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Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study

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ABSTRACT: A process-based carbon gas flux model was developed to calculate total macrophyte and microalgal production, and community and belowground respiration, for a *Peltandra virginica* dominated tidal freshwater marsh in Virginia. The model was based on measured field fluxes of CO_2 and CH_4, scaled to monthly and annual rates using empirically derived photosynthesis versus irradiance, and respiration versus temperature relationships. Because the gas exchange technique measures whole system gas fluxes and therefore includes turnover and seasonal translocation, estimates of total macrophyte production will be more accurate than those calculated from biomass harvests. One limitation of the gas flux method is that gaseous carbon fluxes out of the sediment may underestimate true belowground respiration if sediment-produced gases are transported through plant tissues to the atmosphere. Therefore we measured gross nitrogen mineralization (converted to carbon units using sediment C/N ratios and estimates of bacterial growth efficiency) as a proxy for belowground carbon respiration. We estimated a total net macrophyte production of 536 to 715 g C m^{-2} yr^{-1}, with an additional 59 g C m^{-2} yr^{-1} fixed by sediment microalgae. Belowground respiration calculated from nitrogen mineralization was estimated to range from 516 to 723 g C m^{-2} yr^{-1} versus 75 g C m^{-2} yr^{-1} measured directly with sediment chambers. Methane flux (72 g C m^{-2} yr^{-1}) accounted for 11 to 13% of total belowground respiration. Gas flux results were combined with biomass harvest and literature data to create a conceptual mass balance model of macrophyte-influenced carbon cycling. Spring and autumn translocation and re-translocation are critical in controlling observed seasonal patterns of above and belowground biomass accumulation. Annually, a total of 270 to 477 g C m^{-2} of macrophyte tissue is available for deposition on the marsh surface as detritus or export from the marsh as particulate or dissolved carbon.

KEY WORDS: *Peltandra virginica* · Macrophyte and microalgal productivity · Carbon dioxide · Methane · Belowground respiration · Translocation · Sweet Hall marsh, Virginia

INTRODUCTION

Tidal freshwater marshes are located at the head of the estuarine gradient where a suitable combination of freshwater supply and tidal range permits their development. On the eastern coastal plain of North America, the most expansive tidal freshwater marshes are located between New Jersey and Virginia and in South Carolina and Georgia (Odum et al. 1984). In contrast with east coast salt marshes, which are dominated by one (generally *Spartina alterniflora*) or several (i.e. *S. patens* and *Distichlis spicata*) macrophyte species, it is not unusual to find 50 to 60 plant species in a freshwater marsh (Pickett 1984, Perry 1991). Dominant vegetation changes seasonally and can include fleshy broadleaf plants such as *Peltandra virginica*, *Pontederia cordata*, and *Sagittaria latifolia* and grass-like species such as *Leersia oryzoides*, *Phragmites australis*, *Typha latifolia*, and *Zizania aquatica*.

Intertidal salt and freshwater marshes have long been considered highly productive ecosystems. Salt

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marshes dominated by monospecific stands of *Spartina alterniflora* have been well studied, with aboveground plus belowground net macrophyte production ranging from 1000 to 8000 g dw m^{-2} yr^{-1} (Schubauer & Hopkinson 1984). Most measurements have been made using a variety of biomass harvest techniques which have been shown to produce estimates of plant productivity that can exceed the physiological capacity of *S. alterniflora* (Morris et al. 1984, Dai & Wiegert 1996). Fewer data are available for tidal freshwater marshes, due in part to their high diversity, seasonally variable species composition, and patchy distribution of belowground biomass. Reported annual net aboveground production varies by species, averaging 900 g dw m^{-2} yr^{-1} for *Peltandra virginica* to 1900 g dw m^{-2} yr^{-1} for *Phragmites australis* (Whigham et al. 1978). Although few studies have included belowground production, Booth (1989) reported approximately equal rates of aboveground and belowground production (1634 and 1568 g dw m^{-2} yr^{-1}, respectively) for a monospecific stand of *P. virginica* in Virginia. When belowground components are included, it appears that freshwater marshes are as productive as salt marshes.

Determining community production in tidal freshwater marshes is, at best, a difficult proposition due to the diverse and seasonally changing species composition and the extensive yet patchy distribution of belowground biomass (de la Cruz 1978, Whigham et al. 1978). Most commonly, aboveground production has been measured using either single or multiple harvests where production is either equal to peak biomass (i.e. Doumlele 1981) or biomass adjusted by a mortality or turnover factor (i.e. Pickett 1984, Wohlgemuth 1988, Booth 1989). Few studies have attempted to measure belowground production in tidal freshwater marshes, especially those dominated by *Peltandra virginica* which have rhizomes that extend to a depth of 1 to 2 m (Booth 1989, Chanton et al. 1992). Complete excavation of belowground material and subsequent separation of live and dead roots is a laborious, inexact, and time-consuming effort and does not provide necessary information on turnover rates. An additional level of complexity is added because turnover rates for both above and belowground tissues vary depending on the species (Pickett 1984) and tissue type (Schubauer & Hopkinson 1984). In systems dominated by perennial plants, there can be significant translocation of nutrients and energy from belowground to aboveground components in the spring, and in the reverse direction late in the growing season as aboveground tissues senesce (Lytle & Hull 1980a,b, Hopkinson & Schubauer 1984, Booth 1989). Because translocation is not accounted for in harvest methods, summing aboveground and belowground production will not provide an accurate estimate of true macrophyte productivity.

As an alternative to harvest methods, fluxes of CO_2 and CH_4 have been used to estimate gross and net macrophyte productivity under ambient field conditions (Blum et al. 1978, Giurgevich & Dunn 1978, Howes et al. 1984, Whiting & Chanton 1996) or under experimental conditions such as elevated atmospheric CO_2 concentrations (Drake 1984, Curtis et al. 1989, Azcón-Bieto et al. 1994) or manipulated soil salinities (Pezeshki 1991, Hwang & Morris 1994). The carbon gas flux technique integrates processes that occur within and between aboveground and belowground compartments (e.g. turnover and translocation) and therefore provides a more reliable estimate of total production than harvest methods. If carbon fluxes from the sediments are measured *in situ*, sediment microalgal production can also be calculated (Anderson et al. 1997).

Marsh macrophyte and microalgal organic matter (carbon) can undergo several potential fates: biotic remineralization to CO_2 and CH_4, retention in the marsh system (as accumulated biomass or sediments), consumption by herbivores, or export to adjacent riverine and estuarine environments as particulate (POM) or dissolved organic matter (DOM). The outwelling hypothesis, which proposes that marsh-derived materials can support secondary production in nearby aquatic communities, requires a net export of organic materials from the marsh (e.g. Teal 1962, Odum 1968, Gosselink et al. 1973). Although historically developed for estuarine and salt marsh systems, the outwelling hypothesis is also applicable to tidal freshwater environments. Ecological simulation (i.e. Buzzelli 1996) or mass balance models (Chalmers et al. 1985, Hopkinson 1988, Anderson et al. 1997) can be used to predict overall carbon or nitrogen balances in a marsh system, but accurate production estimates must first be obtained. Sediment microalgae are highly productive (Sullivan & Moncreiff 1988, Pinckney & Zingmark 1993), can be suspended and exported from the marsh by tidal waters (Gallagher 1975), and are often an important food source in aquatic systems (Sullivan & Moncreiff 1990, Hamilton et al. 1992, Currin et al. 1995, Deegan & Garritt 1997). Therefore, any study that attempts to couple marsh productivity and food web dynamics must include sediment microalgae.

In this study, we describe a carbon gas flux technique for determining macrophyte and sediment microalgal productivity in tidal freshwater marshes. We present estimates of total macrophyte productivity and rates of carbon cycling measured using the gas exchange technique and compare these with several traditional harvest methods. Additionally, we report the first known measurements of sediment microalgal productivity in a tidal freshwater marsh system. These data represent a first step in developing coupled car-

bon and nitrogen process-based mass balance models for a mid-Atlantic (Virginia) tidal freshwater marsh.

MATERIALS AND METHODS

Study site. Sweet Hall marsh is an extensive emergent tidal freshwater marsh located on the Pamunkey River, approximately 69 km from the mouth of the York River, Virginia, USA. The marsh is within the Chesapeake Bay National Estuarine Research Reserve system in Virginia (CB-NERRVA), and is bordered by non-tidal hardwood bottomland forests on the mainland side and submerged riverine mud flats along the Pamunkey River. Nearby upland areas on the Pamunkey River include agricultural fields, mixed hardwood and pine forests, and a pine plantation. A tidal channel and the Pamunkey River isolate the majority of the marsh from direct upland and groundwater influences.

Our study site was located along the western branch of Hill's Ditch, a tidal creek that drains into the Pamunkey River on the south end of Sweet Hall marsh. The tidal range is approximately 80 cm and much of the marsh is flooded on high tides. The study site (and on average, the entire marsh) is dominated by the broadleaf macrophytes *Peltandra virginica* and *Pontederia cordata* through most of the summer while the grass *Zizania aquatica* becomes abundant late in the growing season. To minimize disturbances due to repeated sampling, 3 boardwalks (30 m) were built into the interior of marsh in May 1996, roughly perpendicular to the tidal creek. All sampling was conducted from these boardwalks.

