

THE EFFECTS OF INCREASED INUNDATION AND WRACK DEPOSITION ON
PHOTOSYNTHESIS AND RESPIRATION IN A VIRGINIA SALT MARSH

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Master of Arts

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This thesis is submitted in partial fulfillment of the requirements for the degree of

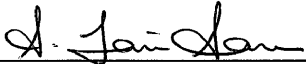
Master of Arts



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DEDICATION

To my parents, for their unending faith and support.

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ABSTRACT

The level of the ocean is constantly changing. In the near future, sea-level is predicted to greatly increase its rate of rise as a result of global warming. As sea-level rises there will be an equivalent increase in frequency and duration of disturbances associated with higher sea-level. Salt marshes provide a transition between the aquatic and terrestrial environments around much of the temperate world. These areas will be the first to feel the effects of an increased rate of sea-level rise. The way in which a salt marsh responds to increased sea-level and its perturbations has great importance to the nearby upland which is often heavily populated. Several hypotheses have been offered to explain the response of the marsh under conditions of sea-level rise.

This study attempted to examine the metabolic response of a common organic-rich high salt marsh to increases in disturbances associated with sea-level rise. We measured changes in community and sediment photosynthesis and respiration in response to the artificially induced disturbances of increased inundation and wrack deposition (dead mats of marsh vegetation). Measurements of photosynthesis and respiration were made by analyzing change in rates of carbon dioxide uptake and release in the light and dark. Data from the seasonal carbon dioxide flux measurements were combined with *in situ* irradiance and temperature data in order to develop a model which estimated gross production and respiration over the course of the entire year.

Results from model output suggest that inundation will reduce both production and respiration but yielding a moderate net loss of carbon to the marsh. The model also predicts a much more severe loss of carbon to areas which are affected by wrack. The consequence of decreased carbon input to the marsh is a reduced ability to accrete material vertically, which is necessary in order to maintain elevation relative to sea-level. If the marsh cannot maintain its elevation it will gradually be submerged causing the entire marsh gradient to migrate landward.

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INTRODUCTION

The level of the ocean relative to the land is always changing. The rate of change is dependent upon geological, biological, and climatic factors. Currently the rate is relatively modest with change occurring on the order of millimeters to centimeters per year; however, the rate may be expected to increase as a result of global warming. Much of the concern over global warming is focused on its potential for accelerating rates of relative sea level rise and its impact on coastal environments. Relative sea-level rise includes two components: eustatic sea-level rise and local land adjustments (Milliman and Haq, 1996).

Eustatic sea-level rise results from changes in the volume and density of ocean water and is largely a function of temperature. Warm water is less dense than cold water and, therefore, occupies a larger volume. Since the ocean contains a tremendous amount of water (70% of the earth surface), even small changes in temperature can have significant effects on ocean height. Increasing temperature can also cause glaciers to melt adding more water to the ocean (Hoffman, 1984). The eustatic component of sea level rise is the one most likely to be influenced by global warming. Much research has been devoted to trying to predict how much sea level will rise with an increase in global temperature. Unfortunately current models have a high degree of variability because of the uncertainty about the size of the temperature change and lack of knowledge about feedback interactions (Titus, 1988). The most often cited estimate for eustatic sea level rise, 1.2 mm yr^{-1} over the last 100 years, was made by Gornitz et al. (1982).

Local land adjustment varies regionally depending upon underlying geology, biological process rates, and depositional environment, as well as within a given environment due to anthropogenic effects. These adjustments are in addition to elevational changes resulting from eustatic sea level rise and they can be either positive or negative. Positive adjustments indicate that the land is rising; they are usually related to isostatic

rebound, common in the higher northern latitudes where reduced weight from glacial retreat allows land elevation to increase (Gornitz and Lebedeff, 1987). More commonly local land adjustments take the form of coastal subsidence, where the land is sinking relative to the ocean. In marsh areas coastal subsidence is due in part to natural geological and biological processes but also may result from anthropogenic disturbance. Sediment elevation may decrease due to compression of unconsolidated organic debris at depth or to organic matter decomposition by oxidation (Stevenson et al., 1986). Withdrawals of water, gas, and oil from coastal sediments are the major anthropogenic disturbances which cause subsidence (Jelgersma, 1996).

Relative sea-level rise is the net result of all factors which might affect the position of the land relative to the sea. Rates of local relative sea-level rise as measured by tide gauge range from -12.8 mm yr^{-1} in Juneau, Alaska (Stevenson et al., 1986), to 10 mm yr^{-1} in southern Louisiana (Penland and Ramsey, 1990). Measurements from the Eastern Shore of Virginia range from $2.8\text{-}4.2 \text{ mm yr}^{-1}$ (Braatz and Aubrey, 1987; Gornitz and Lebedeff, 1987)

Salt marshes exposed to rising sea level must increase their vertical elevation at rates that keep pace with sea level rise or risk transformation to subtidal mudflats/open water. Marshes may maintain elevation by accreting sediments in the form of inorganic clays and sand or as organic matter produced *in situ* (Redfield, 1972). The predominate sediment source depends on marsh type and location (Bricker-Urso et al., 1989).

Marsh type refers to position of the marsh relative to the tides, predominate vegetation, and edaphic conditions. On the Atlantic and Gulf Coasts of North America, low marsh is characterized by daily tidal flooding, monospecific stands of *Spartina alterniflora*, and high bulk density, mineral type soil. Usually the high marsh is only flooded on spring tides, and is vegetated primarily by *Spartina patens*, *Distichlis spicata*, and *Juncus* sp. Characteristically, it has a low bulk density with a thick peat layer

(Brinson et al., 1995). In most situations low marshes accrete the majority of their sediment from allochthonous inorganic clay and sand deposition, which are delivered by daily tidal inundation and storm events (Craft et al., 1993). Some organic matter is necessary to provide structural support (Bricker-Urso et al., 1989), but there is evidence to show that *S. alterniflora* needs the higher bulk density of mineral rich soils, which higher organic matter peats do not have (Nyman et al., 1995). Infrequent flooding in the high marsh does not allow for enough accretion from inorganic sediment deposition; therefore, the majority of vertical accretion must occur as a result of *in situ* organic matter production (Hatton et al., 1983; Bricker-Urso et al., 1989; Craft et al., 1993). Sufficient organic matter can be produced and retained in the high marsh because little biomass is exported via tides (Armentano and Woodwell, 1975), and high marsh vegetation is decomposed very slowly (Valiela et al., 1982; Foote and Reynolds, 1997).

For low marshes, geographic location determines to a large extent the source of inorganic sediment. Riverine marshes accrete silts and clays derived from upland runoff (Day et al., 1995), whereas coastal lagoon marshes trap marine sands from reworked bottoms or along shore flow (Hackney and Cleary, 1987). Marshes in areas with a large tidal amplitude will receive most of their sediment input during normal tidal cycles, while micro- and meso-tidal systems will receive a bulk of their sediment supply during storm events (Stumpf, 1983; Baumann et al., 1984). Many studies have demonstrated the importance of “pulsing” events like storms as natural and necessary components of sediment depositional processes (Stumpf, 1983; Baumann et al., 1984; Stevenson et al., 1985; Day et al., 1995; Christiansen, 1998).

Accretion deficits can result from human activity; for example, in Louisiana channel diversions of the Mississippi River have altered flow and deprived downstream marshes of essential sediment inputs (Hatton et al., 1983; DeLaune et al., 1994; Day et al., 1995). Likewise, damming of rivers allows sediments to settle out in the slow waters behind the

dam, drastically reducing the sediment load to the marshes below the dam. Increased local subsidence rates can also result from groundwater withdrawal (Hatton et al., 1983; Milliman and Haq, 1996).

When the rate of sea level rise exceeds the rate of vertical accretion, changes occur in the structure and composition of the high marsh. The change can be viewed as a transition from organic-rich high marsh to mineral low marsh. This change has been documented in coastal salt marshes from New England (Warren and Niering, 1993), to Maryland (Stevenson et al., 1985), to Louisiana (Nyman et al., 1993; DeLaune et al., 1994). Rising sea level affects all ecosystems along the coastal continuum, from upland to high marsh to low marsh to open water/subtidal mudflats. Therefore, while high marsh is transitioning to low marsh, low marsh is also being converted to subtidal mudflats, and likewise upland is being converted into high marsh. So, as sea level rises the entire coastal ecosystem is migrating landward. The rate and magnitude of the migration depends primarily on the slope of the land and its proximity to tidal creeks (Hmielecki, 1994).

Transition from one marsh type to another at a given point is known as ecosystem state change. It has been hypothesized by Brinson et al. (1995) that there are separate factors which resist or initiate this change for each marsh environment. In the high marsh, the presence of organic-rich sediment is thought to help maintain a state, while disturbances and stresses facilitate change. Identification of factors initiating and resisting state change and the study of processes regulating transition have been the focus of research at the Virginia Coast Reserve, a Long-Term Ecological Research (VCR-LTER) site funded by the National Science Foundation (Hayden, 1991).

Numerous studies have investigated the effects of increased inundation as a stressor on various properties and processes of salt marshes (Phleger, 1971; Smart and Barko, 1978; Smart and Barko, 1980; Morris, 1984; Pezeshki et al., 1987; Burdick and Mendelsohn, 1987; DeLaune et al., 1987; Burdick et al., 1989; Bandyopadhyay et al.,

1993; Pezeshki and DeLaune, 1993; Broome et al., 1995). Researchers have used a variety of approaches including *in situ* measurements, individual plant/greenhouse studies, and single leaf responses. Most studies have examined vegetational responses to changed sediment edaphic properties resulting from increased inundation such as porewater salinity, redox potential (Eh), dissolved oxygen, sulfide, pH, and exchangeable ammonium.

A number of different measures of salt marsh vegetation performance have been used to evaluate inundation effects including: biomass production (Smart and Barko, 1980; 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). The general consensus from this research is that most measures of performance are negatively correlated with inundation.

Morris (1984) and Bandyopadhyay et al. (1993) both showed decreased nitrogen uptake rates with increased salinity and reduced soil Eh, associated with flooding. Similar negative correlations were observed in studies of the relationship between plant gas flux (CO₂), Eh, and salinity (Pezeshki and DeLaune, 1993). Broome et al. (1995) showed the effects of water depth and salinity separately and indicated that *S. patens* is more sensitive to water depth than salinity, possibly related to the poorly developed aerenchyma tissue for belowground aeration. Burdick and Mendelssohn (1987) showed that *S. patens* aerenchyma may not be sufficient to overcome increased waterlogging; a metabolic shift from carbon dioxide to organic acids in respiratory products may be the plant's long term solution to flooding. In correlation matrices including multiple soil factors and plant measures Burdick et al. (1989) determined that the combination of several factors including

soil aeration, sulfide concentrations, and nitrogen levels, may be more important than any single factor.

DeLaune et al. (1987) have reviewed marsh vegetational responses to rising sea level (increased flooding and salinity) in the Mississippi River Delta which is experiencing land subsidence rates of up to 10 mm yr^{-1} , primarily because of decreased inorganic sediment input due to river channelization (Hatton et al., 1983; Baumann et al., 1984). Because of the high rate of marsh loss much of the recent research has come from the Gulf Coast where 40% of the nation's coastal marshes are located (Mitsch and Gosselink, 1993), and 50 square miles of marsh are being converted to open water every year (Titus, 1988). DeLaune et al. (1987) cover all aspects of the changes in soil physicochemical properties, including incomplete decomposition of organic matter, buildup of potentially toxic compounds like sulfides, increasingly anaerobic conditions, ion toxicity, and photosynthesis and stomatal responses.

Although most literature deals with the negative effects of flooding on salt marsh vegetation, it is important to note that under certain conditions flooding may have positive effects. In low marsh environments daily flooding often acts as an energy subsidy by regulating fluxes of nutrients and sediments as well as removing toxic compounds which build up in the soils (Odum, 1980). These benefits from tidal flooding explain the high primary productivity seen in many low marsh systems and especially along creek banks, where primary productivity has been positively correlated with tidal range (Steever et al., 1976). In the low marsh sediment characteristics and steep hydraulic gradients permit flushing of tidal water through the system on a regular basis, whereas in the high marsh the more gradual slope and less frequent flooding leads to stagnant porewater which is flushed at a much slower rate. Thus, structure of the marsh determines whether inundation will act as a subsidy or a stress (Odum, 1980).

As shown by DeLaune et al. (1987) and others, the negative impacts of inundation on high marsh vegetation are greater than simply reducing plant vigor. Increased inundation in the high marsh starts a negative feedback loop which may eventually lead to the conversion of high marsh to low marsh. Flooding reduces production in the high marsh; a large portion of this production is normally retained in the high marsh sediments and is the primary means of vertical accretion for marshes which do not receive daily tidal inundation. The increased inundation is not typically sufficient to supply enough allochthonous inorganic sediments to make up for the accretion deficit from reduced organic matter production (DeLaune et al., 1994). As vertical accretion does not keep up with relative sea level rise, the marsh becomes flooded on a more frequent basis, further reducing the productivity of the high marsh vegetation. The feedback loop continues until the flooding waters have carried in enough inorganic sediment to increase the bulk density of the sediments to values which permit low marsh vegetation and the high marsh vegetation is replaced by mineral-rich low marsh *S. alterniflora* (state change). This transition occurs concurrently with an increase in sea level and therefore the area that was formerly irregularly flooded high marsh, is now daily flooded low marsh (Warren and Niering, 1993).

A second major disturbance to high marshes results from wrack deposition, an accumulation of dead plant debris, which collects into rafts that float around on the tide, eventually to become stranded on the marsh. In sufficient density these mats smother underlying vegetation creating bare areas. Mats are normally created in the winter and spring when strong storms remove standing dead *S. alterniflora* from the low marsh and transport them throughout the salt marsh on high tides. These mats are common in coastal marshes all along the Atlantic and Gulf Coasts of North America (Reidenbaugh and Banta, 1980). There are differing opinions on the relevance and scale of the impact which wrack deposition might have on marsh systems (Valiela and Riestma, 1995).

Many researchers have noted the importance of wrack deposition as a physical disturbance in salt marshes (Redfield, 1972; Reidenbaugh and Banta, 1980; Bertness and Ellison, 1987; Hartman, 1988; Valiela and Rietsma, 1995; Tolley, 1996). Most studies of wrack have considered changes in macrophyte species composition resulting from the disturbance (Hartman et al., 1983; Bertness and Ellison, 1987). Wrack deposition is among the most common disturbances in New England salt marshes (Valiela and Rietsma, 1995). The length of time mats remain in marshes is usually short. Most mats decay or are moved before the end of the following summer. Mats which cover the marsh at the start of the growing season cause the most damage by preventing new year's growth (Valiela and Rietsma, 1995).

Because of its typically short residence time wrack does not usually cause permanent change to a marsh. Wrack mats are frequently moved about within a marsh several times before being broken up, moved out, or decomposed. Even areas completely devegetated by wrack deposits fully revegetate within two to three years (Reidenbaugh and Banta, 1980; Bertness and Ellison, 1987; Valiela and Rietsma, 1995).

Hartman (1988) observed no significant differences in edaphic factors (ammonium, sulfide, or salinity) between a control site and one which had been artificially covered with wrack for a growing season. The study concluded that vegetative propagation, rather than new seed growth, is the primary means of recolonization for bare patches created by wrack. Other studies have been unable to show any long term changes in species composition as a result of wrack deposition (Reidenbaugh et al., 1980; Hartman, 1983; Bertness and Ellison, 1987; Valiela and Rietsma, 1995; Tolley, 1996).

Only a small portion of low marsh *S. alterniflora* production becomes wrack each year. Valiela and Rietsma (1995) estimated that 3% of Great Sippewissett Marsh creekbank *S. alterniflora* biomass was incorporated into wrack mats. Hartman (1988) suggested 4% of this same marsh is covered by wrack annually. Bertness and Ellison

(1987) suggested that as much as 30% of a Rhode Island high marsh was covered by wrack during a June sampling. Along Virginia's portion of the Delmarva peninsula Reidenbaugh and Banta (1980) observed that 11% of a *S. alterniflora* study area was affected by wrack deposition during a single year, leading to an 8% reduction in net aerial productivity. Aside from Hartman's (1988) measurements of edaphic factors, there is little literature available on the effects of wrack deposition on community or belowground respiration.

The higher a mat is stranded in the salt marsh, the more likely it is to break down in place, as opposed to being moved again by future high tides. Marsh responses to wrack deposition are variable and dependent on location, time of year, and duration of stay. Increase in residence time has a deleterious effect on underlying vegetation. The likelihood of wrack deposition to a marsh site is largely dependent on meteorological occurrences such as wind, wave, and storm events (Hartman et al., 1983).

In a well studied Rhode Island high marsh residence times of wrack mats averaged 2-4 weeks and coincided with times of high spring tides. Residence time in the marsh was directly related to distance from the water with increasing residence time farther from the water. While residence time increased with distance from the water, the percentage of the marsh that was covered by wrack for at least 2 days decreased with distance from the water. Results of studies involving artificial wrack coverage of marsh showed that *S. alterniflora* and *D. spicata* were able to survive significantly longer under wrack mats than *S. patens*. Even short term coverage (2-4 weeks) was sufficient to reduce aboveground production of *S. patens* (Bertness and Ellison, 1987).

A much less studied effect of wrack deposition is change in elevation accompanying the disturbance. In a study at a Virginia marsh Reidenbaugh et al. (1983) measured small changes in elevation over three years in order to calculate short-term accretion and erosion rates in a young prograding marsh. Results showed that even though most areas of the

marsh were accreting ($1.6-6.2 \text{ mm yr}^{-1}$) at least enough to keep pace with an observed 2 mm yr^{-1} rise in sea level, areas with wrack deposits and areas still bare or sparsely vegetated from recent wrack deposition had substantial erosion rates (-5.3 mm yr^{-1}). The authors suggested that net erosion resulted from organic matter decomposition and sediment compaction, as opposed to physical processes like waves and wind.

Wrack deposition and resulting erosion, although aurally sparse, may still be significant because of the localized intensity of the disturbance. So even though wrack may be present for only a brief duration, its potential effects on elevational differences can be severe. These small areas of decreased elevation might in turn become areas where salt panne formation begins (Hartman, 1983), or where transition from high marsh to low marsh is initiated (Brinson et al., 1995).

OBJECTIVES and HYPOTHESES

The goals of this research were to determine the effects of wrack deposition and increased inundation frequency on high marsh community metabolism. These disturbances are predicted to increase in frequency and intensity as global warming increases the rate of relative sea level rise. In order to calculate potential organic matter accretion rates and to determine the potential for wrack deposition and increased inundation frequency to perturb those rates, we proposed to develop a carbon budget for an organic-rich high marsh site located in the Virginia Coast Reserve (VCR).

Hypothesis 1: Increased inundation will reduce *S. patens/D. spicata* net community primary production in an organic rich high marsh.

Because inundation and associated increases in salinity have negative impacts on nutrient uptake (Morris, 1984; Bandyopadhyay et al., 1993) and other measures of macrophyte vigor (Phleger, 1971; Smart and Barko, 1978; Smart and Barko, 1980; Burdick and Mendelsohn, 1987; DeLaune et al., 1987; Pezeshki et al., 1987; Burdick et al., 1989; Pezeshki and DeLaune, 1993; Broome et al., 1995), the frequency and duration of inundation is expected to reduce net primary production.

Hypothesis 2: Increased inundation will decrease rates of belowground metabolism in a *S. patens/D. spicata* community.

Increased inundation is expected to raise the water table in flooded areas, increasing anaerobiosis and thereby decreasing belowground decomposition rates (Nyman and DeLaune, 1991).

Hypothesis 3: Wrack deposition will increase rates of *S. patens/D. spicata* community respiration, decrease rates of community production, and result in decreased rates of organic matter accretion.

Although no specific studies have examined the effects of wrack deposition on sediment respiration, inferences from available literature indicate that wrack mats themselves provide a source of refractory carbon for bacterial degradation; however, by killing both above- and belowground plant biomass, inundation is expected to cause rates of sediment respiration to exceed primary production.

METHODS AND MATERIALS

SITE DESCRIPTION

Research was conducted within the Virginia Coast Reserve (VCR) which is located at the southern tip of the Delmarva peninsula (Figure 1). The VCR is part of the National Science Foundation's Long Term Ecological Research (LTER) program. The reserve extends 110 km on the Atlantic side of Virginia's Eastern Shore. The VCR, which encompasses an area of approximately 14,000 hectares, is owned and managed by The Nature Conservancy. It contains a variety of coastal systems, including 14 barrier islands, beaches, mudflats, channels, lagoons, salt marshes and coastal uplands. The VCR/LTER is a multi-institutional research site with investigators from the University of Virginia, East Carolina University, Virginia Institute of Marine Science, Bucknell University, Old Dominion University, and Virginia Commonwealth University contributing. The project is managed by the University of Virginia.

Within the reserve, research for this study was conducted at Upper Brownsville marsh (37° 27' 38" N, 75° 50' 04" W) near the town of Nassawodax VA (Figure 2) (Taylor, 1994). The site is located on the mainland side of Hog Island Bay, along Phillips Creek. The study area is irregularly flooded by the creek which has a tidal prism of approximately 145 cm (Hmieleski, 1994). The marsh is typically flooded only on extreme tides brought about by meteorological events. Vegetation at the study site is dominated by a mixed community of *Spartina patens* and *Distichlis spicata* interspersed with dense monospecific stands of *Juncus roemerianus*. Soils of the high marsh are rich in peat with organic content ranging from 45% to 51% in the top 10 cm. The site is surrounded on three sides by agricultural fields and pine forest. A more complete description of the site and surrounding soils, vegetation, and hydrology is provided by Hmieleski (1994).

