WETLANDS, Vol. 17, No. 2, June 1997, pp. 182–194

THE PRIMARY PRODUCTIVITY OF BENTHIC AND PLANKTONIC ALGAE IN A PRAIRIE WETLAND UNDER CONTROLLED WATER-LEVEL REGIMES

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Abstract: There have been few measurements of primary productivity by benthic (periphytic) and planktonic algae in prairie wetlands so their quantitative importance relative to other primary producers is largely unknown. We measured the daily productivity (inorganic carbon assimilation per m^2 of wetland area) of phytoplankton, epipelon, epiphyton, and metaphyton in ten wetland cells in Delta Marsh, Manitoba over a five-year period. Water levels in the cells were manipulated so that some cells had normal water levels for the wetland, while water depths increased 30 cm or 60 cm in other treatments. With increasing water depth, phytoplankton productivity increased while that of epipelon, epiphyton, and metaphyton decreased. Metaphyton was the largest contributor to total algal productivity (70%), followed by epiphyton (23%), phytoplankton (6%), and epipelon (1%). Phytoplankton had the highest photosynthetic efficiency (C assimilated per unit chlorophyll), despite being a minor contributor to total productivity. Variations in P-I parameters (α, β, I_k, and P_{max}) were considerable, possibly due to temporal and spatial fluctuation in the abiotic environment. Algal productivity was comparable to that of submersed and emergent macrophytes, suggesting that algae are probably important resources in supporting food webs in prairie wetlands.

Key Words: algae, periphyton, epipelon, epiphyton, metaphyton, phytoplankton, photosynthesis, productivity, marsh, wetland, prairie, Canada

INTRODUCTION

Most measurements of primary productivity in freshwater wetlands have focused on submersed and emergent macrophytes (e.g., Brinson *et al.* 1981). As yet, there is comparatively little information on the functional contributions by algae (Vymazal 1994). Therefore, it has proven difficult to delineate the routes of energy flow and the structure of food webs within wetlands (e.g., Batzer and Wissinger 1996, Keough *et al.* 1996). Consequently, management decisions are often based on assumptions of the relative importance of suspended and rooted primary producers rather than direct evidence (Murkin 1989).

Four algal assemblages are present to varying degrees in wetlands. Phytoplankton is comprised of truly planktonic and detached benthic cells suspended within the water column; epipelon is associated with illuminated sediments in open water areas; epiphyton colonizes the submersed surfaces of live and dead macrophytes; and metaphyton, typically macroscopic, filamentous and thalloid green algae, forms submersed and suspended macroscopic mats. Although some studies have quantified the annual areal-based productivity of individual algal assemblages (Stanley 1976, Hooper and Robinson 1976, Reeder and Mitsch 1989, Schalles and Shure 1989, Cronk and Mitsch 1994, Robarts *et al.* 1995), no study has compared concurrently the proportionate contributions to total algal productivity by each of the four assemblages.

Table 1. Algal biomass (mg chlorophyll-a per m^2 of wetland area) in the MERP cells during the ice-free periods of 1985 through 1989. Data are summarized from Robinson *et al.* (1997).

Assemblage	Mean	Range	% of Total
Phytoplankton	7	<1–39	1
Epipelon	4	<1–17.5	1
Epiphyton	67	6–182	11
Metaphyton	530	123–1,309	87

The objectives of this study were three-fold: first, to provide comprehensive long-term data on the productivity (C fixation per unit wetland area) of phytoplankton, epipelon, epiphyton, and metaphyton in a freshwater prairie wetland; second, to determine the relative contributions of these groups to total primary productivity; third, to investigate the effects of experimental water-level manipulation (Murkin *et al.* 1984) on algal productivity. Water level change is an inherent property of prairie wetlands (van der Valk and Davis 1978) but its effect on primary productivity is not well documented, especially in light of forecast climate warming in central North America.

METHODS

Site Description

This study was conducted as part of the Marsh Ecology Research Program (MERP) in Delta Marsh, a 22,000-hectare prairie wetland on the south shore of Lake Manitoba, Canada (50°11′N 98°19′W). The objectives behind MERP are described in detail elsewhere (Murkin *et al.* 1984). One principal objective was to examine the role of water-level regime on marsh productivity. Ten diked mesocosms (cells) of 5.5–7.7 ha area were subjected to controlled water level manipulation. All cells were drawn down in 1984 prior to five years of flooding: three to a "low" depth (mean 7–28 cm) similar to the long-term level of Delta Marsh, four to a "medium" depth (30 cm deeper than normal), and three to a "high" depth (60 cm deeper). The precise depth profiles of each cell were mapped to account for irregular bottom topography. This study was conducted during the five years of experimentally altered water levels (1985–1989).

We used the modeling method of Fee (1973), as adapted by Jones (1984) for epiphyton, to estimate the areal productivity (C assimilated per m^2 of wetland area) of the four algal assemblages. This procedure incorporated regular estimates of algal biomass expressed as area-based chlorophyll-a (Table 1; Robinson *et al.* 1997), numerical relationships between biomass-normalized carbon assimilation rates (specific productivity) and irradiance, and measurements of ambient photosynthetically active radiation (PAR).

Photosynthesis–Irradiance Relationships

Phytoplankton. Three sampling sites were established randomly in each cell on each sampling date. In all cases, depth-integrated phytoplankton samples were collected with a 5.8-cm ID acrylic tube at four times during 1986. Samples were collected to avoid contamination by other algal assemblages.

On each date and at each site, water samples were filtered (Whatman GF/C) and analyzed for chlorophyll-a (Chl-a) following Robinson *et al.* (1997). Three aliquots of water were also dispensed into glass culture tubes for productivity experiments. One tube was blackened with paint and black plastic tape to exclude all light. Tubes were inoculated with a known activity of $NaH^{14}CO_3$ (37 kBq/mL) and placed in a water-filled incubator for two hours at ambient water temperatures. The incubator was front lit by a high pressure sodium vapor lamp (Sylvania Lumalux LU-70), creating a light gradient from ≈ 15–2,000 μmole m^{-2} s^{-1} PAR, similar to the *in situ* range. Samples were positioned in the incubator so that one sample from each site within the cell was exposed to "high" light and the other to "low." Dark samples were held at the rear of the incubator. The irradiance to which each sample was exposed in the incubator was determined with a Li-Cor LI-185 meter equipped with a LI-192SA underwater quantum sensor. Following the incubation, the samples were filtered (Gelman 0.45-μm pore-size filters), fumed over concentrated HCl for one minute to liberate residual inorganic ^{14}C and placed into vials of Scintivers® (Fisher Scientific) scintillation cocktail. Sample radioactivity (dpm) was determined using a Beckman LS3801 liquid scintillation counter, programmed for H-number quench correction. As samples were not digested prior to counting, this method may underestimate the radioactivity of highly quenched samples.

