

Effects of Sea Level Induced Disturbances on High Salt Marsh Metabolism

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ABSTRACT: Salt marshes, which provide a transition between the marine and terrestrial environments around much of the temperate world, will be the first ecosystem to feel the effects of an increased rate of sea level rise. This study examined the metabolic responses of a high salt marsh to increased inundation and wrack deposition associated with sea level rise. We measured changes in ecosystem and soil photosynthesis and respiration by analyzing carbon dioxide fluxes in the light and dark. Data from seasonal flux measurements were combined with continuously measured light and temperature data to develop a model that estimated annual production and respiration. Results suggested that increased inundation will reduce respiration rates to a greater extent than production, yielding a moderate net loss of organic carbon from the high marsh. The model also predicted a substantial loss of organic carbon from wrack-affected areas. This decreased organic carbon input may play an important role in the ability of the marsh to maintain elevation relative to sea level rise.

Introduction

The level of the ocean relative to land is continuously changing. At any given location, the rate of change is dependent upon geological, biological, and climatic factors. Rates of sea level rise along most of the U.S. Atlantic Coast are currently between 0.6–4 mm yr⁻¹ (Stevenson et al. 1986; Warwick et al. 1996). These rates are expected to accelerate because of global warming, resulting in increased melting of glaciers and thermal expansion of the ocean (Hoffman 1984; Milliman and Haq 1996).

Salt marshes, which act as ecotones between terrestrial and marine environments, must increase their vertical elevation at rates that keep pace with sea level rise or risk transformation to a lower position along the marsh gradient. Marshes maintain elevation both by accreting inorganic sediments and accruing soil organic matter produced in situ (Redfield 1972). The predominant accretion method depends on site-specific factors that include position of the marsh relative to the tides, predominant vegetation, edaphic conditions, and geographic location (Bricker-Urso et al. 1989).

On the Atlantic and Gulf Coasts of North America, high marsh is generally located at or above mean high water, is typically only flooded on spring tides or during storm events, is vegetated

primarily by *Spartina patens*, *Distichlis spicata*, and *Juncus* sp. and has organic-rich, low bulk density sediments (Brinson et al. 1995). Because of infrequent flooding, most vertical accretion occurs by in situ organic matter production and retention rather than by sedimentation of inorganic material (Hatton et al. 1983; Bricker-Urso et al. 1989; Craft et al. 1993).

In transgressing systems, structure and composition of the high marsh community is expected to change when the rate of sea level rise exceeds the rate of vertical accretion. The change from organic-rich high marsh to mineral low marsh has been documented in coastal salt marshes from New England (Warren and Niering 1993) to Maryland (Stevenson et al. 1985) and Louisiana (DeLaune et al. 1994). Transition from one marsh type to another at a given point has been described as ecosystem state change. Brinson et al. (1995) hypothesized that in high marshes, presence of organic-rich soils help to maintain the marsh state, whereas disturbances and stresses such as increased flooding and wrack deposition (accumulations of dead marsh grass) expedite change. As sea level rises, the frequency and duration of high marsh disturbances are expected to increase (Brinson et al. 1995). The rate and magnitude of marsh change depends upon the local rate of sea level rise, specific physical characteristics of the marsh, slope at the upland-marsh interface, and marsh proximity to tidal creeks (Hmielecki 1994).

The objective of this research was to examine how increased inundation frequency and wrack de-

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position affect the ability of a high marsh to accrete organic carbon. Although other studies have reported on the effects of wrack and flooding on high marsh biomass production and respiration, none of these studies (Phleger 1971; DeLaune et al. 1987; Burdick et al. 1989; Nyman and DeLaune 1991; Bandyopadhyay et al. 1993; Broome et al. 1995; Tolley and Christian 1999) provided a quantified carbon budget that is necessary to determine how disturbances (wrack and flooding) may alter organic accretion rates in the high marsh. In this study, seasonal CO_2 flux measurements were combined with hourly light and temperature data to create a model of annual carbon flux in a Virginia high marsh exposed to artificially increased inundation and wrack deposition. These carbon budget and data on soil characteristics were used to determine vertical accretion potentials for each disturbance regime and assess the ability of the high marsh to resist state change due to wrack deposition and increased flooding associated with rising sea level.

SITE DESCRIPTION

This research is part of a longer-term study of the effects of sea level rise on ecosystem state change in land margin ecosystems located within the Virginia Coast Reserve (VCR), a National Science Foundation–Long-Term Ecological Research (NSF-LTER) site owned and managed by The Nature Conservancy and located on the Atlantic Ocean side of Virginia's Eastern Shore (Fig. 1) (Hayden et al. 1991). Within the reserve, research was conducted at Upper Brownsville marsh ($37^{\circ}27'38''\text{N}$, $75^{\circ}50'04''\text{W}$) near the town of Nassawadox, Virginia. The site is located on the mainland side of Hog Island Bay, along Phillips Creek (Fig. 1). The creek has a tidal prism of about 145 cm that typically floods the high marsh only on spring tides and exceptional tides resulting from meteorological events. A mixed community of *S. patens* and *D. spicata* dominates vegetation at the site, interspersed with dense monospecific stands of *Juncus roemerianus*. In this study, we worked in the *S. patens*/*D. spicata* portion of the marsh. Hmielski (1994) and Taylor (1995) provide a more complete description of the site, surrounding soils, vegetation, and hydrology.

