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Ecosystem Responses of a Tidal Freshwater Marsh Experiencing Saltwater Intrusion and Altered Hydrology

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Abstract Tidal freshwater marshes exist in a dynamic environment where plant productivity, subsurface biogeochemical processes, and soil elevation respond to hydrological fluctuations over tidal to multi-decadal time scales. The objective of this study was to determine ecosystem responses to elevated salinity and increased water inputs, which are likely as sea level rise accelerates and saltwater intrudes into freshwater habitats. Since June 2008, in situ manipulations in a *Zizaniopsis miliacea* (giant cutgrass)-dominated tidal freshwater marsh in South Carolina have raised porewater salinities from freshwater to oligohaline levels and/or subtly increased the amount of water flowing through the system. Ecosystem-level fluxes of CO_2 and CH_4 have been measured to quantify rates of production and respiration. During the first 20 months of the experiment, the major impact of elevated salinity was a depression of plant productivity, whereas increasing freshwater inputs had a greater effect on rates of ecosystem CO_2 emissions, primarily due to changes in soil processes. Net ecosystem production, the balance between gross ecosystem production and ecosystem respiration, decreased by 55% due to elevated salinity, increased by 75% when freshwater inputs were increased, and did not change when salinity and hydrology were both manipulated. These changes in net ecosystem production may impact the ability of marshes to keep up with rising sea levels since the accumulation of organic matter is critical in allowing tidal freshwater marshes to build soil volume. Thus, it is necessary to have regional-scale predictions of saltwater intrusion and water level changes relative to the marsh surface in order to accurately forecast the long-term sustainability of tidal freshwater marshes to future environmental change.

Keywords Climate change · Primary production · Ecosystem respiration · Carbon dioxide · Methane · Waccamaw River, South Carolina

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Introduction

The existence of tidal freshwater marshes overlying thousands of years of accumulated soil (e.g., Orson et al. 1992; Neubauer et al. 2002) is evidence that these ecosystems have an inherent resilience to environmental fluctuations. Tidal variability over semi-diurnal scales, over spring-neap cycles, and across longer period oscillations modifies soil oxygenation, affects pathways of microbial respiration, and influences tidal marsh plant productivity (Morris 2000; Neubauer et al. 2005; Ensign et al. 2008). Seasonal and interannual variability in precipitation affects freshwater (river) discharge into the coastal zone and influences the transport of watershed-derived nutrients and sediments (Correll et al. 1999; Pont et al. 2002). Global sea level has been rising at ~0.2 mm year^{-1} for thousands of years and at ~1.8 mm year^{-1} during much of the twentieth century (Gornitz et al. 1982; Meehl et al. 2007), yet tidal marshes have been able to exist in equilibrium with sea level by building soil volume (Redfield 1965; Pasternack 2009). Sea level rise can be accompanied by saltwater intrusion, the upstream movement of the salt front, such as has been observed in Chesapeake Bay (Hilton et al. 2008). River discharge also plays a key role in structuring estuarine salinity gradients, and low discharges can lead to significantly elevated salinities in the tidal freshwater zone

(Neubauer and Craft 2009). Global climate change is expected to accelerate sea level rise and modify river discharge to the coastal zone (Burkett et al. 2001; Christensen et al. 2007; Meehl et al. 2007), increasing saltwater intrusion into historically freshwater environments and modifying tidal marsh hydrology.

These environmental perturbations are likely to affect ecosystem processes and, ultimately, long-term marsh stability and persistence. Changes in salinity and hydrology can drive shifts in the composition of plant communities (Pearlstine et al. 1993; Schuyler et al. 1993; Perry and Hershner 1999), affect seed germination (Baldwin et al. 1996; Peterson and Baldwin 2004), and produce physiological changes in photosynthetic efficiency and rates of growth and maintenance respiration (Jackson and Drew 1984; Pezeshki et al. 1987a, b). Furthermore, increased soil water saturation, such as can occur with water inputs regardless of salinity, can shift the balance between aerobic and anaerobic mineralization processes in the soil (Ponnamperuma 1984), which can reduce overall rates of organic matter decomposition (Bridgham et al. 1998). Increases in porewater salinity tend to be coupled with increasing SO_4^{2-} concentrations, which affect microbial competition for electron donors and therefore can shift the dominant anaerobic pathways that are responsible for organic carbon mineralization in marsh soils (e.g., SO_4^{2-} reduction vs. methanogenesis; Neubauer et al. 2005; Weston et al. 2011). Since organic matter accumulation is responsible for 62% of vertical marsh accretion across a diversity of tidal freshwater marshes (Neubauer 2008), changes in rates of organic matter production or loss have the potential to significantly affect the ability of these marshes to keep pace with rising sea levels. For example, Spalding and Hester (2007) found that changes in plant production due to elevated salinity and increased inundation led to decreased organic matter accumulation in freshwater mesocosms.

The objective of this study was to determine ecosystem responses of a tidal freshwater marsh to elevated salinity and increased water inputs. This was achieved by in situ manipulations (additions of brackish and freshwater) that raised porewater salinities from freshwater to oligohaline levels and/or subtly increased the amount of water flowing through the system. Using CO_2 and CH_4 flux measurements, I quantified monthly and annual rates of gross ecosystem production (total gross CO_2 fixation, GEP), ecosystem respiration (measured as CO_2 and CH_4 emissions to the atmosphere, ER_{CO2} and ER_{CH4}), and net ecosystem production (NEP; the balance between gross ecosystem production and ecosystem respiration, Chapin et al. 2006). This approach of measuring individual processes provides mechanistic insight into the processes that drive ecosystem responses, allows generalizable predictions to be generated, and is extensible to other ecosystems since GEP and ER drive organic matter dynamics in all systems. Although NEP is not equivalent to ecosystem carbon accumulation (Chapin et al. 2006; Lovett et al. 2006), changes in NEP due to experimental manipulations should be proportional to changes in carbon accumulation if the manipulations do not influence lateral (i.e., non marsh-atmosphere) fluxes of carbon. The data presented herein cover the first 19 months of experimental saltwater and freshwater additions (Jun 2008 to Dec 2009), but the study is ongoing and will continue through the 2011 growing season.

Materials and Methods

Study Site and Experimental Design

The Waccamaw (3,910 km^2 drainage area) and Pee Dee rivers (37,150 km^2) converge in coastal South Carolina and then flow roughly southwest before joining the Black (5,080 km^2) and Sampit rivers (920 km^2) to form Winyah Bay, the third largest estuary (by watershed area) along the Atlantic coast of North America (Patchineelam et al. 1999). Historically, the tidal freshwater zones of these rivers supported an extensive rice culture industry, with fields leveled and impounded after extensive stands of tidal freshwater forest were cleared (Tufford 2005). Today, the former rice fields in the Winyah Bay drainage contain 6,600 ha of emergent marsh and 3,700 ha of forested wetlands, with roughly 80% of these wetlands exposed to regular tides (the remaining 20% are managed impoundments; Kelley 2009).

This study was conducted at Brookgreen Gardens in a 0.9-ha tidal freshwater marsh (33°31.50′ N, 79°5.51′ W) adjacent to Springfield Creek, a tidal tributary of the Waccamaw River. The intertidal site contains a diverse mix of emergent herbaceous species and represents a transitional state for former rice fields between submerged aquatic vegetation-dominated systems and late successional swamp forests (Kelley and Porcher 1995). Common plants at the site include *Zizaniopsis miliacea* (giant cutgrass), *Apios americana* (groundnut), *Cicuta maculata* (water hemlock), *Hydrocotyle umbellata* (marsh pennywort), *Orontium aquaticum* (goldenclub), *Peltandra virginica* (arrow arum), *Pontederia cordata* (pickerelweed), *Polygonum arifolium*, and *Polygonum sagittatum* (hastate and sagittate tearthumb, respectively), with upward of 30 species distributed through the study site. Surface soils at the site are organic (63.5±2.9% organic matter, 30.0±0.5% C, 2.4±0.02% N; Koren et al., in preparation). Semi-diurnal tides flood the site on most high tides, with typical flooding depths of 10–30 cm.

A total of 15 plots at the study site were randomly assigned to receive diluted saltwater (+salt plots), freshwater (+fresh plots, to account for water addition effects in the absence of elevated salinity), or no water additions (control plots), with five replicates of each of the three treatments. Each plot was defined by a 61×61-cm aluminum collar, inserted 10 cm into the soil, that acted as a stable platform for anchoring the metabolism flux chambers (see "Carbon Flux Measurements" below) and also minimized lateral surface drainage of added salt or fresh water from the plot (see "In Situ Salinity Manipulation" below). The collars contained three 2.5-cm-diameter holes per side, positioned at the soil surface, to allow normal tidal flooding and drainage. The distance between adjacent plots was ~3 m to minimize cross-contamination between plots. A boardwalk allowed access while minimizing disturbance to the marsh.

