Tidal influences on carbon assimilation by a salt marsh

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Abstract. Salt marshes are among the most productive ecosystems on Earth, and play an important role in the global carbon cycle. Net carbon dioxide (CO_2) ecosystem exchanges in coastal salt marshes remain poorly investigated. In *Spartina alterniflora* dominated North American Atlantic coast marshes, the lack of a clear understanding of how *Spartina alterniflora* responds to flooding limits our current ability to understand and predict salt marsh response to sea-level rise. Here we investigate the processes influencing ecosystem-level carbon exchanges between a *S. alterniflora* dominated salt marsh on the eastern shore of Virginia and the atmosphere. We examined the impacts of tidal inundation on the marsh–atmosphere carbon exchanges through a combination of eddy covariance measurements and *in situ* photosynthetic measurements. Maximum daytime carbon fluxes were observed during the middle of the growing season (July and August) and amounted to -10 μmol CO_2 m^{-2} s^{-1}, and the marsh assimilated 130 gC m^{-2} during the 2007 growing season. Our study is the first to quantify the effects of tidal inundation on marsh plants, which caused anywhere from 3% to 91% reductions in atmospheric carbon fluxes, with a mean reduction of 46 ± 26%, when compared to non-flooded conditions.

Keywords: coastal salt marshes, carbon budget, atmospheric carbon fluxes, tidal flooding, sea-level rise

Contents

1. Introduction

Wetlands are among the most biogeochemically active ecosystems in the world (Mitsch and Gosselink 2007), and play an important role in the global carbon cycle (Dixon and Krankina 1995). Coastal salt marshes, in particular, can sequester carbon as they accrete and bury sediments rich in organic matter (Duarte *et al* 2005). Despite the improved understanding of CO_2 cycling in terrestrial and oceanic ecosystems achieved through programs such as FLUXNET (Baldocchi *et al* 2001) and JGOFS (Joint Global Ocean Flux Study) (Doney and Ducklow 2006), uncertainties still exist concerning the processes governing carbon cycling in coastal wetlands. Limited information on net CO_2 ecosystem exchanges in coastal wetlands comes from regional and global budgets (Duarte *et al* 2005), and chamber investigations (Drake *et al* 1996). Although past studies indicate that inter-tidal salt marshes have a high carbon sequestering capacity (Drake *et al* 1996, Duarte *et al* 2005), only limited seasonal investigations exist on the processes controlling ecosystem-level exchanges of carbon and energy between coastal ecosystems and overlying atmosphere (Goulden *et al* 2007, Yan *et al* 2008).

Inter-tidal salt marshes dominate much of the land–sea interface in low energy coastal regions of North America. The smooth cordgrass, *Spartina alterniflora,* is the dominant plant species along the east coast of North America and forms extensive monoculture stands in intertidal environments. These inter-tidal systems are susceptible to global environmental change associated with relative sea-level rise (RSLR) (Simas *et al* 2001). Marshes are undergoing changes due to RSLR, tidal range, and coastal engineering (Adam 2002). Over the last 4000 years, marsh ecosystems have been accreting vertically and have been in equilibrium with RSLR (Morris *et al* 2002). However, current rates of RSLR can threaten marsh ecosystem viability. Increases in RSLR are known to shift this equilibrium towards marsh loss while increases in plant primary productivity enhance marsh stability (Morris *et al* 2002). If marsh accretion does not keep pace with changes in RSLR then these ecosystems can be transformed into barren mudflats. For plant production to counterbalance the effects of RLSR, the marsh must be a net CO_2 sink. Salt marshes have complex carbon flows (Chapin *et al* 2006). For example, during inundation CO_2 and other carbon forms (e.g., bicarbonate and dissolved organic carbon) may move into the estuarine water column, and be transported laterally out of the marsh. In this investigation, we focus on vertical exchanges of carbon between the ecosystem and the atmosphere. Continuous ecosystem-scale measurements of atmospheric carbon fluxes may provide useful insights on the fate of marsh ecosystems under changing sea-level conditions. As such changes continue to be accelerated, marshes will likely modify their carbon sequestration capability. Thus, we investigated the processes influencing ecosystem-level carbon exchange between marshes and atmosphere. We quantified seasonal carbon assimilation rates by a *S. alterniflora* dominated marsh and investigate impacts of tidal inundation on carbon exchange between the marsh and the atmosphere.