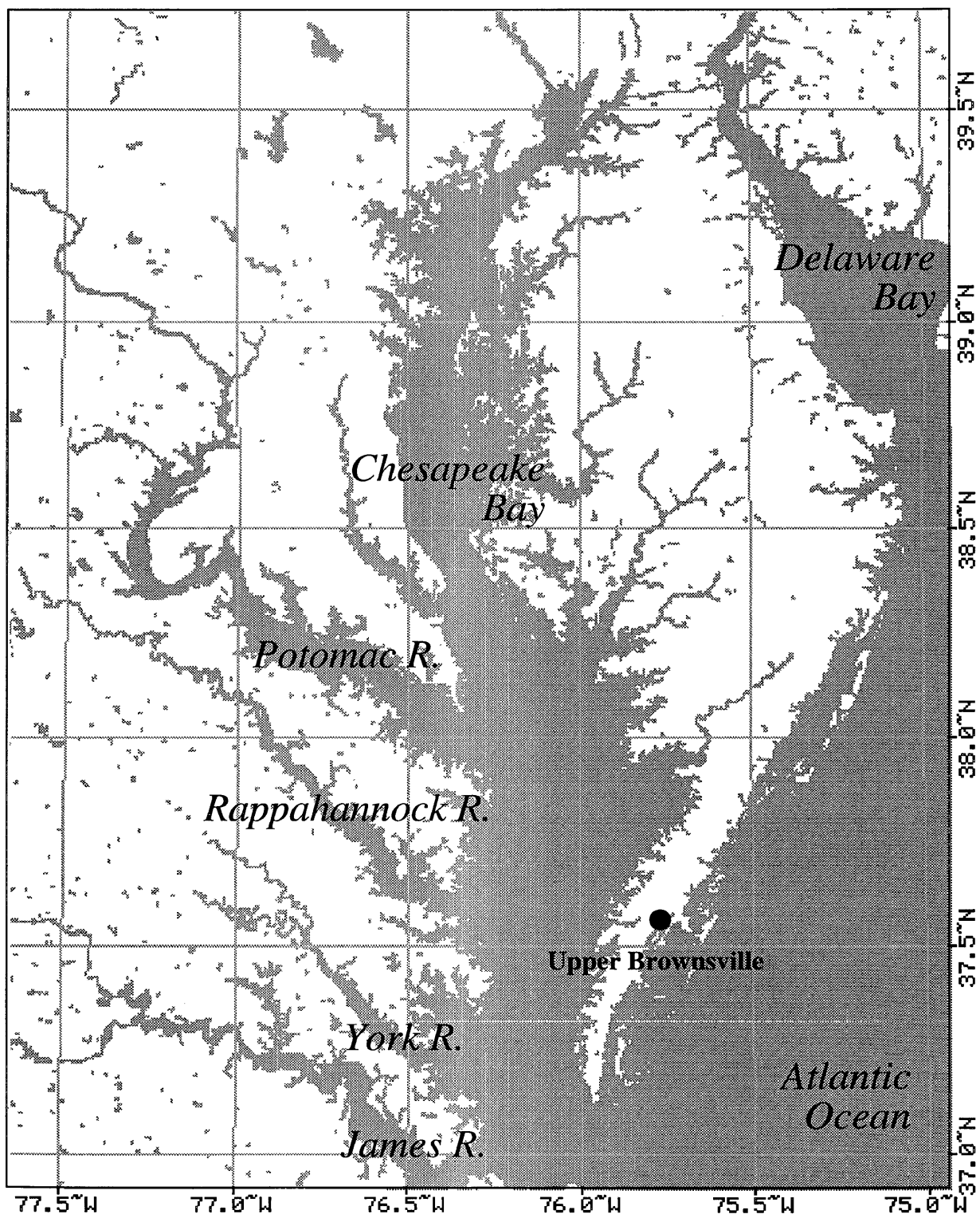


Figure 1. Location of study site in relation to Chesapeake Bay.

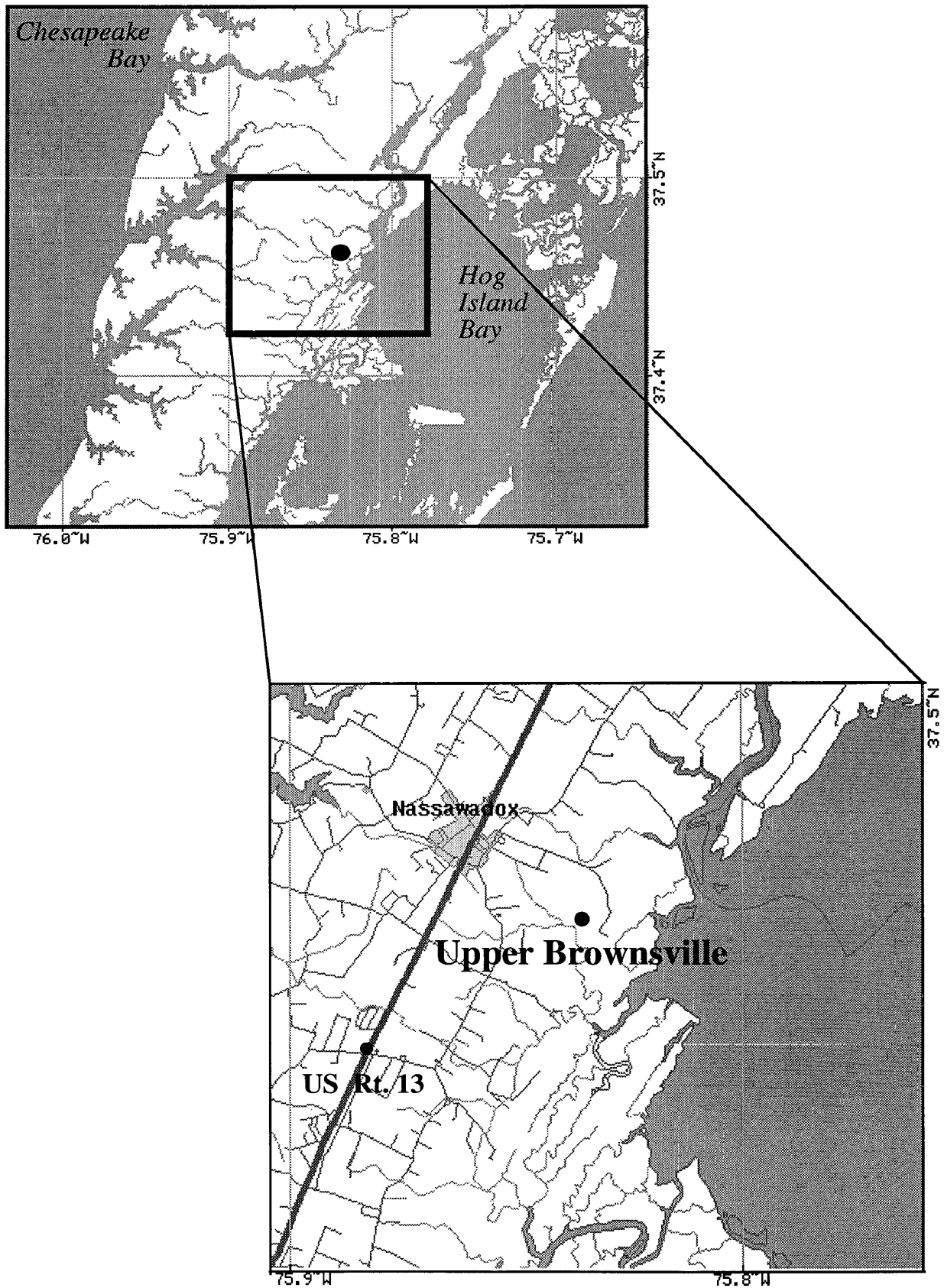


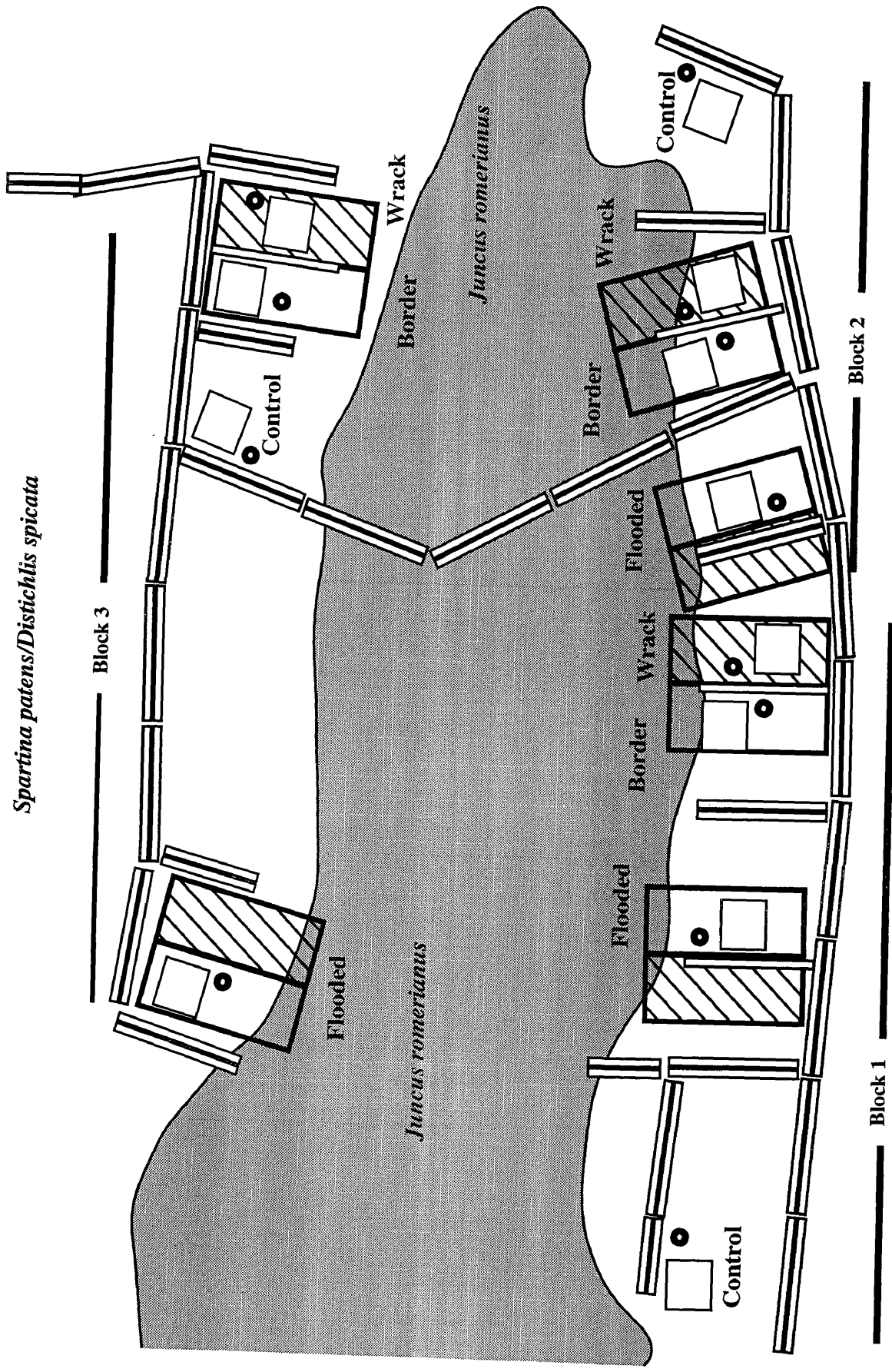
Figure 2. Local area picture of study site near the town of Nassawodax VA

INUNDATION SITE

This study was performed at an experimental inundation site (Figure 3) established by Dr. Robert Christian and his graduate student James Taylor of East Carolina University. The experiment was intended to mimic the effects of increased inundation by artificially flooding, on a daily basis, sections of the marsh not normally flooded. Flooding was accomplished by pumping water from the nearby tidal creek through approximately 30 meters of 1.91 cm diameter PVC pipe to the inundation site using an electric pump powered by photovoltaic cells. The pump was operated by a float switch which was triggered when the tidal creek water rose above 0.50 m MSL. During these experiments the system was strictly solar powered; therefore, it only ran during daylight high tides when there was sufficient light to power the pump ($\sim 50 \mu\text{E m}^{-2} \text{ sec}^{-1}$). Water volume pumped onto the marsh was monitored by a flow meter at the head of the pump. A complete description of the electrical system and previous pumping regimes is provided in Taylor (1995).

Plywood borders with small openings at their corners were constructed around flooded plots (3 x 4 m) in order to slow drainage of pumped water. The border was created by driving weatherproofed 0.95 cm thick plywood 10 cm into the marsh, leaving approximately 10 cm aboveground to trap water. A bordered control treatment was set up to determine if the plywood border alone had any effect on community marsh processes.

Studies were performed between August 1995 and September of 1997. Measurements made are listed in Table 1. Seasonal samplings occurred in February (1996, 1997), April (1996, 1997), June (1996, 1997), August (1995, 1996, 1997), and November (1996, 1997). The pump for the inundation experiment was operational from March 10 to October 26 of 1995 and April 9 to November 11 of 1996. The pump was not installed in 1997. It was removed during the winter to avoid potential damage from freezing. Since there was no living aboveground macrophyte vegetation and thus, little



Spartina patens/Distichlis spicata

Figure 3. Diagram of artificial inundation site. Black rectangles indicate border areas. Hatched area inside border areas represents wrack cover areas. Boardwalks connect all plots. Small circles indicate site of sediment measurements, open squares indicate site of community measurements.

primary production and since water levels were much higher in winter, removal of the pump was not thought to affect results. During 1996, approximately 89,000 liters of water were pumped into the three 12 m² flooded treatment sections of marsh. Sampling dates were scheduled to coincide with midday low tides to insure no flooding of the marsh. Measurements were not made during cloudy, rainy, or exceptionally windy conditions.

EXPERIMENTAL DESIGN

Three replicate blocks (1, 2, and 3) were established within the experimental site. Blocks each contained three 3 x 4 m treatment plots, including: an undisturbed control (C); a bordered control (B), where no water was pumped onto the marsh but a plywood border was installed; and a flooded treatment (F), which was identical to the border control, but was artificially flooded during each daylight high tide during the growing season (April through November). The half closest to the boardwalk of each plot was vegetated by a mixed *S. patens* /*D. spicata* community and the back half with *J. roemerianus*. Every treatment was further divided by covering half of each vegetation type with a layer of locally produced *S. alterniflora* wrack.

Wrack was maintained on designated sections of the bordered (B) plots for the duration of the study, and more wrack was added as needed to maintain complete coverage of the plots. Lysimeters, which sampled porewater at a depth of 10 cm, were located in the middle of each plot. A number of different studies were conducted at the inundation site by several different investigators. Therefore, not all combinations of treatments were studied by all investigators. For this thesis we examined the effects of wrack and flooding separately on the *S. patens*/*D. spicata* community. Measurements were made in the vegetated sections of the control, bordered control and flooded plots as well as the wrack section of the bordered control. Four treatments were sampled in each of the three blocks, for a total of twelve study plots. Aluminum collars were placed in each of the designated areas for CO₂ measurements as described below.

Table 1. Sampling dates and frequencies for major components of study.

UPPER BROWNSVILLE SAMPLINGS											
	August 1995	November 1995	February 1996	April 1996	June 1996	August 1996	November 1996	February 1997	April 1997	June 1997	September 1997
Community CO ₂ (gC/m ² /time)	X	X	X	X	X	X	X	X	X	X	X
Sediment CO ₂ (gC/m ² /time)	X	X	X	X	X	X	X	X	X		
Sediment Chl <i>a</i> (mg/m ²)			X	X	X	X	X	X	X	X	
<i>Pore Water Measurements</i>											
Salinity (ppt)		X	X	X	X	X	X	X	X		
NH ₄ (μM)		X	X	X	X	X	X	X	X		
NO ₂ /NO ₃ (μM)		X	X	X	X	X	X	X	X		
PO ₄ (μM)		X	X	X	X	X	X	X	X		
DIC (mM)		X	X	X	X	X	X	X	X		

OTHER MEASUREMENTS: CH₄ (November 1996), bulk density (July 1997), % organic matter (July 1997), above ground biomass (February & September 1997),

C:N ratio (plant) (August 1995), pH (April 1996)

COMMUNITY CARBON DIOXIDE FLUX MEASUREMENTS

Photosynthesis and respiration rates were determined by measuring changes in CO₂ concentration within a static flux chamber (Figure 4) over short (5-10 minute) time intervals. Design of the chamber and protocol for sampling were modified from Whiting et al. (1992). The chamber was constructed of an aluminum angle frame, covered on three sides by clear 0.1 mm thick Teflon. The fourth side and the top of the chamber were made of 0.32 cm Plexiglas. The chamber was 0.86 m wide, 0.86 m deep and 1.01 m tall, including collar area, with a total volume of 747 liters. It was attached to the marsh by means of 20 cm tall, 0.32 cm thick, aluminum collars which were seated 10 cm into the marsh in each plot as shown in Figure 3. Collars remained in place for the duration of the study to avoid repeated perturbations of the marsh with each sampling. Each side of the collar had three evenly spaced 2.5 cm diameter holes located at the marsh surface to allow exchange of tidal water when experiments were not being conducted. These holes were plugged with rubber stoppers when CO₂ measurements were made. The lip of the collar was sealed to the base of the flux chamber by use of a rubber soaked neoprene gasket which was attached to the chamber and held fast to the collar with twelve large office clips. The Plexiglas top of the chamber was attached to the vertical section of the chamber in the same manner.

Temperature within the chamber was regulated to +/- 2°C of ambient by circulating ice water through a heat exchange radiator attached to the Plexiglas side of the flux chamber. This temperature regulation system was necessary because of the greenhouse-like tendencies of the transparent chamber. Two small battery operated fans behind the radiator moved air across the grill. Another fan was placed closer to the marsh surface to ensure that all air within the chamber was evenly mixed. Fans remained engaged for the duration of the sampling. Water was pumped through the radiator only when temperature regulation was necessary.

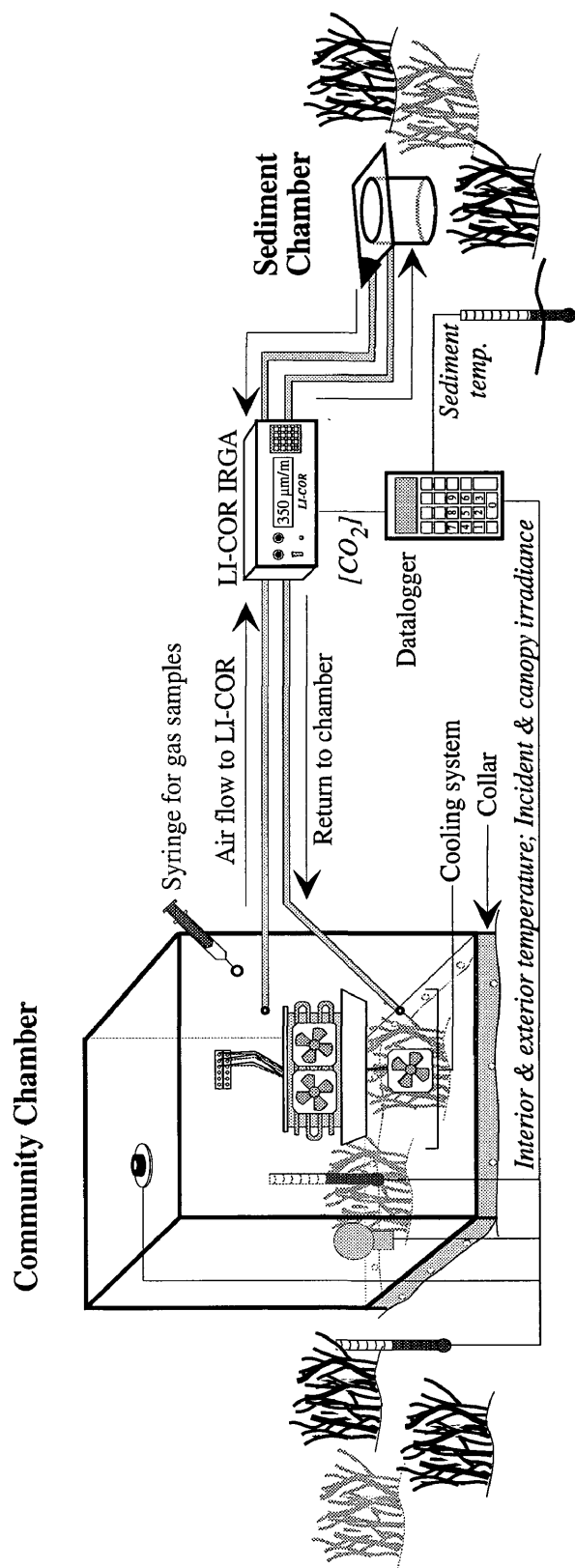


Figure 4. Schematic diagram of field set up for carbon dioxide flux measurements.

Carbon dioxide concentrations were measured with a LiCor model 6252 (Lincoln NE) non-dispersive infra-red gas analyzer (IRGA). The sample was not altered during analysis and was returned to the chamber via a closed loop between the chamber and the gas analyzer so there was no change in the volume within the chamber during sampling. Sample gas was circulated through the IRGA by a small pump (LiCor 6262-04) at the constant rate of 500 ml min^{-1} . Although the IRGA sampled continuously, data were recorded at one minute intervals on a LiCor 1000 data logger. Other environmental data collected simultaneously with CO_2 data included incident photosynthetically active radiation (PAR) and temperature. PAR was measured both with 2π sensors (LiCor quantum flux) which measure only light directed vertically from the sun, and 4π sensors (LiCor spherical) which measure both direct sunlight and reflected light. Temperature was measured with type-T constantan-copper thermocouples inside and outside the chamber, and at a depth of 5 cm in the sediment.

Calibration of the IRGA was performed daily before each field use. Adjustments including zeroing, spanning and corrections for changes in barometric pressure. Zeroing was accomplished by passing a stream of N_2 gas through a soda lime (variable portions NaOH, CaO or CaOH, Fisher Chemical, Fair Lawn NJ) scrubber (to remove CO_2) for 15-30 minutes. Span on the IRGA was set using CO_2 in N_2 calibration gas (Scott Specialty Gases Inc., Plumsteadville PA), typically 350, 408, or 1000 ppmv. All gases were passed through a series of filters to remove moisture and particulates including a physical filter, nafion tubing (Type 815, Dupont perfluorinated polymer, Perma Pure, Inc., Toms River NJ) packed in silica gel, and magnesium perchlorate ($\text{Mg}(\text{ClO}_4)_2$).

Measurements were made at as many different light levels as possible in order to develop a relationship between the rate of photosynthesis and irradiance (P v. I). Starting in November of 1996, shade cloth was employed to sequentially reduce light and thereby provide a greater range of light intensities. These measurements were made at five different

times during the year in order to determine seasonal changes in photosynthetic rate. Respiration measurements were made in the dark, immediately following the light measurements, by placing a black tarpaulin over the chamber. Curves relating respiration rate to temperature (R v. T) were developed from these data.

SEDIMENT CARBON DIOXIDE FLUX MEASUREMENTS

Photosynthesis and respiration by benthic microorganisms were determined as described above for community measurements except that smaller (0.495 L) chambers (Figure 4) were used, and all vegetation was removed from inside of the chamber prior to the August 1995 to sampling. Regrowth of vegetation into the sediment chamber was minimal over the course of the study. The chambers were 11 cm in diameter and were constructed of 0.16 cm thick, 10 cm high aluminum attached to 0.64 cm Plexiglas (5 cm high). The aluminum was sunk into the marsh 10 cm in order to provide an air-tight seal. The only part of the chamber which was removed between measurements was the o-ring gasketed, 1-cm thick, clear, Plexiglas top. No temperature control was used inside the sediment chamber since temperatures rarely varied much from ambient. The chambers had holes flush with the surface of the marsh, like the community collars, to facilitate water drainage.

POREWATER CHEMISTRY MEASUREMENTS

Porewater was sampled from lysimeters within each treatment plot concurrent with seasonal gas flux measurements. Samples were taken from a depth of 10 cm. To collect a sample a lysimeter was purged of water and a vacuum (50 mm Hg) drawn with a hand vacuum pump (Nalgene) and allowed to recharge for 1 hour with fresh pore water. Water taken for dissolved inorganic nutrient analysis was immediately filter sterilized (0.45 μ m; Gelman Supor) into Whirlpak bags and put on ice for later analysis. Samples for dissolved inorganic carbon (DIC) were filtered into acid washed 12.8 ml Hungate tubes and sealed with a rubber septum (Bellco) leaving no air headspace and stored refrigerated until

analysis. When possible pH and salinity were measured in the field with a Fisher pH/Temp Tester and Reichert-Jung temperature-compensated refractometer respectively. In the lab, NH_4^+ analyses were performed according to the phenolhypochlorite method of Solorzano (1969). NO_3^- & NO_2^- were measured using an Alpkem Flow Solution Autoanalyzer (Perstop 1992). Orthophosphate (PO_4^{3-}) was determined by the method of Parsons et al. (1984). DIC analysis was performed by injection of a porewater subsample (50 μl) into 0.05 M H_2SO_4 which was constantly sparged by N_2 gas at a rate of 300 ml min^{-1} into a LiCor model 6252 IRGA for analysis. Results were compared to standards prepared from 1, 5, and 10 mM Na_2CO_3 .

