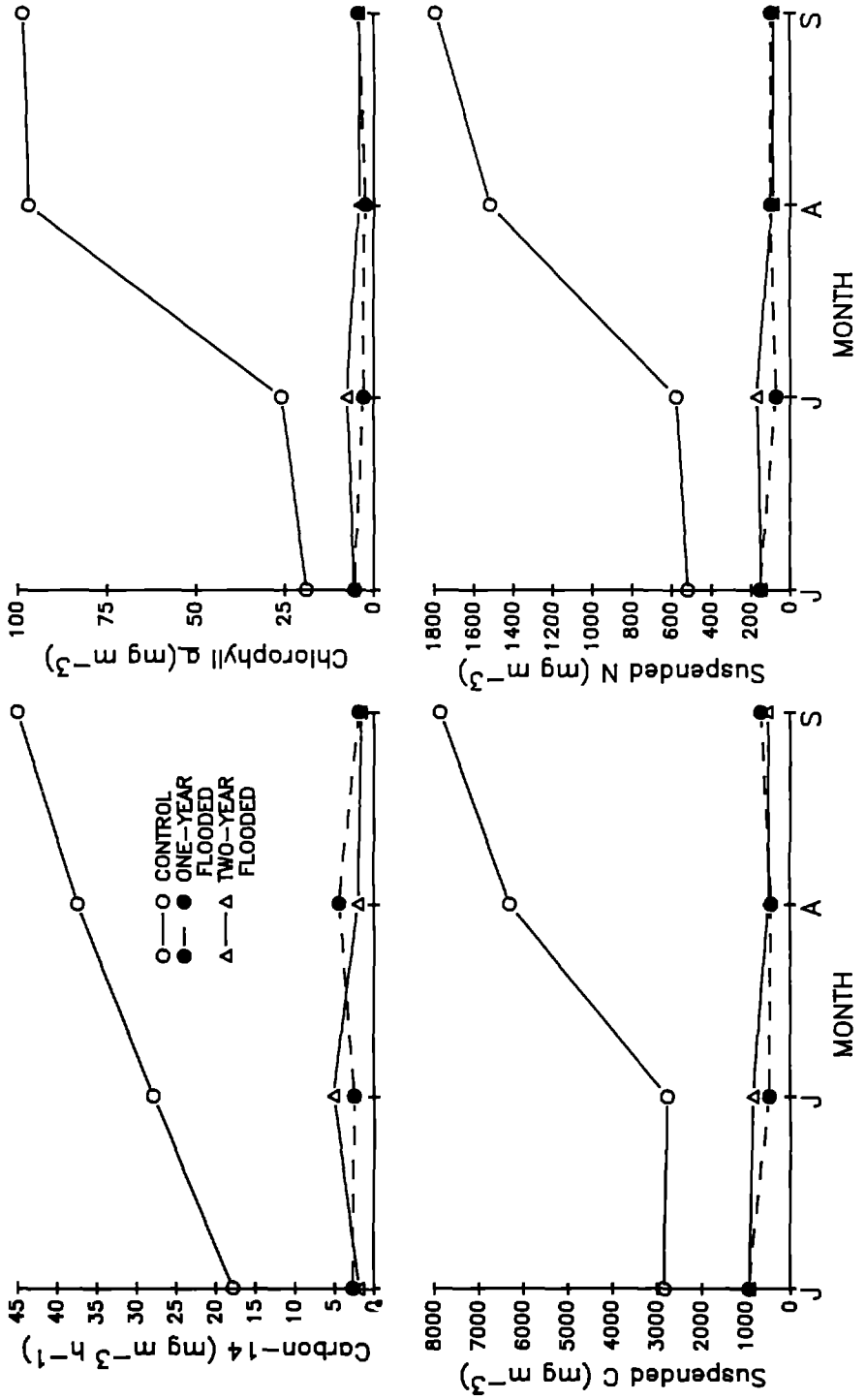

Fig. 4 Mean monthly phytoplankton productivity (^{14}C-bicarbonate uptake) and chlorophyll *a*, suspended carbon, and suspended nitrogen per m^3 in control, 1-year, and 2-year flooded marshes in 1982.

DISCUSSION

Periphytic productivity in marshes flooded 1 year generally was significantly higher than in control marshes. One reason for this higher productivity could have been increased irradiance below the surface due to the elimination of the macrophyte canopy. Only dead standing litter remained in these cells after 1 year of flooding (Murkin and Kadlec, 1986). Hooper and Robinson (1976) and Straskraba and Pieczynska (1970) found that low productivity of periphytic algae within *Phragmites* and dense *Typha* sites was related to low light intensity. Why then was periphyton productivity in marshes flooded for 2 years not significantly different than in the control marshes? One possible reason was the larger biomass of metaphyton in 2-year flooded marshes (Hosseini and van der Valk, this volume). Field observations indicated that metaphyton shaded many of the periphyton sampling sites.