Specific (Chl-a normalized) phytoplankton productivity was determined according to the formula:

$$\mu g\ C\ L^{-1}\ h^{-1}\ \mu g^{-1}\ \text{Chl-a} = \frac{dpm_S \times C \times 1.05}{dpm_T \times T \times \text{Chl}} \quad (1)$$

where dpm_S is the radioactivity of each sample corrected for dark uptake; C is the DIC of marsh water (μg C L^{-1}) as determined from alkalinity, pH and temperature (APHA 1980); 1.05 is an isotope discrimination factor (Strickland and Parsons 1972); dpm_T is the radioactivity of added ^{14}C; T is the incubation time (hours); and Chl is pheophytin-corrected Chl-a (μg L^{-1}), measured according to Marker *et al.* (1980).

Similar experiments (six in 1986, 11 in 1988) were

conducted on phytoplankton samples from a single site in an adjacent undiked region of Delta Marsh. These incubation experiments were combined for the description of the parameters related to specific productivity and irradiance.

Epipelon. Epipelon developed in the cells following flooding of upland vegetation and exposure of bare sediments. Sampling sites were not at permanent locations but were selected at random from representative portions of the progressively expanding area of open sediment. Samples were collected on three dates during the ice-free period of 1986.

The sampling procedure followed Eaton and Moss (1966). At each site, the surface sediment (0–5 mm) within a 5.8-cm ID coring tube was aspirated into a bottle and returned to the laboratory, where it was decanted into a blackened beaker and settled in the dark for 24–30 h. Overlying water was siphoned off until the sediment was exposed. Circular pieces of untreated lens paper of the same diameter as the beakers were placed on the moist sediment surface. All samples were placed on an unshaded outdoor platform and covered with a clear acrylic lid to enable epipelic algae to migrate towards the light, becoming trapped among fibers of the lens paper.

Lens papers were removed from the sediments at 10:00, 14:00 and 19:00 h on the following day and were placed into filtered (Whatman GF/C) site water. For the 10:00 and 14:00 h samples, collected papers were replaced with new ones. Algae was removed from the lens paper by vigorous shaking and dispensed into two clear and one darkened culture tubes for productivity measurements. The remainder of the algal suspension was concentrated onto Whatman GF/C filters for chlorophyll measurement. Biomass-normalized productivity ($\mu g\ C\ cm^{-2}\ h^{-1}\ \mu g^{-1}$ Chl-a) was determined as for phytoplankton. Additional experiments were conducted in 1986 (5) and 1988 (9) using epipelon sampled from an adjacent area of Delta Marsh to establish a relationship between irradiance and epipelon specific productivity.

Epiphyton. Samples were collected from artificial substrata placed adjacent to permanent macrophyte monitoring quadrats (van der Valk 1994) that had been previously established at random within each of ten equal zones in each cell. Only those quadrats in submersed areas (4–7 per cell) were used. At each site 0.60-cm-diameter clear acrylic rods were placed in an upright position among emergent macrophytes after ice-out. Collections were made at four times during the ice-free period of 1986. Segments of rods were collected from a series of depths throughout the water column using two pair of needle-nosed pliers to break the pre-scored substrata (Goldsborough *et al.* 1986). Isolated segments were placed into clear and blackened glass culture tubes containing GF/C-filtered water from the site of sample origin. Each sample was inoculated with $NaH^{14}CO_3$, incubated, and processed for specific epiphyton productivity ($\mu g\ C\ cm^{-2}\ h^{-1}\ \mu g^{-1}$ Chl-a) using standard methods. Samples originating from close to the water surface were incubated at high irradiances, while those from close to the sediments were incubated at lower irradiances. Substratum segments were also collected at each site for chlorophyll measurement.

Additional incubations using epiphyton on artificial substrata collected from a reference site adjacent to the cells were conducted in 1986 and 1988 to determine the relationship between epiphyton productivity and irradiance.

Metaphyton. Three sampling sites were chosen at random from among sites containing metaphyton on four occasions during 1986. Sites were identified by visual checks at 10-m intervals along ten randomly positioned sampling lanes in each cell (Murkin *et al.* 1984). Metaphyton in a defined area was raised near the water surface on a submersed foam block, then three cores ($\approx$ 1.5 cm^2 area) were removed from the algal mat at each site in each cell on each of four sampling periods. Algae in the cores was transferred into culture tubes and chlorophyll-specific productivity ($\mu g\ C\ cm^{-2}\ h^{-1}\ \mu g^{-1}$ Chl-a) was estimated. The relationship between irradiance and metaphyton productivity was derived from 22 experiments (4 in 1986, 18 in 1989) conducted using metaphyton collected from several cells of each water depth.

Photosynthesis Modeling. Several curve-fitting techniques are available for modeling photosynthesis-irradiance (P–I) relationships which give generally equivalent results (Geider and Osborne 1992). We used the technique described by Platt et al. (1980), in which Chl-a specific photosynthesis (P_s) is estimated as follows:

$$P_s = P_{max} \times (1 - e^{(-\alpha \times I)/P_{max}}) \times e^{(-\beta \times I)/P_{max}} \qquad (2)$$

where P_{max} is the maximum observed rate of P_s; α is the slope of light-limited photosynthesis (i.e., photosynthetic efficiency); β is the slope of photoinhibition; and I is the incident PAR. This model was chosen because it made explicit provision for photoinhibition of photosynthesis which, based on our preliminary analyses, was found to occur in wetland algae exposed to high irradiances. This suggested that a three-parameter model was desirable, even though P_{max} could be underestimated when photoinhibition occurred.

For each algal assemblage, all specific productivity values and their corresponding irradiances were combined to derive a single relationship. Such specific

Table 2. Specific parameters of the carbon assimilation/irradiance relationships of the four algal assemblages in the MERP cells (± SE; range shown in brackets). α = slope of light-limited specific photosynthesis (efficiency) (μg C μg^{-1} Chl-a h^{-1} $\mu mole^{-1}$ m^{-2} s^{-1}); β = slope of inhibition (units as for α); P_{max} = light-saturated specific photosynthetic rate (μg C μg^{-1} Chl-a h^{-1}); I_k = irradiance at the onset of P_{max} (P_{max}/α) (μmole m^{-2} s^{-1}); n = number of individual determinations on which parameters were derived. Ranges apply only to those experiments in which biomass was held constant.