SEDIMENT CHARACTERIZATION

Sediment Bulk Density and Composition

In July 1997, one 30 cm deep core was taken from each treatment plot (total of 12 cores) with a 50 cm tall, 8.4 cm diameter, thin walled aluminum core tube. The cores were placed on ice until returned to the lab where they were sectioned at 5 cm intervals. Sections were weighed wet, then dried at 50°C to constant weight (approximately one month). Bulk density was determined by dividing the dry weight by the volume of each section. After drying and weighing, sections were combusted in a muffle furnace at 500°C for 6 hours. The percent organic matter of the core sections was determined by taking the difference of the weights before and after combustion and dividing it by the dry weight. All surface vegetation was removed prior to analysis in all cores; for wrack plots, dead *S. alterniflora* stems were removed from the sediment surface before measurements were made.

Sediment Chlorophyll

Three replicate 2.5 cm diameter cores were taken to a depth of 10-15 mm within each treatment plot during seasonal CO_2 flux studies. Upon removal from the marsh both ends of the small cores were capped and kept on ice in the dark until processed less than 3 hours later. The top 10 mm of each core was removed with a razor blade and placed into a

20 ml scintillation vial. Samples were frozen (-15°C) for less than one month until analyzed by the method of Pinckney et al. (1994). After addition of 10 ml of extractant (45% acetone, 45% methanol, 10% deionized water) samples were placed into a freezer (-15°C) for 72 hr, shaken vigorously twice daily for the first 48 hr and left to settle for the last 24 hr. After extraction samples were filtered through 0.45 µm Teflon Gelman filters into 13 x 100 cc disposable cuvettes. Absorbance was measured by spectrophotometer at 665 nm and 750 nm wavelengths before and after acidification with 150 µl of 10% HCl to determine chlorophyll *a* and phaeophytin following a modified protocol of Lorenzen (1967).

Percent Carbon and Nitrogen of Primary Macrophytes

Percent carbon and nitrogen of *S. patens* and *D. spicata* from the different treatments were determined by the lab of R. Christian at East Carolina University. Only aboveground biomass samples were analyzed for this study. Macrophyte samples were prepared by grinding in a Wiley mill with a #40 mesh screen. Analysis was conducted with a Control Equipment Corporation 440 Elemental Analyzer.

MEASUREMENTS OF RESPIRATION UNDER NATURAL AND ARTIFICIAL CONDITIONS

In Situ Artificial Dark/ Natural Dark Study

In September 1997 an experiment was conducted to determine whether there were differences in respiration rates measured under artificial dark conditions (by placing a black tarpaulin over a flux chamber during the day) and rates measured during natural dark (between 2 and 6 hours after sundown). Artificial dark had been used as the preferred method of determining respiration because of the ability to obtain respiration rates at almost the same time and under similar conditions as photosynthesis measurements and because of the logistical difficulties of working at night in the marsh. For the experiment artificial dark measurements were made over the course of an afternoon on three replicate control plots.

The measurements were continued into the evening, and natural dark measurements were made after sundown in an identical manner to the artificial dark except no dark tarpaulin was used. Measurements were made across the continuum of afternoon light to determine if previous light regime might also affect respiration rate. Flux measurements were made following the same protocol as used for seasonal CO₂ exchange studies.

Growth Chamber Study

Concurrent with the artificial dark/natural dark respiration experiment described above, an additional experiment was conducted in an environmental chamber under controlled light and temperature conditions to determine the effects of prior light intensity on respiration rates in the dark and to determine if changes in respiration rate occur over the course of an evening related to changes in plant physiological status. For this experiment five 30 cm tall cores were harvested from the control areas of the marsh and placed in clear, 1 meter tall by 11.5 cm inside diameter polycarbonate tubes and allowed to equilibrate for three days. During equilibration in the environmental growth chamber cores were provided with fresh water regularly while light and temperature were maintained at constant values of 600 $\mu\text{E m}^{-2} \text{ s}^{-1}$ and 20°C. After equilibration, CO₂ fluxes were measured with an IRGA by placing an o-ring fitted lid on top of the polycarbonate tube for 5-10 minutes and measuring changes in CO₂ concentration at one minute intervals. Measurements were made at intervals of 0, 0.5, 1, 8, 18, 19, 25, 43, and 65 hours after cessation of light.

METHANE FLUX MEASUREMENTS

Samples for determination of CH₄ fluxes were taken by withdrawing 60 ml of gas from the community flux chamber at 10 minute intervals. Thirty-five ml of 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 prevent leakage. Fifty μl gas samples were injected into a Hewlett-Packard model 5890 gas chromatograph equipped with a flame ionization detector and molecular sieve 13x column. Oven temperature was 80°C, and detector temperature

was 220°C. A single point calibration of the instrument was performed routinely before and during analyses using a 9.02 ppmv CH₄ in N₂ standard (Scott Specialty Gases). Samples were only taken in November of 1996 because CH₄ fluxes accounted for less than 1% of the total carbon respired.

DEVELOPMENT OF A PRODUCTION/RESPIRATION GAS FLUX MODEL

To estimate annual community carbon exchange for different marsh treatment groups models were constructed using data from seasonal CO₂ flux measurements and local meteorological data (hourly light and temperature). Meteorological data were obtained from a weather station located 400 m from the inundation site, which is maintained by VCR (Porter and Richardson, <http://atlantic.evsc.virginia.edu/data/metadata/index.html>). The model consisted of two sub-models to calculate gross photosynthesis and gross respiration and to “scale up” short term measurements to monthly, seasonal, and annual budgets (Figure 5). For the purposes of the model seasons were defined as: spring, March 15 to May 14; summer, May 15 to September 14; fall, September 15 to November 14; and winter, November 15 to March 14. Model results are shown for the growing year starting in March of 1996 and ending in March of 1997.

Gross photosynthesis was determined by subtracting net community photosynthesis (light CO₂ flux measurements) from community respiration (dark CO₂ flux measurements). Gross photosynthesis measurements were plotted against their corresponding irradiance values and hyperbolic curves were fit to the data for each treatment and season. The equation for a hyperbolic curve is:

$$P = (A * I) / (B + I)$$

where I is incident irradiance in units of $\mu\text{E m}^{-2} \text{s}^{-1}$, P is the gross CO₂ uptake rate in $\text{mg C m}^{-2} \text{min}^{-1}$, A and B are constants (Whiting et al., 1992). With known P and I values, a best fit regression for the constants A and B was calculated using curve-fitting software (Deltagraph Inc.). The resultant equation, with A and B solved, allows one to solve for

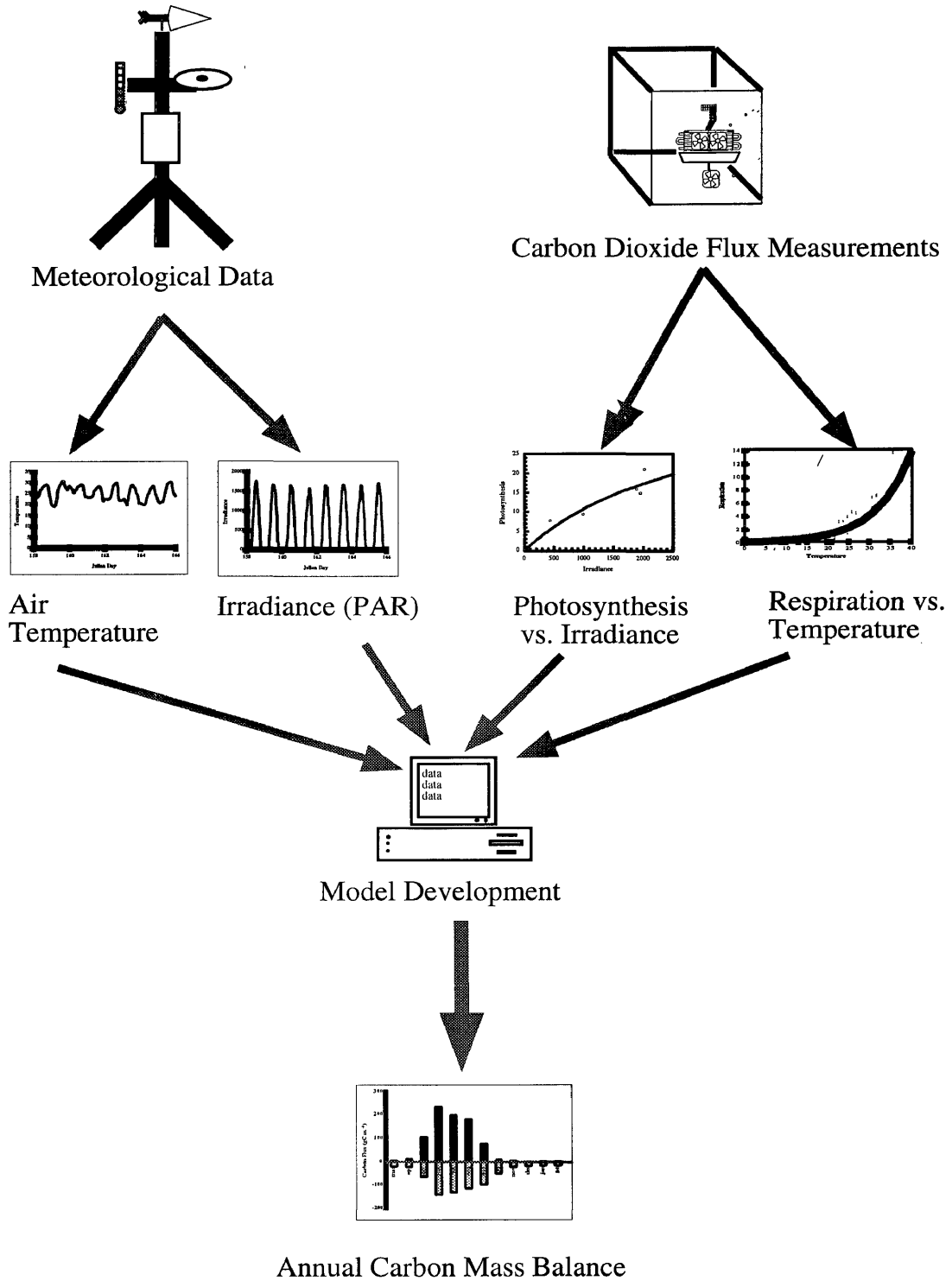


Figure 5. Procedure for 'scaling up' from short term carbon dioxide flux measurements to monthly, seasonal and annual carbon budgets.

photosynthetic rate (P) with irradiance (I) values obtained from a local weather station (VCR-LTER). Production estimates were made for all daylight hours. Values (listed in $\text{mg C m}^{-2} \text{ min}^{-1}$) were multiplied by 60 to give hourly estimates. The hourly estimates were then summed to determine monthly, seasonal, and annual production values. Separate curves were developed for each season (spring, summer, fall, and winter), and treatment (control, bordered control, flooded, and wrack).

For the respiration sub-model CO_2 fluxes measured in the dark were plotted against temperature and best fit exponential curves were calculated using curve-fitting software (Deltagraph Inc.). The exponential equation is described by:

$$R = A e^{B * T}$$

where R is the respiration rate in $\text{mg C m}^{-2} \text{ min}^{-1}$, A and B are constants, e is the natural log, and T is temperature in $^{\circ}\text{C}$. These curves allowed for extrapolation of CO_2 flux rates to all temperatures encountered during a given season. Separate curves were created for each treatment and season. Because respiration was thought to vary with physiological status of aboveground biomass, the seasons were split according to whether or not there was green biomass present (winter/spring and summer/fall). Respiration rates were calculated for 24 hour periods (light and dark) assuming that light had a minimal effect on rates.

Benthic microalgal production estimates were made by modeling seasonal CO_2 fluxes measured over unvegetated sections of marsh sediment. Because of the high variability in measured fluxes, it was not possible to develop P vs. I curves as was done for macrophyte community measurements. Instead a saturating irradiance value ($\sim 500 \mu\text{E m}^{-2} \text{ s}^{-1}$) was assumed based on reported 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 the average of all fluxes occurring at irradiances above $500 \mu\text{E m}^{-2} \text{ s}^{-1}$. Photosynthetic rates for

values lower than $500 \mu\text{E m}^{-2} \text{s}^{-1}$ were calculated as the percentage of P_{max} equal to the ratio of incident irradiance over saturating irradiance ($500 \mu\text{E m}^{-2} \text{s}^{-1}$).

$$\text{If } I_t < 500 \mu\text{E m}^{-2} \text{s}^{-1} \text{ then } P_t = P_{\text{max}} * I_t / 500 \mu\text{E m}^{-2} \text{s}^{-1}$$

As with community production estimates, hourly light values for a full year were substituted into the production equation to give hourly production estimates for the four treatments, with different curves for each season. A single respiration vs. temperature curve was developed and used to determine respiration values for marsh areas devoid of macrophyte stems.

POTENTIAL ACCRETION RATE CALCULATIONS

A potential accretion rate was calculated for each marsh treatment in this study assuming that all of the net carbon fixed by the marsh community is buried in marsh sediment. The carbon potentially accreted by biological activity was compared to that required to support 1 mm of sediment accretion over a surface area of 1 m^2 , based on sediment bulk density and organic carbon content. This calculation assumes that all net carbon taken up by the high marsh is buried and therefore adds accretionary material. Little of the macrophyte biomass is grazed by herbivores and infrequent tidal flushing allows few opportunities for particulate export. Dissolved organic matter export was assumed to be negligible but measurements were not made.

DATA ANALYSIS

All data manipulation and model development were performed on MacIntosh computers using Microsoft Excel (version 5.1). Statistics were run with Statistica (v. 4.1) software. All results are expressed as the means of three replicate plots within the same treatments. Error bars for all graphs indicate +/- one standard deviation. Data for all porewater constituents, instantaneous CO_2 fluxes, and sediment characterization were analyzed using a randomized block ANOVA with treatment as the fixed effect and block as the random effect. Repeated measures ANOVAs were conducted within treatments among

the months of the study for all monthly samplings. When results were significant, Tukey's HSD multiple comparison test was performed to determine specific interactions. An independent t-test was performed to determine the significance of differences between means in the natural dark/artificial dark experiment.

RESULTS

Figure 6 shows monthly mean and extreme temperatures from March 1996 to March 1997. Data were recorded by a meteorological station, maintained by the VCR at Phillips Creek (Porter and Richardson, <http://atlantic.evsc.virginia.edu/data/metadata/index.html>). Seasonal trends in temperature are as expected, with maximum average in June and minimum in January. Figure 28 is a plot of elevations above mean sea level for each treatment plot within the inundation experimental site. These data were collected by J. Taylor (1995). The highest plots are the block 1 control and block 3 flooded, while the lowest plots are the block 2 border/wrack and block 2 flooded. Total difference between the highest and lowest plots is 8 cm. This difference, although small, may differentially affect processes measured during this study. Table 1 lists all seasonal measurements and times when performed. Along with the seasonal measurements shown in the table, there were a number of single time samplings for other measures, including methane, cores for bulk density and percent organic matter, aboveground biomass, and vegetation samples for C:N analyses.

METHANE

Methane fluxes were measured only in November of 1996. Table 2 shows these fluxes and their extrapolated values in milligrams of carbon per minute. Negative values in the table indicate a decrease in methane concentration over time or uptake by the marsh, while positive values indicate an increase in concentration or release by marsh. Correlation coefficients for the relationship between methane concentration and time were variable because there was little change from ambient concentrations. Measurements were discontinued after the November sampling because methane fluxes did not appear to constitute an important component of the carbon budget. Methane fluxes accounted for less than one percent of the November gross community respiration rates. These low flux rates

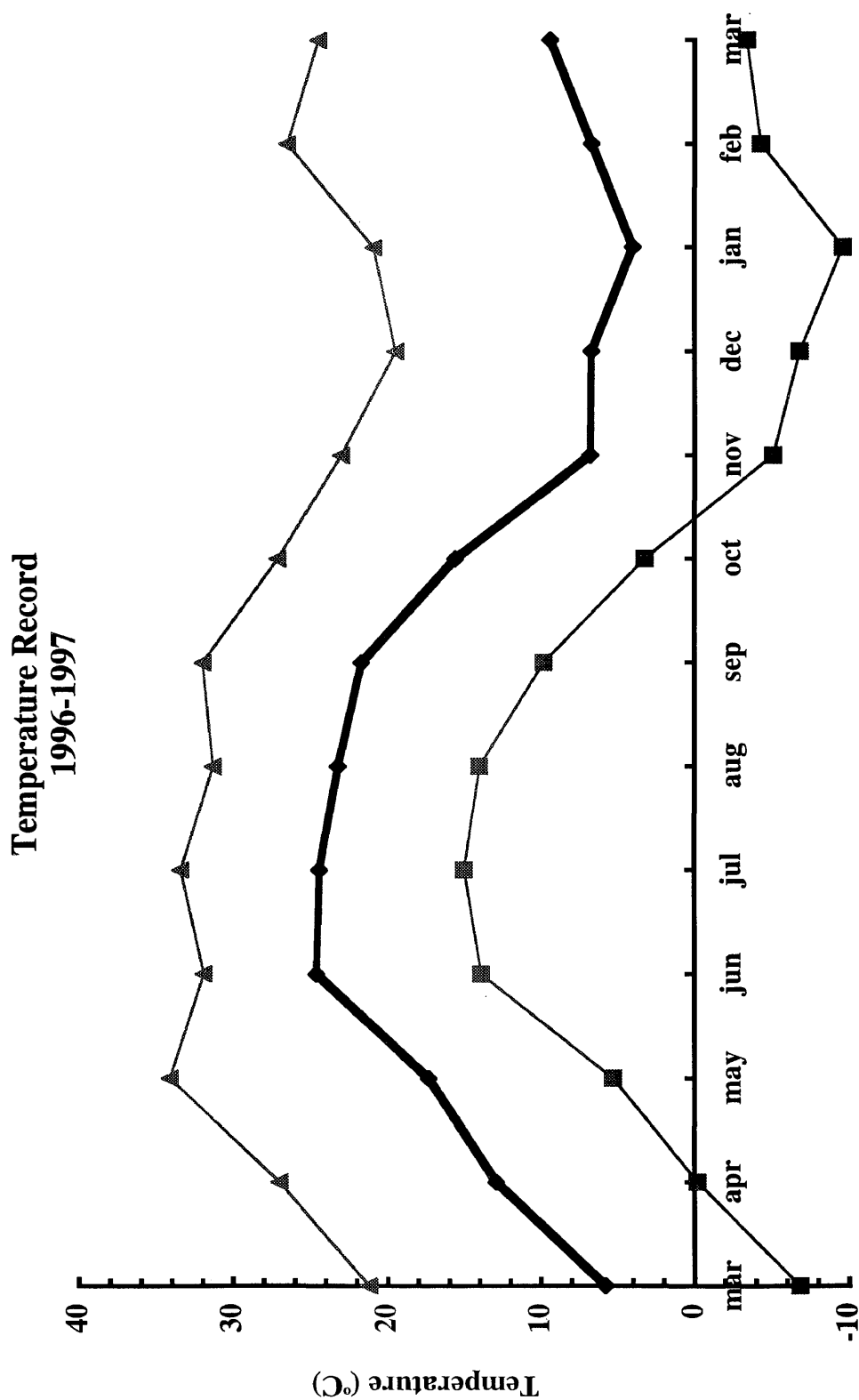


Figure 6. Monthly minimum, maximum, and mean air temperatures for months of model simulation. Data collected from nearby meteorological station owned and maintained by VCR-LTER (Porter and Richardson, <http://atlantic.evsc.virginia.edu/data/metadata/index.html>)

TABLE 2. Methane production from community and selected sediment treatments taken November 11-13 1996. Measurements are based on 30 minute observations with samples taken at 0, 15, and 30 minutes.

Date	Chamber	Slope (ppm/min)	R ²	Chamber Temp. (°C)	CH ₄ Exchange Rate	
					μmol CH ₄ /m ² min	g C/m ² yr ⁻¹
11/13/96	C1	0.006	0.591	20.7	0.265	1.674
11/12/96	C2	0.014	0.413	21.7	0.591	3.730
11/12/96	C3	0.018	0.256	13.8	0.758	4.784
11/13/96	F1	0.004	0.005	15.8	0.186	1.170
11/12/96	F2	-0.018	0.809	12.9	-0.768	-4.843
11/12/96	F3	0.005	0.314	18.2	0.221	1.394
11/13/96	B1	-0.003	0.047	18.6	-0.114	-0.721
11/12/96	B2	-0.011	0.691	14.9	-0.473	-2.981
11/13/96	W1	-0.018	0.845	19.0	-0.750	-4.730
11/12/96	W2	0.007	0.824	12.0	0.294	1.856
11/13/96	Sed C1	0.050	1.000	10.5	0.113	0.711
11/12/96	Sed C2	-0.030	1.000	11.1	-0.067	-0.426
11/12/96	Sed C3	-0.050	1.000	13.2	-0.110	-0.696
11/13/96	Sed F1	0.059	1.000	13.8	0.130	0.817
11/12/96	Sed F2	0.029	1.000	5.6	0.067	0.420
11/12/96	Sed F3	-0.016	1.000	9.6	-0.036	-0.228

Chamber designation: B= border C= control F= flooded W= wrack

are consistent with other measurements of methane flux performed in a variety of Virginia salt marshes (Bartlett et al., 1987).

POREWATER

Ammonium

Figure 7 shows the average ammonium porewater concentration for each treatment during the months of sampling. Average values ranged from a low of 1.94 μM in the June 1996 flooded plots to a high of 31.41 μM in the November 1995 wrack plots. There were no significant differences between the monthly samples within a given treatment at the $p = 0.05$ level. No significant differences between treatments were detected ($p=0.05$) for any of the sampling dates as seen in Table 3. NH_4^+ was relatively low and stable throughout the sampling period with lowest concentrations occurring in summer when available ammonium is likely taken up by macrophytes and maximum values seen in the fall and winter when nitrogen is released by decomposition of marsh vegetation.

Nitrate + Nitrite

Combined values of nitrate and nitrite were consistently low (0-3.6 μM) and fell below detection limits (0.2 μM) on several occasions (April 1996, August 1996, and November 1996). Figure 8 shows the averages of each treatment across all sampling dates. There were significant differences between dates within each of the treatment groups. Typically only one or two of the dates were different from the other seven measurements. Table 3 provides p -values for significant differences in nitrate + nitrite means between treatments. November 1995 and June 1996 samplings were significantly different from the other dates in the flooded and control treatments. The common trend of low nitrogen availability in the summer and higher levels in the winter is seen in the graph along with an unexpected peak in June 1996.