Carbon flux measurements. Marsh community CO_2 and CH_4 flux studies were performed by enclosing an area of marsh (0.69 m^2), including both plants and sediments, within a large temperature-controlled chamber ('community chamber', 696 l, Fig. 1), as described by Whiting et al. (1992). Belowground metabolism (no aboveground plants) was measured using a smaller chamber ('sediment chamber', 79 cm^2, 0.8 l). During spring 1996, 6 aluminum collars for the community chamber were installed along 1 transect and left in place for the duration of the study. Collars, embedded 10 cm into the sediment, provided an air-tight seal between the marsh and community chamber. Holes in each collar at the sediment surface allowed tidal inundation and drainage. Prior to making flux measurements, drainage holes were plugged; the community chamber was clamped to a collar; and the system allowed to equilibrate for 10 to 15 min. Sediment chambers were placed adjacent to each community collar. Fluxes were measured during June, September, and November 1996 and March, April, May, July, and September 1997. With the exception of the September 1997 study (see below), all measurements were made only during daytime low tides. To maximize light intensities for flux measurements, sampling dates were chosen so that slack low water occurred between 11:00 and 13:00 h, and sampling did not take place on excessively cloudy or rainy days. Flux measurements in the community chamber were made in full light and dark and at intermediate light levels (using shade cloths; 6 to 7 meshes cm^{-1} window screening) in order to construct photosynthesis versus irradiance curves. Benthic metabolism was measured only in the light and dark. Flux measurements at all light levels (including dark) for a given chamber were made on the same day; it generally took 2 to 3 d to sample all chambers. To maintain community chamber temperature at ±2°C of ambient, ice water was pumped through a heat exchanger within the chamber and the headspace air stirred by 3 fans. The sediment chambers, which were generally shaded by macrophytes, did not have a cooling system.

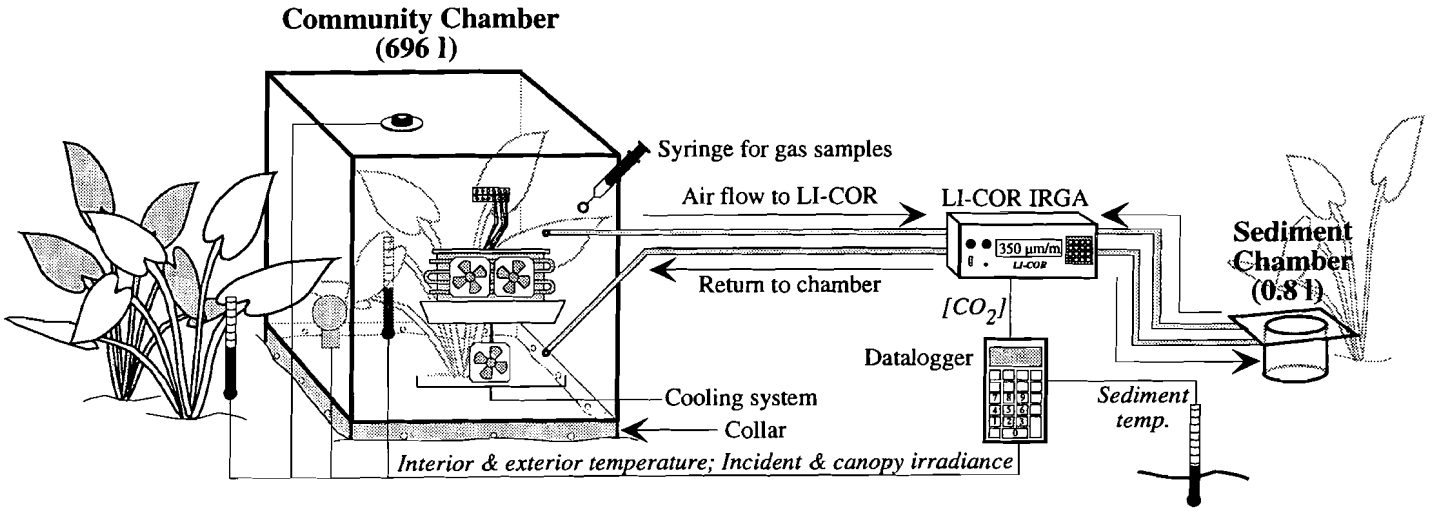

Fig. 1. Schematic of community and sediment chambers used for gas flux measurements

CO_2 concentrations in each chamber were measured in the field using a LI-COR model 6252 infrared gas analyzer (IRGA; LI-COR Inc., Lincoln, NE). Prior to field measurements, the IRGA was zeroed for 15 to 30 min with N_2 passed sequentially through soda lime (to remove CO_2), Nafion tubing (Type 815 DuPont perflourinated polymer, Perma Pure Inc., Toms River, NJ) packed in silica gel (to remove water) and magnesium perchlorate [$Mg(ClO_4)_2$, to remove water]. The instrument was then calibrated with gas standards containing 350, 408, or 1000 ppmv CO_2 in N_2 (Scott Specialty Gases, Inc., Plumsteadville, PA). In the field, air was circulated (500 ml min^{-1}; LI-COR model 6262-04 reference pump) from the chamber through the IRGA and back to the chamber; CO_2 concentrations were measured and recorded at 1 min intervals using a LI-COR model 1000 datalogger. Five to fifteen measurements were made at each light level. Chamber CO_2 concentrations were always between 280 and 350 ppmv—preliminary studies in June 1996 indicated that there was no effect of CO_2 concentration on net photosynthetic rate within this range.

To determine CH_4 fluxes, 60 ml of gas were withdrawn from the community chamber at 10 min intervals. During November 1996 and September 1997, samples were also taken from the sediment chamber at 5 to 7 min intervals. Thirty-five ml of the sample were used to flush, and the remainder to pressurize a gas-tight Hungate tube (12.8 ml). Tubes were stored inverted in brine to reduce gas leakage. Upon return to the lab, 200 µl samples were injected into a Hewlett Packard model 5890 gas chromatograph equipped with a molecular sieve 13× column and flame ionization detector (oven at 80°C, detector at 220°C). A single point calibration of the instrument was performed routinely before and during analyses using a 9.02 ppmv CH_4 in N_2 standard (Scott Specialty Gases, Inc.). Rates of CH_4 flux were linear and showed no response to short-term changes in light.

Concurrent with gas flux measurements, incident irradiance was measured using a LI-COR 2π light sensor placed on top of each chamber, and a 4π sensor within the plant canopy, 15 cm above the sediment surface. Temperatures were measured using thermistors positioned inside and outside the chamber and in the sediment (10 to 15 cm). Light and temperature data were logged at 1 min intervals on a LI-COR model 1000 datalogger.

Tidal effects on CO_2 and CH_4 fluxes were determined during September 1997. Sampling was conducted over 1 full tidal cycle, with measurements made during day and night, on both low and high tides, as described above. When the marsh was flooded, CO_2 and CH_4 fluxes in the chamber headspace and concentrations of dissolved CH_4 in overlying water were measured. Gaseous CO_2 and CH_4 fluxes were measured as above. For dissolved CH_4, 30 ml water samples were shaken for 30 s with an equal volume of CH_4-free argon in a 60 ml syringe. The gas was transferred to a 30 ml syringe with stopcock and analyzed as above within 2 d of collection. CH_4 concentrations in water were calculated using the Ostwald solubility coefficient (0.037 at 20°C, Weiss 1974). Dissolved CO_2 concentrations were not directly measured. Instead, we assumed that air and water CO_2 concentrations were in equilibrium, with the concentration of dissolved CO_2 calculated using chamber headspace CO_2 concentrations and the Ostwald solubility coefficient for CO_2 (0.938 at 20°C, Weiss 1974). Differences in CO_2 and CH_4 respiration rates due to seasonal, diurnal and tidal effects were statistically tested using ANOVA and Tukey's HSD multiple comparison tests (Zar 1996).

Belowground respiration (nitrogen mineralization). In freshwater marsh systems, molecular diffusion or convective throughflow of sediment gases through plant tissues is greater than direct sediment-atmosphere diffusion (Chanton et al. 1992, Chanton & Whiting 1996, Whiting & Chanton 1996). Thus, gas fluxes measured with sediment chambers may underestimate true belowground respiration rates (Morris & Whiting 1986). To account for this we used the sediment gross nitrogen mineralization rate as a proxy for belowground respiration, with N mineralized converted to carbon units using measured sediment C/N ratios and bacterial growth efficiencies (after Linley & Newell 1984, Hart et al. 1994). Although there are potential errors with this approach (see 'Discussion'), we believe this estimate will be more accurate than one based solely on CO_2 and CH_4 efflux into sediment chambers. Gross nitrogen mineralization was determined by $^{15}NH_4^+$ isotope pool dilution as described in Anderson et al. (1997). Sediment cores (10 cm deep) were collected seasonally in triplicate at 5 randomly selected points along each transect using polycarbonate core tubes (20 cm tall × 25.5 cm^2). Each core was uniformly injected with 4.0 ml of argon-sparged ^{15}N-labeled ammonium sulfate [$(^{15}NH_4)_2SO_4$, 10 mM, 99.7 at. %, Isotec Inc., Miamisburg, OH] to an approximate final concentration of 1 mM and 30 at. % ^{15}N in porewater. Cores were incubated at ambient temperature in the dark for either 0, 24, and 48 h (November 1996) or 0, 6, and 24 h (September 1996 and April 1997). After each incubation period, 1 of each set of 3 cores was sacrificed by addition of an equal volume of KCl (255 ml, 2 M) to extract the total exchangeable NH_4^+ pool. Sediment slurries were shaken in Whirl-Pak bags for 1 h on a rotary shaker at room temperature and centrifuged. Supernatants were filter sterilized (0.45 µm Gelman Supor Acrodiscs) and stored frozen in Whirl-Pak bags until analyzed for NH_4^+ using the technique

of Solorzano (1969). Remaining supernatants were transferred to sterile, disposable specimen cups. Magnesium oxide (MgO, 0.2 g) was added to reduce $NH_4^+{}_{(aq)}$ to $NH_{3(g)}$ which was trapped on acidified ($KHSO_4$, 10 µl, 2.5 M) paper filters (Whatman #3, 7 mm) for 6 d, as described by Brooks et al. (1989). Disks were dried overnight in a desiccator over concentrated sulfuric acid (H_2SO_4), wrapped in tin capsules, and analyzed for %N and ^{15}N enrichment using an elemental analyzer coupled to an isotope ratio mass spectrometer at the University of California at Davis. Rates of N mineralization were determined using a model described by Wessel & Tietema (1992) which takes into account both the change in at. % enrichment of the ^{15}N-labeled NH_4^+ pool as well as the change in total concentration of the NH_4^+ pool.

