Midsummer Photosynthetic Carbon Budget for Old Woman Creek Wetland, Ohio: Relative Contribution of Aquatic Macrophytes Versus Phytoplankton[1]

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ABSTRACT. Few data are available on net productivity rates in Laurentian Great Lakes wetland communities. We used several methods (Licor photosynthesis system and various radiotracer methods) to estimate midsummer carbon photoassimilation rates among important phytoplanktonic and aquatic macrophyte assemblages in Old Woman Creek National Estuarine Research Reserve (OWC) on Lake Erie near Huron, OH, during 1993-1995. Our data suggested that the majority of carbon flow into the OWC estuary (approximately 66-99% of the total) occurred through aquatic macrophytes, especially the dominant floating-leaved species *Nelumbo lutea* and the emergent species *Phragmites australis*.

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INTRODUCTION

Coastal wetlands associated with the Laurentian Great Lakes play an important role as "metabolic gates" in processing organic and inorganic materials before they reach recipient waters of the Great Lakes (Wetzel 1992). This is especially true in the western basin of Lake Erie, a body of water essentially ringed by coastal wetlands (Stuckey 1989, Herdendorf 1992). However, information on community-level energetics in Great Lakes coastal wetlands, including photosynthetic budgets, are conspicuously lacking. A consensus research priority for Great Lakes researchers (summarized by Krieger and others 1990, 1992) has thus been the development of an estuarine carbon budget model that incorporates contributions from all photoautotrophs, including aquatic macrophytes as well as algae. In inland wetlands and marine coastal wetlands, annual primary productivity rates are among the highest of any community in the biosphere and the majority of carbon fixation into the ecosystem occurs via macrophytic fixation (reviewed by Wetzel 1983, Mitsch and Gosselink 1993).

In the only published primary productivity studies we are aware on a Lake Erie wetland to date, Reeder and Mitsch (1989) and Reeder (1990, 1994) estimated annual carbon fixation rates in the Old Woman Creek National Estuarine Research Reserve (OWC) near Huron, OH. Using peak biomass transect sampling of dominant aquatic macrophyte *Nelumbo lutea* (American lotus) and a light bottle:dark oxygen evolution assay method to estimate phytoplanktonic productivity, they concluded that, in contrast to "typical" wetlands, annual net primary production by open-water plankton communities (366 g m^{-2} yr^{-1}) greatly exceeded that of lotus beds (approximately 75 g m^{-2} yr^{-1}). However, both aboveground biomass sampling and oxygen evolution techniques represent indirect methods for measuring photosynthetic carbon flow rates into photoautotrophs, and may underestimate total fixation in systems dominated by rhizomatous macrophytes with large underground biomass. The goal of this study was to determine midsummer photosynthetic C flux through various macrophytic and algal components of OWC using a variety of direct measurement techniques.

MATERIALS AND METHODS

Description of Study Site

The Old Woman Creek National Estuarine Research Reserve and State Nature Preserve (OWC) represents one of the few remaining undeveloped coastal wetland systems along the south shore of Lake Erie. It is located in Erie County, OH, at the edge of the Western Basin and the southernmost point on the Great Lakes. Classified as a freshwater estuary, it is characterized by its drowned river mouth as it enters Lake Erie (Herdendorf 1990). The estuary proper is approximately 56 hectares and extends about 2 km south of Lake Erie. Its watershed encompasses an area of approximately 69 km^2. Water level fluctuations are controlled by a barrier sand beach and lake levels. The physical environment of OWC has been the focus of several studies (Klarer and Millie 1989, and reviewed by Whyte 1996). Extant plant communities may be the result of a prolonged period of high water that existed through the 1980s and has continued into the late 1990s. Additional information on the flora and limnology of OWC may be found in Klarer and Millie (1992), Whyte (1996), and Whyte and Francko (1997, 1999).

Primary Productivity

Field measurements of carbon photoassimilation rates in OWC phytoplankton and aquatic macrophytes were conducted in July 1993 and July and August 1994 and 1995, to coincide with the annual wetland peak biomass period (Whyte 1996). Measurements were conducted at mid-day via a "circuit sampling" protocol we developed to permit short-term measurements of all photoautotroph compartments within a single 60-90 min time frame, so that instantaneous C-assimilation rates could be directly compared to determine the relative proportion of C-fixation accounted for by major groups of primary producers at peak biomass. All field experimentation was conducted in the NW embayment of OWC.