Parameter	Phytoplankton	Epipelon	Epiphyton	Metaphyton
α	0.025 ± 0.002	0.006 ± <0.001	0.008 ± <0.001	0.003 ± <0.001
	(<0.001–0.056)	(0.001–0.010)	(<0.001–0.022)	(<0.001–0.010)
β	−0.00005 ± 0.00034	0.00005 ± 0.00014	−0.00030 ± 0.00010	0.00026 ± 0.00032
	(−0.00010–0.01400)	(−0.00020–0.00300)	(−0.00100–0.00200)	(−0.00010–0.00600)
P_{max}	7.2 ± 0.6	2.3 ± 0.3	2.4 ± 0.1	1.1 ± 0.1
	(0.2–23.4)	(0.3–4.9)	(0.1–7.9)	(0.1–10.9)
I_k	282 ± 40	407 ± 75	292 ± 17	399 ± 95
n	1,141	879	2,567	610

productivities were used, along with ambient biomass and irradiance data, to determine their corresponding productivity. The photosynthetic parameters α, β and P_{max} were determined by non-linear regression.

Algal Biomass

The biomass (pheophytin-corrected chlorophyll per m^{-2} of wetland area) of phytoplankton, epipelon, epiphyton, and metaphyton was measured at three-week intervals in all cells throughout the ice-free periods from 1985 to 1989 (Table 1). Details of data collection are presented in Robinson *et al.* (1997). Biomass estimates were used to model the primary productivity of each assemblage in each cell.

Light Environment

Total incident PAR was measured at hourly intervals using a Li-Cor LI-190SA quantum sensor mounted on an elevated platform adjacent to one of the cells. Instantaneous PAR measurements above emergent vegetation and at the water surface were recorded at 10 m intervals along two randomly selected sampling lanes. The lanes were sampled in each of the ten cells over each period of biomass collection. We calculated the percent reduction in incident light to develop an empirical relationship between light loss by shading and water depth at the sampling site. We did not measure light loss due to surface reflection; instead, we followed Jones (1984) in applying a universal 10% reflectance loss (Hutchinson 1975). Light extinction in the water column was assessed at three-week intervals. At 10-m intervals along each sampling lane, light was measured at 5-cm depth increments using an underwater quantum sensor. Extinction coefficients were expressed as % absorbance per 10 cm (Wetzel and Likens 1991). A relationship between the extinction coefficient and water depth was developed to estimate subsurface PAR data needed to compute *in situ* algal productivity.

Productivity Estimates

Biomass data (Chl-a m^{-2}) for each algal assemblage at each isobath were available directly or were interpolated between existing data. Hourly estimates of ambient PAR (μmole m^{-2} s^{-1}) were determined for each isobath by correcting hourly incident PAR (mole m^{-2} h^{-1}) for shading, reflective loss, and extinction in the water column. For each assemblage, algal productivity (mg C m^{-2} h^{-1}) was derived using equation (2) wherein the I term was PAR at the specific isobath.

Daily productivity (mg C m^{-2} d^{-1}) was estimated as the sum of all hourly productivity values. Mean productivity of each algal assemblage (mg C m^{-2} d^{-1}) and the known area of each isobath were used to calculate total algal productivity for each cell (kg C $cell^{-1}$ d^{-1}).

Areal estimates of algal biomass (Chl-a per m^2) were converted to the equivalent C content using a C:Chl-a ratio of 130 determined by Hosseini (1986) for these cells. Annual mean biomass (as mg C m^{-2}) was then divided by annual mean productivity (mg C m^{-2} d^{-1}) to yield biomass turnover times (days).

RESULTS

Photosynthesis–Irradiance Relationships

Of the four algal assemblages studied, phytoplankton had the highest photosynthetic efficiency (α) and P_{max}, and metaphyton had the lowest (Table 2). Epiphyton and epipelon were intermediate for both parameters, although α of epiphyton was greater than that of epipelon. Saturation intensities (I_k) were lowest for phytoplankton and epiphyton (280–290 μmole m^{-2}

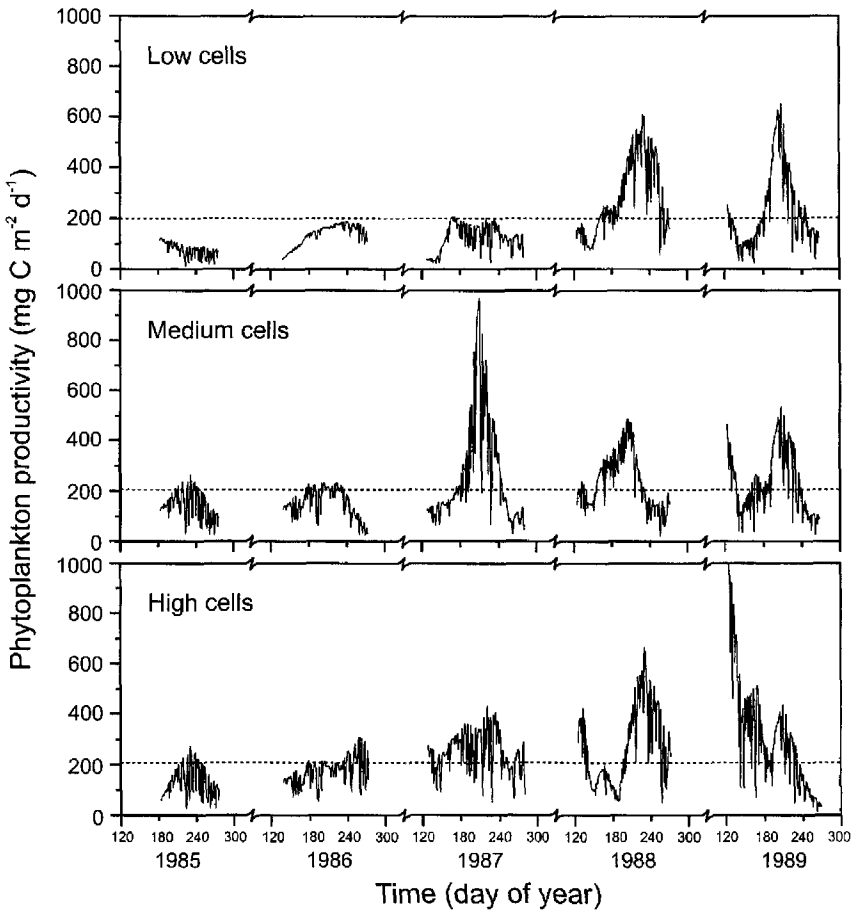

Figure 1. Mean daily productivity (mg C per m² wetland area) of phytoplankton in low, medium, and high flooded wetland cells during the ice-free periods from 1985 to 1989. Horizontal dotted lines represent the overall mean productivity for all cells and times (208 mg m^{-2} d^{-1}).