Sediment characterization. Sediment cores (55 cm^2 × 30 cm deep) were collected seasonally and sectioned into 0–2, 2–5, 10–13, 18–21, and 27–30 cm intervals. Samples were dried at 50°C for 3 to 4 wk. A portion of each sample was ground in a Wiley mill (#40 screen), weighed into ashed silver cups and acidified with 1 to 2 drops of 10% HCl to remove carbonates. Samples were placed on a hot plate to evaporate excess acid. The acidification step was repeated and samples allowed to dry overnight in a 50°C drying oven. Total carbon and nitrogen were measured using a Fison model EA 1108 elemental analyzer.

Aboveground macrophyte biomass. Seasonally, aboveground macrophyte biomass was clipped at 5 points along each of 2 transects in the marsh. Each transect was divided into 5 zones (0–2, 2–8, 8–15, 15–23, and 23–30 m from the tidal creek) and a sampling point within each zone was randomly selected. The 2 zones nearest the creek covered the front and back sides, respectively, of a natural levee, while the 3 interior zones were slightly lower in elevation. A 0.11 m^2 ring was blindly dropped at each sampling point; all vegetation rooted within the ring was clipped and returned to the lab for sorting. Samples were sorted by species into living (50 to 100% green), dying (0 to 50% green), and dead fractions, dried at 50°C for 3 to 4 wk, and weighed. Percents carbon and nitrogen were measured as above without the acidification steps. From these data, aboveground macrophyte productivity was estimated using the peak biomass (i.e. Whigham et al. 1978, Doumlele 1981) and Smalley (1958) harvest methods. The peak aboveground biomass (converted to g C m^{-2}) of each species was summed to calculate productivity. Because different species have their peak biomass at different times of the year, multiple harvests allow a better estimation of aboveground productivity than does a single harvest. Smalley production was calculated by taking into account changes in both the live and combined dying plus dead fractions of biomass for all species over the course of the year (Smalley 1958). To account for leaf mortality and decomposition between sampling dates, we applied a turnover factor of 2.24 yr^{-1} (Wohlgemuth 1988) to our estimates obtained from each method. Seasonal trends in live, dead, and total biomass were analyzed using 1-way ANOVA followed by Tukey's HSD multiple comparison tests.

Sediment chlorophyll *a*. For analysis of sediment microalgal biomass, sediment was collected using 2 cm diameter core tubes to a depth of at least 1 cm. Triplicate cores were taken from the same areas sampled for macrophyte biomass, plugged with rubber stoppers, and stored in the dark until processed. The 0 to 5 mm section of each core was removed and stored frozen. Analysis was performed according to the protocol of Lorenzen (1967), as modified by Pinckney et al. (1994) to include extraction of the sediment (unground) with 10 ml of extractant (45% methanol, 45% acetone, 10% DI water) at −15°C for 72 h. Differences in monthly chlorophyll concentrations were analyzed using ANOVA and Tukey's HSD multiple comparison tests.

RESULTS AND CALCULATIONS

Carbon flux measurements

Mean short-term community CO_2 respiration measured as dark CO_2 flux (CR; see Table 1 for abbreviations) ranged from a low of 0.28 mg C m^{-2} min^{-1} in March 1997 to a high of 6.51 mg C m^{-2} min^{-1} in Sep-

Table 1. List of abbreviations used throughout this paper

Abbreviation	Explanation	Units
GCP	Gross community photosynthesis	Mass C m^{-2} per unit time
GMaP	Gross macrophyte photosynthesis	Mass C m^{-2} per unit time
GMiP	Gross microalgal photosynthesis	Mass C m^{-2} per unit time
TCR	Total community respiration (CO_2 + CH_4)	Mass C m^{-2} per unit time
CR	Community respiration (CO_2 only)	Mass C m^{-2} per unit time
ME	Community respiration (CH_4 only)	Mass C m^{-2} per unit time
BGR	Belowground respiration	Mass C m^{-2} per unit time
MaR	Macrophyte respiration	Mass C m^{-2} per unit time
MiR	Microalgal respiration	Mass C m^{-2} per unit time
GNM	Gross sediment nitrogen mineralization	Mass N m^{-2} per unit time
AGB	Aboveground macrophyte biomass	Mass C m^{-2} or g dw m^{-2}
BGE	Bacterial growth efficiency	%
MOM	Sediment macro-organic matter	–

tember 1997 (Fig. 2). CR was highest during the summer when temperatures and aboveground macrophyte biomass (AGB) were greatest. While there was considerable variability between sampling sites on any given day, average community CH_4 fluxes (ME) were highest in September 1996 (0.54 mg C m^{-2} min^{-1}) and lowest during April 1997 (0.16 mg C m^{-2} min^{-1}; Fig. 2). Sediment CH_4 fluxes were a small percentage (generally <5%) of the total ME flux (data not shown). Community ME rates accounted for 5 (May, June 1996; September 1997) to 46% (March 1997) of short-term total community respiration (TCR; CR + ME; Fig. 2). TCR followed the same general trend as CR: rates were highest between May and September, and significantly lower from November to April (Fig. 2; ANOVA, $F = 18.09$, $p < 0.0001$; Tukey's HSD, $p < 0.05$).

During September 1997, studies were conducted over 1 full tidal cycle. Mean CR ranged from 4.02 (nighttime high tide) to 9.00 mg C m^{-2} min^{-1} (nighttime low), but there were no statistical differences in CR over the tidal cycle (Fig. 3A; ANOVA, $F = 2.68$, $p = 0.14$). In contrast, there were large changes in ME over the tidal cycle (Fig. 3A). All treatments (nighttime low, nighttime high, daytime high) were significantly different than ME measured during daytime low tides (ANOVA, $F = 18.18$, $p < 0.01$; Tukey's HSD, $p < 0.05$). ME was higher during the day than at night, and low tide release rates were higher than when the marsh was flooded. Gross photosynthesis also varied with the tidal cycle (Fig. 3B).

Belowground respiration (N mineralization)

Gross N mineralization in the upper 10 cm of the sediment was highest in September (20 mg N m^{-2} h^{-1}; Table 2) and lowest in November (0.4 mg N m^{-2} h^{-1}). Average sediment C/N ratios in the upper 30 cm ranged from 11.6 to 12.1. Mineralization, the reduction of organic matter to NH_4^+, is largely confined to the live root zone. Our data indicate that sediment organic matter concentrations were fairly uniform (average 19.6% ± 7.0 SD; n = 294) through the top 30 cm of sediment. The high standard deviation reflects occasional high organic matter concentrations (50 to 80%) in the upper 2 cm. In *Peltandra virginica* marshes, the highest organic matter content and root concentrations are observed in the upper 30 cm (Booth 1989, Chambers & Fourqurean 1991, Hussey & Odum 1992, Harvey et al. 1995), although live roots and high concentrations of sediment organic matter (15 to 20%) can be present to depths greater than 1 m (Booth 1989, S.C.N. unpubl.). In our calculations, we extrapolated our measured rates of N mineralization (top 10 cm) to 30 cm depth.

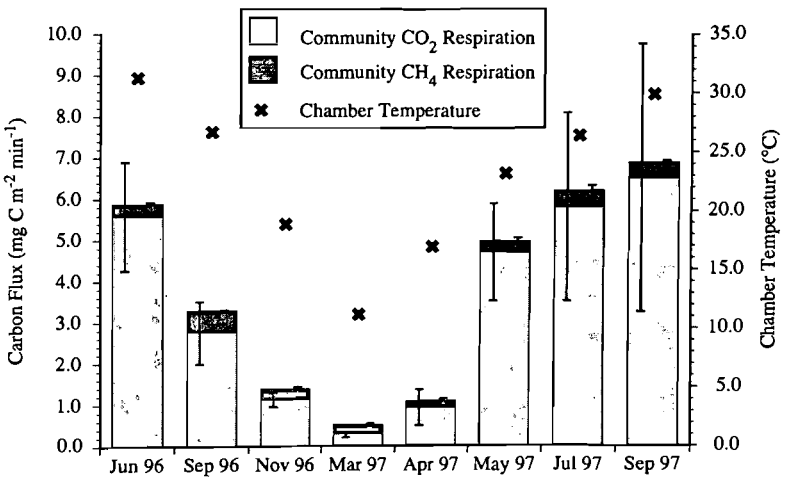

Fig. 2. Seasonal community CO_2 and CH_4 fluxes (mg C m^{-2} min^{-1}), and air temperature within the chamber. Bars are additive; thus combined CO_2 + CH_4 flux = TCR. Error bars are ± 1 standard deviation; n = 3 to 7

Aboveground macrophyte biomass and sediment chlorophyll *a*

There was considerable variability in aboveground biomass (AGB) along each transect with highest live biomass observed near the tidal creek. All sampling locations were generally dominated by *Peltandra virginica* and *Pontederia cordata*, with *Zizania aquatica* increasing in abundance at the end of the growing season. Live biomass was highest during May and June and lowest in November (Fig. 4; ANOVA, $F = 25.63$, $p < 0.0001$; Tukey's HSD, $p < 0.05$). AGB was not measured during winter when few standing stems were observed. Dead and dying biomass peaked in July (ANOVA, $F = 6.84$, $p < 0.001$; Tukey's HSD, $p < 0.01$); nearly 70% of this material was *P. virginica* or *P. cordata*, while 20% was unidentifiable detritus or wrack. Macrophyte C/N ratios ranged from 11.5 (*P. cordata*, June) to 26.0 (*Z. aquatica*, November) and increased during the growing season. Sediment chlorophyll *a* concentrations in the top 5 mm were highest in May (Fig. 4; ANOVA, $F = 19.35$, $p < 0.0001$; Tukey's HSD, $p < 0.01$).