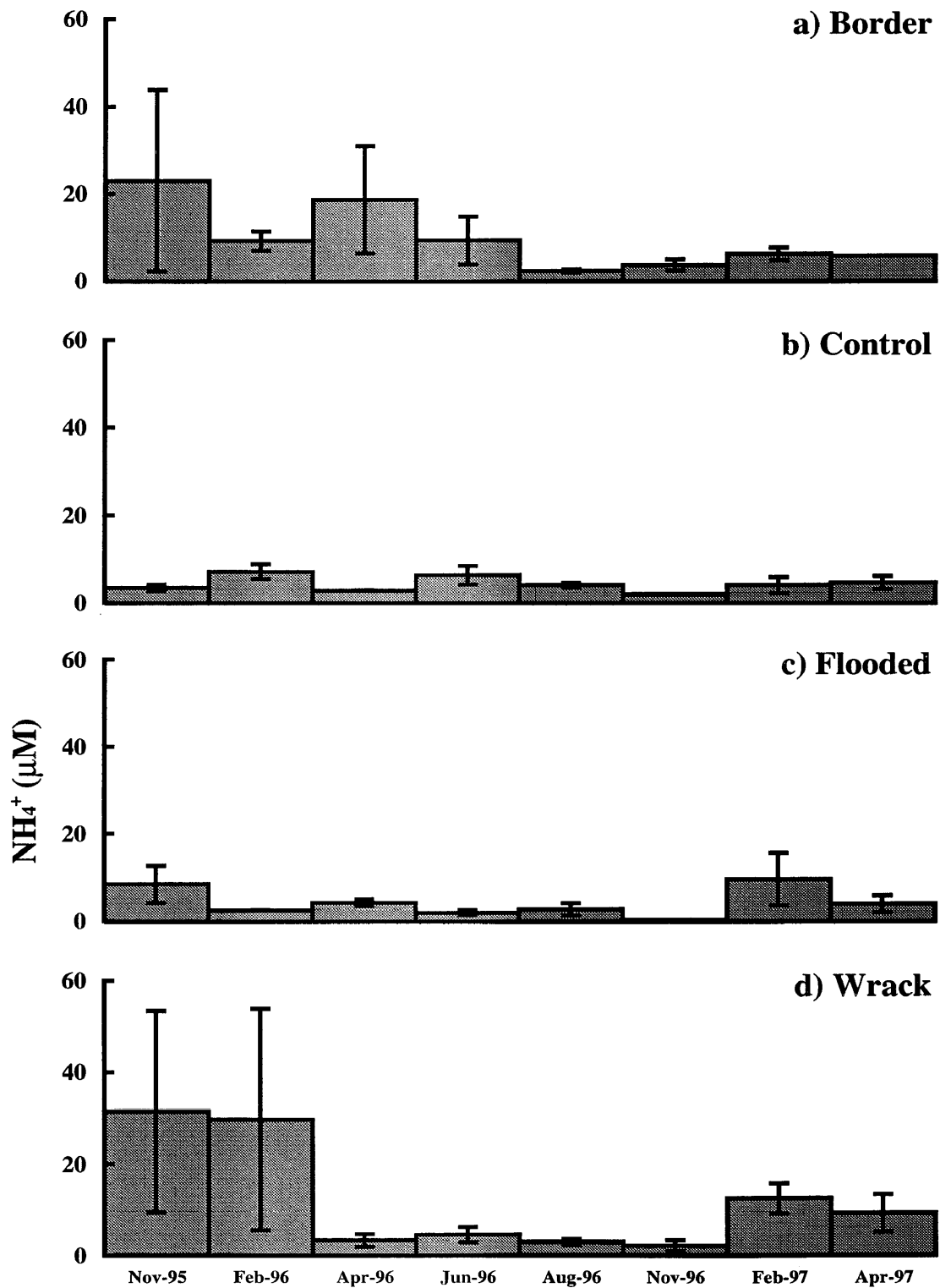


Figure 7. Porewater NH_4^+ concentrations (μM) for each treatment. Lysimeters sampled at depth of 10 cm. Error bars indicate one standard deviation.

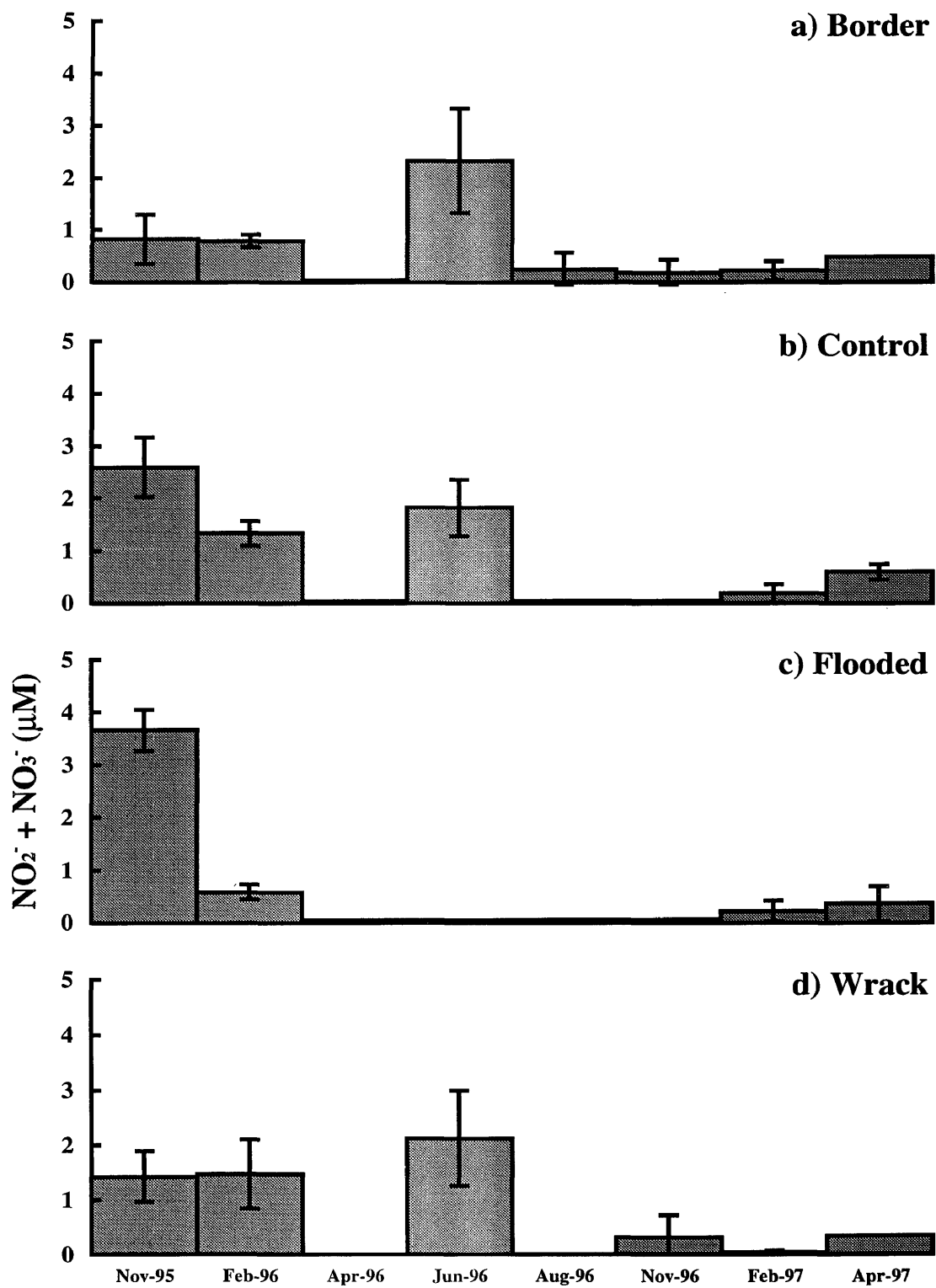


Figure 8. Porewater $\text{NO}_2^- + \text{NO}_3^-$ concentrations (μM) for each treatment. Lysimeters sampled at depth of 10 cm. Error bars indicate one standard deviation.

Dissolved Inorganic Phosphate (DIP)

DIP does not appear to be limiting in this system, as concentrations equal or exceed the total inorganic nitrogen concentrations in most months and thereby exceed the quantity needed by vegetation and microalgae. Values ranged from near 0 to 16.6 μM and were highest in the spring for all treatments. Figure 9 indicates that June 1996 values were significantly different than the other monthly means in the control and wrack treatments, while no differences existed within the border or flooded treatments between months. Table 3 shows that there was only a significant difference between treatments in June of 1996. The DIP spike in June 1996 was also seen in the nitrate + nitrite measurements (Figure 8).

Dissolved Inorganic Carbon (DIC)

DIC is a less frequently measured component of porewater. It was measured to determine if this pool could be a vector for carbon transport into or out of the marsh. The concentrations ranged from 0.8-3.4 mM. There were no significant treatment differences between mean monthly DIC concentrations (Table 3); however, Figure 10 shows that significant differences existed between the monthly measurements within border, control, and wrack treatments. Although largely masked by replicate variability, there appears to be a trend toward higher DIC concentrations in the summer, possibly as a result of higher summer respiration rates.

Salinity

The final component measured in porewater was salinity. Table 3 shows that a significant difference between treatments existed only in February of 1996, when salinities were higher in the wrack than in control and border treatments. Salinity varied from 5-24.6 ppt. The expected seasonal trend in porewater salinity was masked by the variability between replicates. Normally an increase in salinity would be expected in the summer as evapotranspiration removes fresh water and concentrates salts in the porewater.

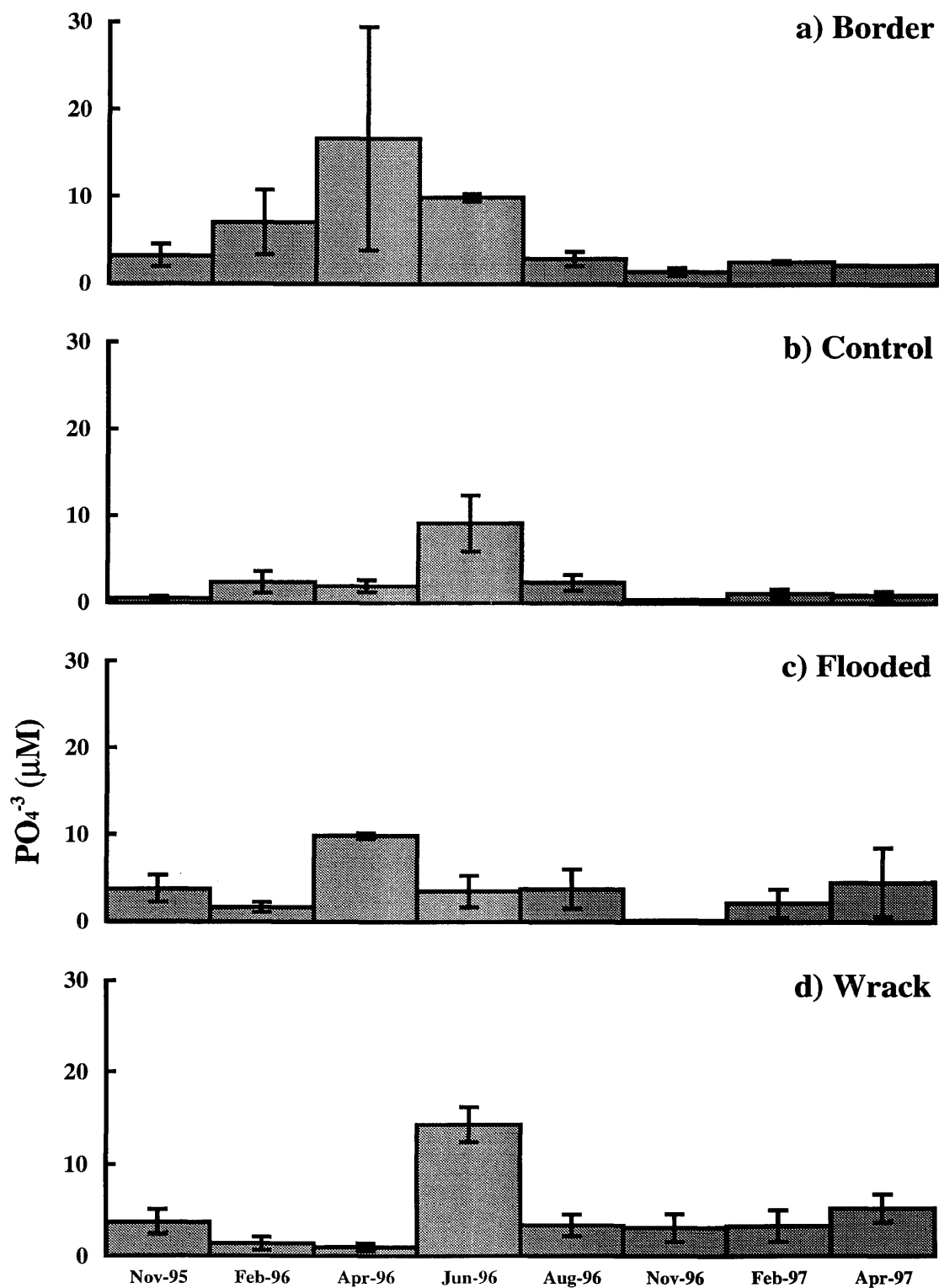


Figure 9. Porewater PO_4^{3-} concentrations (μM) for each treatment. Lysimeters sampled at depth of 10 cm. Error bars indicate one standard deviation.

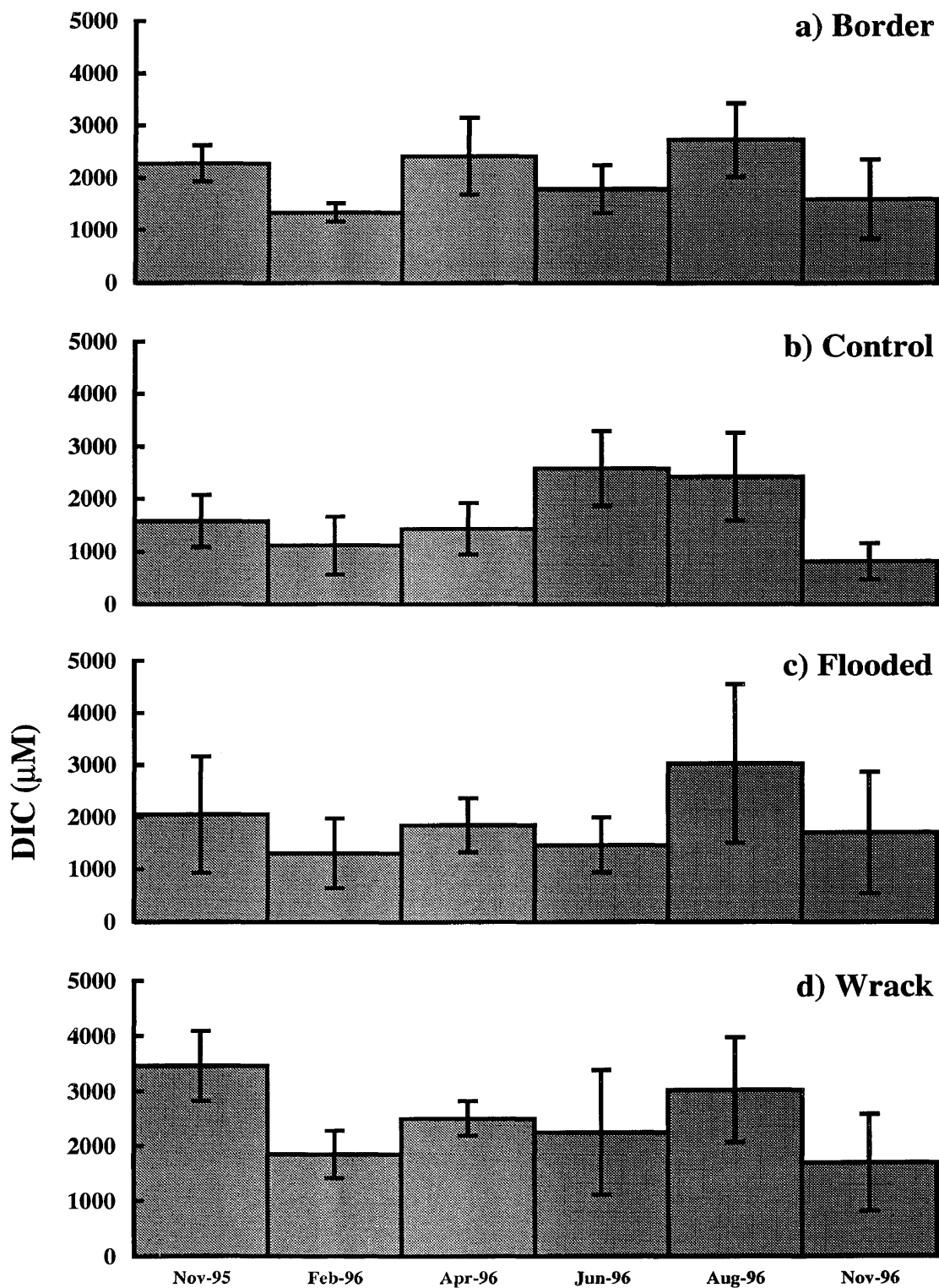


Figure 10. Porewater DIC concentrations (μM) for each treatment. Lysimeters sampled at depth of 10 cm. Error bars indicate one standard deviation.

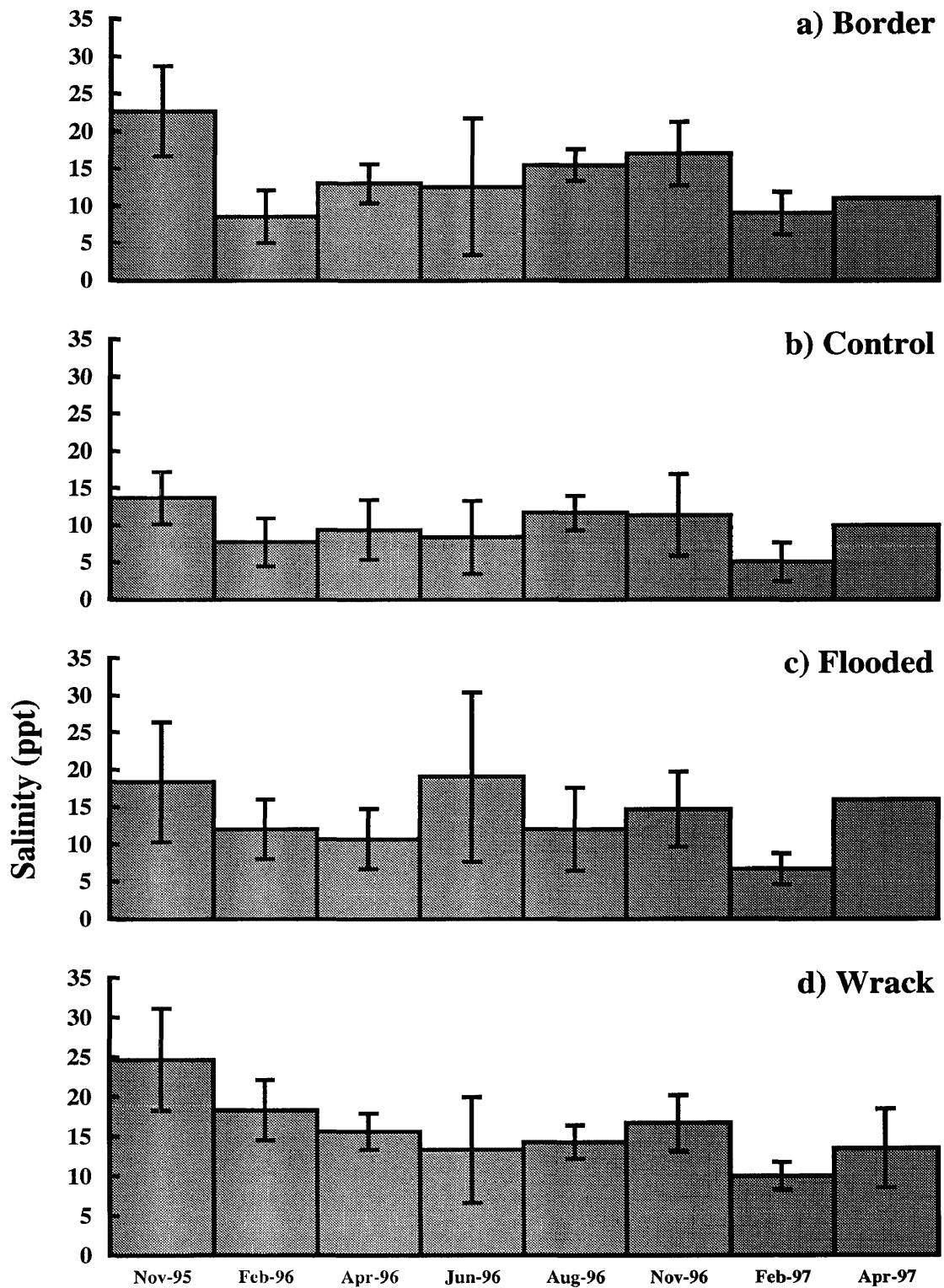


Figure 11. Porewater salinity concentrations (ppt) for each treatment. Lysimeters sampled at depth of 10 cm. Error bars indicate one standard deviation.

Significant differences between months within a given treatment existed only for the wrack treatment, as seen in Figure 11. Lack of a strong seasonal signal and high within-treatment variability might be due to elevational differences between plots (Figure 28).

SEDIMENT CHARACTERIZATION

Sediment bulk density and composition

One 30 cm deep core was taken from each of the twelve study plots in the inundation experiment. Measurements of organic matter content and bulk density were averaged for cores taken from three replicate plots (one from each block) and sectioned at 5 cm intervals over a 30 cm depth profile. One way ANOVAs were performed to identify differences between the treatments at a given depth (Table 4). No significant differences existed between any of the treatments. Figures 12 and 13 show bulk density and percent organic matter by treatment. The low bulk densities in the top ten to fifteen centimeters of all cores (0.13-0.17 g cm³) reflect the high peat content of the surface sediments. These data are supported by the high organic matter content (39-51%) of those same sediments. At depth the bulk densities are high and organic matter content low; this is a function of the fact that a noticeable sand layer occurs at the 25 cm depth. Although statistical differences do not exist between individual sections, there does appear to be a reduced depth of high organic content in the wrack treatment.