2. Materials and methods

Studies were conducted at the Virginia Coastal Reserve Long Term Ecological Research (VCR-LTER) site on the eastern shore of Virginia, USA. The data were obtained during May to October 2007. Marsh–atmosphere carbon exchanges were determined with an eddy covariance system deployed on a tower established at Fowling Point (37°24 'N, 75°50 'W), Virginia. The site is dominated by *S. alterniflora* and twice a day is inundated by high tides. The average plant height recorded at this site was 62.6 ± 1.9 cm with a mean canopy leaf area index of 2.20 ± 0.25 for the 2007 growing season. With a mean relief of only 2 m and high erosion and deposition rates (13 mm per year in the horizontal dimension), the marsh is dynamic and susceptible to forcings associated with RSLR (Van Cleve and Martin 1991). During the 2007 growing season (May–October), unusually dry conditions dominated the area, which experienced a total rainfall of 295 mm, compared to the climatological average of 537 mm. Instruments mounted on the tower permitted to determine marsh–atmosphere carbon and energy exchanges. The eddy covariance system, mounted at 3.7 m above the ground surface, consists of a sonic anemometer (model CSAT3, Campbell Scientific Inc., Logan, UT) and an infra-red gas analyzer (model LI-7500, Licor Inc., Lincoln, NE). Net radiation, photosynthetic active radiation (PAR), air temperature and humidity, sediment temperature, and water level were recorded to study the environmental controls on NEE (net ecosystem exchange of CO_2 is the difference between gross ecosystem production and ecosystem respiration).

Only days with high tide events that peaked during the mid-day period (10:00 and 14:00), combined with water depth exceeding 0.25 m (indicating submergence of the plants), were considered to quantify the effect of tidal fluctuations on marsh–atmosphere carbon exchanges. The midday high tide events were characterized by rapid drop in NEE, corresponding with the increasing water level. The 0.25 m water level was chosen as substantial decrease in CO_2 flux was observed when the water level on the marsh surface was greater than this value. Such conditions prevailed only on 24 days during the period of record. A Fourier series truncated at the 4th order was fitted to the diurnal CO_2 flux data, by excluding those CO_2 fluxes coinciding with the occurrence of midday high tide events. The excluded points were determined based on when the water depth exceeded 0.25 m between 08:00 and 16:00 h. The fourth order Fourier curve fit was expressed as

where t represents time (in hours), F_{CO2} is the CO_2 fluxes, and $\omega = 2\pi/T$ (T is the period of the signal, 24 h). The coefficients $a_0, a_1, ...$ and $b_0, b_1, ...$ were determined using non-linear fitting procedures using the `trusted region' algorithm in Matlab (The Mathworks, Inc., Natick, MA) curve fitting toolbox. To quantify the effects of cloudy conditions on NEE, CO_2 fluxes were further segregated into sunny and cloudy days based on the values of the clearness index (K_t) (Liu and Jordan 1960). The K_t is defined as the ratio of global solar irradiance received at the Earth's surface (S) to the extra-terrestrial irradiance (S_e), $K_t = S/S_e$.

where S_{sc} is the solar constant (1370 W m^{-2}), β is the solar elevation angle, and t_d is day of year. A day was classified cloudless when the average K_t values exceeded 0.65.

S. alterniflora photosynthetic rates were measured using a pulse amplitude modulated fluorometer (Diving PAM, Walz, Hamburg, Germany). Measurements were taken between 11:00 and 13:00 h on day of year 191 and 198 to represent both exposed and submerged plants. Rapid light curves were obtained by exposing leaves to eight increasing PAR levels. For each PAR level, leaves were exposed to light for 10 s, followed by a 0.6 s saturation pulse to determine the effective quantum yield of photosystem II, Φ_{PSII} (Genty *et al* 1989). Values of relative electron transport rates (rETR), a proxy for photosynthesis, were calculated (Beer *et al* 1998) as

where AF is the fraction of light absorbed by the leaf (typically equal to 0.84, Beer *et al* 1998). The rETR rates were used as a measure of photosynthesis to assess whether carbon assimilation occurred while plants were submerged. The dependence between relative electron transport rate (*P*) and incident PAR on leaves was expressed as (Ralph and Gademann 2005).

where P_s is a scaling factor representing the maximum potential rETR, α is the initial slope of the rapid light–response relationship before the onset of saturation, and β represents the slope of the rapid light–response relationship at the point where photosystem II activity declines. To determine photosynthesis at light saturated conditions, the maximum rETR (rETR$_{max}$) was estimated (Ralph and Gademann 2005) as

Photosynthetic light saturating levels (*E*κ) were estimated as $E\kappa = \text{rETR}_{max}/\alpha$.

3. Results

Peak marsh–atmosphere carbon exchanges were recorded during 9:00 to 12:00 h (local time) and corresponded with conditions of maximum air temperatures, PAR levels, and atmospheric turbulence. Rapid declines in assimilation rates during the afternoon can be attributed to increased temperature stress and radiation loading on the plant canopy. Night-time respiration rates increased with growing season, with maximum rates observed in July (> 5 µmol CO_2 m^{-2} s^{-1}). Respiration decreased during September in response to senescing in plants. Marsh–atmosphere carbon exchanges indicate that the marsh is productive in terms of net carbon vertical exchanges, with average maximum values ranging from 6 to 10 µmol CO_2 m^{-2} s^{-1} under midday conditions in July to August. Maximum carbon fluxes were observed in June and July, corresponding with the peak of the growing season and thereafter trends decreased towards the end of the growing season (figure 1).