GASEOUS CARBON FLUX MODEL

As a first step in constructing coupled carbon and nitrogen process-based mass balance models for Sweet Hall marsh, we developed a carbon gas flux model to determine annual rates of macrophyte and microalgal carbon fixation, and community and belowground respiration. To do this, it was necessary to scale our short-term field measure-

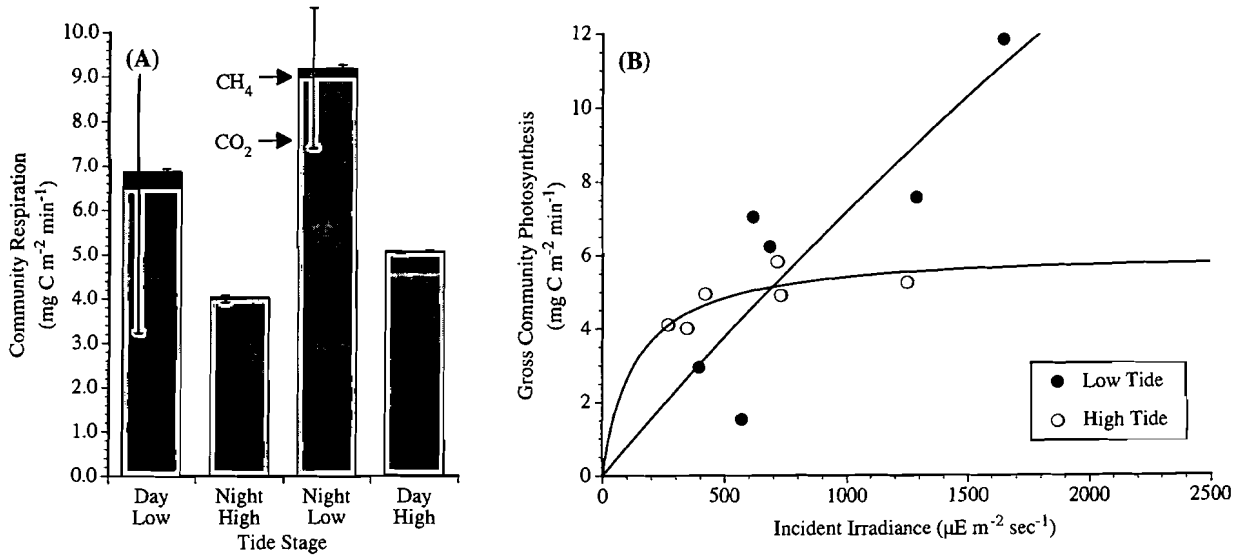

Fig. 3. (A) Community CO_2 and CH_4 respiration (mg C m^{-2} min^{-1}) measured in darkened community chamber over 1 tidal cycle in September 1997. Error bars are ± 1 standard deviation; n = 2 or 3. (B) Gross community photosynthesis versus incident irradiance at high and low tides. Each data point is the slope of CO_2 concentration versus time for a 5 to 10 min sampling interval, minus measured dark respiration

Table 2. Sediment carbon mineralization rates as calculated from measured gross nitrogen mineralization rates, C/N ratios, and estimates of bacterial growth efficiency (BGE). Rates were measured in April, September, and November and extrapolated to seasons as defined below. All rates integrated through the upper 30 cm of the sediment column. n = 16 to 30 for mineralization rates; n = 9 to 29 for sediment C/N

Season	No. of days	N mineralization (mg N m^{-2} h^{-1})	Sediment C/N	C mineralization (g C m^{-2} $season^{-1}$) BGE = 0.5	BGE = 0.4	BGE = 0.3
'Growth' (Mar to Jul)	153	11.32	11.66[a]	243[b]	291	340
'Senescence' (Aug to Oct)	92	20.01	12.06	266	320	373
'Winter' (Nov to Feb)	120	0.43	11.60	7	9	10
Annual totals (g C m^{-2} yr^{-1})				516	620	723

[a]Sediment C/N values are averages of seasonal C/N values for 0–2, 2–5, 10–13, 18–21, and 27–30 cm sediment sections
[b]Calculated by multiplying N mineralization × number of hours per season × sediment C/N × (1 – BGE)

ments of community and sediment CO_2 and CH_4 fluxes to daily, monthly, and annual rates. Our model is driven by these seasonal rates, which, in turn, are controlled by hourly changes in irradiance and temperature (measured at the Virginia Institute of Marine Science, VIMS, ~50 km from Sweet Hall; VIMS 1997) and predicted tidal inundation of the marsh (modeled with a sine curve; 12 to 13 h flooding d^{-1}).

Carbon fluxes were estimated for the 2 yr period from January 1996 through the end of December 1997. For the model, we made the assumption that photosynthesis versus irradiance (P vs I) and respiration versus temperature (R vs T) relationships (see below) did not change from year to year. Thus, interannual variations in modeled carbon fluxes are pri-

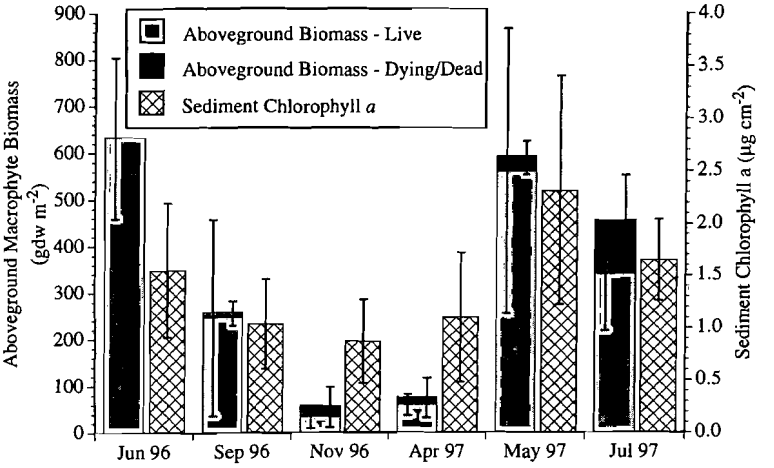

Fig. 4. Seasonal patterns of aboveground macrophyte biomass (g dw m^{-2}) and sediment microalgal chlorophyll (μg cm^{-2}). Error bars are ± 1 standard deviation; n = 10 for macrophyte biomass; n = 30 for sediment chlorophyll

marily due to changes in incident irradiance and temperature. For months where field data were not collected, flux rates were estimated by linear interpolation.

Model construction and assumptions

Gross community photosynthesis

Measurements of gross community photosynthesis (GCP) were made during 8 mo of the 2 yr modeling period, with data collected at a range of light levels (dark to full light) in each season. GCP was calculated from field measurements of net community photosynthesis (light and shaded CO_2 fluxes) plus community respiration (CR; dark CO_2 fluxes) taken immediately following the light measurements. To determine changes in GCP over the course of a day or month in response to changing light levels, GCP versus irradiance (I) curves were developed. Data from 6 chambers, placed along a transect extending from creekbank to marsh interior were used to generate a GCP versus I curve for each season. Hyperbolic curves (after Whiting et al. 1992) were fit to the data using the Levenberg-Marquardt iterative method (DeltaPoint 1996). Hourly GCP was modeled as:

$$GCP_t = \left[\frac{a \times I}{b + I}\right]$$

where GCP_t is calculated gross community photosynthesis (mg C m^{-2} h^{-1}); I is average hourly incident irradiance measured at VIMS (μE m^{-2} s^{-1}); and a and b are empirically derived constants with units of mg C m^{-2} h^{-1} and μE m^{-2} s^{-1}, respectively. Hourly GCP_t rates were summed to determine daily and monthly fluxes.

When data for individual chambers were analyzed, ambient irradiance and GCP were highly correlated (i.e. r^2 = 0.84 to 1.00 for April 1997; Fig. 5A). However, when a month's data for all chambers were pooled (Fig. 5A), the correlation coefficient dropped considerably (r^2 = 0.30 for April 1997 to 0.88 for July 1997), reflecting variability in AGB and species composition along the transect. In spite of this, aggregated GCP versus I curves for each month were used to model the integrated response of the entire, spatially variable, marsh community to changing light conditions (Fig. 5B).

Curves of GCP versus I measured under flooded and non-flooded conditions were markedly different (Fig. 3B). However, when these curves were used to calculate GCP for the entire month of September 1997 (hypothetically assuming the marsh was always flooded or always dry), there was only a small difference between calculated monthly high and low tide GCP (106 vs 108 g C m^{-2} mo^{-1}, respectively). Therefore, we assumed that there was no change in GCP due to tidal flooding.