In Situ Salinity Manipulation

Experimental water additions to the +salt and +fresh plots began on 16 June 2008 and were made every 3–4 days through 11 January 2010. The +salt plots received salt marsh tidal creek water from the flow-through seawater system at the Baruch Marine Field Laboratory (BMFL) that was diluted to a salinity of 10.2 (± 0.9, mean±standard deviation for 159 dates when water was added) before being added to the marsh. The freshwater that was added to the +fresh plots and also used to dilute the salt marsh creek water was from a 180-m-deep groundwater well at the BMFL (salinity=0.5±0.04). On nearly all water addition dates, 40 L of brackish or freshwater, as appropriate, were added to each plot when the surface of the marsh was not flooded. Periodically, due to the rising tide, less than 40 L were added. Water was transported to the site in polyethylene containers and gravity-fed onto the soil surface through a distribution manifold in each plot. It generally took 45–60 min to add the entire 40 L to a single plot. Over the study period, roughly 6,200 L of water were added to each of the +salt and +fresh plots.

Porewater salinity measurements were made regularly throughout the experimental period using porewater samplers ("sippers") that had a 5-cm sampling window of porous sintered plastic (Porex, 25–40 μm nominal pore size) centered around depths of 10 or 25 cm. Each experimental plot contained a pair of sippers (one at each depth). Two additional pairs of sippers ("ambients," 10 and 25 cm depths per pair) were located within the study wetland but were 10–30 m from the experimental plots and were therefore assumed to be entirely unaffected by manipulations within the plots. Before sampling, the sippers were purged of water, with an equal volume of N_2 added to maintain anaerobic conditions. A vacuum was then placed on the sipper by withdrawing 60 mL of headspace. The sippers were allowed to refill for roughly 30 min before a porewater sample was collected with a syringe and stored in a plastic centrifuge tube. Conductivity (at 25°C) and salinity were determined on the porewater samples and on the brackish/fresh water added to the plots using a YSI 3200 conductivity meter that was calibrated daily with 100, 1,000, and 10,000 μS cm^{-1} conductivity standards. The sippers in the plots were sampled within ~1 h after saline or freshwater additions, whereas the ambient sippers were sampled approximately weekly. When gas flux measurements were made, porewater samples were collected daily for 3–5 days. Using these data, porewater turnover was calculated as $Cond_t = [Cond_0 \times e^{(-b \times t)}] + [Cond_{unmanip} \times (1 - e^{(-b \times t)})]$, where $Cond_t$ is the porewater conductivity at time t, $Cond_0$ is the conductivity at time 0 (i.e., at the start of a 3–5-day period), b is the fraction of porewater replaced per day (i.e., the turnover rate), and $Cond_{unmanip}$ is the median conductivity in all unmanipulated plots (i.e., controls and ambients) during the study period (167 μS cm^{-1} at 10 cm, 182.5 μS cm^{-1} at 25 cm, n=1,300–1,303 measurements per depth). Porewater turnover was calculated separately for each depth in the +salt plots for 20 time periods (~once per month).

Carbon Flux Measurements

Plot-scale exchanges of CO_2 and CH_4 were measured with large, transparent, temperature-controlled chambers (0.37 m^2×1.22 m height; after Whiting et al. 1992; Neubauer et al. 2000) that enclosed plants and the marsh soils. Measurements began in May 2008, 1 month before the saltwater additions began, and were made at roughly bi-weekly to monthly intervals through January 2010. Gas flux measurements were made around mid-day low tides, and sampling did not occur on excessively cloudy or rainy days. Prior to making flux measurements, drainage holes in the collars were plugged with rubber stoppers, the metabolism chambers were clamped to collars, and the entire system was allowed to equilibrate for 5–15 min. As necessary, a 1.22-m chamber extension was added to enclose taller plants. Once the chamber temperature was similar to the ambient air temperature (within ~±1°C), a transparent lid was clamped to the top of the chamber and CO_2 and CH_4 flux measurements began. Measurements were made for 5–7 min in full light, at several intermediate light levels (chamber covered with layers of shade cloth) and in the dark (chamber covered with an opaque shroud), so a full cycle of measurements on a single plot took roughly 20–30 min although measurement times were extended during the cooler months when flux rates were lower. For most sampling events, flux measurements were made from all 15 plots over a 2–3-day period although

there were some times when weather or equipment difficulties meant that not all plots were sampled.

The system described herein was capable of simultaneously measuring plot-scale CO_2 and CH_4 gas fluxes from two chambers. Air within each chamber was stirred with four fans while pumps circulated air between the chambers and a LI-COR LI7000 CO_2/H_2O analyzer (LI-COR Biosciences, Lincoln, NE, USA). Using a Valco STF multiposition valve (VICI Valco Instruments, Houston, TX, USA), two chambers were connected to the LI7000. The valve rotated every 15 s to change which chamber's air stream flowed through the LI7000 such that CO_2 concentrations within two separate chambers were measured alternately, resulting in a CO_2 measurement for each chamber every 30 s. The CO_2 concentrations were recorded and the multiposition valve controlled by a Campbell CR1000 datalogger (Campbell Scientific, Logan, UT, USA). To determine CH_4 fluxes, air samples were collected from each chamber roughly every 5–7 min, stored in gas-tight Hungate tubes, and analyzed for CH_4 concentration in the laboratory using a flame ionization detector on a Carle model 211 gas chromatograph (through July 2008; Carle Instruments, Fullerton, CA, USA) or on a Shimadzu GC-14A gas chromatograph (since September 2008; Shimadzu Scientific Instruments, Columbia, MD, USA). Gas fluxes, calculated as the change in gas concentration over time, were typically linear, with median r^2 values of 0.99 for both CO_2 and CH_4 fluxes. CO_2 fluxes were calculated at each light level; CH_4 fluxes were calculated across all light levels for a plot. Implicit in this calculation and subsequent modeling efforts is the assumption that variations in plant activity over hourly to diurnal scales do not significantly affect CH_4 emissions.

During the flux measurements, at 15–30 s intervals, the CR1000 datalogger recorded temperature (measured with thermocouples located inside and outside the chambers and in the soil adjacent to the chambers at 5, 10, 15, 20, and 25 cm depths) and incident photosynthetically active radiation (PAR, LI-COR LI190-SL quantum sensors, located on top of each chamber). The datalogger also controlled a relay (Campbell AGREL-12) that circulated ice water through a heat exchanger when chamber temperatures were ≥0.5°C above ambient. In practice, this automated system kept chamber temperatures from −0.8°C to 1.1°C of ambient (10th to 90th percentiles of all measurements).

The system, as described above, has been in use since mid-April 2009. Prior to introducing the multiposition valve in April 2009, flux measurements were made from a single plot at a time. Before January 2009, when the temperature control relay was added to the system, the cooling system was manually controlled and chamber temperatures were generally between −1.3°C and 1.2°C of ambient (10th to 90th percentiles). The quality of gas flux measurements made prior to April 2009 is equivalent to that of flux data collected since that date. The improvements to the system have focused on automation and increasing sampling efficiency in the field.

Gas Exchange Modeling

Short-term CO_2 and CH_4 flux rates measured in the field were used to generate gross ecosystem production vs. irradiance (GEP vs. PAR) and ecosystem respiration vs. air temperature relationships (ER_{CO2} or ER_{CH4} vs. T; after Neubauer et al. 2000). Individual GEP vs. PAR curves were developed for each plot that was measured during a sampling event (i.e., one curve per plot per month). Since respiratory CO_2 and CH_4 fluxes were only measured once per plot per sampling event, ER_{CO2} and ER_{CH4} vs. T relationships were determined for each plot in both 2008 and 2009 (i.e., one CO_2 and one CH_4 curve per plot per year). Following Neubauer et al. (2000), the ER vs. T curves were combined with respiration rates measured in the field to account for seasonal variability in CO_2 and CH_4 emissions (at similar temperatures) due to, for example, changes in plant phenology or soil oxidation. These environmental relationships were subsequently combined with weather data (air temperature and PAR, measured every 15 min; NOAA-NERRS 2010) collected at the BMFL, ~21 km from the study site, to calculate GEP, ER_{CO2}, and ER_{CH4} every 15 min. Similarly, net ecosystem production was calculated every 15 min from the GEP, ER_{CO2}, and ER_{CH4} rates. Based on the results of Neubauer et al. (2000), which showed that gross ecosystem production and ecosystem CO_2 emissions from a tidal freshwater marsh in Virginia did not vary significantly with tidal inundation, I assumed that the tidal cycle did not affect ecosystem-scale gas exchanges in this system.