Materials and Methods

EXPERIMENTAL DESIGN

The experimental inundation site, designed by R. Christian and students (Taylor 1995), consisted of three replicate blocks; each contained four treatment plots (3×4 m), including an undisturbed control (C), border control (B), wrack addition (W), and artificial inundation (F) treatment

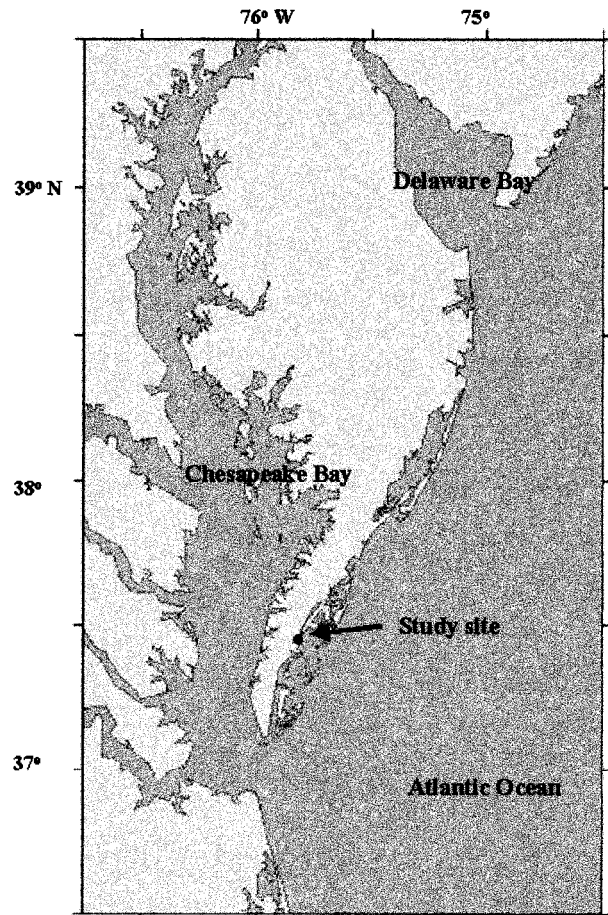


Fig. 1. Location of study site with Chesapeake Bay as reference.

(Fig. 2). Average elevation for each treatment is given in Table 1. A plywood border (0.95 cm thick) with small openings at the corners was driven into the ground around B, W, and F treatments to slow water drainage from the plots. This plywood border was the only manipulation to B plots. A layer of *S. alterniflora* wrack was deposited and maintained on W plots throughout the experiment. In F plots, water was pumped (pump rate varied between 7.5 and 10 l min^{-1}) from Phillips creek through approximately 30 m of 1.91-cm diam PVC pipe to the three flooded plots using a solar-powered electric pump, operated by a float switch and triggered when tidal heights exceeded 0.50 m above mean sea level. This system was operational for the 1994, 1995, and 1996 growing seasons (March–November). Under this pumping regime, F plots were inundated daily to a depth of several centimeters during the growing season while the remaining plots (B, C, and W) were flooded only by natural events.

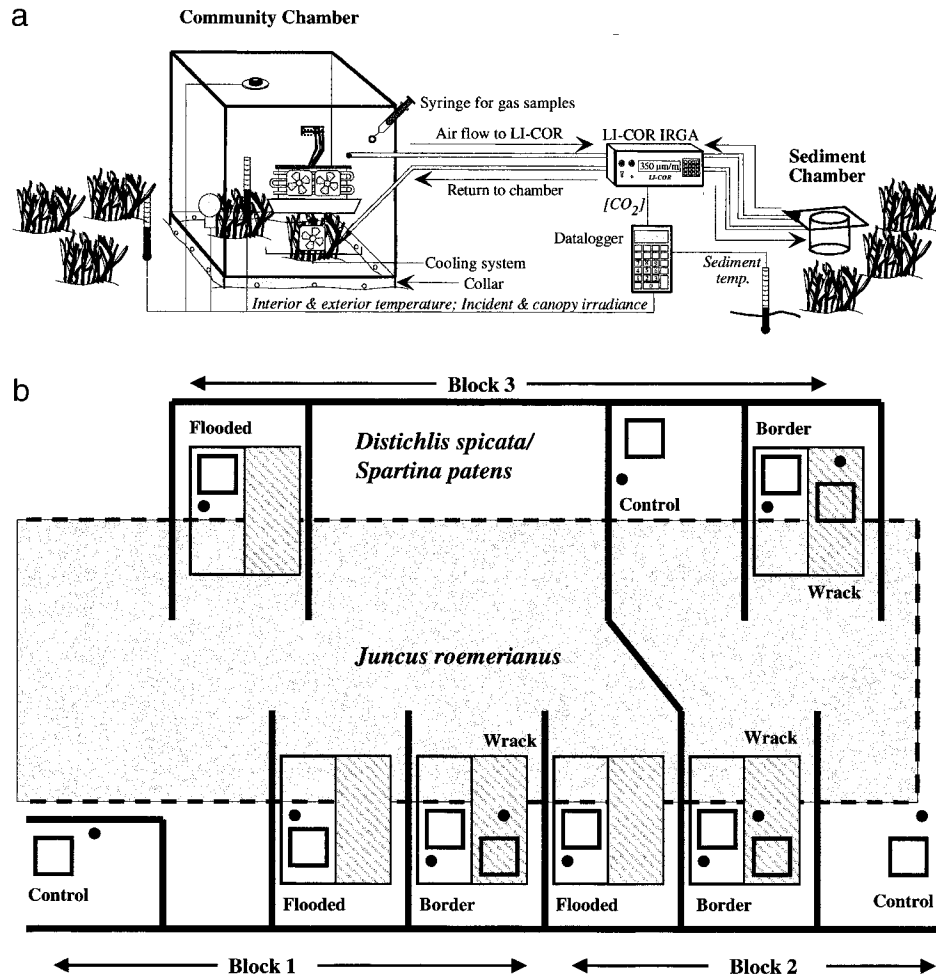


Fig. 2. a) Schematic of field equipment used for carbon dioxide flux measurements. b) Diagram of the experimental inundation site. Black lines indicate boardwalks, black circles indicate site of soil incubation chambers, black squares indicate site of ecosystem metabolism chambers.