s^{-1}) and somewhat greater (≈ 400 μmole m^{-2} s^{-1}) for epipelon and metaphyton. Values for α, β, and P_{max} were not correlated (r^2 = 0.02–0.25, $p > 0.05$) with possible indicators of short-term adaptation and longer term assemblage change such as ambient water temperature, biomass, or three-day, 10-day, and 20-day light-histories. Multiple linear regressions using temperature, biomass, and 10-day light history accounted for only 2–25% of the variance of any of the three photosynthetic parameters.

Light Environment

Water depth affected both the incident irradiance reaching the water surface and its extinction in the water column. The reduction of incoming light by emergent macrophytes (0–100%) was negatively correlated with water depth ($r = -0.49$; $n = 345$, $p < 0.0001$) due to declining macrophyte density with increased depth. The extinction coefficient of the water column was highest at shallow sites and decreased significantly with increasing water depth ($r = -0.71$; $n = 401$, $p < 0.0001$). A curvilinear model applied to these data did not significantly improve the predictive relationship over the range of depths measured.

Algal Primary Productivity

Maximum productivity occurred in mid-summer (July–August) for all four algal assemblages. Phytoplankton also showed occasional maxima in spring, particularly in the last two years of the study (Figure 1). Phytoplankton productivity ranged from 13 to 1,062 mg C m^{-2} d^{-1} around a mean of 208 mg C m^{-2} d^{-1} over the 5-year period. Mean daily phytoplankton productivity generally increased with each successive year of the study (Table 3), with the exception of 1987 in medium cells when mid-summer productivity was higher than at any other time.

Mean epipelon productivity was 31 mg C m^{-2} d^{-1} over five years but it varied erratically from < 1–157 mg C m^{-2} d^{-1} (Figure 2) with no consistent year-to-year trend (Table 3).

Epiphyton productivity ranged from 20–2,978 mg

Table 3. Mean daily productivity (mg C per m^2 wetland area) of planktonic and benthic algae in low, medium, and high flooded wetland cells from 1985 to 1989.

	Phytoplankton			Epipelon			Epiphyton			Metaphyton		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
1985	76	160	134	24	77	26	465	247	205	1,530	1,551	676
1986	137	153	174	1	54	1	478	410	282	2,952	2,064	1,445
1987	125	264	250	44	19	1	1,791	973	325	3,224	2,497	1,371
1988	280	237	271	44	46	17	1,399	1,120	381	3,950	3,202	1,833
1989	229	229	298	46	41	31	881	1,317	572	2,659	2,545	1,366
Mean	169	209	225	32	47	15	1,003	813	353	2,863	2,372	1,338

C m^{-2} d^{-1} (5-year mean = 37 mg C m^{-2} d^{-1}; Figure 3). As with phytoplankton, mean daily productivity of epiphyton increased through time although only in medium and high cells (Table 3).

Metaphyton, which formed dense floating or entrained mats in all cells throughout the study, had the highest 5-year mean daily productivity (2,269 mg C m^{-2} d^{-1}), with a range of 90–7,162 mg C m^{-2} d^{-1} (Figure 4). Annual productivity increased until 1989, when it declined (Table 3).

Total daily algal productivity, calculated for all days for which individual estimates for all four algal assemblages were available, ranged from 216 to 9,157 mg C m^{-2} of wetland area, with a mean of 3,540 mg C m^{-2} d^{-1} between 1985 and 1989 (Figure 5). Mean daily productivity increased to a maximum in 1988, then it

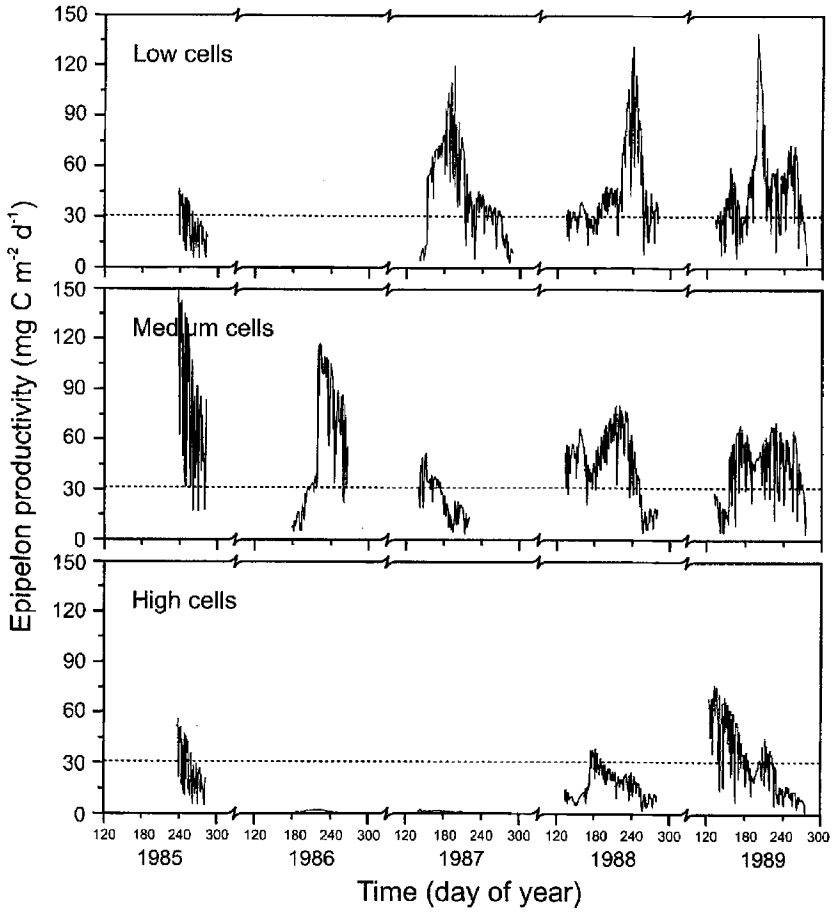

Figure 2. Mean daily productivity (mg per m^2 wetland area) of epipelon in low, medium, and high flooded wetland cells during the ice-free periods from 1985 to 1989. Horizontal dotted lines represent the overall mean productivity for all cells and times (31 mg m^{-2} d^{-1}).