Field gas flux data were collected during 20 sampling events and used to model monthly GEP, ER, and NEP for the 20-month period from May 2008 through December 2009. Fluxes were interpolated between sampling events to allow environmental relationships (e.g., GEP vs. PAR curves) to change from week to week while also allowing ambient weather conditions to force these relationships. During weeks when field flux measurements were made, only the GEP vs. PAR and ER vs. T relationships generated during that week were used to calculate gas exchange rates. When field gas flux measurements were not made, GEP, ER_{CO2}, and ER_{CH4} were calculated using GEP vs. PAR and ER vs. T relationships from the preceding and subsequent sampling events. The final modeled flux was calculated by weighting the fluxes based on the timing of the unmeasured week relative to the surrounding sampling events to produce the final modeled flux. As an example, field flux measurements were made in weeks 20 (12–14 May 2008)

and 24 (09–11 Jun 2008). For weeks 21–23, GEP, ER_{CO2}, ER_{CH4}, and NEP were calculated using the 15-min weather data and both the weeks 20 and 24 GEP vs. PAR and ER vs. T relationships. These fluxes were then weighted on a week-by-week basis to give the final modeled fluxes (i.e., all time points during week 21 were calculated using a 3:1 weighting of the fluxes calculated with the weeks 20 and 24 parameters, time points during week 22 used a 1:1 weighting, and a 1:3 weighting was used for week 23).

A resampling approach was used to compensate for "missing" data (i.e., plots that were not sampled during a sampling event) and to generate monthly and annual GEP, ER_{CO2}, ER_{CH4}, and NEP rates and confidence intervals. For each sampling event, one plot was randomly selected to represent each treatment. Monthly gas exchange rates were calculated using data from these randomly selected plots, weighted as described above. Annual rates were determined by summing monthly rates. The model was then re-run using another set of randomly selected plots (one per treatment per sampling event); this resampling was repeated 1,000 times and the grand mean of the 1,000 model runs was the final rate presented in this paper. Re-running the model (with 1,000 new iterations each time) changed the final monthly flux rates by only 0.1–3.4% (coefficient of variation for triplicate runs for five randomly selected months). All model calculations and resampling were done in Microsoft Excel.

Statistical Analyses

Treatment-related, depth-specific, and temporal differences in porewater salinity were assessed using a standard least squares ANOVA, with treatment, date, and depth as model effects. Similarly, short-term GEP, ER_{CO2}, and ER_{CH4} rates were analyzed by treatment and date using a two-way ANOVA. Regression analysis was used to examine relationships between measured gas fluxes and environmental parameters (PAR, porewater salinity, temperature). For all statistical analyses, significance was set at $p \leq 0.10$ because there is high spatial variability at the study site, but it was logistically unfeasible to increase the number of replicate plots within each treatment. Therefore, type 1 errors (incorrectly rejecting the null hypothesis of no treatment-related differences) are more likely than if a more conservative p value (e.g., 0.05) was used, but type II errors (incorrectly accepting the null hypothesis) are less likely.

Pairwise differences between monthly and annual gas flux rates in the three treatments were calculated for each of the 1,000 model iterations (e.g., $\Delta GEP_{(control\text{-}salt),n} = GEP_{control,n} - GEP_{+salt,n}$, where $GEP_{control,n}$ and $GEP_{+salt,n}$ are modeled rates from iteration n during the time period of interest in the control and +salt treatments). If there was no difference between treatments, the distribution of the 1,000 Δ values would be centered on 0. Conversely, if 0 lies at the upper or lower 5% of the distribution of Δ values (i.e., $p \leq 0.10$), there is a significant difference between the treatments and the null hypothesis of no difference is rejected. This approach has advantages over traditional parametric and non-parametric statistical methods; among others, it is not necessary to assume a particular distribution of the data (here, distributions of Δ values were frequently normal but were often bimodal or undefined), the raw data structure is preserved rather than simplified to ranks as in many non-parametric tests, and the approach is conceptually straightforward (Crowley 1992).

Results

Effectiveness of Saltwater Additions

Following experimental manipulation, porewater salinity in the +salt plots was representative of oligohaline conditions (salinity, S, >0.5) whereas the +fresh, control, and ambient plots had salinities typical of the tidal freshwater zone (S< 0.5; Fig. 1a). During the study period, average porewater conductivity in the +salt plots ranged from 3,026 to 5,924 μS cm^{-1} (salinity=1.6–3.3), compared with 147–379 μS cm^{-1} (S=0–0.1) in the control plots and 139–160 μS cm^{-1} (S=0) in the ambient plots (values are per-plot averages of all dates and depths; there were no date-related differences in porewater conductivity, p=0.62). Average porewater conductivities in the +fresh plots (311–385 μS cm^{-1}; S=0.1) were slightly (but not significantly) elevated relative to the control and ambient plots but were still substantially lower than values in the +salt plots (treatment effect: p<0.0001). The conductivity of tidal floodwater on the marsh was 106–219 μS cm^{-1} (S=0–0.1; n=9 measurements during the 20-month sampling period) and generally was slightly lower than porewater values in the control and ambient plots.

Relative to the 25-cm sippers, conductivities at 10 cm depth tended to respond more quickly to brackish/freshwater additions, with higher values in the shallower vs. deeper wells (depth effect: p<0.0001). This depth effect was most pronounced in the +salt plots but, within several days of the water additions, conductivities at 10 cm decreased substantially and were comparable to or lower than those at 25 cm depth (e.g., Fig. 1b). The median porewater turnover rate at 10 cm in the +salt plots was 0.52 day^{-1} (i.e., 52% per day, range 0.23–0.91 day^{-1}) and was significantly greater than the turnover rate at 25 cm (median 0.27 day^{-1}, range 0.11–0.56 day^{-1}, p<0.0001). A more rapid turnover of shallow vs. deeper porewater has been reported elsewhere (e.g., Reay 1989; Neubauer and Anderson 2003) and presumably reflects depth-related differences in vertical exchanges with

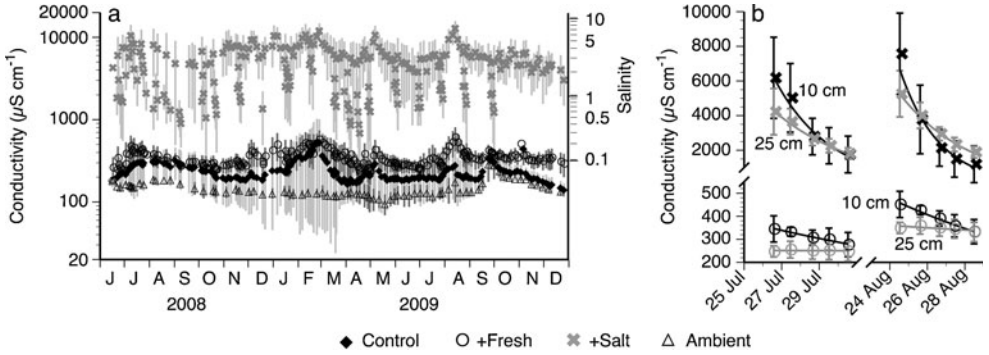

Fig. 1 **a** Porewater conductivities (micro-Siemens per centimeter) and salinities (practical salinity scale) in experimental plots. Values are averages (± standard deviation) for all plots and depths measured during each of the 228 porewater collection events during the study period. n=10 sippers per date for control, +fresh, and +salt points. n=4 sippers per date for ambients. **b** Time-course measurements showing typical dilution profiles of porewater conductivity. Data are presented for 10- and 25-cm-deep sippers in the +fresh and +salt plots for July and August 2009. The samples collected on 26 July and 24 August were collected roughly one hour after 40 L of brackish or freshwater were added to the experimental plots. Values are averages (± standard deviation) of five sippers per data point. Curves are exponential fits to the data

tidal floodwaters, porewater drainage from shallow to deeper soils, and/or lateral exchange between the plots and adjacent (unmanipulated) soils.

Short-Term Carbon Flux Measurements

Across the 20 sampling events, short-term rates of gross ecosystem production in full sun ranged from 0.3 mg C m^{-2} min^{-1} (median for +salt plots, Jan 2009) to 28.7 mg C m^{-2} min^{-1} (control plots, Jun 2009, Fig. 2a). In May and Jun 2008, before the experimental manipulations began, maximum (full-sun) rates of GEP were 12.6–13.9 mg C m^{-2} min^{-1} (May) to 15.9–23.4 mg C m^{-2} min^{-1} (early Jun; Fig. 2a, rates are medians by treatment), with no pre-manipulation differences between the treatments (p>0.05). Although short-term GEP in the +salt plots dropped sharply from late Jun (median of 23.7 mg C m^{-2} min^{-1}) to Jul (11.3 mg C m^{-2} min^{-1}) following the initiation of the saltwater additions, there were no significant differences between the control, +fresh, and +salt treatments during any sampling events in 2008. In contrast, short-term rates of GEP in the +salt plots during 2009 (Fig. 2a) were lower than rates in the control plots for much of the growing season, whereas there were never any significant differences between GEP in the control and +fresh plots. Short-term GEP was well described as a hyperbolic function of incident PAR, with median r^2 values of 0.997. Across all sampling events, all but 3% (seven of 263) of the plot-specific hyperbolic relationships had r^2 values >0.95, with the majority of the relatively poor fits occurring in Jan/Feb 2009 when rates of GEP were low at all light levels.