ECOSYSTEM METABOLISM

Photosynthesis and respiration rates were determined by measuring changes in CO_2 concentrations within a transparent static flux chamber (679 l; 0.82 m wide \times 0.82 m deep \times 1.01 m tall, Fig. 2) over short (5–10 min) time intervals. Design of

the chamber and protocol for sampling were modified from Whiting et al. (1992). To reduce disturbance to treatment plots, aluminum collars (20 cm tall) were sunk into the marsh to a depth of 10 cm within each treatment plot in August 1995 and left for the duration of the study. Immediately before

TABLE 1. Sediment characteristics for each treatment. Bulk characteristics determined over top 10 cm unless otherwise noted. Values inside parentheses indicate \pm SD ($n = 3$).

Treatment	Mean Elevation (m) ^a	Bulk Density (g cm ⁻³)	Organic Content (%)	Organic Carbon ^b (%)	Annual Range Sediment Chlorophyll <i>a</i> ^c (mg chl <i>a</i> m ⁻²)
Border	0.989 (0.027)	0.15 (0.02)	48.0 (1.0)	49.6	10.3 (6.0)–52.8 (44.3)
Control	1.012 (0.028)	0.15 (0.04)	50.1 (4.1)	49.6	16.7 (7.7)–51.5 (34.4)
Flooded	1.014 (0.035)	0.13 (0.02)	47.9 (5.7)	49.6	17.1 (10.5)–70.2 (61.6)
Wrack	0.989 (0.027)	0.17 (0.02)	40.5 (9.4)	49.6	7.0 (5.1)–87.0 (49.3)

^a Meters above mean sea level.

^b Data provided by Christian (unpublished data), from plots close to study site.

^c Sediment chlorophyll *a* in top 1 cm of sediment.

making a flux measurement, drainage holes in the sides of the collar were plugged and the ecosystem flux chamber attached to the collar with clamps. A rubber-soaked neoprene gasket between the collar and chamber provided an airtight seal. Temperature within the chamber was regulated to $\pm 2^\circ\text{C}$ of ambient by circulating ice water through a heat exchange radiator attached to the Plexiglas side of the flux chamber. Two small, battery operated fans behind the radiator moved air across the grill, and a third fan ensured that all air within the chamber was adequately mixed.

Carbon dioxide concentrations were measured by circulating air through a LiCor model 6252 (Lincoln, Nebraska) non-dispersive infrared gas analyzer (IRGA) with a small pump (LiCor 6262-04) at the constant rate of 500 ml min^{-1} . The IRGA was zeroed and calibrated before each field use with gas standards (350, 408, or 1,000 ppmv CO_2 in N_2 ; Scott Specialty Gases, Inc., Plumsteadville, Pennsylvania). Data were recorded at 1-min intervals for 5–10 min on a LiCor 1000 data logger. Simultaneously, temperature was measured with type-T constantan-copper thermocouples inside and outside the chamber, and at a soil depth of 5 cm, while photosynthetically active radiation (PAR) was measured with a LiCor 182 deck sensor at the top of the chamber. Measurements were made at multiple light levels to develop relationships between photosynthesis and irradiance. Starting in November 1996, we used shade cloth to sequentially reduce light and thereby provide a greater range of light intensities. Respiration measurements were made in the dark, immediately after light measurements, by placing a black tarpaulin over the chamber. Curves relating respiration to temperature were developed from these data. Seasonal CO_2 flux studies were performed in February (1996, 1997), April (1996, 1997), June (1996), August (1995, 1996), and November (1995, 1996). Measurements were made over 2–3 consecutive days for each sampling date.

SOIL METABOLISM

Photosynthesis and respiration by soil microorganisms were determined as described for ecosystem measurements except that smaller (0.495 l; 11-cm diam) chambers (Fig. 2) were used and all aboveground vegetation was removed from inside the chambers before the start of the study. Between measurements the O-ring sealed Plexiglas top was removed and the rest of the chamber remained in place. No temperature control was used because temperatures rarely varied from ambient ($\pm 2^\circ\text{C}$). The chambers had holes flush with the surface of the marsh to facilitate drainage; these holes were plugged prior to making gas flux measurements.

SOIL CHARACTERISTICS

In July 1997, upon completion of the metabolism studies, a thin-walled core tube was used to take one 30 cm deep by 8.4 cm diam core from each treatment plot. After removing all live and dead aboveground vegetation, cores were sectioned at 5-cm intervals, dried at 50°C to constant weight, and combusted in a muffle furnace at 500°C for 6 h to determine bulk density and organic content. During each flux sampling three replicate 2.5 cm diam soil chlorophyll cores were taken to a depth of 10–15 mm within each treatment plot, capped and kept on ice in the dark until processing. The top 10 mm of each core was removed, frozen (-15°C) for less than one month, and analyzed by a modified protocol of Lorenzen (1967), as described in Pinckney et al. (1994). Core sections were extracted for 72 h, and absorbance was measured by spectrophotometer at 665 and 750 nm before and after acidification with 150 μl of 10% HCl to determine chlorophyll *a* and phaeophytin.