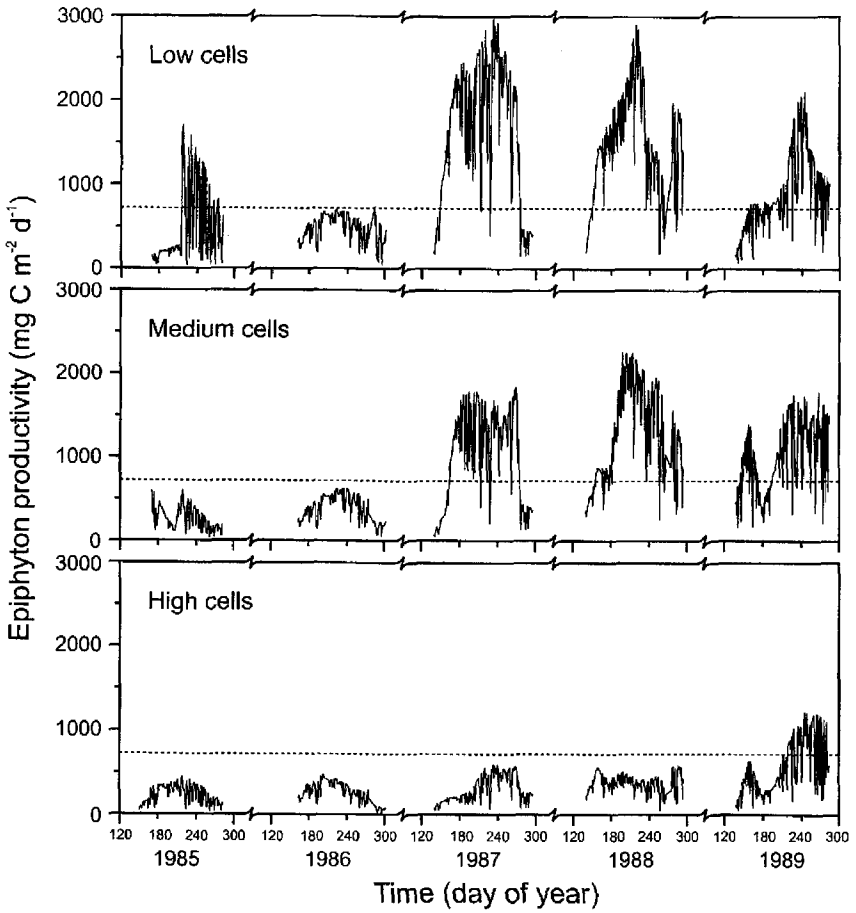

Figure 3. Mean daily productivity (mg per m^2 wetland area) of epiphyton in low, medium, and high flooded wetland cells during the ice-free periods from 1985 to 1989. Horizontal dotted lines represent the overall mean productivity for all cells and times (737 mg m^{-2} d^{-1}).

decreased in 1989. The relative contribution of each assemblage varied spatially and temporally; metaphyton represented 60–80% of the total productivity with smaller contributions by epiphyton (12–35%), phytoplankton (2–13%), and epipelon (< 1–3%).

Turnover Rate of Algal Biomass

The turnover time for phytoplankton biomass (mg Chl-a m^{-2}), based on its mean daily productivity (mg C m^{-2} d^{-1}), ranged from 2 to 7 days (Figure 6). The corresponding range for epiphyton was 8–20 days while turnover was slower for epipelon (9–91 d) and metaphyton (22–48 d). Because of the high proportion of total algal productivity due to metaphyton (Figure 5), weighted average turnover times for total algae (22–48 d) were similar to those of metaphyton. Turnover times for all assemblages generally increased with water depth (Figure 6).

Annual productivity estimates derived from P vs. I models were 269 g C m^{-2} y^{-1} in high cells, 471 g C m^{-2} y^{-1} in medium cells, and 454 g C m^{-2} y^{-1} in low cells (Table 4). In contrast, annual productivity estimates increased when calculations were based on mean daily productivity, calculated turnover times, and a 200-day ice-free period for high (386 g C m^{-2} y^{-1}), medium (688 g C m^{-2} y^{-1}), and low cells (813 g C m^{-2} y^{-1}) (Table 4).

DISCUSSION

Photosynthetic Parameters

Parameters for the photosynthesis-irradiance relationships of wetland algae are rarely published, and existing data have generally been derived from measurements of oxygen evolution rather than carbon assimilation. However, when converted using a photosynthetic quotient of 1.0, reported values for photosynthetic efficiency (α), saturating irradiance (I_k), and maximum photosynthetic rate (P_{max}) compare favorably to those calculated here (Table 5). Relative to ambient irradiance at the site of up to 2,000 μmoles m^{-2} s^{-1}, I_k values suggest that algal growth is not light-