Rates of ecosystem CO_2 emissions ranged from 0.3 mg C m^{-2} min^{-1} (median rates, +fresh and +salt plots, Jan 2010) to 15.6 mg C m^{-2} min^{-1} (control plots, Jun 2008, Fig. 2b). CH_4 emissions were roughly 20-fold lower and ranged from 0.01 mg C m^{-2} min^{-1} (+fresh plots, Jan 2010) to 1.0 mg C m^{-2} min^{-1} (control, Sep 2008, Fig. 2c). None of the 263 individual CH_4 flux measurements indicated net CH_4 oxidation (i.e., CH_4 fluxes were always from the marsh to the atmosphere). As was the case with short-term GEP rates, there were no treatment-related differences in ER_{CO2} or ER_{CH4} before the experimental manipulations began in mid-Jun 2008, with median rates of ER_{CO2} from 5.3–5.7 mg C m^{-2} min^{-1} (May) to 11.2–15.6 mg C m^{-2} min^{-1} (Jun). ER_{CH4} before manipulation ranged from 0.2 to 0.6 mg C m^{-2} min^{-1} and did not vary significantly between May and early Jun. There were no individual sampling events in 2008 with treatment-related differences in ER_{CO2}. Across all of 2009, short-term ER_{CO2} was significantly different in each of the three treatments (control > +fresh > +salt; p<0.001). On an annual basis, in 2008 and 2009, ER_{CH4} was significantly lower in the +salt plots relative to the other treatments (p= 0.009 and p<0.001 in 2008 and 2009, respectively). Multiple comparison tests indicated that Sep 2008 and the two sampling events in Jun 2009 were the only times when there were significant differences in measured ER_{CH4} rates between the control and +salt plots.

For all treatments, log(ER_{CO2}) and log(ER_{CH4}) were positively correlated (p<0.001) with chamber air temperatures, with r^2 values of 0.86–0.89 for CO_2 and 0.33–0.63 for CH_4. Multiple regression analysis indicated that conductivity improved the fit of the prediction (r^2) by 0.02 or less, so the final gas flux model used only temperature to drive ecosystem CO_2 and CH_4 fluxes. Q_{10} values (that is, the proportional change in flux rate with a 10°C change in temperature) ranged from 3.0 to 3.4 for dark CO_2 fluxes and did not vary by year or treatment. For CH_4 emissions, the Q_{10} values were 3.5–3.6 in the control plots, 3.2–3.5 in the +fresh plots and considerably lower in the +salt plots (Q_{10}=1.6–2.5).

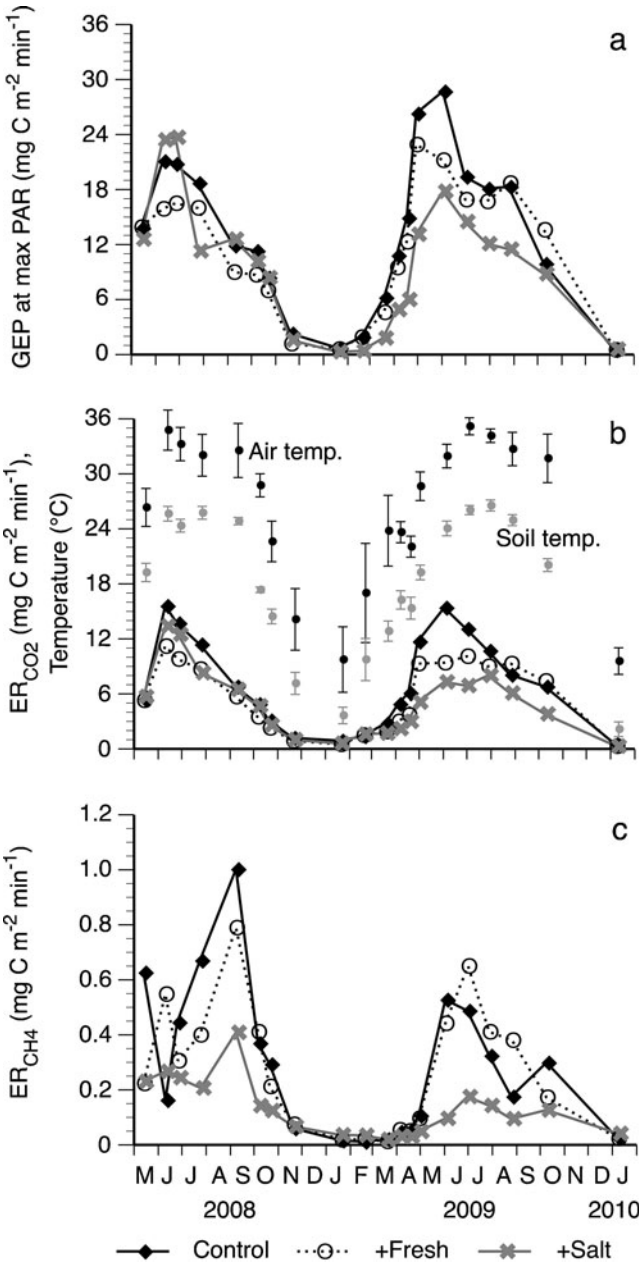

Fig. 2 Short-term gross ecosystem production (**a**) and ecosystem respiration as CO_2 and CH_4 emissions (**b** and **c**; milligrams C per square meter per minute). GEP was measured at multiple light levels but here GEP is plotted for only the highest light level per sampling event (i.e., "full sun"). GEP, ER_{CO2}, and ER_{CH4} values are the median rates from two to five chambers measured in the field, with *error bars* omitted for clarity. Air temperature was measured inside chambers during dark flux measurements. Soil temperature was measured at 10 cm depth and is averaged across all light levels. Temperatures are means±standard deviation

Gaseous Carbon Flux Model

In the control marsh, rates of modeled gross ecosystem production ranged from 8.7 (Jan 2009) to 332.6 g C m^{-2} $month^{-1}$ (Jun 2009; Fig. 3a). In 2008, there were no treatment-related differences in monthly GEP, either before or after the experimental water additions began. However, when integrated from May to Dec 2008, GEP was significantly lower in the +fresh than in the control treatments (1,193 vs. 1,401 g C m^{-2}, $p=0.06$), with rates in the +salt treatment (1,309 g C m^{-2}) that were intermediate and not significantly different from the other treatments (Table 1). In 2009, beginning in Feb and continuing through Jun, monthly rates of GEP were 35–71% lower in the +salt treatment relative to the controls ($p\leq 0.003$). Similarly, rates of GEP were lower by 22–63% in the +salt vs. +fresh treatments ($p\leq 0.014$) from Mar to Jun 2009. May 2009 was the only month when GEP was significantly greater in the controls than the +fresh treatment ($p<0.10$) although rates of GEP were consistently (but not significantly) higher in the control areas from Jan to Aug 2009. For the rest of 2009, there were no treatment-related differences in GEP (exception = Nov 2009, when control > +salt). When integrated across all of 2009, annual GEP ranged from 1,227 g C m^{-2} (+salt) to 1,667 g C m^{-2} (+fresh) to 1,829 g C m^{-2} (control) and was significantly different in each treatment ($p\leq 0.06$, Table 1).

Rates of CO_2 emissions ranged from 29.3 (Jan 2009) to 281.3 g C m^{-2} $month^{-1}$ (Jul 2008) in the unmanipulated marsh (control, Fig. 3b). With the exception of Jul 2008, when emission rates were greater in the control treatment relative to the +salt and +fresh treatments (281 vs. 199 and 184 g C m^{-2} $month^{-1}$, respectively; $p<0.10$), there were no treatment-related differences in monthly CO_2 emissions in 2008. In 2009, ER_{CO2} was greater in the control than the +salt treatment from Mar to Jul and Sep to Dec ($p\leq 0.07$). For much of 2009 (all months except Apr), there were no differences in ER_{CO2} between the +fresh and +salt treatments ($p=0.27$–0.97). Rates in the +fresh treatment tended to be lower than in the controls, although the differences were rarely significant ($p=0.10$–0.59, except for May, Jun, and Oct when $p\leq 0.04$). Across all of 2009, annual gross plant and soil CO_2 emissions ranged from 961 g C m^{-2} (+salt) to 1,098 g C m^{-2} (+fresh) to 1,491 g C m^{-2} (control) and were significantly different between all treatments ($p\leq 0.06$, Table 1).