PRODUCTION-RESPIRATION GAS FLUX MODEL

To estimate annual ecosystem carbon exchange for the different marsh treatments, models were constructed from seasonal CO_2 flux measurements and local meteorological data (hourly irradiance and temperature) obtained from a VCR-LTER weather station (Krovetz et al. 1996) located ~ 400 m from the study site. The model calculated hourly gross photosynthesis and respiration and extrapolated the short-term measurements to monthly, seasonal, and annual time scales (Fig. 3).

Gross photosynthesis (*P*) was determined by subtracting ecosystem respiration (dark CO_2 flux measurements) from net ecosystem photosynthesis (light CO_2 flux measurements). Hyperbolic curves (Eq. 1) were fit to plots of *P* versus *I* for each treatment and season:

$$P = (A \times I) / (B + I) \quad (1)$$

where *I* was incident irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$), *P* was gross CO_2 uptake ($\text{mg C m}^{-2} \text{min}^{-1}$), and *A* and *B* were empirically determined constants (Whiting et al. 1992). Best-fit regressions for the constants *A* and *B* were calculated for each season and treatment using curve-fitting software (Deltagraph v4.0; DeltaPoint Inc., Monterey, California). Seasonal and annual values of production were then calculated from hourly irradiance data for the season in the VCR-LTER database. For purposes of model calculations, seasons were defined based on growing season and average temperature; i.e., spring: March 16 to May 15; summer: May 16 to September 15; fall: September 16 to November 15, and winter: November 15 to March 15.

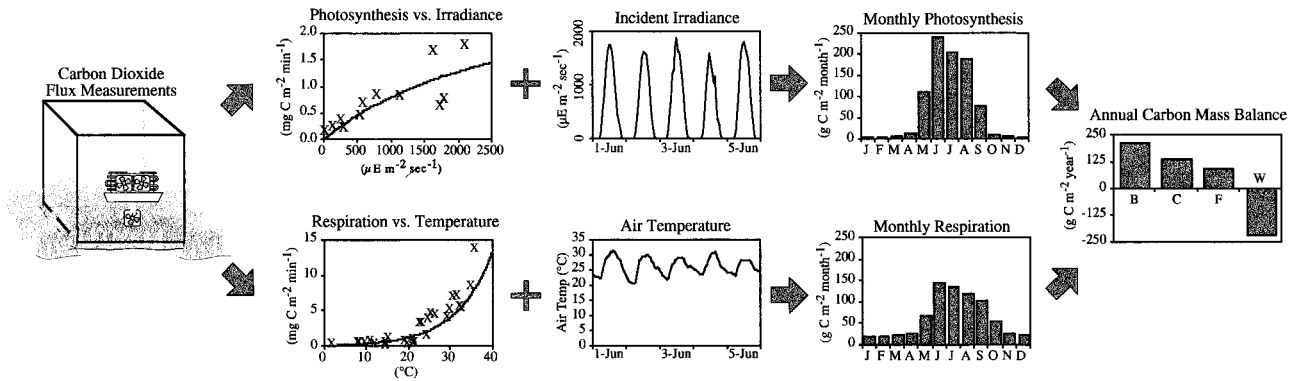


Fig. 3. Flowchart showing the procedure for scaling up from short-term carbon dioxide flux measurements to monthly, seasonal, and annual carbon budgets.

For the respiration model, CO₂ fluxes measured in the dark were regressed against temperature and fitted to exponential curves (Eq. 2) using curve-fitting software (Deltagraph v.4.0).

$$R = Ae^{B \times T} \quad (2)$$

where R was respiration rate (mg C m⁻² min⁻¹), A and B were constants, and T was temperature (°C). These curves allowed for extrapolation of CO₂ flux rates to all temperatures encountered during a given season. For determinations of ecosystem respiration, separate curves were created for each treatment and according to whether or not there was green biomass present (winter/spring and summer/fall). For soil respiration, a single respiration versus temperature curve, incorporating flux data from all seasons, was developed for each treatment. Respiration rates were calculated for 24 h periods (light and dark) assuming that light had a minimal effect on respiration rates. All photosynthesis and respiration curves used in the model can be seen in Miller (1998).

Soil microalgal production was estimated by modeling seasonal CO₂ fluxes from unvegetated sections of marsh soil. Because of the high variability in measured fluxes, it was not possible to develop P versus I curves as was done for the whole ecosystem. We assumed a saturating irradiance value (500 μE m⁻² s⁻¹) based on literature values for intertidal benthic microalgal communities (Holmes and Mahall 1982; Whitney and Darley 1983; Pinckney and Zingmark 1993). A maximum gross photosynthesis rate (P_{max}) was determined for each treatment based on averages of all fluxes occurring at irradiances above 500 μE m⁻² s⁻¹. Photosynthetic rates for values lower than 500 μE m⁻² s⁻¹ were calculated as the percentage of P_{max} equal to the ratio of incident irradiance over saturating irradiance (500 μE m⁻² s⁻¹; Eq. 3).

$$\text{If } I_t < 500 \mu\text{E m}^{-2} \text{ s}^{-1}$$

$$\text{then } P_t = P_{\max} \times I_t / 500 \mu\text{E m}^{-2} \text{ s}^{-1} \quad (3)$$

where I_t and P_t were incident irradiance (μE m⁻² s⁻¹) and gross photosynthesis (mg C m⁻² min⁻¹), respectively, at time t.