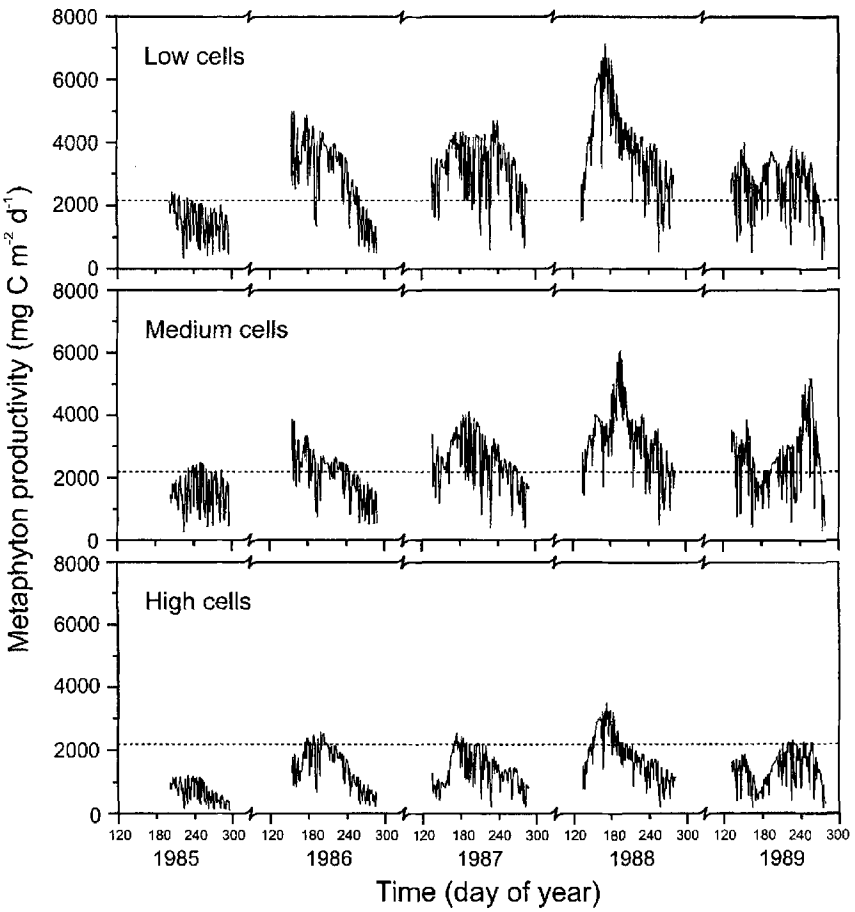

Figure 4. Mean daily productivity (mg per m^2 wetland area) of metaphyton in low, medium, and high flooded wetland cells during the ice-free periods from 1985 to 1989. Horizontal dotted lines represent the overall mean productivity for all cells and times (2,269 mg m^{-2} d^{-1}).

limited, except under exceptional circumstances of high turbidity after strong winds (Kotak and Robinson 1991) or when the water surface is occluded with a thick metaphyton or macrophyte mat. The occurrence of photoinhibition was extremely rare.

Phytoplankton was a minor contributor to total algal productivity in Delta Marsh as a whole (Table 1, Figure 5; Goldsborough and Robinson 1996) despite having the highest α and P_{max} and lowest I_k of the four algal assemblages. The efficiency of light use (α = 7 mg C mg Chl-a^{-1} mole^{-1} m^{-2}) is typical of most phytoplankton assemblages (6–18 mg C mg Chl-a^{-1} mole^{-1} m^{-2}; Reynolds 1984) and was greater than that of epiphyton, epipelon, and metaphyton (2.2, 1.7, and 0.8 mg C mg Chl-a^{-1} mole^{-1} m^{-2}, respectively). It is unclear why benthic algae should have substantially lower α values than algae entrained in the water column.

Variation in Photosynthetic Parameters

The parameters that define the P–I relationship vary as a function of environmental conditions, including light exposure history (Savidge 1988), ambient temperature (Prezelin and Ley 1980, Tilzer *et al.* 1986), nutrient availability (Williams 1978, Fee *et al.* 1987), and diel environmental periodicity (Prezelin and Ley 1980). Parameters varied greatly here; α varied over a range from 10× for epipelon to as much as 200× for epiphyton (Table 2). Multivariate analyses suggested that changes in ambient temperature, biomass, and light history explained < 25% of this variability.

The role of environmental factors in regulating P–I relationships merits further attention. Fee *et al.* (1987) suggest that variability in primary productivity may be related to the size and stability of aquatic systems. By these criteria, small or shallow wetlands may be more variable than other ecosystems. For example, wind-induced turbulence in wetlands decreases irradiance and increases nutrient levels through sediment resuspension (Carper and Bachmann 1984). In an unenclosed, shallow area of Delta Marsh, up to 90% of all wind events have sufficient velocity to resuspend sediments (Kotak and Robinson, unpublished data) and attenuate light (Kotak and Robinson 1991), particular-

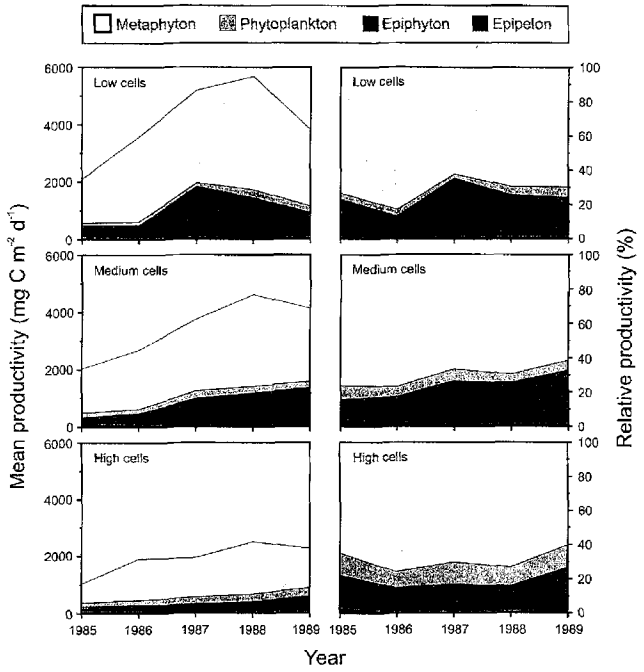

Figure 5. Absolute (left; mg m^{-2} d^{-1}) and relative (right; % total) contributions by phytoplankton, epipelon, epiphyton, and metaphyton to total algal productivity in low, medium, and high flooded wetland cells from 1985 to 1989.

ly in May to June. Further, the large population of carp (*Cyprinus carpio* L.) in Delta Marsh is another source of sediment resuspension, although fish were excluded from the cells.

Individual algal cells within epiphyton and metaphyton may be subject to considerable variability in light (e.g., Losee and Wetzel 1983, Turner *et al.* 1995), temperature, and nutrient availability (Pasciak and Gavis 1974). High metaphyton biomass may lead to additional variability in nutrient regimes by sequestering essential nutrients during growth and releasing them during decomposition, changing redox conditions at the sediment interface, and releasing dissolved organic matter, which chelates metals and alters microbial processes (Turner *et al.* 1995).