Gross microalgal photosynthesis

Because of a lack of low light intensity measurements during field studies (less than 200 μE m^{-2} s^{-1}), gross microalgal photosynthesis (GMiP) versus I curves could not be developed. To scale short-term rates to daily and monthly fluxes, we assumed maximum GMiP at irradiances greater than 500 μE m^{-2} s^{-1}. Between 0 and 500 μE m^{-2} s^{-1}, there was a linear increase from 0 to full GMiP. Holmes & Mahall (1982) showed that net CO_2 exchanges for water-saturated intertidal sediments from California plateaued between 500 and 750 μE m^{-2} s^{-1}. Similarly, Darley et al. (1981) observed saturating irradiances in a *Spartina alterniflora* marsh of 500 μE m^{-2} s^{-1} during summer and 100 μE m^{-2} s^{-1} in

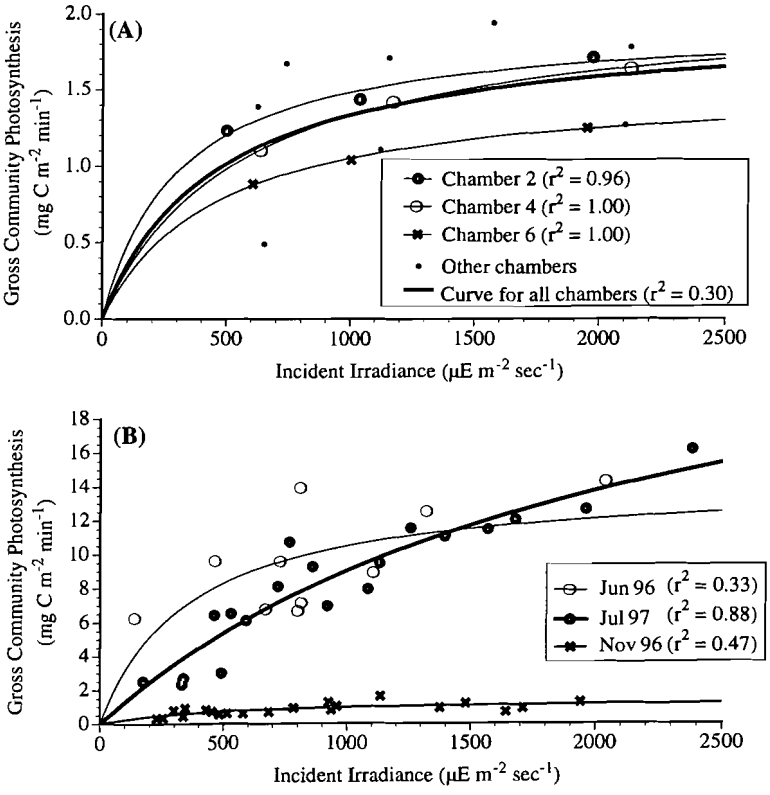

Fig. 5. (A) Relationship between incident irradiance (I) and gross community photosynthesis (GCP) for April 1997, showing strong correlation for individual chambers, but much lower correlation when all chambers are considered. (B) Representative GCP versus I curves used in carbon gas flux model

winter. Whitney & Darley (1983) and Pinckney (1994) reported saturating irradiances ranging from 500 to greater than 1000 μE m^{-2} s^{-1}, depending on the habitat (i.e. creekbank vs marsh interior). Short-term GMiP rates were multiplied by 60 to obtain hourly rates which were then summed to determine daily and monthly rates.

In our tidal inundation study, we were unable to calculate GMiP during high tide. Using the data of Holmes & Mahall (1982), we calculated that gross CO_2 uptake rates decreased by an average of 49% when the sediments were flooded with only a few mm of water. Pinckney & Zingmark (1993) calculated that microalgal production decreased by less than 25% during periods of flooding. To be conservative, we applied the 49% relative decrease from Holmes & Mahall (1982) to simulate a depression in Sweet Hall GMiP rates due to increased light attenuation and vertical migration (downward) of microalgae during tidal flooding (Pinckney & Zingmark 1993, Pinckney 1994). When modeling tidal effects on carbon flux rates, we assumed that the depth of water overlying the marsh did not affect process rates; the important factor was whether the marsh was 'wet' or 'dry'.

Community respiration

In April, July and September, Q_{10} values were calculated from plots of respiration versus air temperature (CR vs T). Values ranged from 1.94 (July) to 3.2 (April). In other months there was not a significant CR versus T relationship; so values from April, July or September were substituted based on similarities in overall vegetation characteristics (AGB and species composition).

Monthly Q_{10} values were combined with hourly weather data measured at VIMS and average monthly respiration rates to calculate hourly CR rates:

$$CR_t = CR_i \times Q_{10}^{\left[\frac{t_t - t_i}{10}\right]}$$

where CR_t is calculated hourly respiration (mg C m^{-2} h^{-1}); CR_i is the average CR rate during season i (mg C m^{-2} h^{-1}); Q_{10} varies seasonally; and t_t and t_i are air temperatures (°C) at time t and the time the field measurements were made, respectively. There were no tidal effects on CR (Fig. 3; ANOVA, $F = 2.68$, $p = 0.14$). Respiration was calculated 24 h d^{-1}; hourly rates were summed to obtain daily and monthly CR rates.

Methane release

Community CH_4 release (ME) was not significantly related to either air or sediment temperature; thus we assumed that the rates we measured were applicable throughout a month. The tidal effects study indicated that there were significant differences in ME over a tidal cycle (Fig. 3; ANOVA, $F = 18.18$, $p < 0.01$; Tukey's HSD, $p < 0.05$). Nighttime rates were 50% of daytime rates, suggesting that a light-dependent process was responsible for some of the CH_4 transport. For modeling purposes, night was defined as any time when average hourly irradiance was less than 50 μE m^{-2} s^{-1}. Rates at high tide were only 12% of corresponding low tide rates. Hourly rates of CH_4 release were calculated as:

$$ME_t = ME_i \times (0.50)^* \times (0.12)^*$$

where ME_t is calculated CH_4 release rate (mg C m^{-2} h^{-1}); ME_i is average ME rate during season i (mg C m^{-2} h^{-1}); and the factors 0.5 and 0.12 are added (*as needed) to convert daytime low tide rates in response to diurnal or tidal changes, respectively. Hourly rates were summed to obtain daily and monthly fluxes.

Belowground respiration

Gross N mineralization (GNM) rates measured in April, September, and November were integrated over a sediment depth of 30 cm. Rates of GNM were converted to carbon units using sediment C/N ratios and estimated bacterial growth efficiencies (BGE, or microbial growth yield) of 30 to 50% (Linley & Newell 1984, Hart et al. 1994):

$$\text{Belowground C respiration} = \left(C/N\right)_{substrate} \times GNM \times (1 - BGE)$$

To convert rates from discrete seasons to an annual rate, seasons were defined based on vegetation processes. Early spring to summer (March to June) was defined as the 'growth' period since AGB rises from near 0 in March to maximum values in mid-June. Large amounts of *Peltandra virginica* and *Pontederia cordata* biomass begin to die in July (Fig. 4), and total community AGB continues to decline through the end of the growing season. Thus, July to September was classified as the period of 'senescence'. From November to February ('winter'), AGB was near 0. Within a season, no corrections were made for changes in sediment temperature.

Model results

Photosynthesis

Total gross community photosynthesis (GCP) averaged 1062 (± 102 SD) g C m^{-2} yr^{-1} over the 1996 to 1997 model period. Results from the sediment chambers show that 66 (± 12 SD) g C m^{-2} yr^{-1} were fixed by sediment microalgae (GMiP). By difference, the remaining 996

(± 114 SD) g C m^{-2} yr^{-1} was gross macrophyte photosynthesis (GMaP). GCP was low during winter and early spring, but increased from 26 to 174 g C m^{-2} mo^{-1} between April and May (Fig. 6). This large increase in GCP was reflected in the large accumulation of AGB during the same period (Fig. 4), although measured photosynthetic rates were not sufficient to explain the entire biomass accumulation (see 'Discussion'). Following a maximum in June, and coincident with decreases in AGB, there was a steady decline in GCP through the end of the growing season. GCP rates during winter were relatively constant (12 to 14 g C m^{-2} mo^{-1}), reflecting low AGB during this time. Statistically, GCP rates were significantly higher ($p < 0.05$) during the summer (May to September) than during the rest of the year (November to April). Highest GMiP rates occurred in May (14.3 g C m^{-2} mo^{-1}), before the growth of dense macrophyte biomass restricted light penetration to the sediment surface. In June, GMiP rates were the lowest of the yr (2.1 g C m^{-2} mo^{-1}; Fig. 6). GMiP rates again increased toward the end of the growing season, possibly due to senescence of the dense *Peltandra virginica* and *Pontederia cordata* cover and subsequent replacement by the tall, thin grass *Zizania aquatica*, which allowed more light to reach the sediment surface.

Respiration

Total community carbon respiration (TCR; CR + ME) exceeded GCP, 1269 (± 130 SD) versus 1062 g C m^{-2} yr^{-1}. Although not the focus of this paper, we hypothesize that sedimentation during tidal flooding provided sufficient carbon to the marsh to account for the high respiration rates and maintain rates of marsh surface accretion. Alternately, if GCP and TCR vary annually and are out of phase, high autotrophic production in 1 yr might not be decomposed until the following year leading to an imbalance between GCP and TCR. Total community respiration rates were significantly greater during the summer ($p < 0.05$; May to September) than during the remainder of the year. Of the community respiratory flux, 6% (72 ± 4 g C m^{-2} yr^{-1}) was due to CH_4 release (ME); the remaining 94% (1197 ± 134 g C m^{-2} yr^{-1}) was CO_2 efflux (CR). CR rates were highest during July (285 g C m^{-2} mo^{-1}; Fig. 6), perhaps due to the large amount of dead and dying *Peltandra virginica* and *Pontederia cordata* biomass (Fig. 4). ME rates were highest during the late growing season (August to September; 8.4 to 8.6 g C m^{-2} mo^{-1}).