POTENTIAL ACCRETION RATE

The annual contribution of net ecosystem production to potential marsh accretion or loss was determined for each treatment. Potential annual organic accretion (mm yr⁻¹) was calculated (Eq. 4) based on surface bulk density (g sed cm⁻³), soil percent organic matter, percent carbon of organic matter, and net carbon flux (g C m⁻² yr⁻¹).

$$\text{organic accretion potential} = \frac{\text{net C flux}}{(\text{bulk density} \times \% \text{OM} \times \% \text{C}_{\text{OM}})} \quad (4)$$

Net carbon flux was calculated as the difference between gross ecosystem photosynthesis and ecosystem respiration. The calculation of potential marsh accretion rates assumed that all net carbon fixed by the marsh ecosystem was buried in marsh soils. It was assumed that grazing of macrophyte biomass by herbivores was insignificant at this site and that export of particulate or dissolved organic or inorganic carbon was negligible due to infrequent tidal flushing. There is not always a direct relationship between accretion and changes in marsh elevation (Cahoon et al. 1995). Violating any of these assumptions will result in an actual accretion rate that is lower than the calculated potential rate.

DATA ANALYSIS

Variability in monthly and annual photosynthesis and respiration rates was determined using a mod-

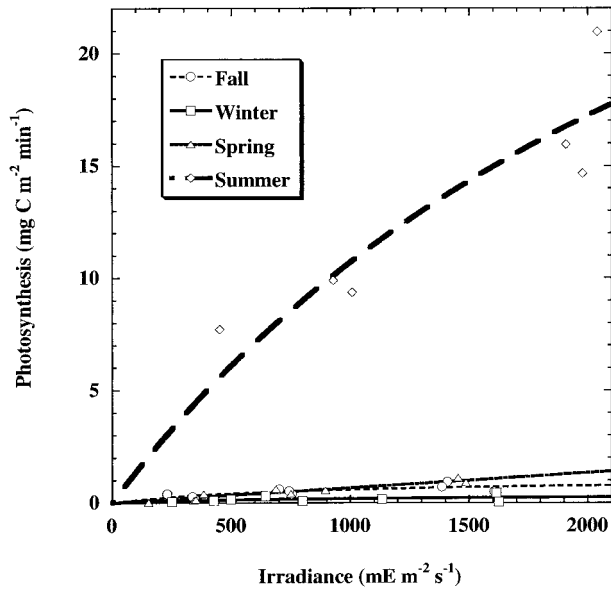


Fig. 4. Example of an ecosystem photosynthesis ($\text{mg C m}^{-2} \text{ min}^{-1}$) versus irradiance ($\mu\text{E m}^{-2} \text{ s}^{-1}$) curve. The four lines on the graph represent best-fit hyperbolic curves for each season. Data are from the 1996–1997 growing season.

ified Monte Carlo sampling strategy (StatSoft Inc. 1999). All calculated parameters (e.g., A and B in Eqs. 1 and 2) were randomly varied by $\pm 20\%$ and the model was re-run to give new rates of marsh carbon flux. This procedure was repeated 500 times and average rates of ecosystem and soil photosynthesis and respiration were calculated. Treatment effects on gas fluxes were analyzed using one-way ANOVA. Soil characterization data were analyzed using a randomized block ANOVA with treatment as the fixed effect and block as the random effect. When significant ($p \leq 0.05$), Tukey's HSD multiple comparison tests were performed to determine specific interactions (Zar 1984). All statistics were run with Statistica (v. 4.1) software.

Results

SOIL CHARACTERIZATION

Organic matter content (40.5% wrack; 50.1% control; 47.9% flooded; 48.0% bordered) and bulk density (0.17 g cm^{-3} wrack; 0.15 g cm^{-3} control; 0.13 g cm^{-3} flooded; 0.15 g cm^{-3} bordered) were characteristic of soils from this type of high marsh (Table 1). Although not statistically significant, the higher bulk density ($p = 0.47$) and lower percent organic matter ($p = 0.33$) found in the wrack treatment would be expected in soils with a lower organic accretion rate. Soil microalgae (measured as soil chlorophyll) demonstrated significant variation, but there was no discernible trend to the var-

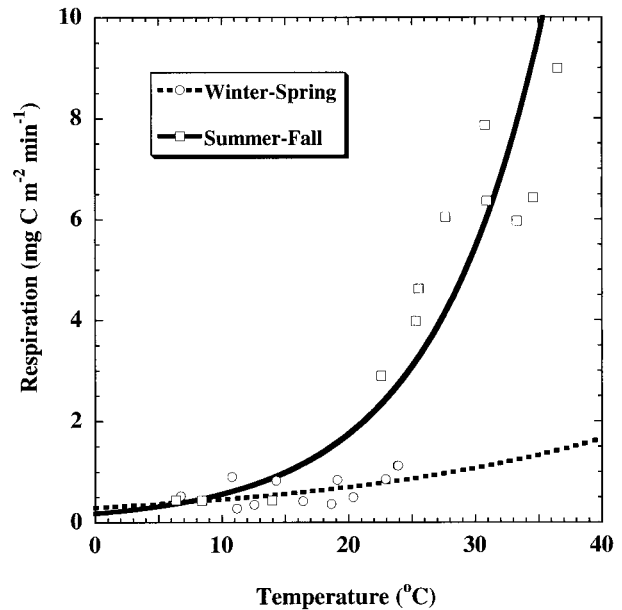


Fig. 5. Example of an ecosystem respiration ($\text{mg C m}^{-2} \text{ min}^{-1}$) versus temperature ($^{\circ}\text{C}$) curve. The two lines in the graph represent best-fit exponential curves for either winter/spring or summer/fall. Data are from the 1996–1997 growing season.

iation nor was there a consistent difference between treatments.