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A Licor 6200 portable photosynthesis system (1000-ml chamber) was used to measure CO_2-fixation rates in aerial leaves of *Nelumbo lutea* and *Phragmites australis* (giant reed), the dominant floating-leaved and emergent macrophytes in OWC, respectively. Replicate 30-second incubations of leaves that remained attached to the plant (N = 5 leaves of each species on each sampling date) were used to provide adequate replication for statistical analysis. The section of plant leaf enclosed by the chamber was excised for later measurement of leaf surface area and conversion of rate functions into µmol C taken up m^{-2} leaf surface s^{-1}.

Radiotracer techniques utilizing ^{14}C-bicarbonate were employed to estimate photosynthetic rates in plant/algal samples where the Licor chamber could not be used. We utilized a sealed air chamber technique for measuring photosynthetic carbon flow into the upper surfaces of *Nelumbo* floating leaves. Chamber systems (350-ml) were constructed from magnetic-closure filter holder systems. The reservoir chamber was sealed at the top with parafilm and placed on the upper surface of the leaf a few cm from the petiole. The seal at the surface of the leaf was maintained by placing the magnetic ring filter holder on the underside of the floating leaf, restricting air exchange into the chamber without damaging the leaf. Ampules of ^{14}C-bicarbonate solution (5 µCi ml^{-1}) were opened immediately before use and a 100-µl aliquot was added to replicate chambers placed on different leaves at time zero. In preliminary experiments we found that 30-min incubations produced adequate C-incorporation with minimal reduction in chamber CO_2 partial pressure. A chamber covered with foil was run concurrently to serve as a dark control. After incubation chambers were collected and placed in a darkened box for transport to the shoreline where samples were processed for transport to the Miami campus.

Aqueous ^{14}C bottle assays were used for analyses of the dominant submerged aquatic macrophyte species (*Potamogeton pectinatus* [sago pondweed] and *Ceratophyllum demersum* [coontail]) and their attached epiflora, and for open water/littoral zone phytoplankton samples, using standard methodology (Francko and Wetzel 1984; Wetzel and Likens 1991). Assays were conducted in replicate 250-ml polycarbonate screw-cap flasks spiked with 100 µl of non-acidified, ampulated ^{14}C-bicarbonate solutions. Light/dark flasks containing macrophyte material (approximately 0.1 g fresh wt, collected immediately before assays) or whole littoral zone or pelagic waters, were incubated at the 10-cm and 50-cm depths for 30 to 60 min (attached to stakes driven into the littoral/pelagic sediment), removed, placed in dark boxes, and returned to the shoreline where samples were fixed for transport back to Miami University for liquid scintillation spectrographic analysis. Due to methodological difficulties, epiflora attached to lotus petioles and benthic algae associated with littoral sediments were not sampled in our investigation.

On the shoreline, planktonic samples were filtered though 0.2-µm pore-sized Nuclepore filters (0.3 atm vacuum), and triplicate filters from each bottle were placed in glass scintillation vials containing 0.5 ml of 0.5 N perchloric acid to solubilize cells and drive off unincorporated inorganic carbon. Portions of macrophytes samples were withdrawn from incubation bottles, blotted dry, weighed, and immediately added to perchloric acid-containing vials. In *Nelumbo* leaves, 1-cm leaf disk samples (N = 5 from each leaf) were excised with a cork borer from leaf sections exposed to ^{14}C and disks were placed in perchloric acid as above (Francko 1986).

Ancillary measurements of PAR and water temperature were made during the time of incubation and water samples were collected in 1-liter brown polyethylene bottles for analyses of pH and alkalinity. Radiolabel incorporation in fixed samples was measured using a Beckman model 1800 liquid scintillation counter. Data for each water or plant sample on each sampling date were pooled and mean radiolabel uptake rates (+/- SD) were converted to total C-assimilation rates using a ^{12}C:^{14}C uptake ratio method (Francko and Wetzel 1984, Wetzel and Likens 1991).