When hourly N mineralization rates were extrapolated to seasonal rates and converted to carbon units using measured sediment C/N ratios and bacterial growth efficiencies (BGE) ranging from 0.3 to 0.5, 'growth' and 'senescence' periods accounted for nearly equal amounts of belowground respiration (BGR; 243 to 340 and 266 to 373 g C m^{-2} $season^{-1}$, respectively; Table 2). Although 'winter' accounted for 120 d of the yr, BGR during this season (7 to 10 g C m^{-2} $season^{-1}$) was less than 2% of the annual total.

Total BGR estimated from sediment nitrogen mineralization was 516 to 723 g C m^{-2} yr^{-1}. In contrast, carbon respiration (CO_2 + CH_4) measured using sediment chambers was 75 (± 2 SD) g C m^{-2} yr^{-1}, suggesting that over 85% of CO_2 and CH_4 produced in the sediments was transported through macrophytes before being released to the atmosphere. Methane release (72 g C m^{-2} yr^{-1}) accounted for 11 to 13% of total BGR. However, nearly all CH_4 passed through plant tissues—sediment CH_4 fluxes were generally <1% of total sediment chamber respiration (data not shown). While gross CH_4 production may be much larger than net release due to methane oxidation in the sediment (Yavitt 1997), gas transport through plant stems appears to provide a more efficient mechanism of releasing CH_4 to the atmosphere than direct sediment-atmosphere diffusion.

The difference between TCR and BGR (546 to 753 g C m^{-2} yr^{-1}) can be divided among marsh macrophyte and microalgal respiration (MaR and MiR,

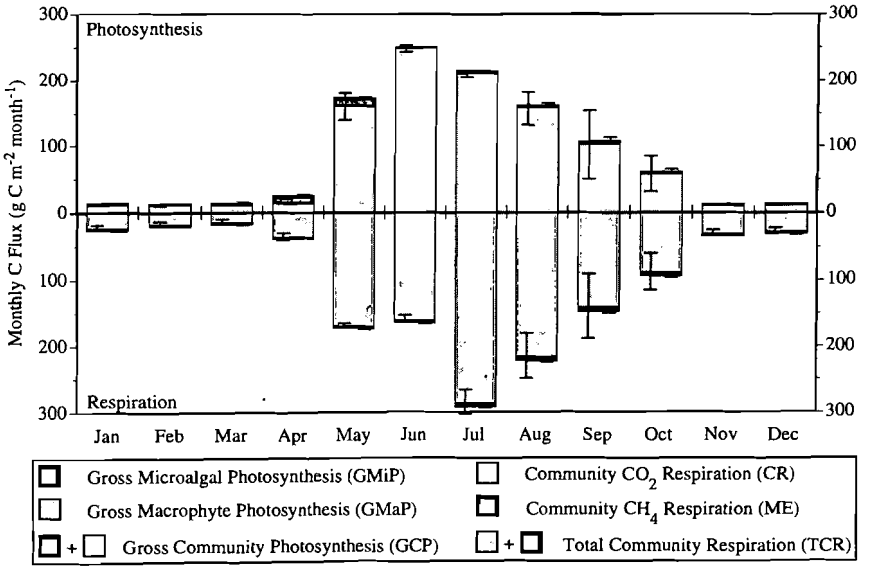

Fig. 6. Monthly rates of gross macrophyte and microalgal photosynthesis and community CO_2 and CH_4 respiration (g C m^{-2} mo^{-1}) from carbon gas flux model. Values are averages of 1996 and 1997 model output (± 1 standard deviation; error bars do not include prediction error of the *P* vs *I* or *R* vs *T* regressions)

respectively). Pomeroy (1959) stated that MiR was less than 10% of GMiP. Using this value, we calculated a MiR rate of 7 g C m^{-2} yr^{-1} and a net microalgal photosynthesis rate of 60 (± 10) g C m^{-2} yr^{-1}. This will underestimate total microalgal production to the extent that the algae utilize porewater DIC in addition to atmospheric CO_2. The remaining 539 to 747 g C m^{-2} yr^{-1} of respiration was due to macrophyte growth and respiration costs and decomposition.

Macrophyte carbon budget

On an annual basis, 996 g C m^{-2} yr^{-1} (Table 3) were fixed by marsh macrophytes (GMaP). During the early growing season (March to June), there was little decaying AGB (Fig. 4); therefore, measured TCR included MaR necessary for growth and maintenance and BGR. MaR, calculated as TCR – BGR – MiR, was subtracted from GMaP to give a net macrophyte photosynthesis rate of 232 to 309 g C m^{-2} ($\bar{x}$ = 271 g C m^{-2}; March to June only). As the growing season progresses, decomposition of AGB makes up an increasing proportion of TCR. To calculate MaR while accounting for decomposition, we assumed that growth and maintenance respiration costs were a constant percentage of GMaP, regardless of the time of year. During March to June, we calculated that macrophyte respiration was 28 to 46% of GMaP. Based on this estimate, MaR for the remainder of the yr would range from 159 to 261 g C m^{-2} yr^{-1} ($\bar{x}$ = 210); the remaining 259 to 287 g C m^{-2} ($\bar{x}$ = 273 g C m^{-2}) would result from plant decomposition. Annual net macrophyte photosynthesis was thus calculated to range from 536 to 715 g C m^{-2} yr^{-1} ($\bar{x}$ = 625 g C m^{-2} yr^{-1}). Based on studies by Hwang & Morris (1992) in a *Spartina alterniflora* marsh, 5 to 37 g C m^{-2} yr^{-1} ($\bar{x}$ = 21 g C m^{-2} yr^{-1}) were fixed via DIC uptake by the roots (0.5 to 3.7% of GMaP). Therefore, net macrophyte production (net photosynthesis + DIC uptake) was 557 to 736 g C m^{-2} ($\bar{x}$ = 646 g C m^{-2}; Fig. 7).

Early summer translocation of carbon from belowground rhizomes to aboveground tissue is critical to support accumulation of aboveground biomass (AGB). Production of peak AGB required a total of 676 g C m^{-2} between the start of the growing season (March) and the time of peak biomass (June; calculated from peak AGB, species-specific % carbon values, and a turnover of 2.24 yr^{-1}). During this 4 mo period, net photosynthesis accounted for only 35 to 45% of the carbon required. The remaining 367 to 444 g C m^{-2} ($\bar{x}$ = 405 g C m^{-2}) was likely supplied by translocation from below to aboveground tissues. Following peak biomass, AGB disappeared from the surface of the marsh. Possible fates include respiration to CO_2 or CH_4, leaching as DOC during tidal flooding, translocation to belowground tissues, and other losses which include herbivory, deposition on the sediment surface or export from the marsh. Using our carbon gas flux model, some literature values, and a few simplifying assumptions, we have completed a conceptual carbon flux model, described below, for macrophytes in *Peltandra virginica* dominated tidal freshwater marshes (Fig. 7).

Leaching of DOC from plant tissues can occur both during tidal submergence and aerial exposure (Gallagher et al. 1976, Turner 1978, Pakulski 1986, Moran & Hodson 1990, Turner 1993, Mann & Wetzel 1996).

Table 3. Model output and sensitivity analysis for conceptual carbon flux model (Fig. 7). Case 1 to 3: variations in the bacterial growth efficiency from 30 to 50%. Cases 4 and 5: variations in the ratio of (MaR) macrophyte respiration to (GMaP) gross macrophyte photosynthesis. Units are g C m^{-2} yr^{-1}

	Case 1	Case 2	Case 3	Case 4	Case 5
	Bacterial growth efficiency (%)			MaR/GMaP (%)	
	50	40	30	40	50
System gas fluxes					
Gross macrophyte photosynthesis	996	996	996	996	996
Macrophyte respiration	459	370	281	398	497
Macrophyte decomposition	287	273	259	277	293
Macrophyte respiration/gross photosynthesis (%)	46	37	28	40	50
Belowground respiration	516	620	723	587	472
Carbon inputs					
Net macrophyte photosynthesis	536	625	715	597	498
DIC uptake	21	21	21	21	21
Internal cycling					
Spring translocation	444	405	367	417	461
Autumn translocation	460	460	460	460	460
Carbon outputs					
Dissolved losses (leaching terms)	66	66	66	66	66
Particulate losses ('other losses')	204	307	410	275	160
Maximum C for export (dissolved plus particulate)	270	374	477	341	226

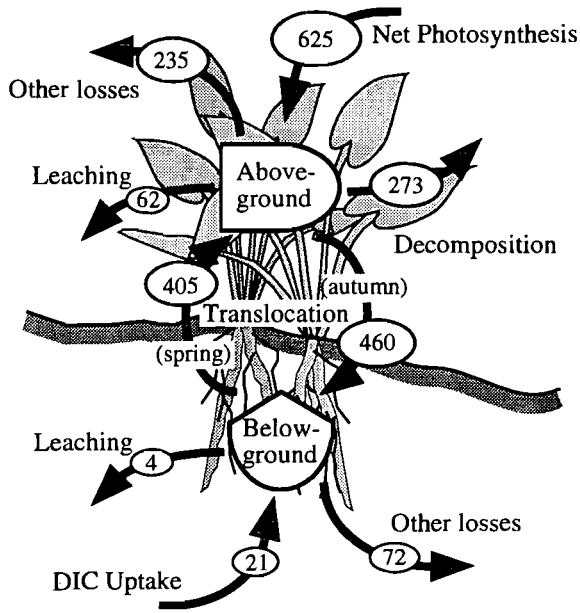

Fig. 7. Conceptual model of carbon fluxes in a *Peltandra virginica* dominated tidal freshwater marsh. Bacterial growth efficiencies from 30 to 50% were used in the calculations presented in the text. For visual simplicity, only results using a median efficiency of 40% are shown here. Units are g C m^{-2} yr^{-1}

Working in *Spartina alterniflora* salt marshes, Turner (1993) calculated that 5 to 10% of total aboveground production was leached from plant tissues. From our biomass harvests, seasonal and species-specific percent carbon data, and an annual live biomass turnover of 2.24 yr^{-1} (Wohlgemuth 1988), we calculated aboveground productivities using the peak biomass (845 g C m^{-2} yr^{-1}) and Smalley methods (776 g C m^{-2} yr^{-1}). Combined with Turner's (1993) data, we estimated a leaching rate of 41 to 85 g C m^{-2} yr^{-1} ($\bar{x}$ = 62 g C m^{-2} yr^{-1}). Using Booth's (1989) nitrogen leaching rates for *Peltandra virginica* and a C/N ratio of 16.3 for aboveground tissues (this study), 34 g C m^{-2} yr^{-1} were leached from aboveground tissues. Both of these values are likely underestimates of true leaching rates as *S. alterniflora* is more resistant to degradation than fleshy plants like *P. virginica* (Odum & Heywood 1978, Webster & Benfield 1986), and Booth's (1989) study examined only live standing leaves; leaching rates are higher from dead and dying tissues (Mann & Wetzel 1996).