Subsurface irradiance in the MERP cells was determined by emergent macrophyte cover and extinction in the water column. Emergent macrophytes (*Phragmites australis* (Cav.) Trin. ex. Stend., *Scolochloa festucacea* (Willd.) Link., *Scirpus acutus* Muhl. and *Typha* × *glauca* Godron) reduced incident radiation by as much as 90%, similar to the reduction observed in dense *Phragmites* stands elsewhere (Roos and Meulemans 1987). The amount by which macrophytes reduced incident radiation decreased as water depth increased, probably because macrophyte biomass decreased in deeper water (van der Valk 1994). However, the negative correlation between light extinction rate

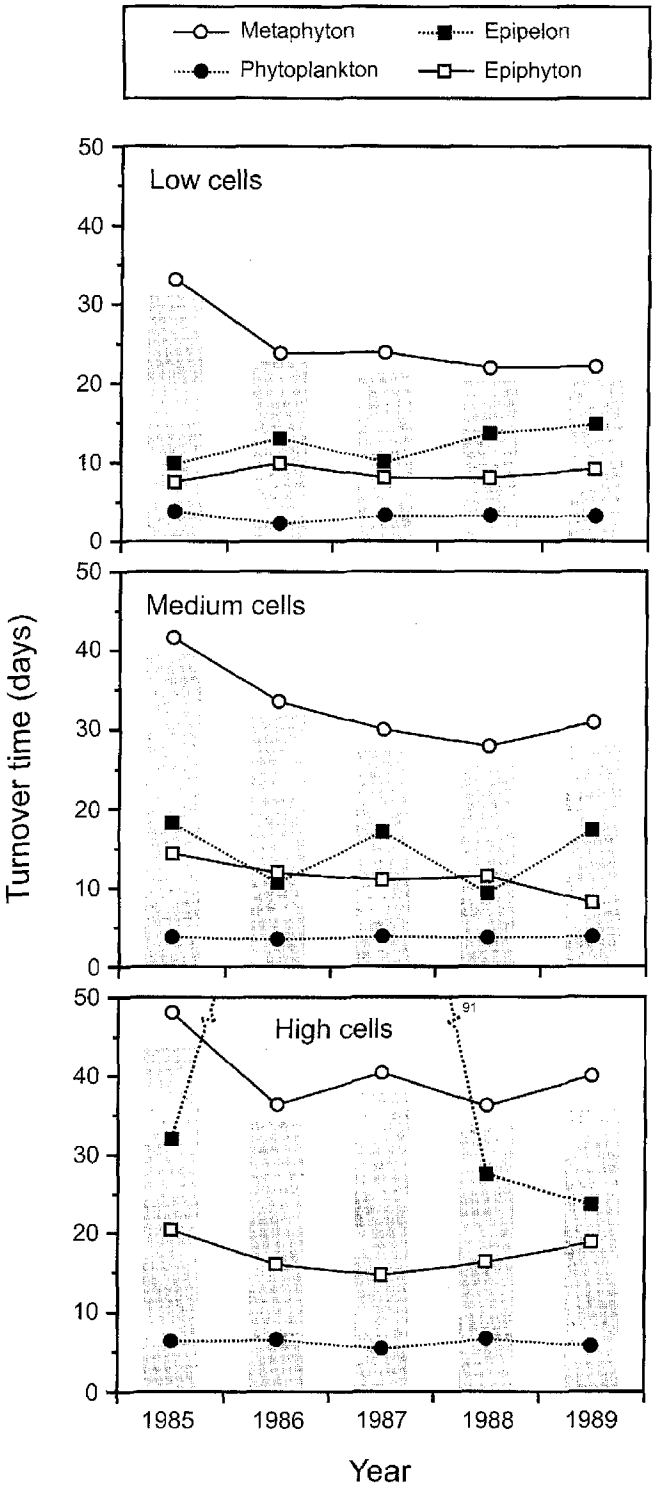

Figure 6. Turnover times (d) of metaphyton, phytoplankton, epiphyton and epipelon in low, medium, and high flooded wetland cells from 1985 to 1989. Estimates were based on a C:Chl-a ratio of 130 (Hosseini 1986). Vertical bars represent the weighted average turnover times of all algal assemblages combined.

Table 4. Mean and range (in brackets) of annual productivity (g C m^{-2}) of planktonic and benthic algae in low, medium, and high flooded wetland cells, as estimated by two methods: 1) P vs. I models, and 2) turnover times calculated on the basis of a 200-day annual ice-free period.

	Phytoplankton	Epipelon	Epiphyton	Metaphyton	Total
Calculated using P vs. I models					
Low cells	24	4	144	282	454
	(7–42)	(0–7)	(52–278)	(96–414)	(159–668)
Medium cells	29	4	110	328	471
	(14–40)	(1–7)	(28–194)	(145–474)	(188–709)
High cells	32	2	52	185	269
	(12–44)	(0–4)	(30–85)	(63–271)	(105–370)
Calculated using turnover times					
Low cells	34	6	201	573	813
	(15–56)	(0–9)	(93–358)	(306–790)	(419–1,135)
Medium cells	42	9	163	474	688
	(31–53)	(4–15)	(49–263)	(310–640)	(407–921)
High cells	45	3	71	243	386
	(27–60)	(0–6)	(41–114)	(135–367)	(208–500)

and water depth was unexpected and suggested that relatively more light reached the sediments in deep than in shallow water. Profuse epiphyton, metaphyton, and macrophytes can reduce water transparency and we found that algal productivity (Figures 5, 6) and biomass (Robinson *et al.* 1997) also varied inversely with water depth. Thus, high light extinction in shallow waters was probably a consequence of high macrophyte, metaphyton, and epiphyton biomass. When combined together with the effects of shading by macrophytes, extinction-depth relationships produced the surprising result that subsurface irradiance did not vary

Table 5. Parameters of P–I relationships for wetland algae; α = photosynthetic efficiency (μg C μg^{-1} Chl-a h^{-1} μmole^{-1} m^{-2} s^{-1}); I_k = irradiance at onset of P_{max} (μmole m^{-2} s^{-1}); P_{max} = light saturated specific photosynthetic rate (μg C μg^{-1} Chl-a h^{-1}).