From the above data, it was possible to estimate photosynthetic rates in each compartment per unit time for the whole estuary, using aerial and ground-truth data on macrophyte bed sizes and volumes of water present in open water/littoral zones to calculate compartment sizes (Whyte 1996, Whyte and Francko 1997). The mean depth of OWC is 0.5 m and in this extremely turbid system (approximately 30-35 NTU; Whyte 1996) limited phytoplanktonic production occurs below the 0.5-m depth. To compute total phytoplanktonic C-assimilation rates in the entire water column, we plotted rate functions for the 0.1-m and 0.5-m depths within both the open water/pelagic zone (defined as all waters outside lotus beds, or 64% of the estuarine surface area) and the littoral zone (within lotus beds), and used the resultant slope to compute mean fixation in the top 50 cm and bottom 50 cm volumes of water. By summing these values and dividing by two, an estimate of total areal fixation by phytoplankton per unit time could be derived. During the course of our study, *Nelumbo* beds covered 36% of the estuary surface area, and within a bed, aerial and floating leaves accounted for an average of 1.6 m^{-2} and 0.7 m^{-2} of leaf surface area, respectively, per m^2 of bed surface area. In 1993, *Phragmites* beds containing approximately 10.2 m^{-2} of leaf surface area per m^2 of bed area were found in about 2% of the estuarine surface area, and by 1994 and 1995 that percentage had increased to 5%. We estimated that submerged aquatic macrophytes occurred in about 5% of the estuarine surface area (approximately 10 kg fresh wt biomass m^{-2} water surface) in 1993 and 1995, and were absent from the flora in 1994.

RESULTS

Midday photosynthetic carbon assimilation rates for important phytoplanktonic and aquatic macrophyte compartments, expressed in whole-estuary units, are shown in Table 1. Absolute C-photoassimilation rates for the estuary varied considerably from date to date (about 1.4-3.4 x 10^4 mol C h^{-1}) and between compartments, since solar insulation, water pH, and other photosynthetic

parameters varied from date to date. However, several patterns were noted in relative C-photoassimilation rates on a whole-estuary basis. On all sampling dates over the 3-year period where Licor data could be collected, lotus aerial leaves represented the largest single source of carbon photoassimilation into the estuary. Lotus floating leaves and *Phragmites* consistently fixed much less carbon than lotus aerial leaves and their contribution to total estuarine fixation each approximated that of the pelagic phytoplankton. The smallest portion of fixation consistently occurred in littoral phytoplankton and submerged macrophyte communities. With the exception of 9 July 1994, when a malfunctioning Licor instrument prevented collection of aerial-leaf data, 66 to 99% of the total photosynthetic carbon flow on an estuary-wide basis could be accounted for by aquatic macrophytes.

DISCUSSION

Our data suggest that in terms of peak-season carbon assimilation into the OWC estuary as a whole, macrophytes play a more important role than phytoplankton. Although our data cannot be translated into precise annual productivity figures, it is possible to make rough calculations, assuming typical diel macrophyte productivity patterns (Wetzel 1983, Francko and Wetzel 1984), Allen curve-biomass data for OWC lotus populations (Whyte and Francko 1997), and OWC phytoplankton seasonal patterns (for example, Klarer and Millie 1992). Under such rough assumptions, our mean *Nelumbo lutea* peak-season productivity value of approximately 1.5 x 10^{10} µmol fixed h^{-1} (aerial and floating leaves) would translate to approximately 1200 g biomass m^{-2} yr^{-1} for lotus beds alone, or about 400 g biomass m^{-2} yr^{-1} on an estuary-wide basis—within the published range for productive temperate emergent wetlands (Wetzel 1983, Mitsch and Gosselink 1993), but approximately 5-fold higher than the value reported by Reeder (1990, 1994) and Reeder and Mitsch (1989). Our phytoplankton productivity data were more variable from sampling date to sampling date, due largely to high storm-event-induced turbidity associated with the 18 Aug 1995 sampling date, and would translate to roughly 6 to 330 g C m^{-2} using 18 Aug 1995 and 16 July 1993 data, respectively. If the 18 Aug date is deleted, the predicted annual planktonic productivity (pelagic and littoral) would range between 70 and 330 g C m^{-2}, within the typical range for a shallow, turbid hypereutrophic system (Wetzel 1983) and similar to the annual OWC planktonic productivity value reported by Reeder (1990, 1994) and Reeder and Mitsch (1989).