We assumed that DIC uptake occurred at a constant rate of 1.75 g C m^{-2} mo^{-1}, for an annual total of 21 g C m^{-2}. Belowground leaching rates (4 g C m^{-2} yr^{-1}) were estimated from Rovira (1969) who reported that root leaching rates from a range of species are rarely more than 0.4% of GMaP. Combined root and rhizome mortality (defined here as loss to sediment macro-organic matter, MOM) was estimated based on Booth (1989). Total loss of root matter during the early growing season (March to June) was 474 g C m^{-2}. Of this, 33 to 110 g C m^{-2} ($\bar{x}$ = 72 g C m^{-2}) were transferred from belowground biomass to the sediment MOM pool (474 g C m^{-2} total loss – 367 to 444 g C m^{-2} translocation loss – 3 g C m^{-2} leaching loss + 7 g C m^{-2} DIC uptake), although the ultimate fate (e.g. respiration to CO_2 and CH_4, export from the marsh) of this MOM is unclear. Because belowground biomass standing stocks are similar at the beginning and end of the year (Booth 1989), we balanced all inputs to the belowground compartment (DIC uptake and fall translocation) with outputs (leaching, spring translocation, and other losses) to calculate an autumn translocation rate of 460 g C m^{-2} yr^{-1}. Similarly, we balanced all inputs and outputs from the aboveground compartment (assuming that AGB is 0 at the beginning and end of the year) and determined that 171 to 300 g C m^{-2} yr^{-1} ($\bar{x}$ = 235 g C m^{-2}) of AGB was lost by herbivory, detritus deposition on the sediment surface, or export from the marsh by tidal waters. The partitioning between these loss terms is currently unknown.

DISCUSSION

The gas exchange technique described herein provides a non-destructive means of determining total macrophyte and microalgal production. Because production numbers are based on actual process modeling, a relatively large amount of data (e.g. GCP vs *I*, CR vs *T* curves) are needed to construct a robust model. Additionally, there are a series of assumptions (see 'Gaseous carbon flux model') that must be made to successfully extrapolate short-term (5 to 30 min) field measurements to monthly and annual budgets. However, if these process relationships can be described and all assumptions confidently justified, a gas flux modeling approach can provide a degree of process-related insight into differences in primary productivity over the course of several years or between different marshes in the same year.

Gas exchange technique versus harvest methods

Annual net macrophyte production (557 to 736 g C m^{-2} yr^{-1}) determined using our gas flux model was lower than that based on AGB harvest methods (776 to 845 g C m^{-2} yr^{-1}) adjusted by a turnover rate of 2.24 yr^{-1} (Wohlgemuth 1988). As previously discussed, harvest techniques tend to bias production estimates by failing to account for seasonal translocation while the gas exchange technique implicitly includes translocation and biomass turnover in production calculations.

Several studies have measured both aboveground macrophyte biomass and production in tidal freshwater marshes (Fig. 8). Because there is a wide range in aboveground productivity depending on marsh species composition (Whigham et al. 1978), we limited our comparison to *Peltandra virginica* and *Pontederia cordata*, the 2 dominant species at our study site. In order to compare annual production values, we converted literature production values from g dw m^{-2} yr^{-1} to g C m^{-2} yr^{-1} assuming a percent carbon of 48.5% (our data, *P. virginica*, June). Our values of peak aboveground biomass fall within the wide range of values reported for other east coast *P. virginica* and *P. cordata* dominated tidal freshwater marshes (Fig. 8), while our annual production is among the highest reported. This reflects the high biomass at our site, but also indicates the sensitivity of the production estimate to the assumed rate of biomass turnover. The studies reported in Whigham et al. (1978), Doumlele (1981), and the peak biomass and Smalley methods of Wohlgemuth (1988) do not account for complete turnover of leaf material during the growing season. These studies will underestimate true macrophyte production as *P. virginica* leaves can lose up to 50% of their dry weight after only 9 d of immersion (Odum & Heywood 1978). The remaining data points on Fig. 8, with the exception of Booth (1989), fall between the lines indicating a turnover (production/peak biomass) of 2 and 2.5 yr^{-1} and represent a more accurate estimate of aboveground marsh production.

Microalgal production

Sediment microalgal production rates measured in this study fall in the wide range of 30 to 200 g C m^{-2} yr^{-1} reported for salt marshes and intertidal habitats (Table 4). Estimates from a *Spartina alterniflora* salt marsh show that, given the assumptions and limitations inherent in each approach, the gas exchange and ecophysiological techniques provide similar production rates (Anderson et al. 1997).

Nitrogen mineralization

In spite of the uncertainties associated with using N mineralization rates to calculate belowground C respiration, we believe that this method is more accurate than directly measuring CO_2 and CH_4 gas effluxes into sediment chambers. Few studies have simultaneously measured both carbon respiration and gross nitrogen mineralization; none have done so in tidal marshes. Working in grassland and cropland soils in North Dakota, Schimel (1986) reported no correlation between CO_2 evolution and gross N mineralization over the course of a 4 d laboratory incubation and attributed this to changes in substrate quality (i.e. C/N ratio) during the incubation. In contrast, studies in an old-growth forest in Oregon (Hart et al. 1994) and a pine plantation in New Zealand (Scott et al. 1998) found strong correlations between CO_2 evolution and gross N mineralization rates. Hart et al. (1994) calculated the C/N ratio of the respired substrate as 10 to 12, compared with a C/N ratio of 26.8 for forest soils. This difference suggests the presence of 2 sediment organic pools, one that is labile and rapidly mineralized (i.e. proteins and sugars) and another more recalcitrant pool (i.e. cellulose and lignin). Because emergent marsh macrophytes contain less cellulose and lignin than woody terrestrial plants (Odum & Heywood 1978), the C/N ratio of respired marsh organic matter will be similar to that of marsh sediments. Thus, we converted N mineralization rates to C respiration using the C/N

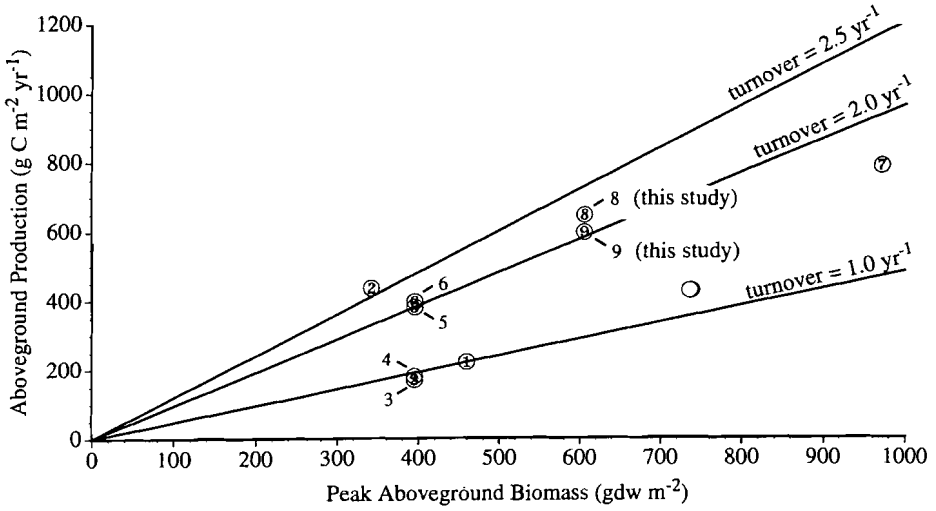

Fig. 8. Aboveground production versus peak biomass for *Peltandra virginica* and/or *Pontederia cordata* only in tidal freshwater marshes. Symbols as follows: O Whigham et al. (1978); ① Doumlele (1981); ② Pickett (1984); ③ Wohlgemuth's (1988) peak biomass, ④ Smalley, ⑤ mortality, and ⑥ Allen curve methods; ⑦ Booth (1989); ⑧ this study's peak biomass, and ⑨ Smalley methods. Lines indicate turnover (production/peak biomass) of 1, 2, and 2.5 yr^{-1}

Table 4. Comparison of methods used to determine benthic microalgal production for intertidal marsh and sand/mudflat habitats

Location	Marsh type	Method	Annual production (g C m^{-2} yr^{-1})	Source
Delaware	Salt marsh	O_2	61–99	Gallagher & Daiber (1974)
Tijuana Estuary, California	Salt marsh	^{14}C	185–341	Zedler (1980)
Global survey	Intertidal and shallow coastal sediments	^{14}C and O_2	50–200	Colijn & de Jonge (1984) and references therein
East Galveston Bay, Texas	Salt marsh	^{14}C	71	Hall & Fisher (1985)
Graveline Bay, Mississippi	Salt marsh	^{14}C	28–151	Sullivan & Moncreiff (1988)
Sheepscot River Estuary, Maine	Intertidal sand/mudflats	O_2	28–29	Cammen (1991)
North Inlet, South Carolina	Salt marsh	O_2 microelectrode, ecophysiological model	56–234	Pinckney & Zingmark (1993)
Goodwin Islands, Virginia	Salt marsh	Process-based simulation model	101–169	Buzzelli (1996)
Phillips Creek marsh, Virginia	Salt marsh	Ecophysiological model	27.8	Anderson et al. (1997)
		Ecophysiological model	4.9 g C m^{-2}; July only	
		CO_2 gas flux	3.8 g C m^{-2}; July only	
Upper Brownsville marsh, Virginia	Salt marsh	CO_2 gas flux	24–68	Miller (1998)
Sweet Hall marsh, Virginia	Tidal freshwater marsh	CO_2 gas flux	59	This study

ratio of the sediments (11.6 to 12.1). Our measure of belowground respiration (516 to 723 g C m^{-2} yr^{-1}) may include some root respiration since no attempts were made to separate fine roots from the sediment matrix prior to the N mineralization studies.