During the 20-month study period, rates of CH_4 emissions ranged from 0.03 g C m^{-2} $month^{-1}$ (Feb 2009) to 26.3 g C m^{-2} $month^{-1}$ (Sep 2008) in the control treatment (Fig. 3c). During late summer 2008 (Aug, Sep) and late spring 2009 (May, Jun), CH_4 emissions increased in the control and +fresh treatments relative to the +salt treatment. In Aug and Sep 2008, ER_{CH4} was roughly three times greater in the control marsh relative to the +salt treatment but, due to high variability in the controls, the differences were not significant ($p=0.13$–0.28). In these 2 months, ER_{CH4} was significantly greater in the +fresh vs. +salt treatment ($p\leq 0.03$); these are the only months in

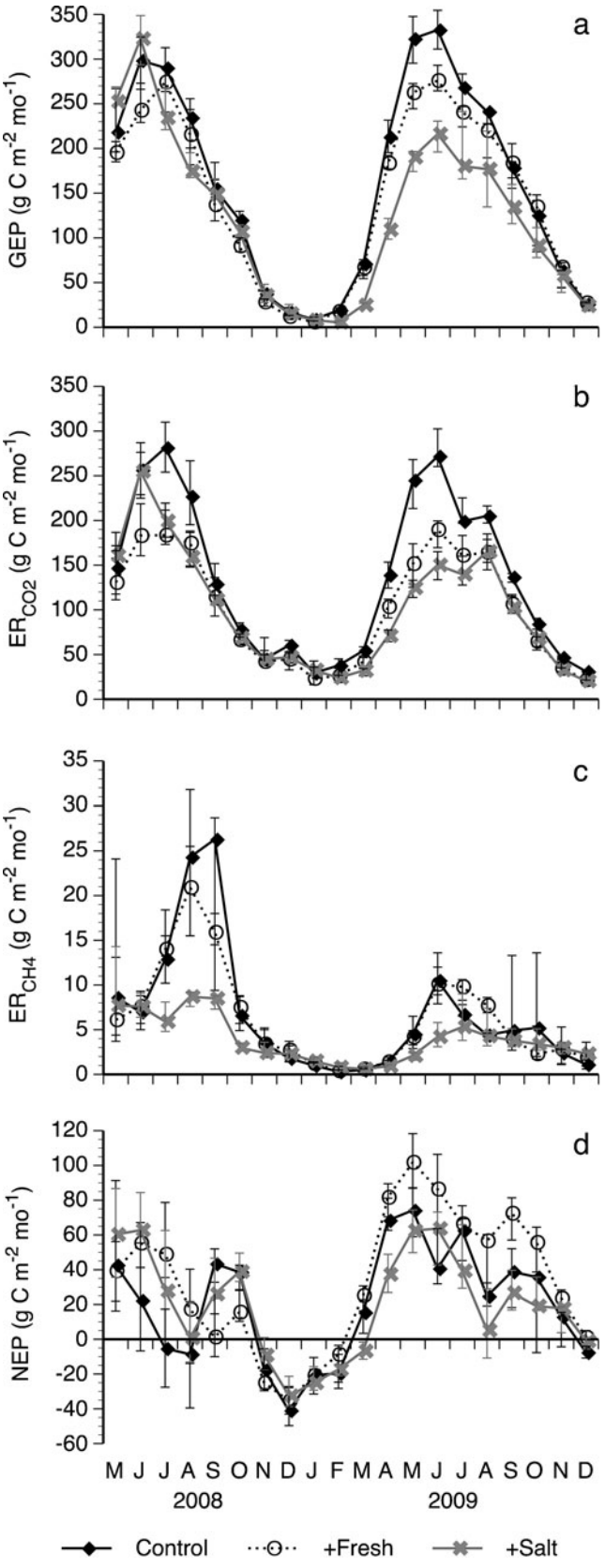

Fig. 3 Modeled monthly gross ecosystem production (**a**), ecosystem respiration as CO_2 and CH_4 emissions (**b** and **c**), and monthly net ecosystem production (**d**; grams C per square meter per month). For net ecosystem production, positive values indicate a flux of carbon from the atmosphere into the marsh and negative values indicate the reverse. Values are the medians from 1,000 model runs, with *error bars* indicating the 25th to 75th percentiles of the model output. Note the scale change from the GEP and ER_{CO2} panels to the ER_{CH4} panel

2008 with significant treatment-related differences in ER_{CH4}. Similarly, the only differences in ER_{CH4} in 2009 were in May and Jun when rates were greater in the +fresh relative to the +salt treatment ($p \leq 0.06$). There were never any significant differences in monthly ER_{CH4} between the control and +salt treatments although rates during the growing season tended to be higher in the control areas. When summed across all of 2009, annual ER_{CH4} rates ranged from 37 g C m^{-2} (+salt) to 42 g C m^{-2} (control) to 53 g C m^{-2} (+fresh, Table 1). Methane emissions from the +fresh treatment were significantly greater than those from the +salt treatment ($p=0.08$); annual rates from the unmanipulated marsh (control) were not significantly different from either experimental treatment ($p=0.28$–0.55).

Net ecosystem production varied widely from month to month, with control treatment rates from −41 g C m^{-2} $month^{-1}$ (Dec 2008; negative NEP = net flux of C from marsh to atmosphere) to 74.2 g C m^{-2} $month^{-1}$ (May 2009, Fig. 3d). In a qualitative sense, NEP tended to be the highest during late spring (Apr–Jun), lower during mid-summer (Jul, Aug) with a secondary peak in late summer (Sep), and negative during winter. In all treatments, median monthly NEP rates were negative from Nov 2008 to Feb 2009; median rates were periodically negative in other months (e.g., Jul, Aug 2008 in control treatment) but not significantly different from zero during those times (Fig. 3d). Throughout the 2009 growing season, NEP tended to be greater in the +fresh treatment and the lowest in the +salt treatment, with significant differences between these treatments from Mar to May 2009 and Sep 2009 ($p \leq 0.10$). However, due to high spatial variability, there generally were few treatment-related differences in monthly NEP in either 2008 or 2009. In 2009, annual NEP was positive in all treatments, indicating that the marsh fixed more carbon through gross production than was lost to the atmosphere as respiratory CO_2 and CH_4 emissions. Rates were greater in the +fresh treatment (515 g C m^{-2}) than the control (295 g C m^{-2}, $p=0.004$) and +salt treatments (230 g C m^{-2}, $p<0.001$) but rates were not different between the control and +salt treatments ($p=0.39$, Table 1).

In addition to the treatment effects highlighted above, there were significant interannual differences in ecosystem C flows driven by treatment effects and natural temporal

Table 1 Modeled rates of GEP, ecosystem respiration as CO_2 and CH_4 emissions (ER_{CO2} and ER_{CH4}, respectively), and NEP

Flux	Time period	Treatment	2008 (g C m^{-2} $time^{-1}$)		2009 (g C m^{-2} $time^{-1}$)
GEP	01 May–31 Dec	Control	1,401[a] (1,334–1,495)	=	1,519[a] (1,479–1,557)
		+Fresh	1,193[b] (1,148–1,244)	<	1,394[a] (1,354–1,432)
		+Salt	1,309[ab] (1,262–1,355)	>	1,075[b] (1,029–1,132)
	Annual	Control	nd		1,829[a] (1,784–1,871)
		+Fresh	nd		1,667[b] (1,623–1,707)
		+Salt	nd		1,227[c] (1,176–1,283)
ER_{CO2}	01 May–31 Dec	Control	1,239[a] (1,174–1,315)	=	1,222[a] (1,182–1,262)
		+Fresh	965[b] (915–1,016)	=	898[b] (861–934)
		+Salt	1,051[b] (1,010–1,095)	>	803[b] (777–831)
	Annual	Control	nd		1,491[a] (1,445–1,531)
		+Fresh	nd		1,098[b] (1,057–1,136)
		+Salt	nd		961[c] (934–990)
ER_{CH4}	01 May–31 Dec	Control	94[a] (79–110)	>	39[ab] (35–43)
		+Fresh	85[a] (76–95)	>	49[a] (43–55)
		+Salt	49[a] (45–57)	>	33[b] (30–36)
	Annual	Control	nd		42[ab] (39–46)
		+Fresh	nd		53[a] (47–59)
		+Salt	nd		37[b] (34–41)
NEP	01 May–31 Dec	Control	81[a] (10–148)	=	255[b] (223–291)
		+Fresh	142[a] (91–188)	<	447[a] (418–475)
		+Salt	201[a] (149–255)	=	243[b] (213–275)
	Annual	Control	nd		295[b] (259–335)
		+Fresh	nd		515[a] (480–550)
		+Salt	nd		230[b] (199–265)

Values are median modeled rates (grams C per square meter per time), with 25th to 75th percentiles in parentheses. For each combination of C flux × time period (e.g., GEP for all of 2009), values with the same superscripted letters are not significantly different from each other. The <, =, and > symbols compare fluxes over the same time period between 2008 and 2009. All comparisons are significant at $p \leq 0.10$

GEP gross ecosystem production, *NEP* net ecosystem production, *nd* indicates no annual rate data for 2008, since measurements did not begin until May 2008

variability. Most of the significant year-to-year changes in C fluxes were seen in the first half of the growing season (01 May to 15 Jun), presumably because this comparison includes a comparison of rates before manipulations began (2008) with fluxes after 1 year of experimental treatment (2009). During the 01 May to 15 Jun period, GEP in the control treatment increased by 35% from 2008 to 2009 (371 to 502 g C m^{-2}, $p=0.04$). In contrast, GEP in the +salt treatment over the same time period decreased from 410 to 310 g C m^{-2} (−24%, $p=0.08$). This same time period also saw a 20% decrease in ER_{CO2} and a 67% decrease in ER_{CH4} in the +salt treatment from 2008 to 2009 ($p=0.01$ and 0.03, respectively). In both the control and +fresh treatments, NEP was ~2 times higher in 2009 than 2008, although the effect was significant only in the +fresh treatment ($p=0.05$). For the remainder of the year (16 Jun to 31 Dec), there were no year-to-year differences in GEP ($p=0.10$–0.91 across treatments). ER_{CO2} in the +salt treatment was 20% lower in 2009 than in 2008 ($p<0.01$). Because the dramatic late summer peak in ER_{CH4} (Figs. 2c and 3c) was seen only in 2008, rates of ER_{CH4} from 16 Jun to 31 Dec were 38–57% of the modeled rates in 2008 in the control and +fresh treatments ($p \leq 0.02$). The net effect of the year-to-year changes in these fluxes resulted in a trend toward higher NEP in all treatments during the 16 Jun to 31 Dec period, although the effect was significant only in the +fresh treatment ($p=0.002$). From 01 May to 31 Dec (the common time between years) and in the absence of experimental manipulations (i.e., control treatment), there were no interannual changes in GEP or ER_{CO2} ($p \geq 0.47$), a 41% decrease in ER_{CH4} ($p<0.001$), and no change in median NEP rates ($p=0.12$) from 2008 to 2009.