Sediment chlorophyll

Chlorophyll results were statistically analyzed as was porewater, in that comparisons were made between treatments, by month, and between months by treatment. Over the course of the study sediment chlorophyll ranged from 15-90 mg chl_a m⁻². Between treatment differences occurred in April and August of 1996 as well as June 1997 (Table 3) with wrack having statistically higher chlorophyll concentrations in those months. Because of the large variability (both within plot replicates and within treatment replicates) within a given month significant differences within a treatment across dates were

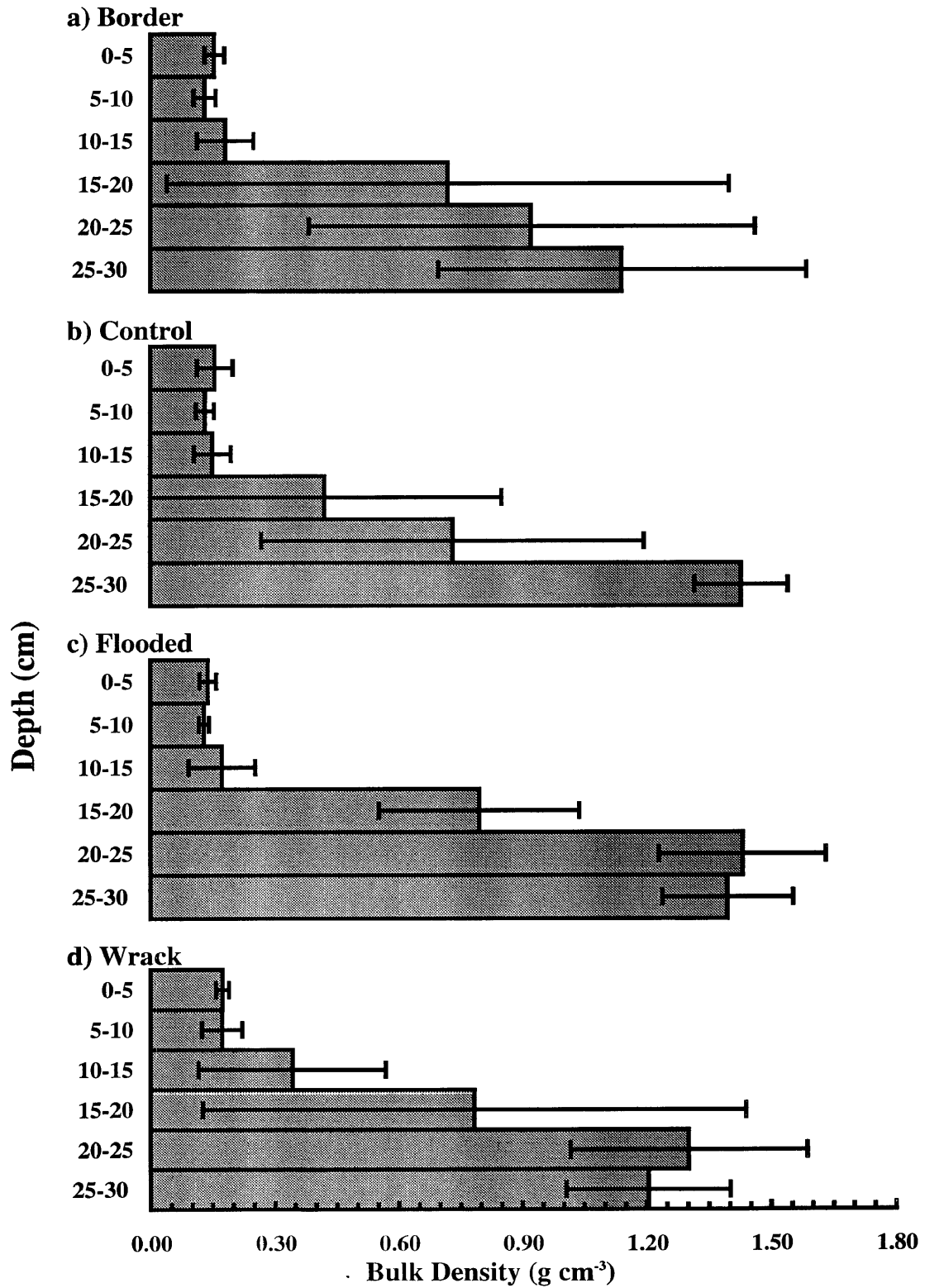


Figure 12. Sediment bulk density sections measured at 5 cm depth intervals for each treatment. Error bars indicate one standard deviation

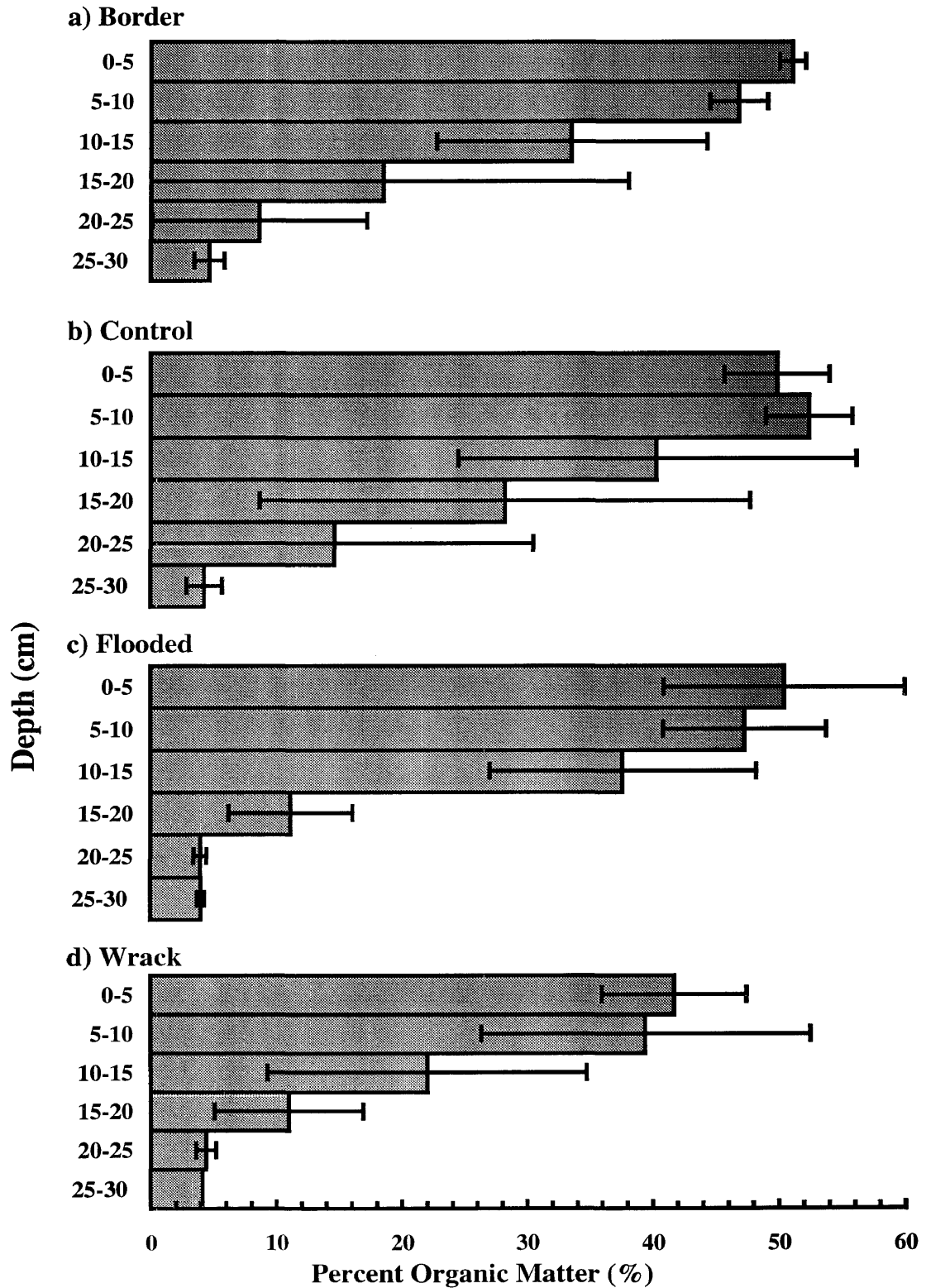


Figure 13. Organic matter content of sections measured at 5 cm depth intervals for each treatment. Error bars indicate one standard deviation

Table 3. P-values for 2 way Randomized Block ANOVAs (between treatments) with treatment as the fixed effect and block as the random effect. Significant interactions are highlighted in bold. Respiration results are comparisons of instantaneous fluxes. Dashed lines indicate no data for statistics.

MEASURE	DATE									
	Nov-95	Feb-96	Apr-96	Jun-96	Aug-96	Nov-96	Feb-97	Apr-97	Jun-97	
Chlorophyll a	-----	P=0.07	P=0.01	P=0.93	P=0.005	P=0.07	P=0.07	P=0.76	P=0.004	
NH4	P=0.57	P=0.54	P=0.36	P=0.44	P=0.59	-----	P=0.42	P=0.57	-----	
PO4	P=0.27	P=0.23	P=0.33	P=0.04	P=0.89	-----	P=0.64	P=0.71	-----	
NO2/NO3	P=0.0003	P=0.12	-----	P=0.01	P=0.22	P=0.34	P=0.46	P=0.52	-----	
SALINITY	P=0.22	P=0.04	P=0.18	P=0.51	P=0.58	P=0.51	P=0.12	P=0.83	-----	
DIC	P=0.06	P=0.40	P=0.12	P=0.14	P=0.89	P=0.55	P=0.17	-----	-----	
RESPIRATION										
Community	-----	P=0.97	P=0.65	P=0.18	P=0.005	P=0.48	P=0.10	P=0.75	P=0.03	
Sediment	-----	P=0.41	P=0.005	P=0.02	P=0.74	P=0.37	P=0.11	P=0.56	-----	

Table 4. Results of ANOVAs comparing between treatment differences at a given depth interval.

DEPTH	ORGANIC MATTER		BULK DENSITY	
	F-statistic	P- value	F-statistic	P- value
0-5	1.34	0.34	0.929	0.47
5-10	1.34	0.32	1.55	0.27
10-15	1.17	0.38	1.61	0.26
15-20	0.95	0.46	0.33	0.80
20-25	0.90	0.48	2.14	0.17
25-30	0.20	0.89	0.525	0.68

only detected in the wrack covered plots (Figure 14). While no seasonal trends are apparent from the data, wrack appeared to have higher sediment chlorophyll concentrations in most months.

C:N Analysis

Percentages of carbon and nitrogen were analyzed in live and dead aboveground vegetation sampled within each treatment plot in August 1995 (Table 5). Because of the cost of analysis, sample replication was limited. Available data shows a significant difference in the C:N ratio between *S. patens* and *D. spicata* ($P < 0.001$) and dead vegetation having a significantly higher C:N ratio than live within a vegetation type (*S. patens* $P < 0.02$, *D. spicata* $P < 0.005$). Tolley (1996) showed that there is much more *S. patens* in the plots than *D. spicata*. The higher C:N ratio for *S. patens* (17.9, $n=10$) indicates a lower nitrogen requirement than for *D. spicata* (10.9, $n=10$) and possibly a competitive advantage in this nitrogen limited marsh.

INSTANTANEOUS SEDIMENT and COMMUNITY RESPIRATION RATES

Measurements of instantaneous community and sediment respiration rates were compared among treatments with a 2 way randomized block ANOVA. Rates were only compared among treatments within a given season because of the need for similar temperatures in order to make comparisons. Figures 15 and 16 show community and sediment instantaneous respiration rates and temperature mean for that month. Since respiration is largely a function of temperature both figures show the expected seasonal trends of highest respiration rates during the summer. These graphs also show that the majority of both community and sediment respiration occurs during the growing season (May-September). Statistical differences among community rates occurred only in August 1996 and June 1997 (Table 3) where wrack rates were significantly lower than the other treatments. Although not significant, rates from the flooded treatment look lower in comparison to the border and control treatments for most months. For the sediment

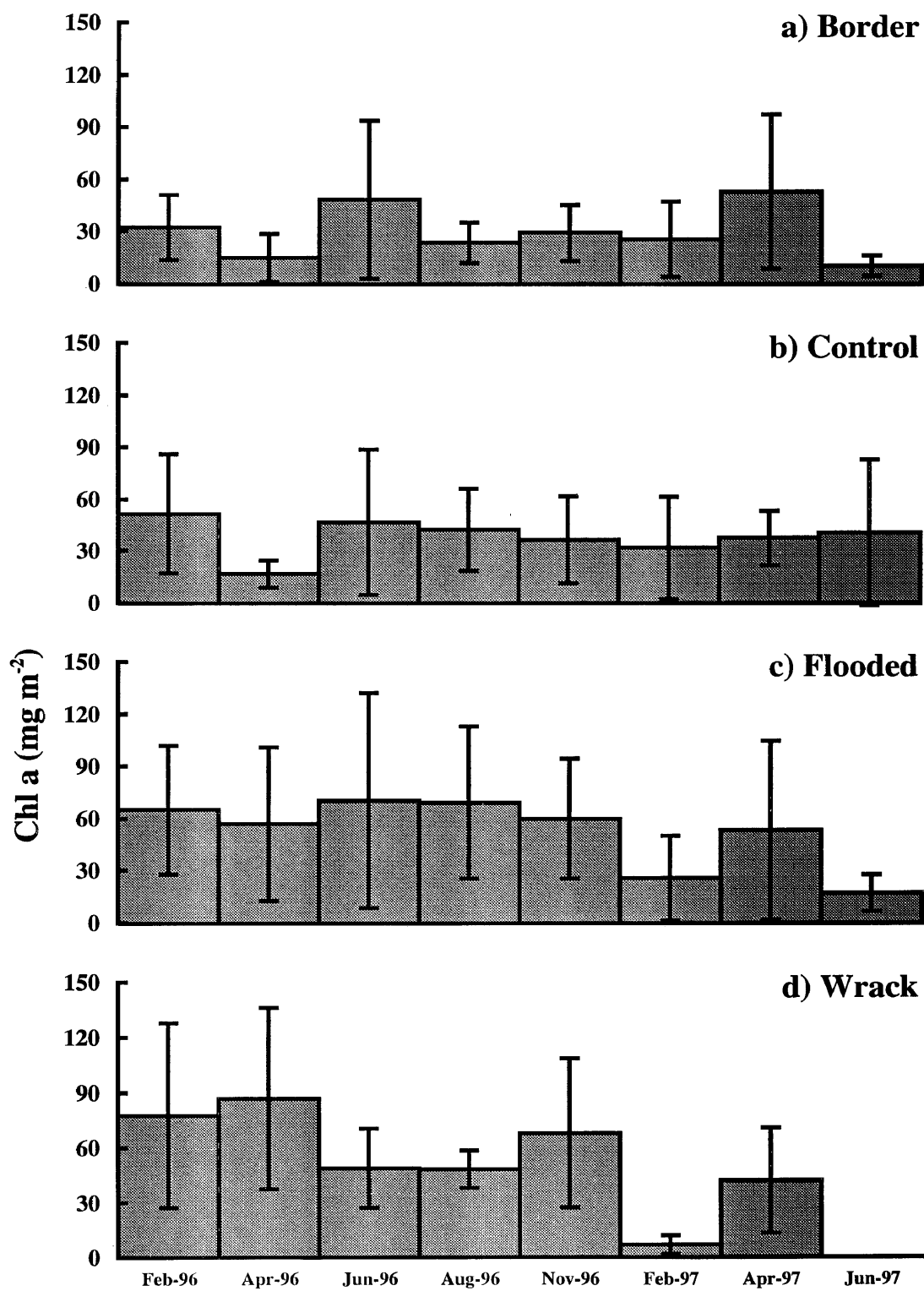


Figure 14. Sediment chlorophyll concentrations (mg m^{-2}) for each treatment. Error bars indicate one standard deviation.

TABLE 5. Percent carbon and nitrogen of vegetation in the different study plots. Samples taken August 1995.

SAMPLE	VEGETATION	% C	% N	C:N
control live	<i>Spartina patens</i>	44.27	2.13	20.78
control live	<i>Spartina patens</i>	42.40	2.01	21.09
control live	<i>Spartina patens</i>	44.78	2.26	19.81
control dead	<i>Spartina patens</i>	46.39	2.43	19.09
control dead	<i>Spartina patens</i>	51.27	2.71	18.92
control dead	<i>Spartina patens</i>	45.64	2.32	19.67
flooded live	<i>Spartina patens</i>	39.13	2.97	13.18
flooded dead	<i>Spartina patens</i>	47.17	2.18	21.64
border live	<i>Spartina patens</i>	36.02	3.37	10.69
border dead	<i>Spartina patens</i>	35.94	2.60	13.82
control live	<i>Distichilis spicata</i>	39.11	3.16	12.38
control live	<i>Distichilis spicata</i>	34.69	2.90	11.96
control live	<i>Distichilis spicata</i>	39.82	2.76	14.43
control dead	<i>Distichilis spicata</i>	41.24	3.49	11.82
control dead	<i>Distichilis spicata</i>	46.28	4.31	10.74
control dead	<i>Distichilis spicata</i>	41.27	3.71	11.12
flooded live	<i>Distichilis spicata</i>	35.46	3.36	10.55
flooded dead	<i>Distichilis spicata</i>	19.81	3.00	6.60
border live	<i>Distichilis spicata</i>	37.13	3.28	11.32
border dead	<i>Distichilis spicata</i>	24.96	3.25	7.68

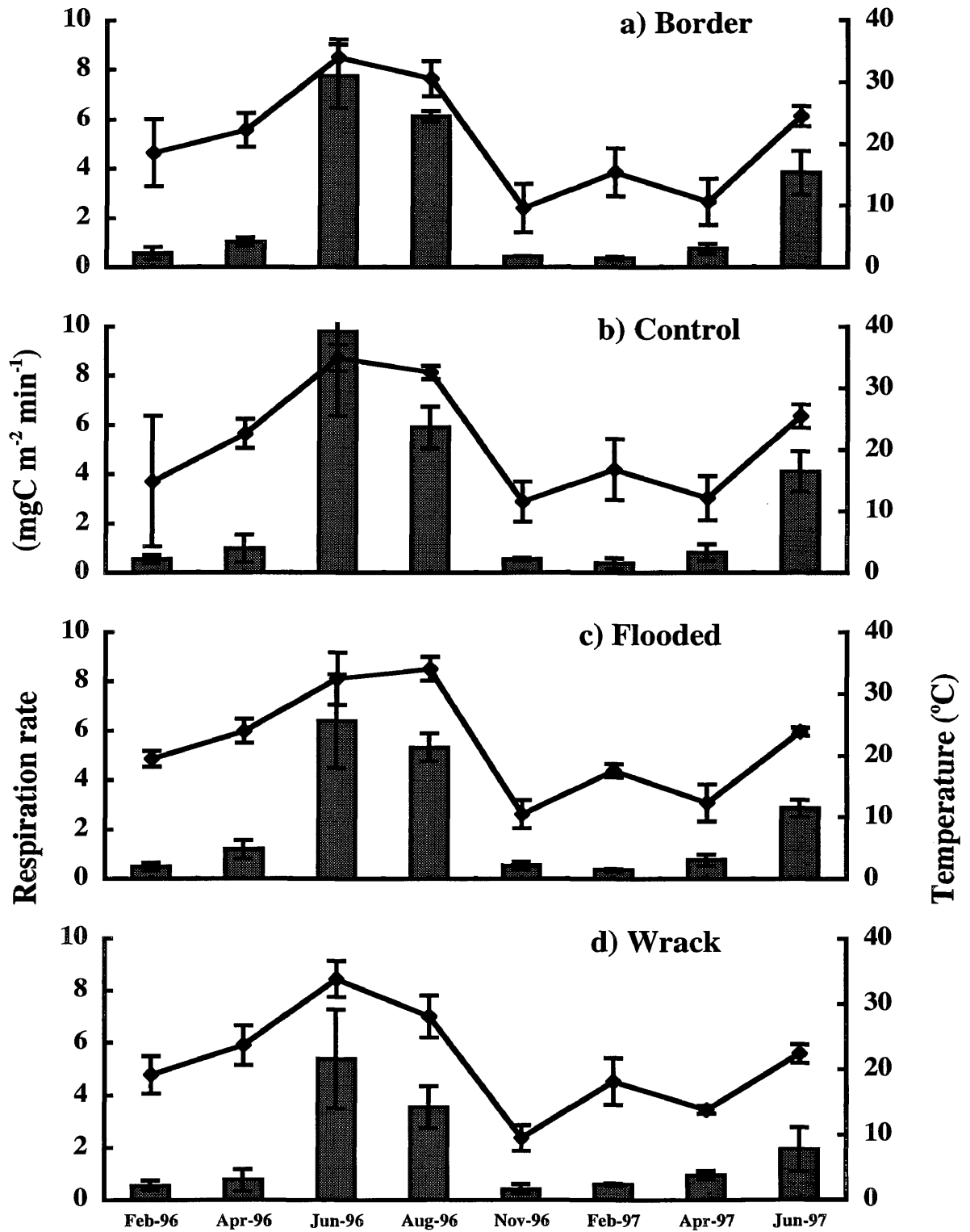


Figure 15. Average instantaneous community respiration rates and mean air temperatures for treatment. Error bars indicate one standard deviation.

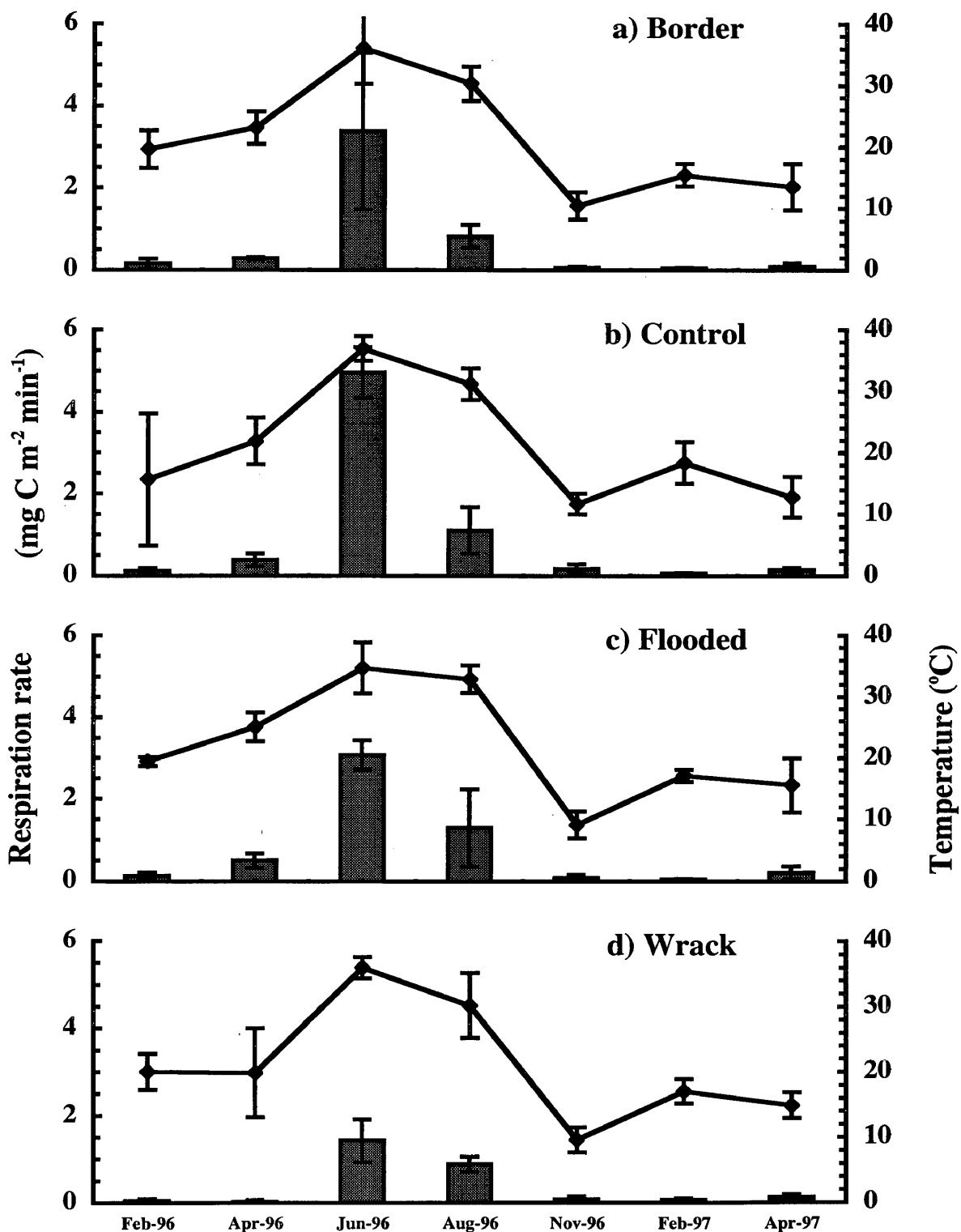


Figure 16. Average instantaneous sediment respiration rates and mean air temperatures for various treatments. Error bars indicate one standard deviation.

respiration rates, differences were significant only in April and June 1996 (Table 3) with the same trends in wrack and flooded treatments. Instantaneous sediment respiration rates varied from 2.7 to 50.6% of instantaneous community respiration with an average of 23.1%.