ECOSYSTEM METABOLISM

Seasonal photosynthesis versus irradiance relationships were used as the basis for the production component of the gas flux model. A typical P versus I curve developed from the gas flux data can be seen in Fig. 4. Curves for the other three treatments looked similar, except for the drastically reduced rates in the wrack treatment. Maximum ecosystem photosynthesis was roughly 10 times greater in summer than in the other three seasons for all treatments. Photosynthesis and respiration were depressed in all seasons in the wrack treatment (Fig. 5). Respiration rates in winter/spring showed a smaller temperature effect than summer/fall when more biomass was present.

MODEL RESULTS AND ACCRETION POTENTIAL

Using photosynthesis and respiration models for each treatment, we calculated net carbon fluxes for both the whole marsh ecosystem and for soils. Based on the measured carbon fluxes, soil bulk densities, soil percent organic matter, and carbon content of the organic matter (Christian personal communication) for each treatment, we determined the elevational change that might accrue due to net carbon fixation on an annual basis. We

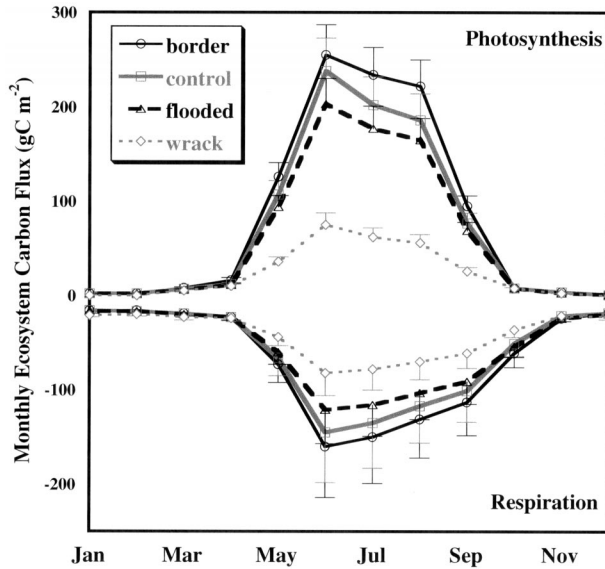


Fig. 6. Monthly model estimates of ecosystem photosynthesis and respiration for each treatment ($\text{g C m}^{-2} \text{ mo}^{-1}$). Positive values indicate photosynthesis (carbon uptake) and negative values indicate respiration (carbon release). Data are from the 1996–1997 growing season.

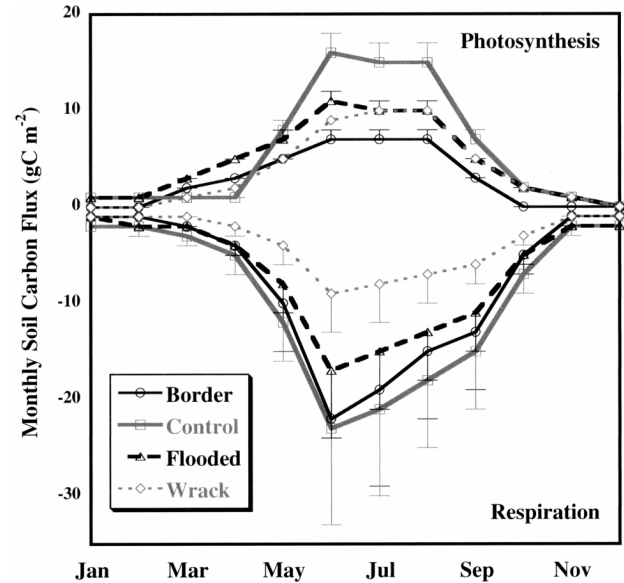


Fig. 7. Monthly model estimates of sediment photosynthesis and respiration for each treatment ($\text{g C m}^{-2} \text{ mo}^{-1}$). Positive values indicate photosynthesis (carbon uptake) and negative values indicate respiration (carbon release). Data are from the 1996–1997 growing season.

recognize that this estimate does not take into account carbon losses due to export or grazing. In addition, there is not always a direct correlation between carbon inputs and elevation gain due to processes such as soil compaction and dewatering. Monthly ecosystem model outputs are shown in Fig. 6, while model outputs for soil metabolism are shown in Fig. 7. Although soil processes were included in the ecosystem measurements, separation of the components allowed us to better distinguish specific responses to marsh disturbances. Photosynthesis and respiration were maximal in the summer when light, temperature, and biomass were greatest. Soil processes accounted for only 10–20% of ecosystem metabolism. Photosynthesis and respiration were consistently lowest in the wrack treatment.