Environmental Conditions

Soil temperature at 10 cm (Fig. 2b), which was measured in conjunction with gas flux samplings, ranged from a low of 3.8°C (Jan 2009) to a high of 26.7°C (late Jul 2009). From June to mid-Sep, 10-cm soil temperatures were between 24°C and 27°C, with little difference between sampling events. There were no treatment effects on soil temperature ($p=0.95$). The annual range in soil temperature at 5 cm

depth (2.9–28.1°C, Jan and late Jul 2009) was slightly greater than at 10 cm whereas the range was narrower at 25 cm (7.0–26.2°C, Jan and late Jul 2009; data not shown). The temperature difference between 5 and 25 cm depths ranged from −4.5°C (i.e., warmer at depth, Nov 2008) to +3.3°C (warmer at surface, Jun 2009) although the temperature variation across the depth profile was ≤±2°C during 13 of 20 sampling events.

Average daily air temperatures during the study period ranged from −2.5°C to 29.6°C and were generally similar in 2008 and 2009; temperatures during field measurements (Fig. 2b) were higher than these daily averages. Across all sampling dates, daytime soil temperatures at 10 cm were highly correlated with the average daily air temperature on the same date (soil temp=0.81×air temp+3.4, r^2=0.96, all temperatures in degree Celsius). Both years had a similar number of days with measurable precipitation (≥0.1 mm, 110 and 118 days for 2008 and 2009, respectively) but 2008 contained 32% more days with precipitation≥10 mm (37 vs. 28 days), 40% more days with precipitation≥25 mm (14 vs. 10 days), and twice as many days with precipitation ≥100 mm (2 vs. 1 days). Overall, 2008 was a wetter year, with cumulative annual precipitation of 141.7 vs. 109.6 mm for 2009; the 30-year (1971–2000) median for the region is 142.0 mm year^{-1} (National Climatic Data Center station "Georgetown 2 E, SC"; www.ncdc.noaa.gov)

Discussion

The effects of salinity and inundation on freshwater marsh plants and soil biogeochemistry have been previously studied (e.g., Conner et al. 1997; Spalding and Hester 2007; Weston et al. 2011), but many questions still remain about how historically freshwater ecosystems will respond to rising sea levels and saltwater intrusion. The changes in ecosystem-level fluxes reported herein reflect responses by the plant community and soil microbes that drive key biogeochemical reactions. Field gas exchange measurements provide process-related insights into responses to environmental stress and do so in a way that integrates all components of the ecosystem (plants, microbes, soils) under naturally variable environmental conditions. In contrast, lab studies are typically conducted under relatively homogeneous conditions (e.g., constant water level) and may exclude portions of the ecosystem (e.g., plant-free soil cores). Further, gas flux approaches can provide insight into responses over relatively short time scales (months to years) that will be missed by other commonly used techniques. For example, organic matter accumulation and/or elevation change can be quantified with sedimentation-erosion tables (Childers et al. 1993) or radiometric dating (Craft 2007), but these approaches would require sustained change over years to decades before treatment effects could be determined.

Below, I use the results of this study to isolate the effects of increasing salinity from those due to increased water inputs (Table 2). Comparing the +fresh and +salt treatments provides insight into the effects of elevated salinity alone since both treatments are receiving extra water relative to the controls. Similarly, by comparing rates between the control and +fresh treatments, it is possible to isolate the consequences of altered hydrology (higher freshwater inputs) in the absence of salinity changes. The integrated effects of elevated salinity and increased water throughput can be determined by comparing the control and +salt treatments.

Salinity Effects on Ecosystem Carbon Fluxes

Saltwater intrusion increases concentrations of ions (e.g., Na^+, Cl^-) and metabolic products (e.g., sulfides), stressors that reduce the growth and productivity of freshwater wetland plants (Koch et al. 1990; Munns and Tester 2008). Even *Spartina alterniflora* (saltmarsh cordgrass), a plant common in salt marshes around the world, tends to be more productive when grown at lower salinities (Morris 2000). Plant responses to elevated salinity are manifested at the whole-plant and physiological levels. In this study, elevated salinity reduced annual GEP by 26% (Table 2), with most of the significant effects occurring during the first half of the growing season (Mar–Jun). Increased salinity combined with increased water throughput resulted in an even larger decrease in GEP (−33%). Field and laboratory studies have indicated that biomass and growth rates of many freshwater wetland plants including *Panicum hemitomon* (maidencane), *Sagittaria lancifolia* (bulltongue arrowhead), *Taxodium distichum* (baldcypress), and *Typha domingensis* (southern cattail) decline as salinities increase (e.g., DeLaune et al. 1987; McKee and Mendelssohn 1989; Glenn et al. 1995; Greiner La Peyre et al. 2001; Spalding and Hester 2007; Krauss et al. 2009b). Throughout 2009, the plant canopy in the +salt plots was visually more open than in the other treatments, an observation that suggests decreased aboveground biomass due to the loss of understory species. Reductions in plant biomass likely would have decreased plot-scale CO_2 fixation. Pezeshki et al. (1987a, b) measured lower stomatal conductance and leaf-level photosynthesis in *P. hemitomon* and *S. lancifolia* after short-term salinity exposure, factors that also would lead to lower growth rates. Similarly, leaf-level CO_2 exchange and growth of *T. distichum* were reduced at higher salinity during permanent flooding (Krauss et al. 2007), but salinity effects on plant physiology largely disappeared under simulated tidal conditions (Krauss et al. 2009a). Plants can deal with elevated salinity through the

Table 2 Effects of altered hydrology (increased water flow through system) and elevated salinity (with and without changes in hydrology) on ecosystem carbon flows

Parameter	Treatment comparison	GEP (%)	ER_{CO2} (%)	ER_{CH4} (%)	NEP (%)	$\frac{ER_{CH4}}{(ER_{CO2}+ER_{CH4})}$ (%)
Salinity	+Fresh vs. +salt	−26.3**	−12.4*	−29.9*	−54.9**	−19.2 ns
Hydrology	Control vs. +fresh	−8.9*	−26.2**	26.0 ns	74.7**	67.3**
Salinity and hydrology	Control vs. +salt	−33.0**	−35.4**	−12.9 ns	−22.3 ns	34.7 ns

Percent changes are relative to the first treatment listed in the "Treatment comparison" column (e.g., percent change in GEP due to altered hydrology=$(GEP_{+fresh}-GEP_{control})/GEP_{control}\times 100$). Values were calculated for each of the 1,000 model iterations for the annual 2009 budget; median percent changes and statistical significance are presented.

ns not significant ($p>0.10$)

*$p\leq 0.10$; **$p\leq 0.05$

production of osmolytes such as proline and glycine betaine, although the production of these molecules incurs an energetic cost and may be limited by nitrogen availability (Cavalieri and Huang 1981). Alternately, plants may accumulate ions in biomass, with reductions in growth as a potential consequence (e.g., McKee and Mendelssohn 1989; Munns and Tester 2008). Future research is needed to determine which combination of mechanisms is responsible for the observed salinity effects on GEP in the present study.

Decreases in plant productivity were accompanied by changes in the species composition of plots exposed to elevated salinity. Plot inventories in April 2009 showed that species richness was approximately twice as high in the control (13.4±3.7 species $plot^{-1}$; mean±standard deviation) and +fresh plots (14.2±1.8 species $plot^{-1}$) relative to the +salt plots (7.0±2.1 species $plot^{-1}$). This pattern is common across broad estuarine gradients, where plant species richness and diversity are typically higher in tidal freshwater marshes compared to brackish and salt marshes (Odum 1988; Latham et al. 1994). Sustained plant community shifts can be achieved within 6 to 18 months of marsh exposure to elevated salinity, with a greater number of salt-sensitive species lost than salt-tolerant species gained (Wetzel et al. 2004). In contrast, Baldwin and Mendelssohn (1998) found that elevated salinity over 1 year did not affect species richness, unless experimental sods were also subjected to disturbance (clipping to simulate herbivory). Reduced species richness at elevated salinity is probably driven by salinity or sulfide-induced death of non-halophytes (Koch et al. 1990; Lamers et al. 1998) as well as reduced seed germination and seedling emergence of both perennials and annuals (Baldwin et al. 1996). In the present study, *Z. miliacea*, *H. umbellata*, and *Phyla lanceolata* (lanceleaf fogfruit) were found in all plots, regardless of treatment. In contrast, *P. arifolium*, *Galium tinctorium* (stiff marsh bedstraw), and *Murdannia keisak* (Asian spiderwort) were found in four or five of the control and +fresh plots but not in any of the +salt plots, suggesting that these species are sensitive to even low levels of salinity. There were no species found only in the +salt plots, although this may be an experimental artifact. By design, the study site was selected to be far upstream of the normal limit of saltwater intrusion (roughly 25 km), but one consequence is that the site is far from sources of brackish/salt-tolerant plants and seeds.