RESPIRATION Vs. TEMPERATURE CURVES

In order to predict marsh community or sediment respiration rates based on air temperature, equations describing the relationship between air temperature and respiration rate for different treatments must be developed. These equations allow extrapolation of respiration measured at a given temperature to temperatures observed throughout the season. Figures 17 and 18 show instantaneous community respiration rates in the dark plotted against the temperature at which the measurements were made. An exponential curve was fit to the data using data analysis software (Microsoft Excel). Separate curves were developed for times of the year when live vegetation was and was not present. The winter/spring curves represent times when there was little or no living vegetation, while during summer/fall vegetation was present. The low correlation coefficients (r^2) for winter/spring curves (Figure 17) reflect low values observed during this period. In the summer when activity was much higher (Figure 18), r^2 values were high. The higher rates seen in the summer/fall community curves when vegetation is present indicate the importance of macrophytes as a source of respiration. For bare sediments, a single curve was used to describe the temperature-respiration relationship (Figure 19). Sediment respiration accounted for a small but important portion of total community respiration (border, 11%; control, 14%; flooded, 12%; and wrack, 8%).

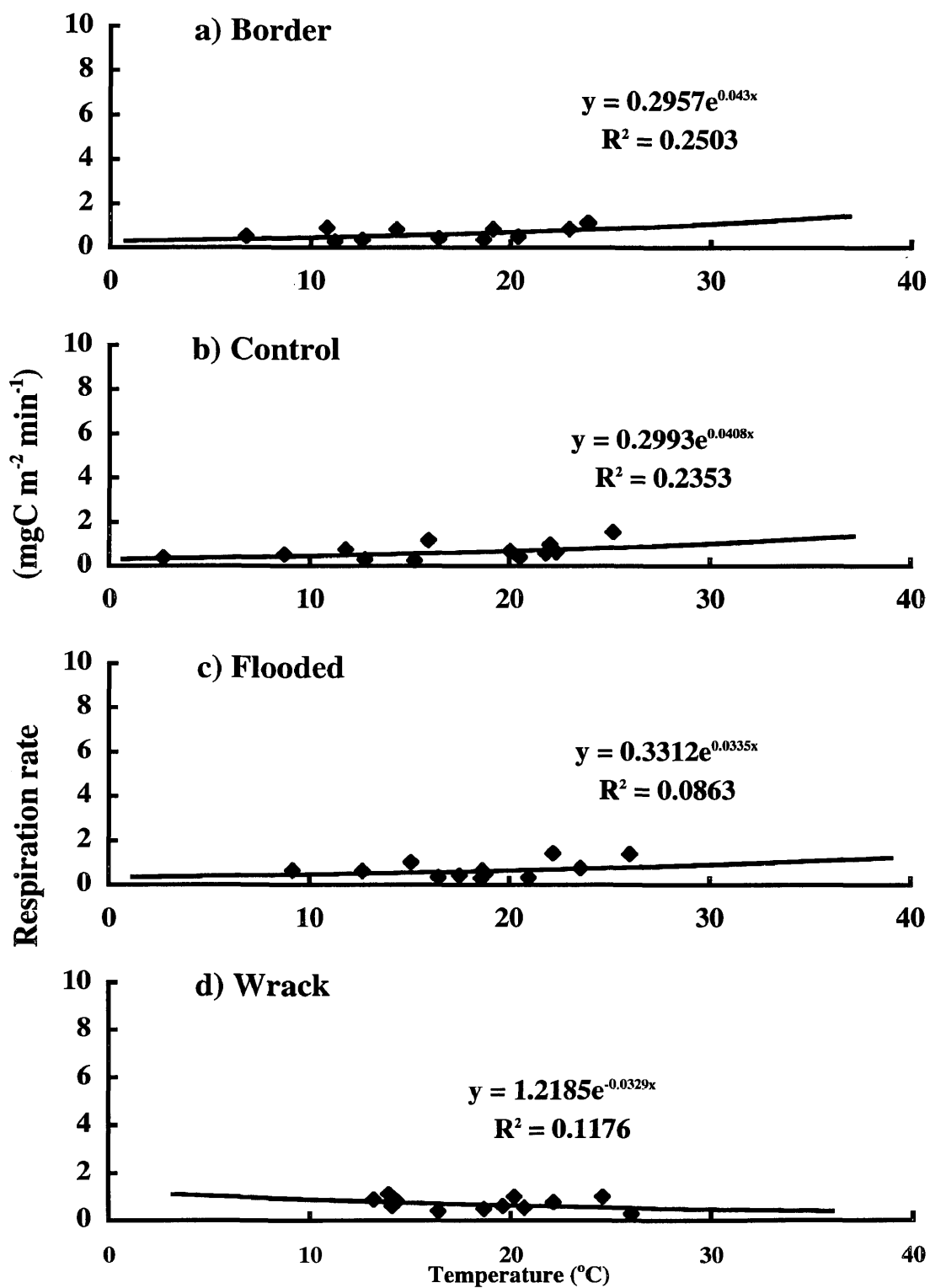


Figure 17. Community respiration vs air temperature relationships for winter-spring. Equations are for exponential curves shown.

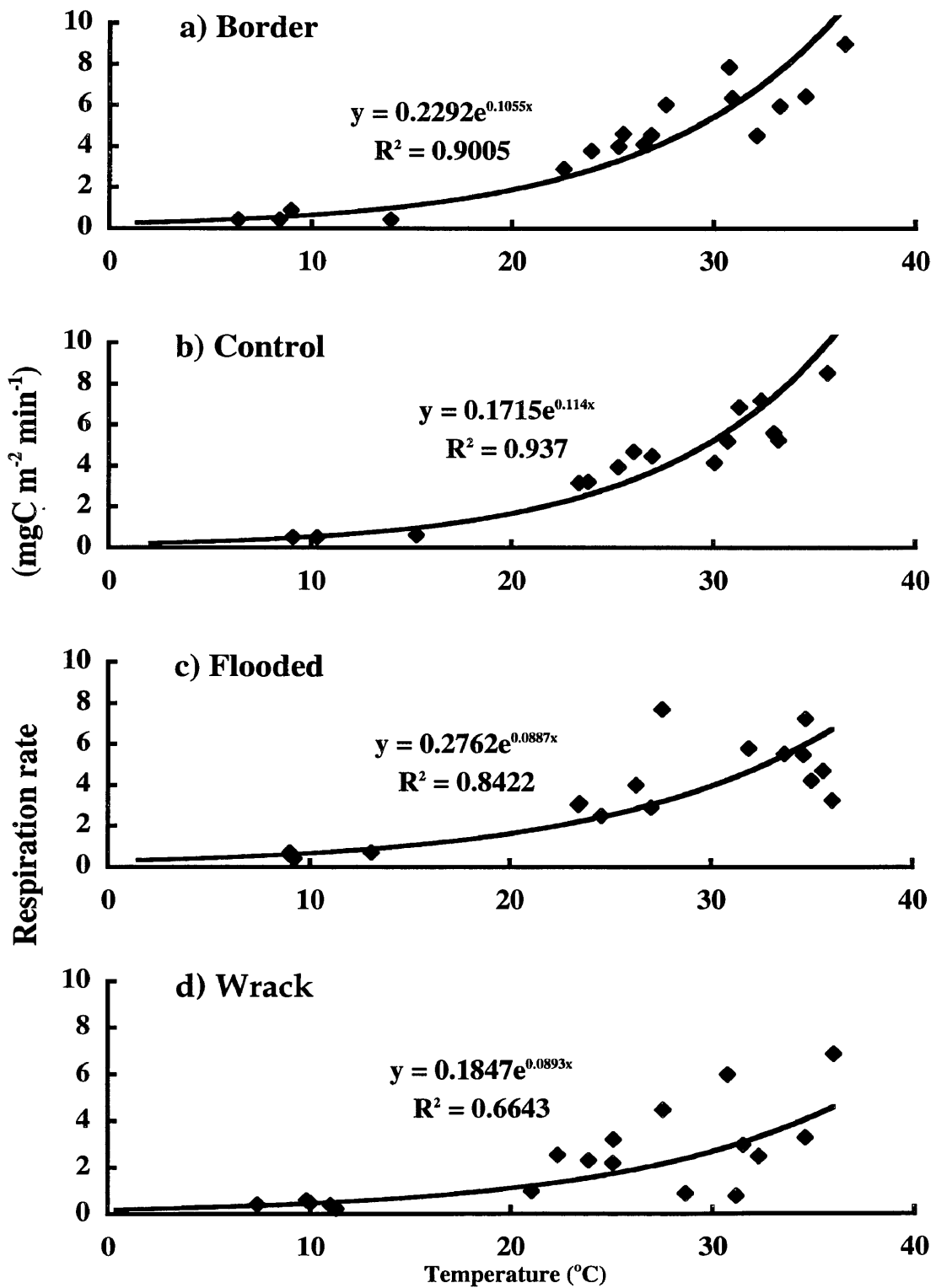


Figure 18. Community respiration vs air temperature relationships for summer-fall. Equations are for exponential curves shown.

PHOTOSYNTHESIS Vs. IRRADIANCE CURVES

Similar to the temperature-respiration relationship, a well investigated relationship exists between irradiance and gross photosynthetic rate for *S. patens* and *D. spicata* (Drake and Read, 1981; Turitzin and Drake, 1981; DeJong et al., 1982; Pezeshki et al., 1987). The relationship is not exponential, but rather hyperbolic, which means the effect of increased light above a certain point (saturation point) does not further increase the photosynthetic rate. Seasonal samplings of community CO₂ exchange rates in the light allowed determination of P vs. I relationships for each season. Separate curves were derived for each season to take into account changes in quantity of biomass, physiological state of vegetation, and temperature range. Figure 20 shows the spring curves for each treatment, with photosynthetic rate on the y-axis and irradiance (PAR) on the x-axis. Figure 21 shows the summer curves. Note the change of the scale on the y-axis; rates are significantly higher in the summer because of the amount of biomass present. Figures 22 and 23 show fall and winter curves with the lower y-axis scale. These curves, along with continuous hourly light data (from VCR-LTER database), were used to develop a production estimate for each of the treatments.

RESPIRATION EXPERIMENT

Artificial Dark/Natural Dark In Situ Experiment

Figure 24 shows the results of an experiment to determine whether respiration measurements made using artificial darkness (i.e. black tarp covering chamber) accurately reflected true dark respiration rates. The graph shows the respiration rates over the course of an afternoon into night. During the light hours (1300-1700) a black tarp was used to simulate darkness inside the chamber, while the measurements in real darkness (1900-2300) had no tarp. A two-tailed t-test comparing the means of the artificial dark (4.17, n=5) and real dark (4.28, n=9) measurements showed no significant difference (p=0.78).

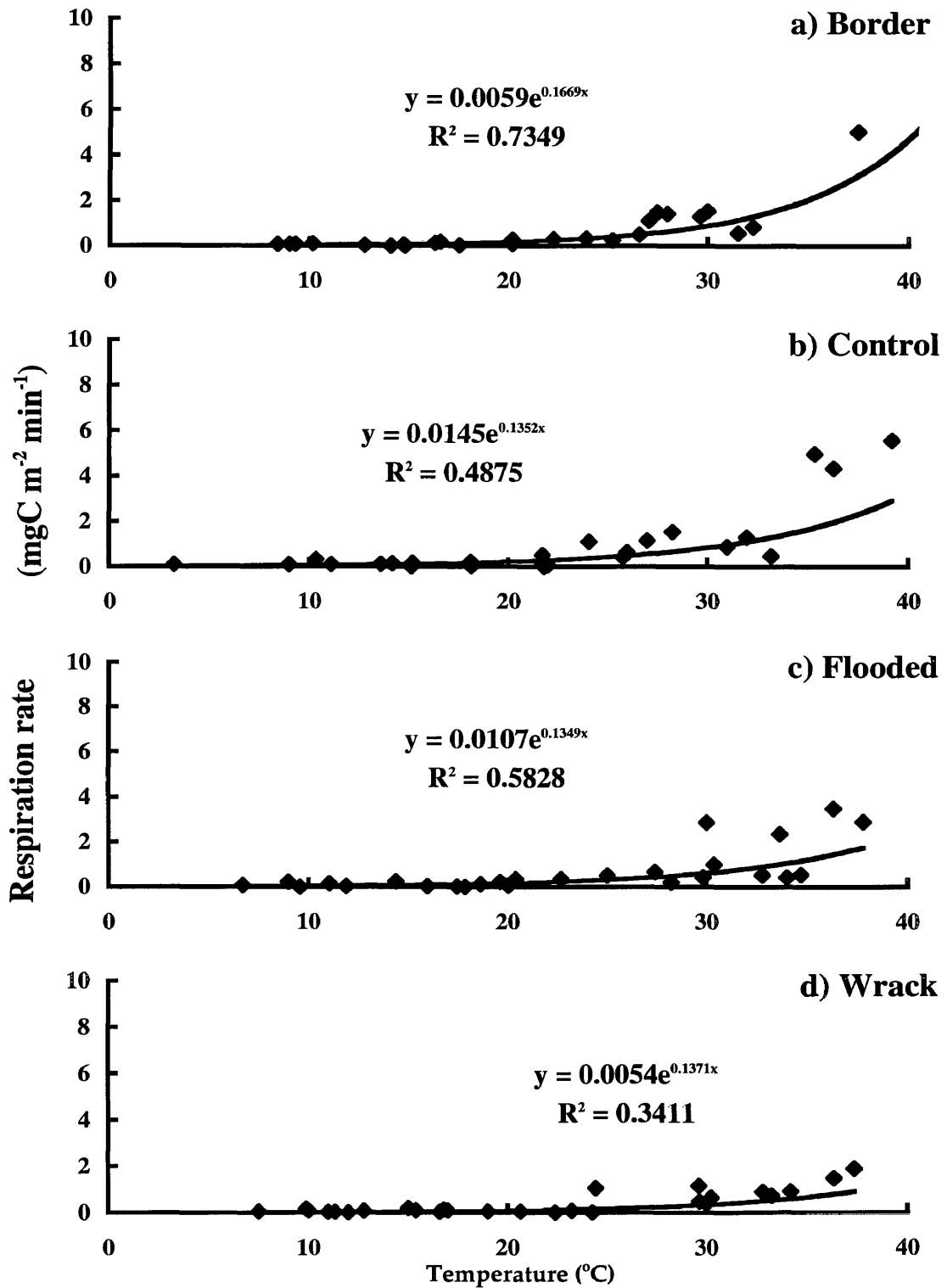


Figure 19. Sediment respiration vs air temperature relationships. Equations are for exponential curves shown. Data from all seasons by treatment.

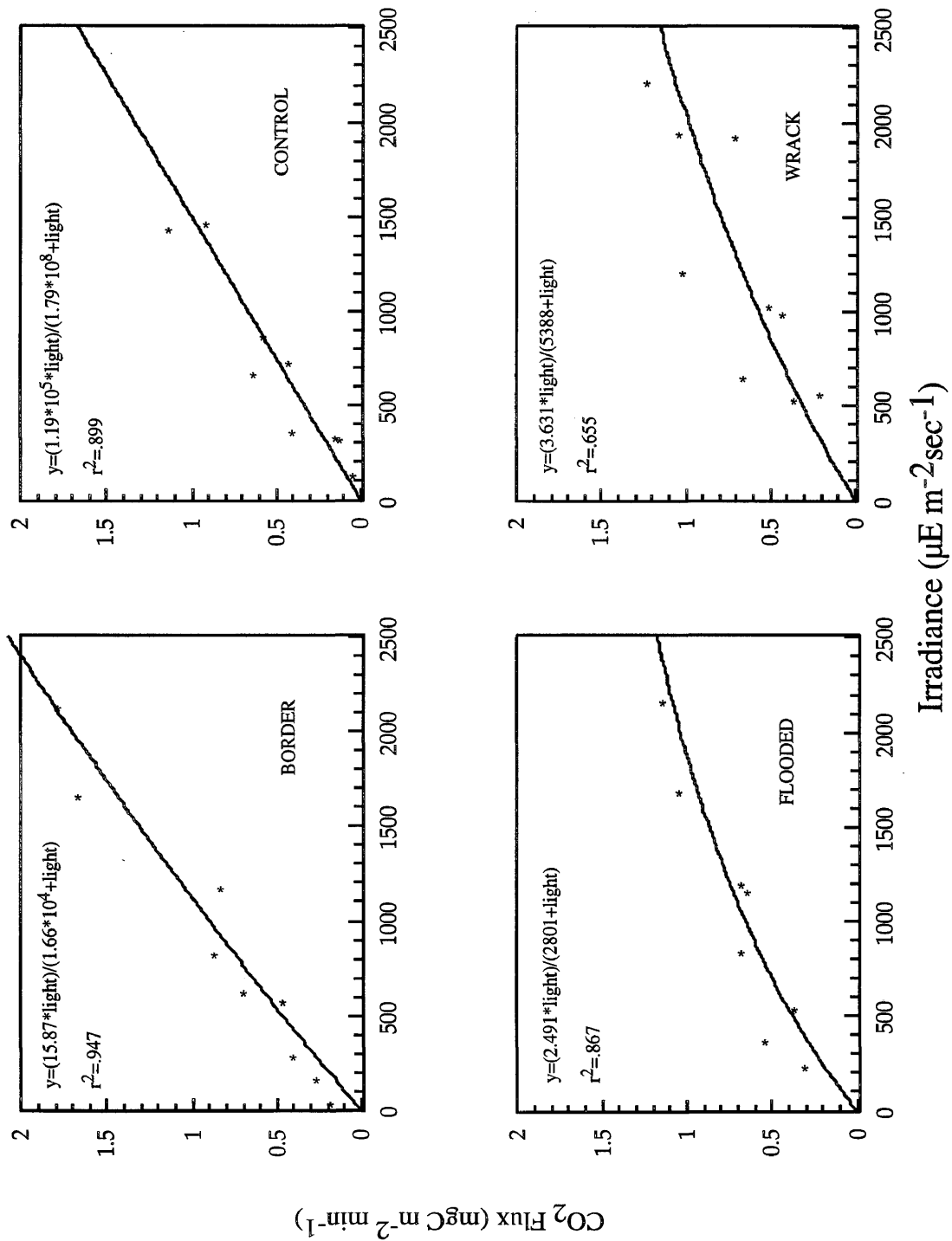


Figure 20. Photosynthesis vs Irradiance curves for each treatment measured during the spring. Equations are given for the hyperbolic curves shown.

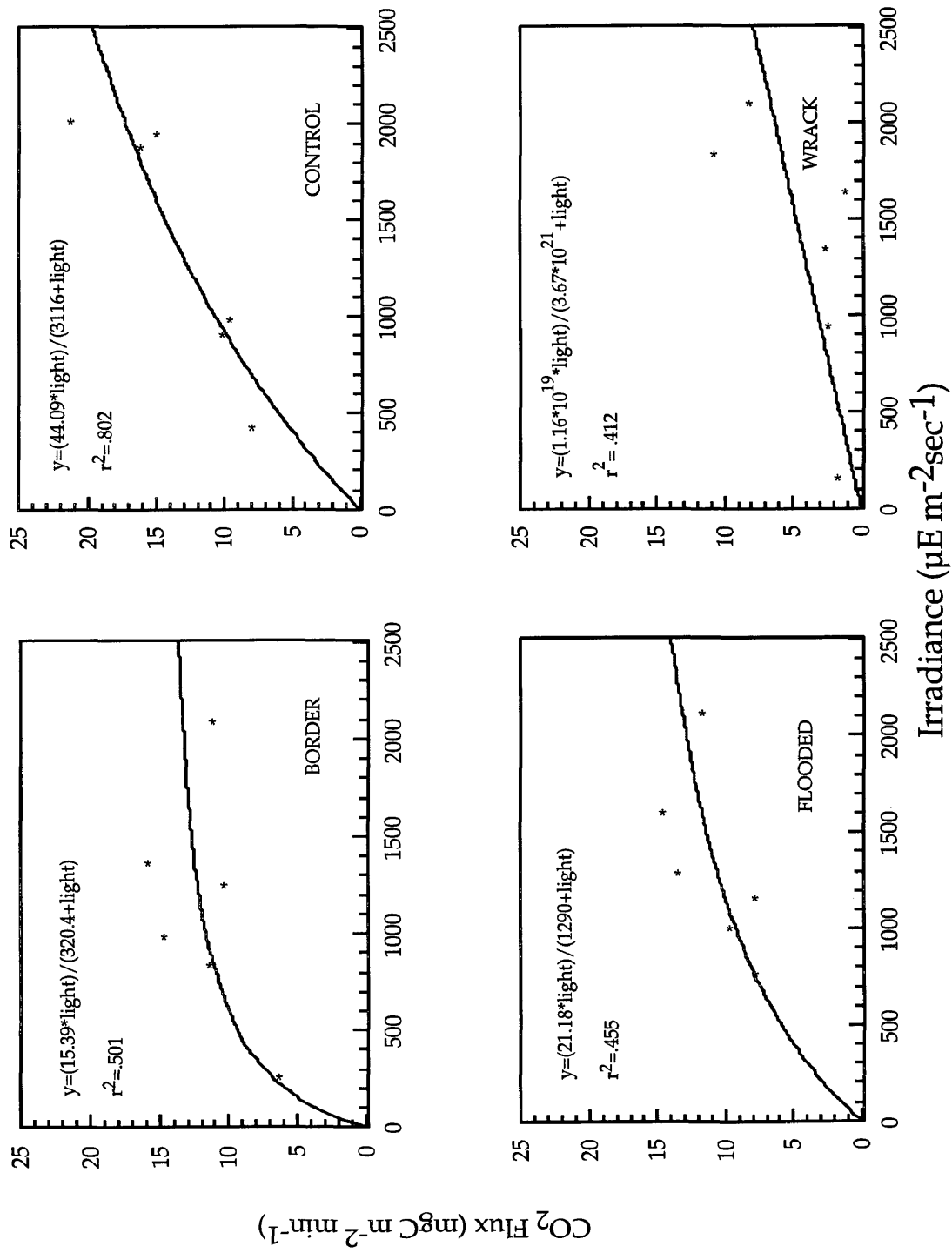


Figure 21. Photosynthesis vs irradiance curves for each treatment measured during the summer. Equations are given for the hyperbolic curves shown.