Ecosystem respiration and photosynthesis were partitioned into whole system, macrophyte and microalgal/soil components. Negative values denote carbon export (i.e., respiration) whereas positive

values show carbon fixed by the marsh (i.e., photosynthesis). Annual ecosystem photosynthesis ranged from $280 \pm 42 \text{ g C m}^{-2}$ for the wrack treatment to $973 \pm 115 \text{ g C m}^{-2}$ for the border control, whereas ecosystem respiration ranged from $-502 \pm 100 \text{ g C m}^{-2}$ for the wrack treatment to $-803 \pm 215 \text{ g C m}^{-2}$ for the border control (Table 2). Macrophytes had the largest effect on carbon flux within the marsh (Table 2). Soil respiration (-42 ± 17 to $-112 \pm 42 \text{ g C m}^{-2} \text{ yr}^{-1}$) was almost balanced by microalgal photosynthesis (34 ± 3 to $67 \pm 7 \text{ g C m}^{-2} \text{ yr}^{-1}$). Mean net carbon fluxes, the difference between gross ecosystem photosynthesis and total respiration, were positive in the control ($117 \pm 234 \text{ g C m}^{-2} \text{ yr}^{-1}$), border control ($169 \pm 238 \text{ g C m}^{-2} \text{ yr}^{-1}$), and flooded plots ($77 \pm 177 \text{ g C m}^{-2} \text{ yr}^{-1}$), indicating net autotrophy. In the wrack treatment, however, there was a net loss of carbon from the marsh ($-222 \pm 111 \text{ g C m}^{-2} \text{ yr}^{-1}$). Based upon these data, biological accretion potentials in the control, border control, and flooded plots were 3.2

TABLE 2. Model results of annual rates of marsh metabolism ($\text{g C m}^{-2} \text{ yr}^{-1}$) and accretion potential (mm yr^{-1}). Values inside parentheses indicate \pm SD.

Treatment	Gross Ecosystem Photosynthesis	Ecosystem Respiration	Gross Microalgal Photosynthesis	Soil Respiration	Gross Macrophyte Photosynthesis	Macrophyte Respiration	Net Carbon Flux	Accretion Potential
Border	973 (115)	-803 (215)	34 (3)	-94 (44)	939 (115)	-710 (210)	169 (238)	4.6 (6.5)
Control	846 (118)	-730 (209)	67 (7)	-112 (42)	779 (118)	-618 (204)	117 (234)	3.2 (6.5)
Flooded	741 (95)	-664 (149)	54 (5)	-80 (29)	687 (95)	-584 (146)	77 (177)	2.3 (5.4)
Wrack	280 (42)	-502 (100)	39 (4)	-42 (17)	242 (42)	-460 (99)	-222 (111)	-6.2 (3.3)

± 6.5 , 4.6 ± 6.5 , and 2.3 ± 5.4 mm yr⁻¹ respectively, while the wrack plot would suffer a net loss in elevation of -6.2 ± 3.3 mm yr⁻¹ (Table 2).

Discussion

The effects of increased inundation on salt marsh vegetation have previously been evaluated by measuring biomass production (Bandyopadhyay et al. 1993), survival (Phleger 1971), stem density and length (Broome et al. 1995), as well as physiological indicators such as photosynthetic rate (DeLaune et al. 1987; Pezeshki and DeLaune 1993), root alcohol dehydrogenase activity, adenylate energy charge ratio (Burdick and Mendelssohn 1987; Burdick et al. 1989), ammonium uptake rate (Morris 1984; Bandyopadhyay et al. 1993), and water-use efficiency (Pezeshki and DeLaune 1993). Most measures of performance were negatively correlated with increased inundation, but the intensity of the response varied with intensity of the disturbance and the effects were often only seen after long periods of time. Reed (1995) reviewed the effects of inundation on the ability of the marsh to maintain vertical elevation and concluded that whereas inundation does reduce production available for accretion, the specific mechanism may vary depending on vegetation type.

Increased inundation has been shown to slow belowground decomposition, measured as a decrease in CO₂ emissions, in several Louisiana marshes (Nyman and DeLaune 1991). Decreased decomposition could result in greater marsh accretion, provided that primary production remained constant. Pezeshki and DeLaune (1993) observed decreased net photosynthesis for *S. patens* under the hypoxic and high salinity conditions associated with increased inundation. Decreased net photosynthesis resulted in less fixed carbon available for accretion, thereby counteracting the potential increase in accretion due to decreased decomposition. The intensity, frequency, and duration of the inundation may influence whether the net effect of flooding on accretion is positive or negative.

Data from our study (Table 2) support the findings of Nyman and DeLaune (1991) and Pezeshki and DeLaune (1993) that increased inundation depresses high marsh metabolism. There was both lower total ecosystem and soil respiration as well as reduced gross production in the flooded plots as compared to either control or border control plots. The net result of both reduced respiration and photosynthesis resulting from increased inundation in this ecosystem-level study was an overall decrease in carbon available for burial and accretion.

Several studies have shown that wrack deposition can substantially alter aboveground biomass in an area, depending on the quantity and duration of wrack deposition (Reidenbaugh and Banta 1980; Bertness and Ellison 1987; Tolley 1996). We were unable to locate any data in the literature related to the effects of wrack on belowground processes. Our study examined the effects of long-term wrack stranding and should be seen as an example of maximum wrack disturbance. Wrack treated plots displayed reduced ecosystem respiration (Fig. 6), perhaps related to the lack of live vegetation in the treatment that would help aerate the soil and provide fresh dissolved organic matter for microbial decomposition. However, the near total reduction in photosynthesis due to the absence of aboveground biomass was likely the primary mechanism responsible for the reduced organic deposition. At these sites, respiration far exceeded photosynthesis but respiration was still reduced relative to control areas (Table 2).