Higher periphytic productivity in flooded marshes might be expected also because of increased nutrients in the water column released by the dead macrophytes. In fact, mean ammonia and TDP were lower in flooded marshes, compared to control marshes (Table 1), and no significant correlation was found between these chemical parameters and periphytic productivity. However, this does not mean that changes in nutrient levels have had no effect on periphyton productivity, since it is not possible to determine what amounts of available nitrogen and phosphorus were present in the three treatments.

TABLE 1

Annual Mean of Chemical Parameters Measured in Control, 1-Year, and 2-Year Flooded Marshes in 1982

	Flooding Treatments		
	Control	1-Year	2-Year
pH	7.96	8.05	8.30
Alkalinity (mg l^{-1} as $CaCO_3$)	539	620	543
Conductance (μmhos cm^{-1})	2521	2831	2501
Ammonia-N ($\mu g\ l^{-1}$)	296	159	110
Total dissolved nitrogen ($\mu g\ l^{-1}$)	733	3986	3815
Total dissolved phosphorus ($\mu g\ l^{-1}$)	778	208	183

Periphyton productivity and biomass are expressed per unit area of artificial substrata. However, in flooded marshes, total available surface area for periphyton increased fourfold to fivefold over control marshes (mean water depth of 0.20 m for control versus 1.0 m for flooded marshes), and the percentage of the marsh surface area that was flooded also increased significantly. Therefore, the total annual productivity and biomass per unit marsh area were significantly higher in flooded than in control marshes. Periphyton 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, Michigan (Allen, 1971), and Crescent Pond, Delta Marsh, Manitoba, Canada (Hooper and Robinson, 1976).

Mean productivity and biomass of phytoplankton were significantly higher in control than in flooded marshes. 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 likely are not due to light limitation. The primary productivity of phytoplankton is positively correlated with TDN and TDP concentrations. Lower nutrient concentrations in the water column of the flooded marshes may have reduced phytoplankton productivity.

Another potential reason for the low phytoplankton productivity of flooded marshes may have been heavy grazing by zooplankton. Murkin (1983), who also worked in the MERP complex during 1981 and 1982, reported a one-hundred-fold increase in cladocerans, which are primarily planktivores, in the water column of flooded marshes compared with controls. Timms and Moss (1984) have also reported a reduction in phytoplankton populations due to grazing. Low phytoplankton productivity in flooded marshes could also potentially 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 the mean biomass of control marshes is still twofold to threefold higher than that of flooded marshes (7.8 mg C m^{-2} vs 2.8 mg C m^{-2} for control and flooded marshes). Nevertheless, total phytoplankton production in the flooded marshes is higher than in the control marshes because of the much greater area with standing water in the flooded marshes.

Phytoplankton chlorophyll *a* was positively correlated with productivity, perhaps since less chlorophyll *c* and degraded phaeophytin generally are found in phytoplankton compared to periphytic communities. Though all components of organic carbon, such as algae, zooplankton, invertebrates, fungi, and so forth, were included in measurements of suspended carbon, the high correlation with productivity suggests that suspended carbon may be used to estimate algal biomass.

Periphyton productivity and two of the three measures of biomass per unit area of substrata generally increased in flooded marshes, whereas phytoplankton productivity and biomass decreased. Why these two communities should respond so disparately to flooding is not at all obvious and needs further investigation. Our data suggest two hypotheses. One hypothesis is that periphyton communities, and also metaphyton (Hosseini and van der Valk, this volume), are able to respond more rapidly than phytoplankton to nutrient releases from dying plants and the associated increased irradiance. Periphyton productivity per unit area of substrata and metaphyton biomass increased throughout the first year of flooding and remained high during the second year. This increased productivity of periphyton plus a significant increase in the colonizable surface area and in metaphyton biomass seem to have resulted in the sequestering of nutrients released by dying plants by these communities, as well as a decrease in available nutrients in the water column that has adversely affected the production of phytoplankton.

Our second hypothesis is that phytoplankton production per unit volume in the flooded cells has been reduced by overgrazing by cladocerans and other planktivores whose numbers increased dramatically after flooding. This hypothesis may explain why phytoplankton productivity and biomass declined after flooding, but it does not explain why periphyton productivity and biomass per unit of substrata increased. These hypotheses may begin to explain why phytoplankton and periphyton respond so differently to flooding in prairie wetlands.

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