Thus, our carbon budget, which is based on short-term measurements of C-photoassimilation and not plant biomass accumulation, produced a macrophyte: phytoplankton productivity ratio nearly the mirror-image of the Reeder-Mitsch model. The differences implicit in these models could be ecologically significant. Organic carbon (and energy) entering ecosystems through phytoplankton and bacteria largely passes into higher trophic levels through grazing food webs, while macrophytic C tends to reach other ecosystem components largely upon fall senescence via detrital food webs, with major implications for heterotrophs (Wetzel 1983, 1992).

One of the reasons for the discrepancy between our lotus productivity numbers and those of Reeder-Mitsch probably lies in the propensity of rhizomatous perennials like lotus and related water lilies to translocate the majority of photosynthate to underground root-rhizome

Table 1

Midday carbon assimilation rates (µmol C fixed h^{-1} x 10^{-8} (SD)) in Old Woman Creek primary producer compartments during the midsummer biomass maximum.

Date	Macrophytes			Phytoplankton			
	Nelumbo		*Phragmites*	Other	Pelagic	Littoral	%Macrophyte
	Aerial	Floating		Submerged	Phyto.	Phyto.	Fixation
16 Jul 93	88.0 (3.0)	ND	5.1 (1.0)	4.4 (2.0)	51.8 (7.0)	ND	66
9 Jul 94	ND	12.2 (0.8)	ND	Absent	41.3 (5.6)	ND	-
9 Aug 94	113.4 (24.3)	9.7 (4.1)	8.9 (2.4)	Absent	10.5 (5.7)	1.1 (0.1)	92
7 Jul 95	153.9 (69.7)	52.7 (34.0)	34.8 (14.6)	0.2 (0.1)	13.8 (2.4)	0.4 (0.3)	95
18 Aug 95	243.0 (121.5)	68.9 (6.5)	13.0 (0.8)	0.6 (0.3)	0.6 (0.1)	0.3 (0.2)	99

ND = Not Determined

systems. Although this carbon flow would have been measured by our methods, it was not accounted for factored by Reeder-Mitsch's above-ground biomass harvesting. Another factor is that the Reeder-Mitsch model was calculated during the late 1980s when lotus covered roughly one half as much of the estuary as during our study periods.

The finding that lotus floating leaves fixed approximately 10-30% as much C per unit area as lotus aerial leaves was somewhat surprising, in that functional stomates are found only on the upper surface of these leaves and floating leaves have access to atmospheric C (Hutchinson 1975). However, we feel that our method probably underestimated real C-uptake capacity in lotus floating leaves and therefore in this species as a whole. First, the chambers themselves shaded the surface of the leaf and reduced PAR. Second, we did not acidify bicarbonate solutions prior to use to create free CO_2 because of the need to reuse ampules for several minutes after opening, and this could have cause a reduction in available CO_2 in some experiments over the very short incubation times we employed. Finally, our method could not account for fixation of CO_2 transported via the petiolar lacunar system from the root-rhizome to the floating leaves.

We have no ready explanation for the disappearance of submerged macrophytes in 1994 and their subsequent re-appearance in 1995, although a combination of water depth and underwater light attenuation may have been the most important abiotic regulator of submerged plant community structure in OWC during 1993-95 (Whyte and Francko 1997). For example, in both 1994 and 1995, the mean turbidity for waters in the NW embayment was statistically identical (35 and 33 NTU, N = 14 and 18, respectively), but the mean water depth was 18 cm higher in 1994 versus 1995. This meant that in 1995 the 1% compensation depth for photosynthesis encompassed nearly all of the areal extent of this shallow system. In that 1995 saw enhanced submerged macrophyte production and extension of submerged macrophyte beds, we suggest that the lower mean water depth permitted more light to penetrate through the water column, enhancing the growth of light-limited plants. We lack a data set complete enough for the years prior to 1993 to speculate on the relative abundance of submerged macrophytes in that year as well. As noted earlier, we were unable to measure the photosynthetic contribution of periphytic algae that heavily coat submerged lotus petioles nor patches of epipelic algae that colonize nearshore areas, further underestimating algal C fixation.

Nonetheless, the data suggest that macrophytic C-fixation is extremely important in OWC, and by extension in other wetlands along the south shore of Lake Erie (for example, Sheldon's Marsh, DuPont Marsh, Pickerel Creek, etc.), dominated by floating-leaved macrophytes and/or *Phragmites*. Annual productivity studies would shed much light on the role of macrophytic versus algal photosynthesis in overall Lake Erie estuarine dynamics.

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