Although wrack is a potential carbon source for decomposition by detritivores it is composed mostly of recalcitrant organic matter (Moran and Hodson 1990) and is therefore likely to contribute little to the respired carbon flux. Detrital particles derived from wrack are likely to be incorporated into soil organic matter. We have not taken into account the increased accretion that might result from inclusion of wrack into soils. The small amount of photosynthesis measured in the wrack treatment was performed by benthic microalgae, epiphytes growing on the wrack, and occasional *S. alterniflora* shoots growing through the wrack mat. Wrack deposition, although aerially sparse, may be significant because of the localized intensity of the disturbance. Even though wrack may be present for only a brief time, its potential effects on elevational differences can be severe. These small areas of decreased elevation may become areas where salt panne formation begins (Hartman et al. 1983), or where transition from high marsh to low marsh is initiated (Brinson et al. 1995).

We observed higher gross primary production in the border control treatment compared to the unbordered control (973 ± 115 versus 846 ± 118 g C m⁻² yr⁻¹, 1996 estimates) (ANOVA $p < 0.00001$; Tukey's HSD $p < 0.01$) suggesting a border effect on marsh metabolism. Tolley and Christian (1999) used the same inundation site but different sampling techniques for estimating production and had similar results ($1,280$ versus 993 g biomass m⁻² for border versus control plots, 1994 data). This experimental artifact might have existed in the flooded and wrack treatments that also had borders, but the larger treatment effects would have masked the border effects.

We estimated primary productivity of benthic microalgae by modeling seasonal CO_2 fluxes from measurements made over unvegetated sections of marsh soil. Based on seasonal model estimates, maximum microalgal production occurred in the summer. Although biomass samplings did not show higher levels of chlorophyll *a* in the summer, higher turnover rates and herbivory could keep biomass at constant levels while providing a labile carbon source for high marsh macrofauna such as the fiddler crab (*Uca pugnax*) (Sullivan and Moncreiff 1988). Pomeroy (1959) explained the increased summer microalgal productivity in a Georgia *S. alterniflora* marsh as a function of higher summer temperatures. Annual gross microalgal production estimates for treatments in our study ranged from 34 ± 3 to 67 ± 7 g C m^{-2} . Although only a small fraction of total gross ecosystem production (border, 3.5%; control, 8.0%; flooded, 7.2%; wrack, 13.7%), this source of carbon may be very important to the high marsh food web because it is more labile than that produced by macrophytes (Van Raalte et al. 1976). These results suggested that benthic microalgae can be a small but important source of primary production in the high marsh and should be considered in future carbon and production estimates for the high marsh ecosystem.

Estimated annual biotic accretion potentials (Table 2) suggested that high marshes exposed to increased flooding would be able to maintain a positive carbon flux while wrack disturbed areas would lose carbon. Calculated accretion potentials must be considered in reference to the rates of local sea level in the area of the study. Braatz and Aubrey (1987) and Gornitz et al. (1982) estimated relative sea level rise on the southern tip of the Delmarva Peninsula, near the study site, at between 2.8 and 4.2 mm yr^{-1} . Based on calculated accretion potentials, the border control (4.6 ± 6.5 mm yr^{-1}), control (3.2 ± 6.5 mm yr^{-1}), and flooded (2.3 ± 5.4 mm yr^{-1}) plots would keep pace with sea level rise whereas wrack (-6.2 ± 3.3 mm yr^{-1}) areas would not. Wrack areas would be more likely to undergo ecosystem state change. It is important to remember that these calculations assumed that all excess carbon fixed as marsh biomass was buried within the system and none was lost to export. The similarity between our calculated rates of marsh accretion and rates of elevation change measured close to our sites at Brownsville marsh using a sedimentation-erosion table (SET; 1.3 to 6.0 mm yr^{-1} ; Christian and Brinson unpublished data) suggests that these carbon loss mechanisms were not quantitatively significant. The short-term nature of these estimates did not take into account the large degree of interannual variability that occurs both in

mean sea level and in aboveground production in coastal intertidal systems (Morris 2000). Estimates of biotic accretion potential made in this paper suggest possible scenarios for marsh building or loss that might result in a given year from the applied disturbance.

The annual biotic accretion deficit created by flooding and wrack deposition could generate a negative feedback; i.e., lower elevation resulting from decreased accretion in conjunction with a gradual increase in sea level would result in more frequent inundation, further reducing production and vertical accretion. This feedback loop could continue until high marsh vegetation is replaced by more flood-tolerant low marsh species (*S. alterniflora*). With increasing inundation frequency, inorganic sediment input would increase and higher bulk density mineral sediments would replace organic-rich peats leading to a state change to low marsh (Brinson et al. 1995).

Conclusions

Results from our gas flux and modeling efforts have led us to conclude that the disturbances of wrack deposition and increased inundation both negatively affect marsh vertical position by reducing organic matter inputs. Wrack deposition is a severe disturbance that occurs over small spatial scales and brief time scales (months) but has an acute effect. Increased inundation occurs over wider spatial scales and occurs for longer periods of time but its effects are much more gradual. Wrack deposition provides a mechanism for rapid loss of organic matter from high marsh soils by preventing input of new organic matter. In this study, flooding reduced production more so than respiration thereby decreasing carbon available for deposition relative to undisturbed areas. These two disturbances act on different temporal and spatial scales but have the same result of reduced organic carbon available for accretion.

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