Assemblage	Location	α	I_k	P_{max}	Source
Phytoplankton	Delta Marsh	0.007–0.008	253–446	2.0–3.0	Gurney and Robinson (1988)
	Delta Marsh	0.092	303	3–79	Kotak (1990)
	Delta Marsh		235–392	6–14	Robinson (1988)
	Delta Marsh	0.025	282	7.2	this study
Epipelon	North Inlet Estuary, S. Carolina, USA	0.002–0.003[1]	579–834	1.0–3.0[1]	Pinckney and Zingmark (1993)
	Delta Marsh		237–563	0.8–4	Robinson (1988)
	Delta Marsh	0.006	407	2.3	this study
Epiphyton	Delta Marsh	0.016	430	3–21	Kotak (1990)
	Delta Marsh		198–659	0.5–4	Robinson (1988)
	Delta Marsh	0.008	292	2.4	this study
Metaphyton	Delta Marsh	0.002–0.005	36–360	0.2–0.7	Gurney and Robinson (1988)
	Delta Marsh	0.007[1]	344[3]	2.0	Richmond (1992)
	Fish ponds, South Bohemia	<0.005–0.001[2]	186–>460[3]	0.8[1,4]	Eiseltová and Pokorný (1994)
	Canal, Merseyside, England		322[3]		Simpson and Eaton (1986)
	Green Bay, Michigan, USA		161[3]		Adams and Stone (1973)
	Laurentian Great Lakes			0.8[1,4]	Auer *et al.* (1983)
	Lake Erie			3.2[1,4]	Wood (1975)
	Delta Marsh	0.003	399	1.1	this study

[1] Converted to C assimilation from O_2 evolution using a photosynthetic quotient of 1.0. [2] Derived from P_{max} and I_k. [3] Assuming 4.6 μmole m^{-2} s^{-1} $\approx$ 1.0 W m^{-2}. [4] Assuming Chl-a content $\approx$ 0.25% of dry weight.

Table 6. Net annual productivity (g C per m^2 wetland area) of macrophytes and algae (based on turnover times) in freshwater wetlands. Dry weights were converted to carbon units on the basis of 45% C content. Asterisks indicate ranges based on aboveground productivity alone and aboveground and belowground productivity combined.

Primary Producer	Location	Annual Productivity (g C m^{-2} y^{-1})	Source
Emergent macrophytes (aboveground)	Delta Marsh	109–1,762	Murkin (1989)
	Delta Marsh	76–1,754	Shay and Shay (1986)
	Delta Marsh	42	van der Valk (1994)
Emergent macrophytes (belowground)	northern prairie marshes	504–1,779	Murkin (1989)
	Delta Marsh	157–1,137	Shay and Shay (1986)
	Delta Marsh	252	van der Valk (1994)
Macrophytes (high-water fluctuating marshes*)	various	284–756	Brinson *et al.* (1981)
Macrophytes (low-water fluctuating marshes*)	various	68–1,106	Brinson *et al.* (1981)
Macrophytes (other non-forested wetlands*)	various	293–756	Brinson *et al.* (1981)
Submersed macrophytes	northern prairie marshes	5–117	Murkin (1989)
Phytoplankton	temporary ponds, Alberta, Canada	2–11	Robarts *et al.* (1995)
	Lake Erie coastal wetland	366	Reeder and Mitsch (1989)
Phytoplankton and epiphyton	Carolina bay wetland, S. Carolina, USA	81	Schalles and Shure (1989)
Epiphyton	Delta Marsh	<1–49	Hooper and Robinson (1976)
	constructed wetlands, Illinois, USA	2–85	Cronk and Mitsch (1994)
Epipelon	tundra ponds	4–10	Stanley (1976)
All benthic and planktonic algae	low MERP cells, Delta Marsh	419–1,135	this study
	medium MERP cells, Delta Marsh	407–921	this study
	high MERP cells, Delta Marsh	208–500	this study

with water column depth over the range studied here (0–115 cm). PAR at the mean depth of each cell (7–64 cm) was consistently 35–45% of incident PAR.

We found that algal biomass was the best single predictor of daily productivity. The amount of variation in productivity explained by variation in biomass, determined using simple linear regressions, ranged from 64% for phytoplankton to 81% for epiphyton. Productivity increased (phytoplankton) or decreased (epipelon, epiphyton, and metaphyton) with depth in response to changes in biomass of the respective algal groups (Robinson *et al.* 1997). Therefore, we conclude that effects of water depth on algal productivity are directly related to flood-induced changes in the availability of algal substrata and hence algal biomass.

Algal Productivity in Prairie Wetlands

This study addresses only the algal portion of total primary productivity in flooded prairie wetlands. When compared to previous estimates of annual macrophyte productivity in the MERP cells and elsewhere (Table 6), these data illustrate that the contributions by shallow water algae are at least as great as those of emergent and submersed macrophytes. For example, Sullivan and Moncreiff (1988) found that epipelon productivity in an estuarine salt marsh ranged from 10–61% of macrophyte productivity. Cronk and Mitsch (1994) calculated that phytoplankton and epiphyton productivity in riparian wetlands subjected to differing hydrologic flow regimes was 17–57% of total organic productivity. This conclusion supports the contention that algal productivity in wetlands may be an important determinant of secondary productivity (e.g., Browder *et al.* 1994, Campeau *et al.* 1994).

In view of the magnitude of algal productivity demonstrated here, the relative consistency of supply of algal biomass over time (Robinson *et al.* 1997), and the acceptability of that biomass to wetland herbivores (Batzer and Wissinger 1996), detailed investigations of the trophic structure of prairie wetlands are warranted (Keough *et al.* 1996). Definition of the role that algae

play as a base of the wetland food web may necessitate revision of wetland management strategies.

ACKNOWLEDGMENTS

This project was supported by the Marsh Ecology Research Program (MERP), a collaborative project of the Delta Waterfowl Foundation and Ducks Unlimited Canada. Additional support was received from the University of Manitoba (GGCR) and the Natural Sciences and Engineering Research Council of Canada (GGCR, LGG).

Numerous field assistants ("Merpies") helped with sampling, and Colleen Barber, Leslie Goodman, and Nicole Armstrong assisted with data collation. Logistic support for sample collection and analysis was provided by Henry Murkin, Bruce Batt, the Delta Waterfowl and Wetlands Research Station, Ducks Unlimited Canada through the Institute for Wetland and Waterfowl Research, and the University Field Station (Delta Marsh). Rob Balshaw of the Statistical Advisory Service, University of Manitoba assisted with data analyses. The helpful comments of two referees on an early draft of this paper are gratefully acknowledged.

This is Paper 87 of the Marsh Ecology Research Program, Paper 257 of the University Field Station (Delta Marsh), and Paper 7 of the Prairie Wetland Ecology Team.

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Manuscript received 18 August 1995; revision received 23 September 1996; accepted 2 December 1996.