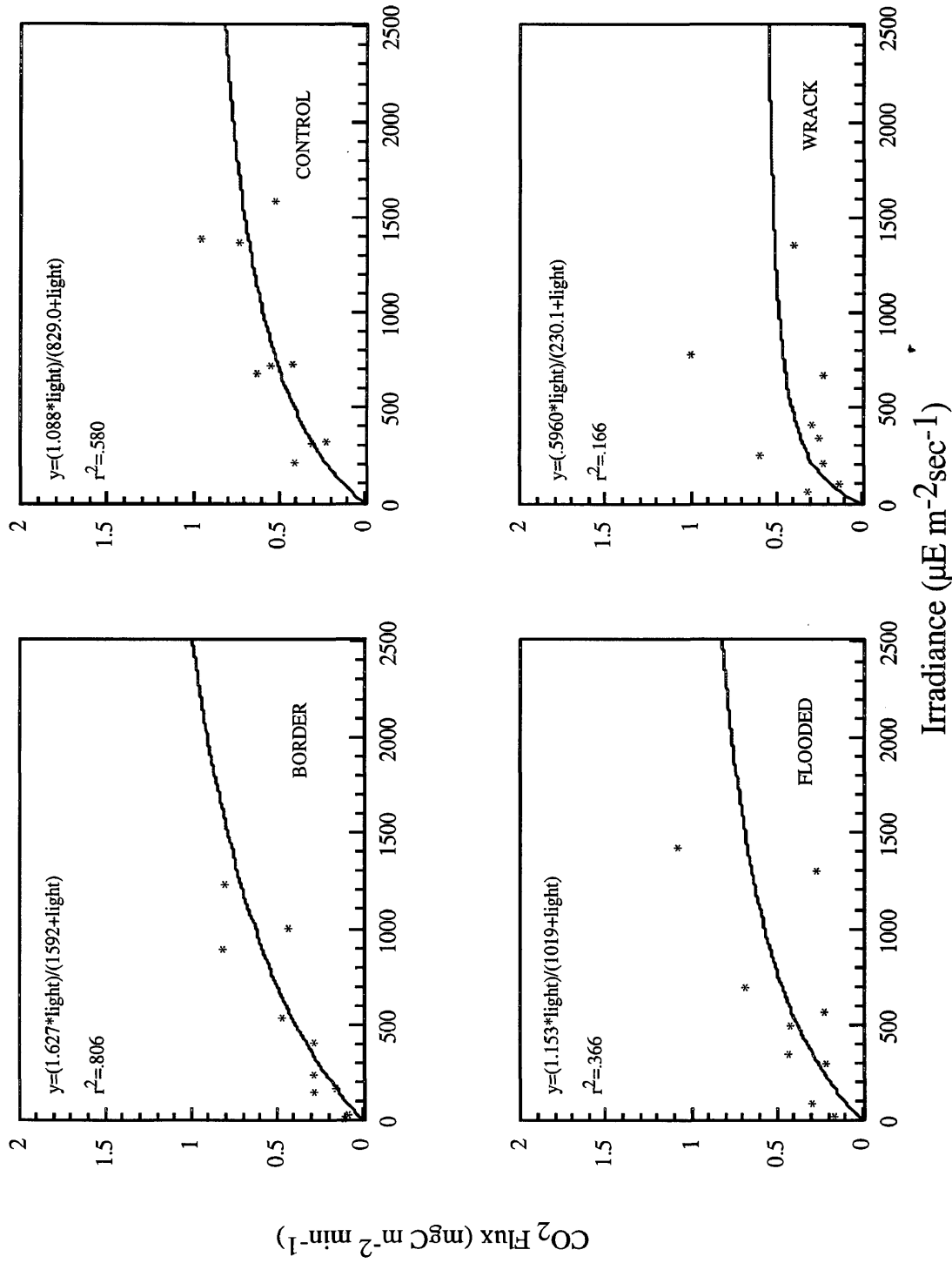


Figure 22. Photosynthesis vs irradiance curves for each treatment measured during the fall. Equations are given for the hyperbolic curves shown.

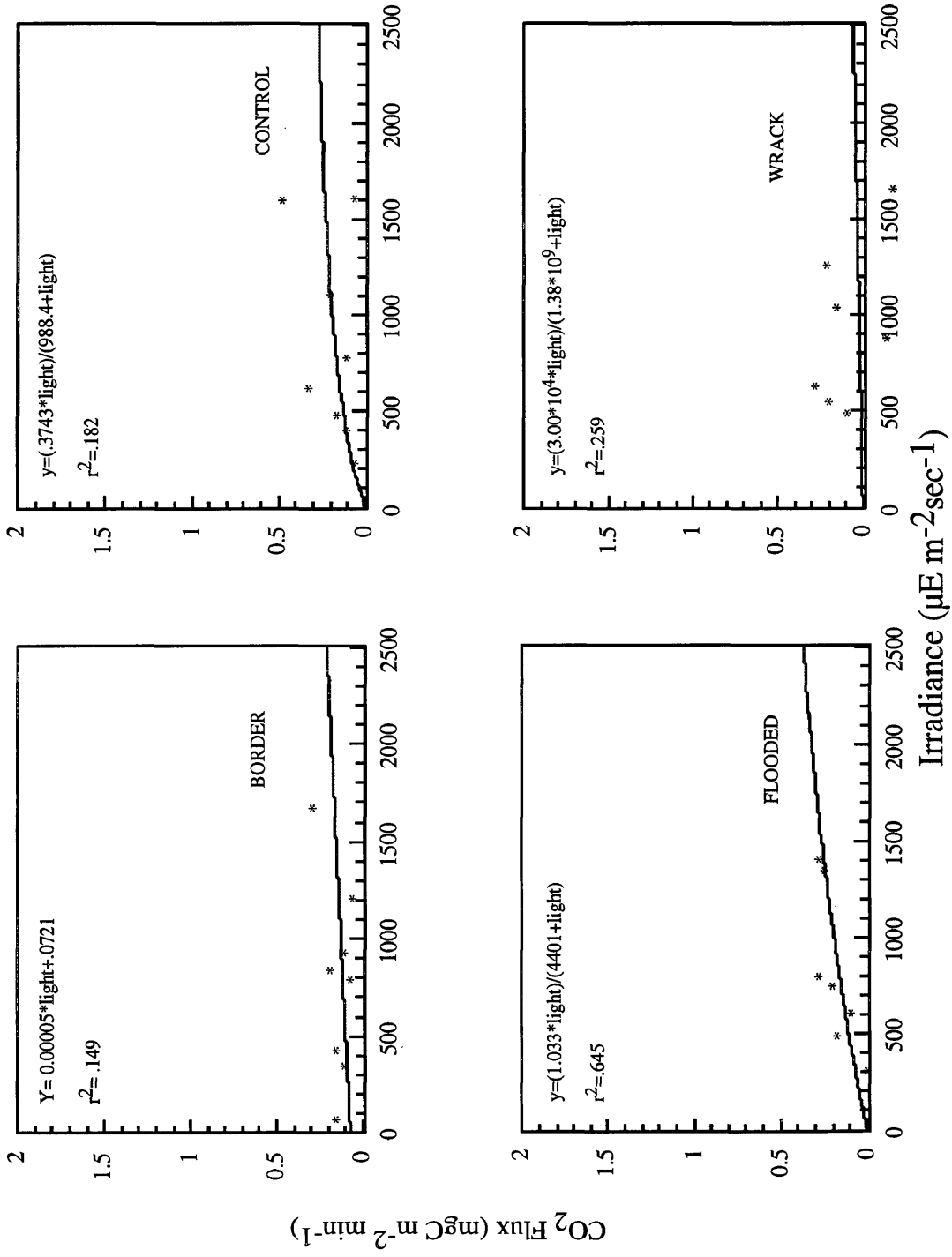


Figure 23. Photosynthesis vs irradiance curves for each treatment measured during the winter. Equation are given for the hyperbolic curves shown.

Growth Chamber Experiment

At the same time as the *in situ* artificial/natural dark respiration experiment, a growth chamber experiment was performed to determine if respiration rates vary with time after cessation of light at constant temperature. Figure 25 shows the results of that experiment, with respiration rate on the y-axis and hours of darkness on the x-axis. Results are shown as the mean of five replicates with error bars indicating +/- 1 standard deviation. Data were analyzed with a repeated measures ANOVA. A significant difference in respiration rates only existed at 25 hours of darkness, which is ecologically irrelevant at this latitude because darkness does not continue for that long. Rates of respiration and CO₂ concentrations were much higher than field measurements made at similar temperatures. Since these were cores harvested from a marsh, there is a possibility that the increased respiration is a function of core degradation rather than actual change in respiration with time following onset of darkness.

MODEL RESULTS

Tables 6 and 7 show gross monthly, seasonal and total output from the community and sediment models which were developed from the R vs. T curves (Figures 17,18 and 19) and P vs. I curves (Figures 20-23). These curves were combined with hourly light and temperature data (from VCR-LTER) over the course of a growing year. Hourly photosynthesis and respiration values were summed to determine monthly, seasonal and annual production and respiration. Table 8 shows the contribution of the different components to community photosynthesis and respiration. Microalgal photosynthesis accounts for only a small portion of total community photosynthesis in the summer (2.8-9.4%) when macrophytes dominate, while in the winter months the microalgae contributes significantly to a much smaller value of community production (17.3-39.5%). Figures 26 and 27 show the gross fluxes graphically. On both graphs, production is listed as a positive flux and respiration as a negative one. The importance of the growing season in

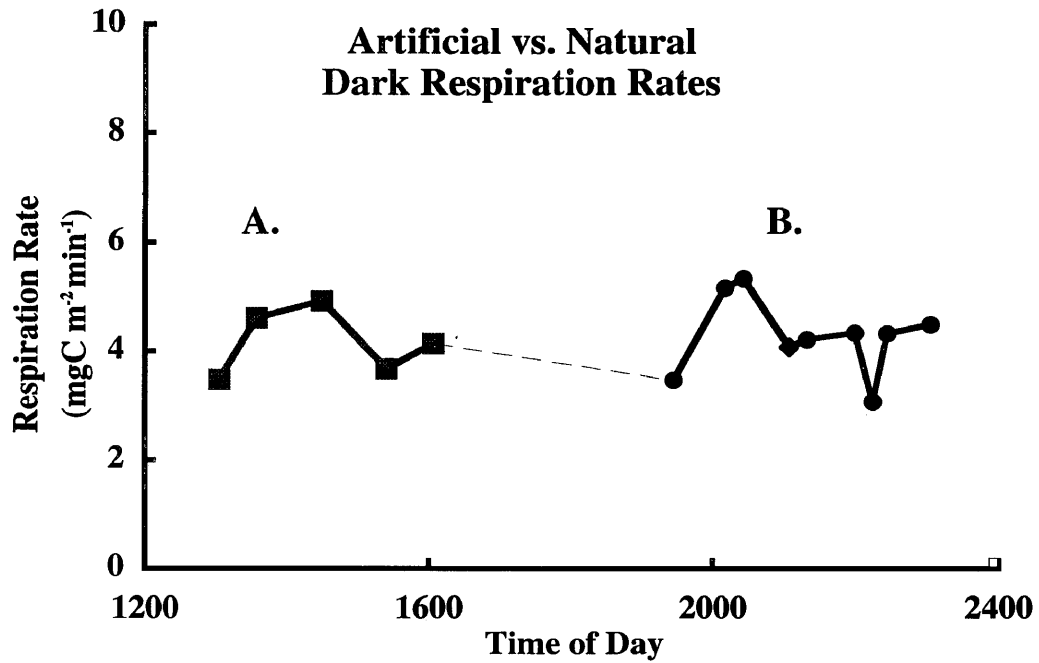


Figure 24. Community respiration rates (mgC m⁻² min⁻¹)
A. artificial dark: during the day chamber covered by tarpaulin
B. natural dark: at night no tarpaulin

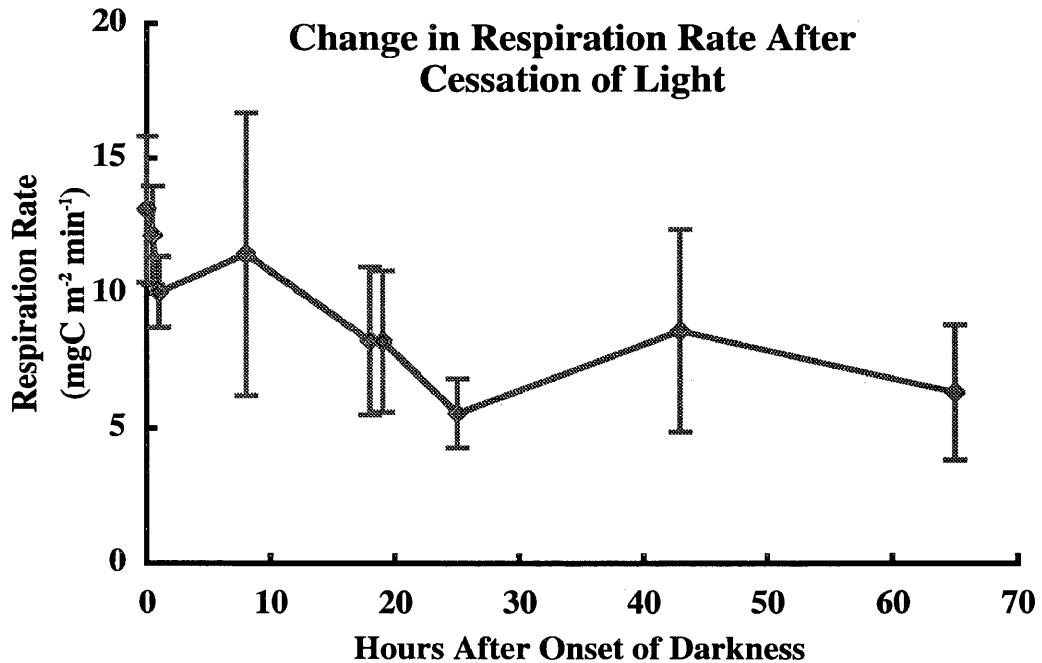


Figure 25. Respiration rates (mgC m⁻² min⁻¹) measured in a light and temperature controlled growth chamber. Error bars indicate one standard deviation.

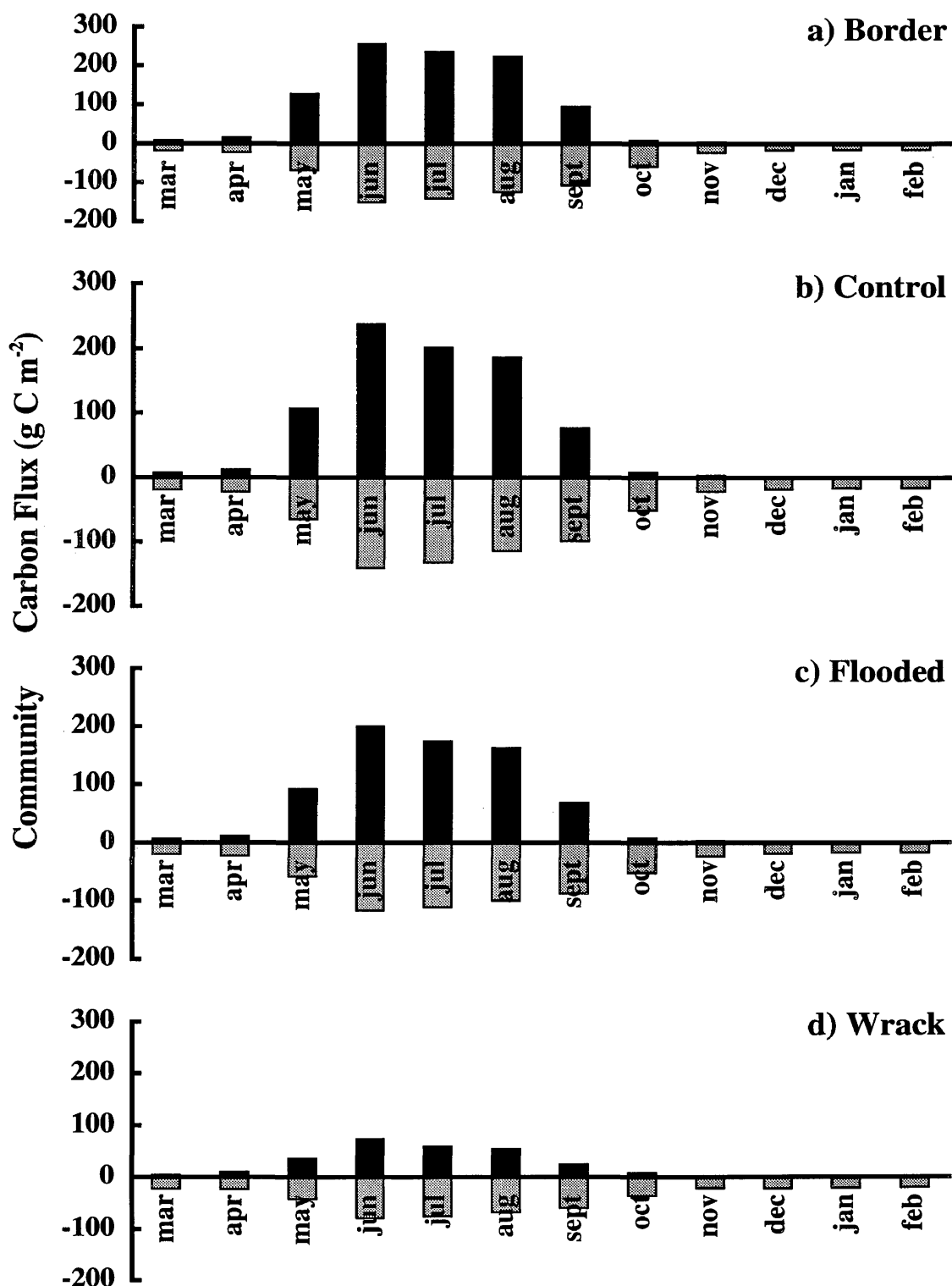


Figure 26. Model calculations of gross carbon fluxes for community respiration and photosynthesis. Positive values indicate carbon uptake by the marsh while negative numbers indicate carbon release.

the overall carbon budget is highlighted in these figures; almost all production occurs in the summer months (May-September) of the vegetated plots. Those figures show reduced production and respiration for the wrack treatment in both sediment and whole community measurements. Because the data are the result of model output no statistics can be run to determine significant differences between estimates. The production seen in the wrack treatments where most vegetation is smothered is explained by microalgae, epiphytes on the wrack, and stray shoots growing through the wrack.

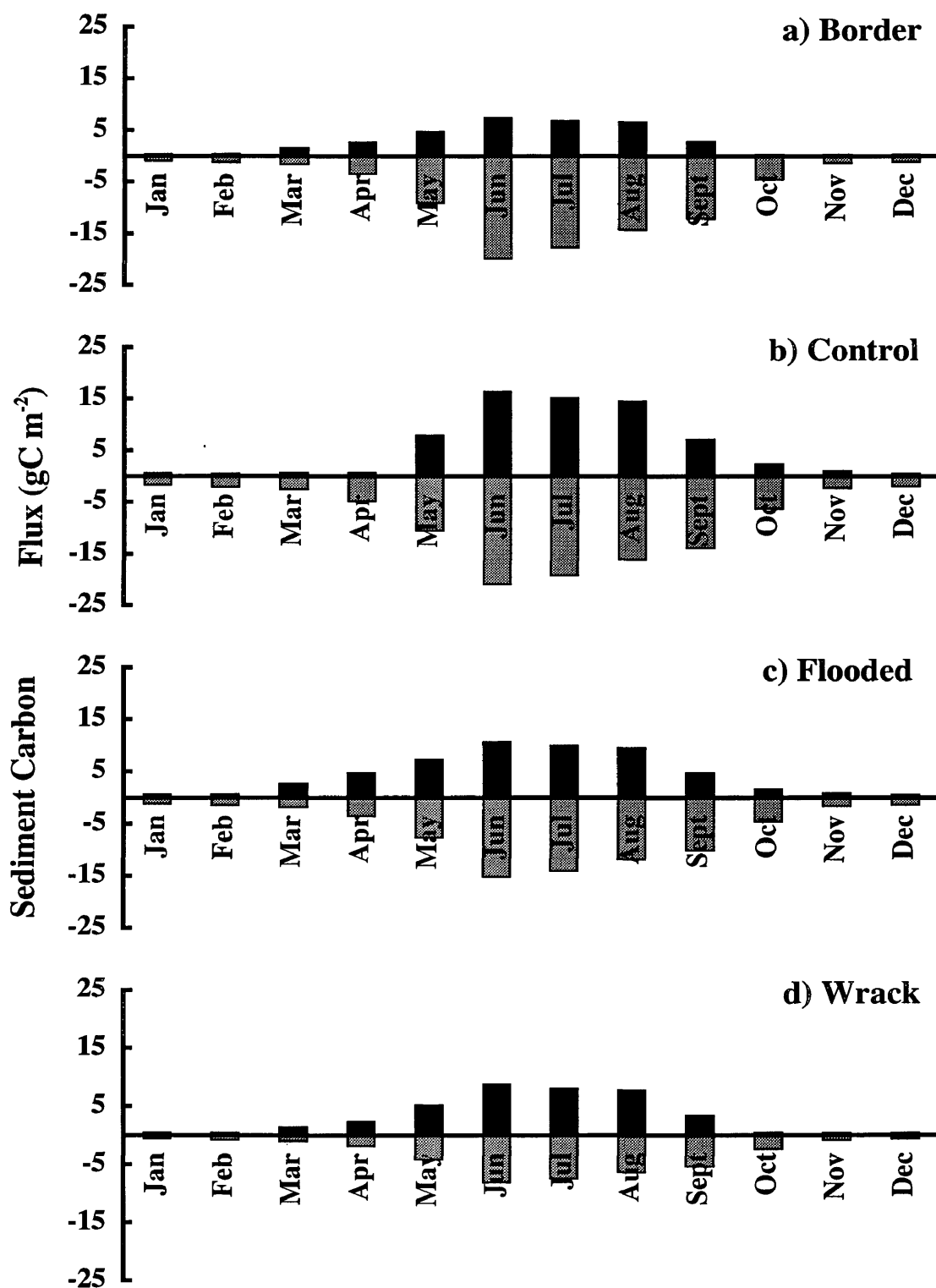


Figure 27. Model calculations of gross carbon flux for sediment respiration and microalgae. Positive values indicate carbon uptake by the marsh while negative numbers indicate carbon release.

Table 6. Model results for community. Calculation based on the 1996 growing season.

COMMUNITY PHOTOSYNTHESIS (gC/m²)				
	Border	Control	Flooded	Wrack
January	2	2	2	0
February	2	2	2	0
March	8	6	6	5
April	16	12	11	10
May	127	107	93	36
June	256	237	200	74
July	236	202	175	61
August	223	186	163	55
September	95	76	68	25
October	8	8	7	8
November	4	4	3	3
December	2	1	1	0
Spring	31	23	22	19
Summer	925	797	689	241
Fall	15	15	14	15
Winter	8	7	6	1
Total	979	842	732	275
COMMUNITY RESPIRATION (gC/ m²)				
	Border	Control	Flooded	Wrack
January	16	16	17	21
February	16	16	17	20
March	19	19	20	22
April	23	23	22	23
May	69	65	58	43
June	150	141	117	79
July	142	132	112	76
August	124	114	100	68
September	108	99	88	60
October	59	51	53	36
November	24	21	24	21
December	18	18	19	22
Spring	45	44	44	47
Summer	538	499	425	288
Fall	118	103	105	71
Winter	68	68	71	84
Total	770	715	646	490

Table 7. Model results for sediments. Calculation based on the 1996 growing season.