Elevated salinity caused decreases in ecosystem CO_2 and CH_4 emissions (ER_{CO2} −12%, ER_{CH4} −30%, $ER_{CO2}+ER_{CH4}$ −13%, Table 2) that were correlated with changes in GEP (Fig. 4). In contrast, elevated salinity in combination with increased water flow through the system resulted in decreases in ER_{CO2} and $ER_{CO2}+ER_{CH4}$ (−35% for each) but no changes in CH_4 emissions. Plant growth and maintenance respiration rates are tightly linked with photosynthetic activity (Cannell and Thornley 2000) so the decline in ER_{CO2} can be partially explained by salinity-related decreases in GEP. In 2009, elevated salinity decreased GEP from 1667 g C m^{-2} $year^{-1}$ (+fresh treatment) to 1,227 g C m^{-2} $year^{-1}$ (+salt), which would have resulted in a 123–202 g C m^{-2} $year^{-1}$ decrease in plant CO_2 emissions (assuming that plant respiration was 28–

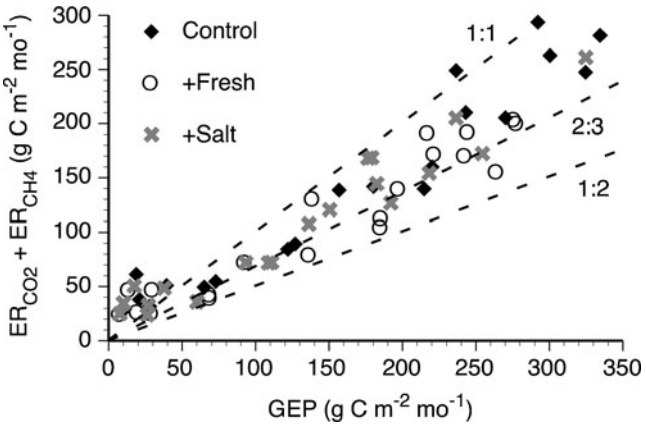

Fig. 4 Relationship between monthly CO_2+CH_4 emissions and gross ecosystem photosynthesis. Regression lines (not shown) are of the form $ER_{CO2}+ER_{CH4}=a\times GEP+b$. For control plots, a=0.79 and b=13.4; for +fresh plots, a=0.65 and b=15.2; for +salt plots, a=0.71 and b=15.2. The r^2 values were 0.92–0.93 for each curve

46% of gross plant production, Neubauer et al. 2000) The actual decrease in annual ER_{CO2} due to elevated salinity was 137 g C m^{-2} (Table 1), suggesting that declines in photosynthetic activity can potentially explain all of the decreases in ER_{CO2}. Similar calculations for the combined stressors of salinity and water input suggest that decreases in plant respiration driven solely by changes in rates of GEP may explain 32–52% of the change in ER_{CO2}. Reduced photosynthate inputs to the soil may also contribute to the decreases in both ER_{CO2} and ER_{CH4} since there is a tight coupling between plant activity and CO_2/CH_4 production when electron donor availability (e.g., organic C) limits soil heterotrophic activity (van der Nat and Middelburg 2000; Kuzyakov and Cheng 2001). Although a decline in ER_{CO2} and ER_{CH4} due to increased salinity was observed here, previous studies have documented increased rates of soil/sediment carbon mineralization (Nietch 2000; Weston et al. 2006, 2011) and root decomposition (Craft 2007) at higher salinities. Simple calculations suggest that 34–70% of ER_{CO2} is due to plant respiration, with the remaining 30–66% due to the decomposition of plant production and soil organic matter (range across all treatments, calculated using annual 2009 data and assuming that plant respiration is 28–46% of GEP). These ranges are large but suggest that plant respiration and microbial carbon mineralization rates are similar in magnitude. Thus, decreases in plant respiratory CO_2 emissions may be partially offset by increases in rates of microbial carbon mineralization. With the present data set, however, it is impossible to determine the relative importance of CO_2 emissions coupled to plants vs. changes in the utilization of soil carbon pools.

The finding that elevated salinity decreased CH_4 emissions from the marsh (by 30%, Table 2) was expected based on thermodynamics (Schlesinger 1997; Megonigal et al. 2004), previous work showing a negative correlation between CH_4 emissions and salinity (Bartlett et al. 1987; Neubauer et al. 2005), and the tight coupling between plant production and CH_4 fluxes (Whiting and Chanton 1993; Megonigal and Schlesinger 1997; Vann and Megonigal 2003). However, even though higher salinity resulted in lower monthly (Aug, Sep 2008, May, Jun 2009) and annual CH_4 emissions, porewater salinity was a poor predictor of short-term CH_4 fluxes. This suggests that methanogenic populations and CH_4 emissions are influenced by the longer-term trend of higher salinity in the +salt plots (Fig. 1a) rather than instantaneous porewater values, which change from day to day (Fig. 1b). On an annual basis, the proportion of GEP that was mineralized and emitted as CH_4 did not change as a function of salinity (annual ER_{CH4}/GEP= 0.030 and 0.032 in +fresh and +salt treatments). Further, the proportional changes in GEP and ER_{CH4} due to elevated salinity were similar (−26% and −30%, respectively, Table 2), suggesting a coupling between plant production and CH_4 emissions. However, on a month-to-month basis, this relationship is weak (r^2=0.34–0.56 for monthly CH_4 vs. GEP), and CH_4 fluxes were similar regardless of salinity for the majority of the sampling period (Fig. 2c and 3c). Thus, while SO_4^{2-} inhibition of methanogenesis (especially when ER_{CH4} peaks in control and +fresh treatments) and declines in plant production due to saltwater intrusion may contribute to decreased CH_4 emissions, other factors such as site hydrology and soil oxidation status probably play a larger role in controlling marsh CH_4 fluxes throughout the year.

The finding of decreased CH_4 emissions with elevated salinity runs counter to a recent report showing that tidal freshwater marsh soil CH_4 emissions increased dramatically following saltwater intrusion (by 70–1200% in selected months, roughly double across the 1-year experiment, Weston et al. 2011). It is difficult to reconcile the expected (and in the present study, observed) decrease in CH_4 emissions under elevated salinity with the large increase found by Weston et al. (2011). Annual rates of CH_4 emission from freshwater flooded soils were similar between these two studies (53 vs. 47 g C m^{-2} $year^{-1}$; this study, +fresh treatment in 2009, vs. Weston et al. 2011) although there is considerable interannual variability in field CH_4 fluxes (Figs. 2c and 3c; Table 1). The soil-only cores studied by Weston et al. were considerably more methanogenic than the vegetated marsh at Brookgreen (21.5 vs. 2.8% of annual CO_2+CH_4 emissions as CH_4). With the increase in salinity, the $ER_{CH4}/(ER_{CO2}+ER_{CH4})$ ratio increased to 30.2% in the lab study following saltwater exposure but did not significantly change in this field study (Table 2). While plant respiration surely drives some of the proportionally higher CO_2 fluxes from the field site, the surface soils at this site appear well-drained and do not flood on every high tide (SCN, personal observation), factors that may lead to higher rates of aerobic mineralization processes and/or CH_4 oxidation (resulting in CO_2 production) and less anaerobic CH_4 production. Weston and co-authors speculated that there was a previously unused pool of labile C that was made available with saltwater intrusion and/or that saltwater increased the supply rate of low-molecular weight dissolved organic carbon via hydrolysis and/or fermentation. The rate at which organic carbon is made available following saltwater intrusion may depend on soil properties (Koren et al., in preparation), and differences in the chemical properties of the organic matter (e.g., C/N ratio, molecular size, chemical structure) will influence its availability to methanogens (Valentine et al. 1994; Megonigal et al. 2004). It is unknown if and how these factors differ between the soils examined in this study and those studied by Weston et al. (2011).