Based on belowground biomass and sediment organic matter profiles for Sweet Hall and other *Peltandra virginica* dominated freshwater marshes, we assumed that mineralization was constant through the top 30 cm of the sediment column. Bowden et al. (1991) measured depth profiles of sediment mineralization in peat sediments along the North River, Massachusetts, and observed minimal N production or consumption between 10 and 30 cm. However, their study location was dominated by *Zizania aquatica*, *Carex* spp., and *Typha latifolia*—species with relatively shallow root distributions. Bowden et al. (1991) observed a distinct organic matter minimum at 30 cm; we observed constant concentrations (15 to 20%) to greater than 1 m. These factors suggest that mineralization will occur to a greater depth at Sweet Hall than observed by Bowden et al. (1991), but this assumption needs to be experimentally verified. However, it is a daunting task to determine mineralization rates over a 1 m sediment profile in an extremely patchy environment where rates can be expected to vary both spatially (horizontally and vertically) and temporally.

There are few estimates of BGE on marsh plants or sediment organic matter. In the absence of exogenous nutrient sources, the theoretical maximum microbial growth yield is equal to the C/N ratio of bacteria divided by the C/N ratio of the substrate (Linley & Newell 1984). Assuming a bacterial C/N of 5 and measured sediment C/N ratios for Sweet Hall (11.6 to 12.1), bacterial growth efficiency is theoretically no greater then ~40%. However, in the presence of available nitrogen (e.g. DIN) in excess of that present in the substrate, actual growth efficiencies can be greater than the theoretical maximum (Newell et al. 1983, Benner & Hodson 1985, Benner et al. 1988, Bano et al. 1997, del Giorgio & Cole 1998). Because fleshy emergent freshwater marsh plants are lower in lignin and humic compounds than salt marsh or woody plants and generally have lower C/N ratios, they are degraded more easily (Odum & Heywood 1978, Odum et al. 1984, Webster & Benfield 1986) and may be expected to support microbial communities with higher growth efficiencies. Therefore, we used a range of bacterial growth efficiencies ranging from 30 to 50% ('theoretical' maximum ± 10%) to convert sediment N mineralization to C respiration.

Model sensitivity analysis

We performed sensitivity analyses to determine how our conceptual model responds to variations in BGE and MaR rates (Table 3). When BGEs used in our analyses were varied from 30 to 50% (cases 1 to 3), calculated BGR varied by over 200 g C m^{-2} yr^{-1}. Although a BGE of 30% (case 3) is most similar to microbial yields on plant detritus (del Giorgio & Cole 1998), it may overestimate the true BGR rate since macrophyte respiration (281 g C m^{-2} yr^{-1}) is only 28% of GMaP. In contrast, the ecophysiological model of Dai & Wiegert (1996) calculated total macrophyte respiration rates of 43 to 50% of GMaP for *Spartina alterniflora*. Because BGR and

MaR are directly linked in our calculations, overestimating BGR will underestimate MaR and reduce the apparent respiration/photosynthesis ratio. Alternatively, it is possible that the BGR rates in case 3 are accurate since respiration costs are proportionally higher in salt marsh than freshwater plants due to salt (Cavalieri & Huang 1981, Mendelssohn & Burdick 1987) and sulfide stresses (King et al. 1982). Cases 4 and 5 forced annual MaR to 40 to 50% of GMaP (the range reported by Dai & Wiegert 1996) by increasing MaR (rather than by decreasing GMaP). The results from these cases were similar to those obtained from BGE estimates of 40 and 50%, suggesting that these growth yields are close to the true values for this system.

To further constrain our results, we estimated rates of GMaP and MaR using leaf-only gas flux measurements. In *Peltandra virginica*, there is restricted gas transport along the length of the petiole (Frye 1989, Chanton et al. 1992). Instead of passing through leaves, CH_4 and sediment-produced CO_2 diffuse directly from the petioles to the atmosphere. Therefore, measuring gas fluxes from leaves provides an independent means of measuring growth and maintenance respiration and partitioning BGR and MaR. Using mid-summer (July) leaf-only flux rates measured in a mixed *Zizania aquatica* and *P. virginica* tidal freshwater marsh on the Edisto River, South Carolina (C. Nietch pers. comm.) and Sweet Hall biomass numbers (this study), we calculated an average GMaP rate of 310 g C m^{-2} (July only) and a leaf respiration rate of 154 g C m^{-2}. These rates were higher than measured at Sweet Hall using the community chamber (Fig. 6). Because photosynthesis and respiration rates are higher in leaves than in petioles and stems, using leaf-only flux measurements and total AGB (leaves + stems + petioles) will tend to overestimate rates. With this approach, MaR was 50% of gross photosynthesis. For comparison, using a BGE of 50% to convert gross sediment N mineralization to C respiration (Table 3, case 1) we produced a MaR to GMaP ratio of 46%. The similarity of these numbers is additional evidence that our conversion of gross N mineralization to C respiration using sediment C/N ratios and BGEs was valid.

Macrophyte carbon budget

Our conceptual model of macrophyte-mediated carbon flows in *Peltandra virginica* dominated tidal freshwater marshes is the first effort of this type. Few studies have attempted to couple aboveground productivity with belowground biomass (translocation and re-translocation), thereby limiting their utility in a larger ecological context. The production of aboveground biomass is supported by net macrophyte photosynthesis ($\bar{x}$ = 625 g C m^{-2} yr^{-1}; range 536 to 715 g C m^{-2} yr^{-1}) and the spring translocation of 'recycled' carbon stored in belowground rhizomes ($\bar{x}$ = 405 g C m^{-2} yr^{-1}; range 367 to 444 g C m^{-2} yr^{-1}). In autumn, a slightly larger quantity of carbon (462 g C m^{-2} yr^{-1}) is moved back to belowground tissues as plants senescence, contrasting with N cycling where significantly greater quantities of nitrogen are translocated aboveground in the spring than belowground in the autumn (Walker 1981, Hopkinson & Schubauer 1984, Booth 1989). Presumably this difference reflects the dominant sources of carbon (atmospheric fixation) and nitrogen (belowground uptake) to the plants.

We have attempted to examine the fates of net macrophyte production as a first step in determining the role that these highly productive plants play in supporting detrital or microbially based food webs in adjacent tidal waters. We estimate that 66 g C m^{-2} yr^{-1} (combined above + belowground) are leached from standing stems, roots, and rhizomes. This leachate may be potentially important as a source of DOC to microbial food webs in adjacent tidal waters or it may be respired *in situ* and form a portion of measured belowground respiration. Labile DOC leached from *Spartina alterniflora* has been correlated with enhanced rates of water column community respiration in waters adjacent to Georgia salt marshes (Turner 1978, Pakulski 1986), while Mann & Wetzel (1996) demonstrated high rates of bacterial production on leachates from aquatic macrophytes. Thus, marsh macrophytes can contribute to microbially-based food webs in adjacent ecosystems.

The ultimate fate of 204 to 410 g C m^{-2} yr^{-1} ($\bar{x}$ = 307 g C m^{-2} yr^{-1}; combined above and belowground 'other loss' terms) is unknown. These plant tissues are either consumed by herbivores, deposited as detritus on the sediment surface or macro-organic matter in the sediment matrix, or exported from the marsh as dissolved or particulate carbon. With the exception of a couple of species (notably *Hibiscus moscheutos*), direct consumption of plant tissues by insects and birds is reportedly minimal, accounting for less than 10% of plant production (Odum et al. 1984, Cahoon & Stevenson 1986). The particulate carbon that is not directly consumed by herbivores falls to the sediment surface and enters the detrital pool where it contributes to belowground respiration, vertical marsh accretion, or is exported from the system. Interestingly, the relative lability (high nitrogen and low cellulose/lignin content) of freshwater marsh macrophyte tissues may limit their importance in aquatic food webs. Utilization of a food source by a consumer depends not only on the quality of the food item, but also on the availability of that food. If decomposition and leaching are rapid enough to remove detritus (as CO_2, CH_4 or DOC) before particulate matter can be exported from the marsh, labile detritus may play only a small role in supporting sec-

ondary production (Findlay et al. 1990). Because the partitioning between these fates has important implications in the role of marsh macrophytes as sources of energy and nutrients to riverine food webs, further research should address the cycling of carbon both within tidal freshwater marshes and between these marshes and adjacent ecosystems.

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