MICROALGAL PHOTOSYNTHESIS (gC/ m²)				
	Border	Control	Flooded	Wrack
January	0.4	0.6	0.6	0.4
February	0.4	0.5	0.5	0.4
March	1.5	0.7	2.7	1.4
April	2.6	0.7	4.7	2.4
May	4.6	7.8	7.2	5.2
June	7.3	16.3	10.7	8.7
July	6.8	15.1	9.9	8.1
August	6.5	14.5	9.5	7.8
September	2.8	7.2	4.8	3.4
October	0.2	2.3	1.6	0.4
November	0.3	1.1	0.8	0.3
December	0.3	0.4	0.4	0.3
Spring	5.2	1.4	9.5	4.7
Summer	26.7	59.3	38.9	31.8
Fall	0.4	4.3	3.0	0.8
Winter	1.4	2.1	2.1	1.5
Total	33.7	67.1	53.5	38.8
SEDIMENT RESPIRATION (gC/ m²)				
	Border	Control	Flooded	Wrack
January	0.9	1.6	1.2	0.6
February	1.3	2.1	1.5	0.8
March	1.5	2.5	1.8	1.0
April	3.4	4.8	3.6	1.9
May	9.2	10.5	7.7	4.1
June	19.8	20.9	15.3	8.2
July	17.7	19.2	14.1	7.5
August	14.3	16.2	11.8	6.3
September	12.1	13.8	10.1	5.4
October	4.6	6.3	4.6	2.4
November	1.4	2.3	1.7	0.9
December	1.1	2.0	1.4	0.7
Spring	6.4	9.0	6.6	3.5
Summer	66.7	72.4	53.0	28.3
Fall	9.7	13.0	9.5	5.0
Winter	4.6	7.8	5.7	3.0
Total	87.4	102.2	74.9	39.7

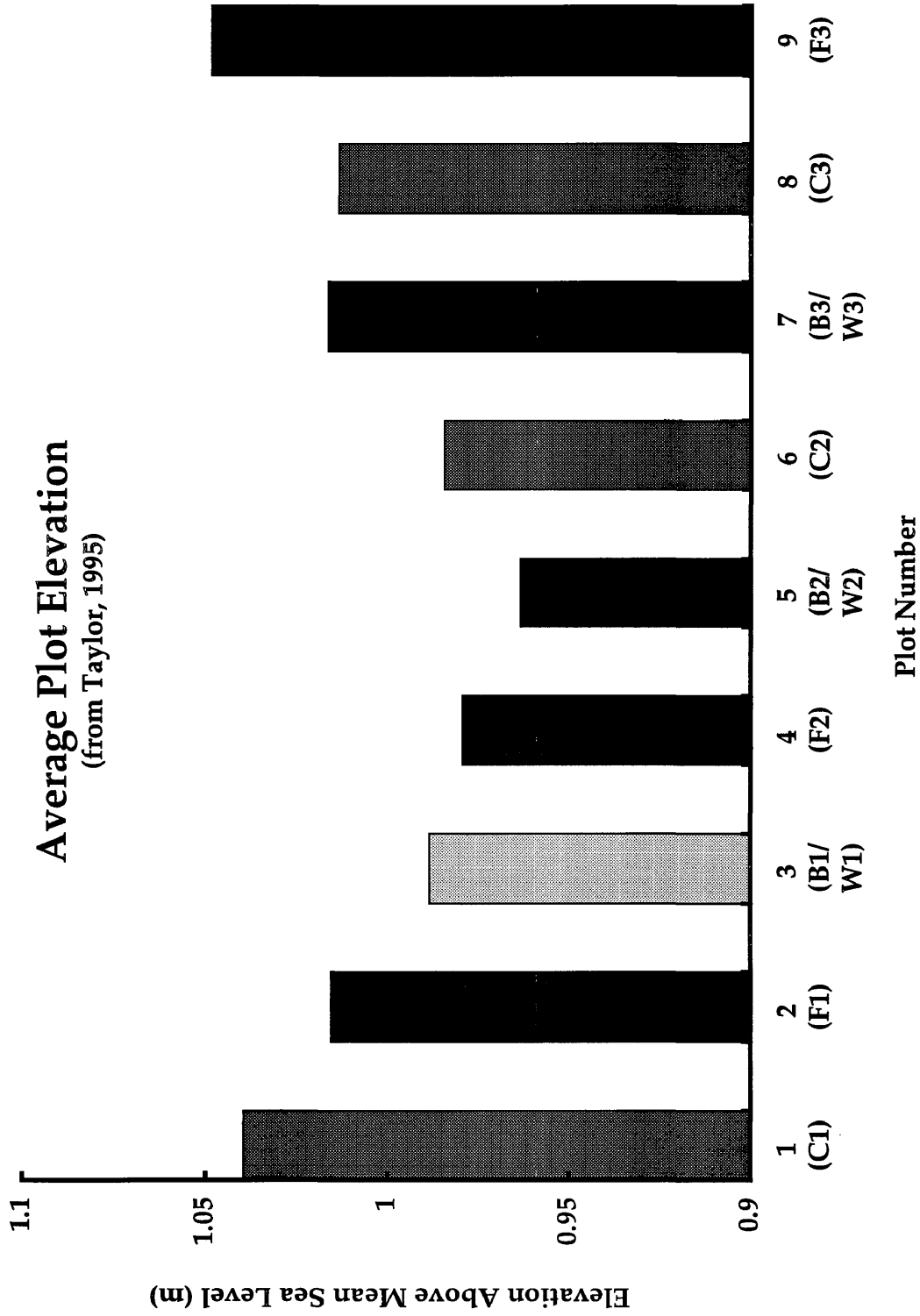


Figure 28. Average elevation for each plot in the inundation experiment . Data taken from the thesis of J. Taylor of East Carolina University. Labels in parentheses indicate block number and treatment (C= control B= border F= flooded W= wrack).

DISCUSSION

We have subjected an organic-rich high marsh to two disturbances, increased inundation and wrack deposition. These disturbances are expected to increase in frequency as a result of accelerated sea-level rise associated with global warming. The organic rich high salt marsh in this study is normally only flooded in the growing season by spring high tides. We increased the frequency of that flooding to once per day by pumping tidal creek water onto selected plots, thereby mimicking the effects of rapid sea-level rise. Another potential effect from accelerating sea-level rise would be the increase in wrack deposition associated with more frequent tidal inundation.

Increased inundation has been shown to slow belowground decomposition, measured as a decrease in CO₂ emissions, in several Louisiana marshes (Nyman and DeLaune, 1991). A decrease in decomposition would result in greater marsh accretion, provided that primary productivity remains constant. Pezeshki and Delaune (1993) observed decreased net photosynthesis for *S. patens* under the hypoxic and high salinity conditions associated with increased inundation. With decreased net photosynthesis less fixed carbon is available for accretion thereby counteracting the potential increase in accretion due to decreased decomposition. The intensity, frequency, and duration of the inundation may determine whether the net effect on accretion is positive or negative. Data from this study (Table 8) support our hypothesis that increased inundation will depress high marsh metabolism. There was both lower total community and sediment respiration as well as reduced gross community production in the flooded plots as compared to either control or border control plots. The net result of reduced respiration and reduced photosynthesis resulting from increased inundation in this community-level study was an overall decrease in carbon available for burial and accretion.

We were unable to locate any data in the literature related to the effects of wrack on belowground processes; however, several studies have shown that wrack deposition will decrease or completely remove aboveground biomass from a given area, depending on the quantity and duration of wrack deposited. This study examined the effects of long term wrack stranding and should be seen as an example of maximum wrack disturbance. Table 6 demonstrates that wrack treated plots had reduced respiration rates, perhaps related to the lack of live vegetation in the treatment which would help aerate the soil and provide fresh organic matter for microbial decomposition. Reidenbaugh et al. (1983) suggested that accretion deficits observed in wrack deposition areas resulted from increased organic matter decomposition and sediment compaction rather than physical movement of material (erosion). In the high marsh examined in this study, the near total reduction in photosynthesis due to the absence of above-ground biomass caused by wrack deposition was probably the primary mechanism responsible for the accretion deficit. At these sites respiration far exceeded photosynthesis (Table 8). Although wrack is a potential carbon source for decomposition by detritivores it is composed mostly of recalcitrant organic matter that is difficult to break down (Moran and Hodson, 1990) and is, therefore, not likely to contribute much to the respired carbon flux. The small amount of production in the wrack treatment was performed by benthic microalgae, epiphytes growing on the wrack, and occasional *S. alterniflora* culms growing through the wrack. Results from this study indicate that areas affected by wrack deposition experience a substantial carbon shortage, which can lead to large accretion deficits (-6.2 mm yr^{-1}) as seen in Table 10.

The fundamental question to be resolved with these disturbance experiments was whether there was net gain or loss of carbon in salt marshes exposed to either increased inundation or wrack deposition. In this study, there was a greater reduction in gross primary production than in community respiration (Table 8) and, therefore, a net loss of

Table 8. Various components of community production and respiration. All values are indicated in grams carbon per meter squared per year. Values calculated by combining P vs. I and R vs. T curves with hourly meteorological observations from the LTER database (Porter & Richardson, VCR/LTER). Meteorological data from the 1996 growing season used for calculations.

Treatment	Gross Community Photosynthesis	Gross Community Respiration	Gross Microalgal Photosynthesis	Gross Sediment Respiration	Gross Macrophyte Photosynthesis	Gross Macrophyte Respiration	Net Carbon Flux
Border	979	-770	34	-87	945	-682	209
Control	842	-715	67	-102	775	-613	127
Flooded	732	-646	53	-75	678	-571	86
Wrack	275	-490	39	-40	236	-450	-215

carbon in both disturbed treatments relative to the control sites. The reduced carbon flux into the marsh resulted in less organic material available for burial and accretion in disturbed areas. Although intense in effect, wrack deposition affects only a small percentage of the marsh each year (Valiela and Riestma, 1995). Although the inundation effect is much less intense, it affects a much greater area on an annual basis.

The annual accretion deficit created by these disturbances could generate a negative feedback mechanism in which lower elevation as a consequence of the accretion deficit in conjunction with gradual increase in sea level results in more frequent inundation, further reducing production and vertical accretion. This feedback loop might continue until high marsh vegetation is replaced by more flood-tolerant low marsh species (*S. alterniflora*) and organic-rich peats are replaced by higher bulk density mineral sediments. This scenario of state change in a salt marsh has been hypothesized by Brinson et al. (1995). A second negative feedback loop might develop in wrack areas as accretion deficits causes increased microtopographic relief, exposing more sediment to air and increasing oxidation of organic matter (R. R. Christian et al., unpublished).

Calculations (Table 10) of accretion potentials based on soil bulk density, organic carbon content, and net carbon fluxes suggest that in border control (7 mm yr^{-1}) and control (4.2 mm yr^{-1}) treatments enough carbon is buried to increase elevation at a pace sufficient to keep up with sea-level rise estimated between $2.8\text{--}4.2 \text{ mm yr}^{-1}$ (Braatz and Aubrey, 1987; Gornitz and Lebedeff, 1987). On the other hand, in flooded areas (3.2 mm yr^{-1}) carbon accretion is sufficient to only marginally keep up with sea-level rise. In the wrack treatment, the negative carbon balance (-6.2 mm yr^{-1}) will result in rapid loss of elevation. These calculations assume that all excess carbon fixed as marsh biomass is buried within the system and none is lost to export. These assumptions are supported by the lack of herbivores which graze on the vegetation and the fact that tidal water in the high marsh does not have enough volume, force, or frequency to export significant quantities of biomass.

Table 9. Summary of sediment microalgal production values in the literature. After Neubauer et al., (in prep.)

Location	Marsh Type	Method	Annual Production (g C m ⁻² yr ⁻¹)	Reference
Delaware	salt marsh	O ₂	61 to 99	Gallagher and Daiber (1974)
Tijuana Estuary, California	salt marsh ^a	¹⁴ C	185 to 341	Zedler (1980)
global survey	intertidal and shallow coastal sediments	¹⁴ C and O ₂	50 to 200	Colijn and de Jonge (1984) and references therein
East Galveston Bay, Texas	salt marsh ^b	¹⁴ C	71	Hall and Fisher (1985)
Graveline Bay, Mississippi	salt marsh ^c	¹⁴ C	28 to 151	Sullivan and Moncreiff (1988)
North Inlet, South Carolina	salt marsh ^d	microelectrode, ecophysiological ⁱ	56 to 234	Pinckney and Zingmark (1993)
Goodwin Islands, Virginia	salt marsh ^e	process-based simulation model	101 to 169	Buzzelli (1996)
Phillips Creek marsh, Virginia	salt marsh ^f	ecophysiological model CO ₂ gas flux	27.8 58	Anderson et al. (1997)
Upper Brownsville marsh, Virginia	salt marsh ^g	CO ₂ gas flux	24 to 68	this study
Sweet Hall marsh, Virginia	tidal freshwater marsh ^h	CO ₂ gas flux	74 (6) ⁱ	Neubauer et al., in prep

a Blue green algal mats under *Spartina foliosa*, *Jaumea carnosa*, *Batis maritima*, and *Monanthochloa littoralis* canopies.

b Blue-green algal mat under mixed *S. patens* and *Distichlis spicata* canopy.

c Sediment microalgae under monospecific *S. alterniflora*, *Juncus roemerianus*, *Distichlis spicata*, and *Scirpus olneyi* canopies.

d Sediment microalgae in five habitats; shallow subtidal, intertidal mud- and sandflats, tall and short form *S. alterniflora*.

e Sediment microalgae in four habitats; vegetated and non-vegetated subtidal, and vegetated and non-vegetated intertidal.

f Sediment microalgae under short form *S. alterniflora*.

g Sediment microalgae under mixed *S. patens* and *D. spicata* canopy with various flooding treatments.

h Sediment microalgae under mixed *Peltandra virginica*, *Pontederia cordata*, *Zizania aquatica* canopy.

i Two year average (standard deviation in parentheses).

We observed higher gross primary production in the border treatment compared to the control ($978.5 \text{ gC m}^{-2} \text{ yr}^{-1}$ vs. $842.0 \text{ gC m}^{-2} \text{ yr}^{-1}$, 1996 estimates), although not statistically different, this raises the question of what effects the borders themselves have on marsh metabolism (Table 8). The borders may act as traps for freshwater precipitation and keep brackish flood water out. This is likely to enhance production in bordered areas not affected by other treatments. Similar results were seen by Tolley (1996) using the same inundation site but different techniques for estimating production ($1280 \text{ g biomass m}^{-2}$ vs. $993 \text{ g biomass m}^{-2}$, 1994 data). This experimental artifact might also have existed in the flooded and wrack treatments which had borders, but the effects would have been masked by the larger treatment effects.

We know of no estimates of sediment microalgal biomass and/or production for high marsh, *S. patens*/*D. spicata* communities. The high stem density in this vegetation type would not appear to allow for significant light penetration to the sediment surface and, therefore, little sediment microalgal biomass would be expected to develop. Seasonal chlorophyll *a* (chl *a*) samplings (Figure 14) in our plots show average chl *a* values ranging from 10.3 mg m^{-2} in June 97 border plots to 77.6 mg m^{-2} in February 96 wrack plots. Because of the high variability of samples within a treatment we did not observe significant differences among treatments and seasonal differences within treatments were not pronounced. Since performing these studies we have noted that the 72 hr extraction used for these analyses may have caused us to underestimate the actual chl *a* value by 10-20% (Neubauer and Miller 1998, unpublished). This correction only affects the absolute values and has no bearing on the relative differences between treatments.

We estimated primary productivity of benthic microalgae by modeling seasonal CO_2 fluxes using measurements made over unvegetated sections of marsh sediment. Based on both instantaneous and seasonal model estimates, maximum microalgal production occurred in the summer. Although biomass samplings do not show higher levels of chl *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 like the fiddler crab (*Uca pugnax*) (Gallagher and Daiber, 1974; Sullivan and Moncreiff, 1990). Pomeroy (1959) explained the increased summer microalgal productivity he observed in a Georgia *S. alterniflora* marsh as a function of high summer temperatures. Annual gross microalgal production estimates for treatments in our study ranged from 33.7 to 67.1 gC m⁻². Although only a small fraction of total gross community production (Border, 3.4%; Control, 8.0%; Flooded, 7.3%; Wrack, 14.1%), 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). The estimates determined for this high marsh fall at the lower end of values derived from a large number of benthic microalgal production estimates made in a number of coastal environments (Table 9). However, these results show that benthic microalgae can be a small but significant source of primary production in the high marsh and should be considered in future carbon and production estimates for the high marsh community.

Questions raised about how accurately the artificial dark technique mimics natural dark conditions were addressed in a field experiment in September of 1997. The primary concern was whether instantaneous darkening of the community, as applied in the artificial dark technique by draping a black tarpaulin over the community chamber, would cause plant physiological changes which may occur with gradual onset of darkness under natural conditions. The experiment (Figure 24) demonstrated no significant differences ($p = 0.78$) between means (artificial dark = 4.17 ± 0.61 vs. natural dark = 4.28 ± 0.72) of the artificial dark fluxes measured during the day and the natural dark fluxes measured at night. Although specific mechanisms of respiration were not examined, results at the community level indicate that respiration measured using the artificial dark technique accurately represented true night respiration rates.

Table 10. Calculated accretion potentials based on sediment characteristics and gas flux model estimates.

	Annual Carbon Flux (gC m ⁻²)	Sediment Bulk Density (g cm ⁻³)	Percent Carbon of Sediments* (%)	Accretion Potential** (mm yr ⁻¹)
Border	209	0.149	20%	7.0
Control	127	0.151	20%	4.2
Flooded	86	0.134	20%	3.2
Wrack	-215	0.174	20%	-6.2

* Percent Carbon (organic) of sediments obtained from a range of high marsh literature values (Hatton et al., 1983; Craft et al., 1988; Craft et al., 1993; Buzzelli, 1996).

** Accretion potential calculated by determining the number of grams of carbon needed in a volume of sediment based on bulk density and sediment percent carbon and dividing that number by the net flux of carbon calculated from the gas flux model.

Another question concerning macrophyte physiological response to natural darkness was whether labile carbohydrates stored in the plant during daylight photosynthesis would be rapidly metabolized, thereby enhancing respiration rates early in the evening. This would lead to an overestimate of respiration rates in short term artificial dark measurements. The error would be further amplified by scaling up to seasonal and annual time scales. We performed an *in situ* experiment during September 1997 at control plots to measure changes in respiration rates over the course of an evening following the onset of darkness. As shown in Figure 24 there were no consistent decreases in respiration rate over the course of an evening (7pm - 11pm).

In addition, a controlled environment lab experiment was conducted to insure that any changes in respiration rate over an evening were not a function of changing temperature during that time period. Variability within the five cores masked any significant statistical trends, except for hour 25 which was significantly different. This result is ecologically irrelevant, however, because at no time do marshes receive 25 hours of continuous darkness. There did appear to be a trend of decreasing respiration rate in the first hour of measurements (Figure 25), but these differences were not statistically significant.

We were concerned about the physiological status of vegetation in our cores since flux rates ($6.3\text{-}13.1 \text{ mg C m}^{-2} \text{ min}^{-1}$) and CO_2 concentrations (1000 ppm CO_2) were well above what we normally measured *in situ*. These higher than expected rates and concentrations might indicate disturbance to the vegetation resulting in respiration rates higher than normal ($4 \text{ mg C m}^{-2} \text{ min}^{-1}$, 350 ppm CO_2). In the field stagnant porewater keeps most belowground processes anaerobic. In removing the cores from the marsh, some of that water is likely to have drained from the cores allowing roots and rhizomes contact with oxygen and, therefore, more efficient aerobic respiration. This would lead to unnaturally high rates of respiration. Therefore, growth chamber data should be viewed with some reservation. However, the field experiment did not show changes in respiration

rates over time and, therefore, artificial dark measurements should be considered accurate reflections of nighttime respiration rates.

We did not observe the expected variations in concentrations of porewater constituents over seasons and with different treatments (Table 3, Figures 7-11). No dissolved organic carbon (DOC) porewater measurements were made. This porewater component might have been expected to show differences between treatments (Moran and Hodson, 1990; Gallagher et al., 1976; Howes et al., 1985); however, its contribution to the overall carbon budget is likely to be minor. These porewater results are contrary to the majority of other studies which have examined the effects of inundation on porewater chemistry (Broome et al., 1995; Burdick et al., 1989). These anomalous results might be explained by the consistently high water table found at the study area. Other research being conducted at the VCR indicates that the water table in the study area rarely drops below 10 cm from the surface (L. Stasavich, pers. com.). This high water table could effectively mask any effects from disturbances because of the 10 cm sampling depth of the lysimeters.

In addition, earlier work by Hmeleski (1994) demonstrated that slope and elevation play important roles in determining salinity, redox potential, and hydroperiod in a given marsh. Elevation measurements made at each plot by Taylor (1995) show an eight centimeter difference between the highest and lowest plots (Figure 28). This natural elevational variation between plots may be important in determining the intensity of disturbance effects in that the higher plots may be less affected by increased inundation than the lower plots. Therefore, porewater constituents may already be responding to natural variations in conditions at this location rather than the experimental alterations.

Methane flux measurements were discontinued after an initial sampling because the carbon lost as CH_4 was negligible relative to community respiration. Extrapolation to daily fluxes yielded less than 10 mg d^{-1} (less than 1% of total carbon respired) and no substantial differences were detected between treatments. A summer sampling should have been

conducted to insure that CH₄ fluxes were also low at times of maximum temperature. Other studies have reported methane emissions varying from 1gC m⁻² yr⁻¹ for *S. patens* peat in Chesapeake Bay (Atkinson and Hall, 1976) to 73 gC m⁻² yr⁻¹ for vegetated *S. patens* marsh along the Gulf Coast (DeLaune et al., 1983). Bartlett et al. (1987) developed a regression between annual methane flux and sediment salinity. Based on this regression and soil salinities at the inundation site we have calculated that methane would contribute no more than 2-4% to the respired carbon budget of the high marsh.

CONCLUSIONS

Increased inundation caused a decrease in both photosynthesis and respiration in this Virginia high marsh community. The net effect was an overall decrease in carbon fixed by the flooded marsh relative to the controls. Therefore, less material was available for burial and vertical accretion. This finding supports our first two hypotheses regarding decreased photosynthesis and respiration rates.

- Based on carbon dioxide flux model estimates, control (7 mm yr^{-1}) and border control (4.2 mm yr^{-1}) sites accumulate enough carbon to accrete organic material at a rate in excess of current rates of relative sea-level rise ($2.8\text{-}4\text{-}2 \text{ mm yr}^{-1}$).
- Sites exposed to increased inundation frequency (3.2 mm yr^{-1}) have a positive carbon balance, but accumulate carbon at a rate which can only marginally keep pace with relative sea-level rise.

Wrack deposition also caused a decrease in community respiration; however, the near-total removal of aboveground biomass led to a more substantial reduction in photosynthesis and resultant net loss of carbon from the marsh. The results from this study do not support our hypothesis that wrack deposition would increase respiration rates. Wrack had covered our treatment sites for a year prior to the beginning of this study. If our measurements had taken place immediately following placement of wrack on the site we may have observed an initial but transient increase in respiration rate.

- Wrack sites (-6.2 mm yr^{-1}) experienced a negative carbon balance, indicating net loss of carbon from the marsh and subsequent loss in elevation in addition to that due to relative sea-level rise.

The combination of techniques used in this study offer a novel approach for looking at how two specific disturbances affect metabolic processes in a high marsh. Although some of the response seen may have been an artifact of the artificial reproduction of the disturbances we still feel the results are valid.

- Carbon dioxide flux techniques offer valuable insights into the dynamics of community salt marsh metabolism through separation of metabolism into its various components.
- Sediment microalgal production makes a small but significant contribution to total community production. Its exclusion from previous high marsh carbon budgets is an oversight that should be remedied in future studies.
- Decrease in the ability of a marsh to accrete organic matter at a rate sufficient to keep up with relative sea-level may create a negative feedback, where loss of elevation results in increased flooding which then causes increasing elevational loss.

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