Hydrologic Effects on Ecosystem Carbon Flows

This study shows that even subtle changes in water inputs (~80 L plot^{-1} week^{-1}, or ~21 cm plot^{-1} week^{-1}, is roughly equivalent to the amount of water over a plot during a single slack high tide) can have significant effects on ecosystem primary production, CO_2 emissions, and net ecosystem production (Fig. 3; Tables 1 and 2). Although within-plot water levels and soil redox data are not available, the observed changes are consistent with responses that would be expected if the water inputs increased soil water saturation, leading to more reducing conditions and an increasing importance of anaerobic processes. In contrast to the relatively subtle water additions in this study, most previous experimental hydrological manipulations in tidal freshwater systems have involved relatively large-scale changes in marsh elevation and/or flooding depth (e.g., McKee and Mendelssohn 1989; Nyman and DeLaune 1991; Peterson and Baldwin 2004; Spalding and Hester 2007).

As inundation increases, plant photosynthesis typically decreases as reducing soil conditions lead to plant O_2 stress and the increased production of soil phytotoxins (Pezeshki 2001). The distribution of tidal freshwater wetland plants is, in large part, a function of plant inundation tolerance, with flood-tolerant species such as *Nuphar lutea* (yellow-pond lily) and *P. virginica* occupying lower elevations than high marsh species such as *Bidens* spp. (beggarticks) and *Impatiens capensis* (jewelweed) (Odum et al. 1984; Parker and Leck 1985; Leck et al. 2009). Thus, there is a gradient of freshwater wetland plant tolerance to inundation that depends on ecophysiological adaptations within individual species; some plants respond negatively to increasing inundation whereas others grow better in flooded vs. drained conditions (e.g., McKee and Mendelssohn 1989; Baldwin et al. 1996; Willis and Hester 2004; Spalding and Hester 2007). In this study, increasing freshwater inputs to the soil surface resulted in a 9% decrease in gross ecosystem productivity (Table 2). Species richness was similar between control and +fresh plots, and there were no large differences in species composition (i.e., species that were common in control plots were also common in +fresh plots and vice versa; data not shown). Given that the study site is perched high in the tidal frame (it does not flood on every high tide), the observed decrease in GEP may represent an initial sign of flooding stress in the plant community. Over time, the response to increased water inputs would likely lessen as flood-tolerant plants replace those that are more sensitive to flooding. Pezeshki et al. (1987a) reported that net photosynthetic activity (leaf level) of *S. lancifolia* decreased with inundation and can contribute to declines in productivity (whole-plant level) for this species (e.g., Spalding and Hester 2007). Similarly, increasing the flooding frequency of salt marsh field plots resulted in a 12% decrease in GEP (Miller et al. 2001). However, other salt marsh work has shown that the productivity of *S. alterniflora* is positively correlated with sea level anomalies, such that plant productivity increases as inundation depths increase (Morris 2000; Morris et al. 2002), until the optimal flooding depth is exceeded. In salt marshes, the effect of increasing inundation is to flush out the soils and lower porewater salinity and sulfide concentrations that reduce plant growth and inhibit nitrogen uptake (Morris 1995; Mendelssohn and Morris 2000). In freshwater marshes, increased water inputs may serve to increase soil anaerobisis without the benefit of removing salts and sulfides; in fact, the freshwater inputs in this study slightly increased porewater salinities relative to control plots (Fig. 1a) because the salinity of the added freshwater was slightly higher than that of tidal floodwaters at the site.

The decrease in ecosystem CO_2 emissions (−26%) with increased water additions was proportionally greater than the decline in GEP (Table 2). I estimate that plant respiration decreased by only 45–75 g C m^{-2} year^{-1} in response to increasing water flow through the system (calculated as described above), compared with a total decrease in ER_{CO2} of 393 g C m^{-2} year^{-1} (Table 1), suggesting there was a large decline in CO_2 emissions from microbial sources. As soil water saturation increases and soil anaerobisis increases, carbon mineralization rates tend to slow because anaerobic pathways have a lower energy yield than aerobic decomposition, complex organic molecules must be processed through a consortium of organisms with specialized substrate demands, and extracellular enzyme activity can be limited by low O_2 availability (Fenchel and Finlay 1995; Freeman et al. 2001; Megonigal et al. 2004). In line with these expectations, Nyman and DeLaune (1991) found that increased inundation of freshwater mash soil cores over a range of water tables from 22.5 cm below soil to +4 cm above led to lower CO_2 emissions. Similarly, increasing the flooding frequency of salt marsh field plots that were normally only flooded by spring high tides decreased ecosystem CO_2 emissions more than would be expected if only plant respiration was affected (Miller et al. 2001).

Water table depth is a key factor regulating CH_4 emissions in wetlands (Roulet and Moore 1995) since O_2 penetration into soils both inhibits methanogenesis and positively influences CH_4 oxidation rates (Megonigal et al. 2004). Therefore, it was unexpected that adding more freshwater to the marsh did not increase annual CH_4 emissions (Table 1), although the system became more methanogenic in that the importance of CH_4 emissions relative to total respiratory CO_2+CH_4 emissions increased (Table 2). Further, water additions, regardless of salinity, increased the annual fraction of GEP emitted as CH_4, from 2.3% (control treatment) to 3.0–3.2% (+salt and +fresh;

$p<0.10$). When considering the monthly gas flux data, there were significant correlations between ER_{CH4} and GEP for all treatments, with slopes of 0.021 to 0.033 g CH_4-C emitted per g CO_2-C fixed ($r^2=0.18–0.56$, $p<0.06$). Similar relationships, with slopes that vary as a function of site water level, have been reported in bogs and fens (Updegraff et al. 2001). Given the high level of scatter in the monthly data, there were no significant differences in the slopes of the ER_{CH4} vs. GEP relationships between the three treatments. Mean sea level along the southeast US coast varies over monthly (±24 cm) and interannual scales (±2.9 cm, Morris 2000) and can affect rates of anaerobic processes in tidal marsh soils (Neubauer et al. 2005), potentially confounding linkages between plant productivity and CH_4 production/emission as the water table changes over tidal, monthly, and interannual scales.

Net Ecosystem Production and Potential Carbon Accumulation

Elevated salinity and increased freshwater inputs had contrasting effects on annual rates of net ecosystem production in this tidal freshwater marsh. In the presence of elevated salinity, NEP was decreased by 55% (Table 2). In contrast, NEP increased by 75% due to additional inputs of freshwater to the ecosystem. When both salinity and water throughput were increased, there was no change in annual NEP. A comparison of the changes in carbon fixation (GEP) and emission terms (ER_{CO2}, ER_{CH4}) under elevated salinity shows that the change in GEP (−26%, −440 g C m^{-2} $year^{-1}$) was much larger than the change in ER_{CO2} (−12%, −137 g C m^{-2} $year^{-1}$, Tables 1 and 2), implicating the inhibitory effect of salinity on marsh primary production as the primary driver of the observed NEP decrease. Although the relative change in ER_{CH4} (−30%) was similar to that of GEP under elevated salinity, the magnitude of ER_{CH4} is small (−16 g C m^{-2} $year^{-1}$) and therefore has very little effect on total system NEP. When water inputs were increased in the absence of a salinity change, there was very little change in GEP (−9%, −162 g C m^{-2} $year^{-1}$) and a much larger decrease in ER_{CO2} (−26%, −393 g C m^{-2} $year^{-1}$), suggesting that decreased rates of mineralization due to increasing soil anoxia was a key factor in increasing NEP. Given this, it is interesting to speculate that subtle increases in freshwater inputs may not have the same magnitude of effect on ecosystem carbon flows in tidal freshwater wetlands that currently experience more frequent and deeper flooding than the present study site, as the autotrophic and heterotrophic communities in those low marsh habitats are presumably already adapted to wetter and more anoxic conditions.

The annual rates of NEP measured herein (230, 295, and 515 g C m^{-2} $year^{-1}$ for +salt, control, and +fresh treatments, Table 1) are comparable to long-term rates of soil carbon sequestration in tidal freshwater marshes (typically ~100–300 g C m^{-2} $year^{-1}$; Craft 2007; Neubauer 2008). However, NEP is not equivalent to ecosystem carbon sequestration (Lovett et al. 2006) because there are other carbon inputs (e.g., sediment deposition, Neubauer et al. 2002) and loss terms (e.g., hydrological export of dissolved inorganic and organic carbon, Neubauer and Anderson 2003; Tzortziou et al. 2008) in hydrologically connected tidal marshes. As an illustration of this, a tidal freshwater marsh in Virginia had a negative annual NEP (respiration exceeded photosynthesis, by 145 g C m^{-2} $year^{-1}$) but still accumulated soil carbon at a rate of 229 g C m^{-2} $year^{-1}$ because large amounts of sediment-associated carbon were deposited on the marsh during tidal flooding (Megonigal and Neubauer 2009 and references therein). With this very important caveat in mind, the gas flux data presented herein suggest that the potential for future carbon sequestration and marsh accretion is going to vary depending on whether a site experiences saltwater intrusion (decreased NEP), increased water inputs in the absence of salinity change (increased NEP), or altered hydrology in combination with saltwater intrusion (no change in NEP). Thus, it is necessary to have regional-scale predictions of saltwater intrusion (a function of sea level rise and river discharge) and water level changes relative to the marsh surface (a function of eustatic sea level rise, regional subsidence, and local marsh accretion) in order to accurately forecast how these marshes will respond to future environmental change.

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