Figure 1. Average NEE estimated for each month of the growing season for a salt marsh in the eastern shore of Virginia. The shaded areas represent the standard deviations around the mean.

Tidal influences on marsh–atmosphere carbon exchanges were observed when the water level was high enough to partially or completely submerge the vegetation. For example, during day of year 244 (1 September 2007), a high tide occurred between 10:00 and 16:00 h, causing an abrupt decrease in CO_2 assimilation with the rising tide (figure 2(A)). Surface energy fluxes also changed in response to the tidal level, with increased latent heat and decreased sensible heat fluxes (figure 2(B)) occurring during the midday high tide event. Tide-induced changes in diurnal patterns of energy fluxes and reduction in the carbon fluxes were observed when unusually high tidal levels were recorded. When high tides did not occur concurrently with midday peaks in solar irradiance levels, no changes in diurnal carbon and energy fluxes were observed (data not shown).

Figure 2. Shown are the diurnal course of (A) NEE and water level, and (B) energy fluxes (Rnet, H, LE) observed when a high tide occurred in the middle of the day for day of year 244 (1 September 2007).

An example of tidal influences on carbon fluxes is represented in figure 3. Declines in flood-induced CO_2 fluxes were estimated as the area comprised between F_{CO2} curve fit and eddy covariance CO_2 fluxes (shaded area in figure 3). On average, CO_2 fluxes decreased by 0.83 ± 0.75 g CO_2 m^{-2} d^{-1} due to tidal activity. Maximum losses in CO_2 assimilation capacity were observed on day of year 243 (2.44 g CO_2 m^{-2} d^{-1}) and minimum losses were estimated on day of year 259 (0.009 g CO_2 m^{-2} d^{-1}). Clear conditions produced larger losses in CO_2 assimilation rates (1.00 g CO_2 m^{-2} d^{-1}) compared to cloudy days (0.41 g CO_2 m^{-2} d^{-1}).

Figure 3. Estimation of carbon assimilation due to tides. The shaded region indicates the loss in carbon assimilation due to the high tide event.

Even when fully submerged, our data suggests that *S. alterniflora* plants assimilate considerable amounts of carbon. *S. alterniflora* plants continue to photosynthesize throughout flooding events, although the photosynthetic rates were considerably reduced (figure 4). Light levels reaching the canopy were often an order of magnitude greater than the levels needed to sustain light saturating rates of photosynthesis (E_k), however, *S. alterniflora* plants assimilated carbon at reduced rates. Mean $\pm$ SE rETR$_{max}$ were estimated as 29.6 ± 1.4 μmol electrons m^{-2} s^{-1} ($n = 243$) for submerged plants, while non-flooded plants exhibited two-fold greater rETR$_{max}$ rates 87.9 ± 5.4 μmol electrons m^{-2} s^{-1} ($n = 296$). To maintain higher rates of photosynthesis, non-flooded *S. alterniflora* plants had nearly twice the light requirement of 247 μmol photons m^{-2} s^{-1} (E_k value for non-flooded plants) compared to flooded plants. As expected, E_k values were lower compared to ambient light levels ($\sim$ 2000 μmol photons m^{-2} s^{-1}) observed at noon, suggesting that *S. alterniflora* plants are not light limited even under cloudy conditions. The quantum efficiency (α), the initial slope of the light response curve, was determined to be 0.207 and 0.318 (dimensionless) for flooded and non-flooded plants, respectively.

Figure 4. The relationship between PAR and relative electron transport rates in (A) submerged and (B) exposed conditions for *S. alterniflora* plants. Solid black lines indicate the best fit line obtained by fitting the line to equation (2).

4. Discussion

The Fowling Point marsh had lower (~ 10 µmol CO_2 m^{-2} s^{-1}) carbon fluxes than those reported for other marshes. Using aerodynamic flux methods, Houghton and Woodwell (1980) estimated daytime maximum carbon fluxes of 22 µmol CO_2 m^{-2} s^{-1} for a *S. alterniflora* dominated marsh in Long Island, NY. Studies on marshes in California and Yangtze Delta in China reported maximum ecosystem–atmosphere carbon exchanges of 30 µmol CO_2 m^{-2} s^{-1} (Goulden *et al* 2007, Yan *et al* 2008). Lower carbon fluxes for the present study are attributed to shorter canopy and less active biomass. When the carbon fluxes are integrated over a full growing cycle, the marsh assimilated 130 gC m^{-2}. This amount of carbon assimilation is a fraction of the yearly maximum net primary production of about 1600 gC m^{-2} estimated for salt marshes (Duarte *et al* 2005). To obtain such primary productivity estimates, previous methods considered either small-scale destructive biomass harvests at end of year (< 1 m^2) (Shew *et al* 1981) or allometric relationships to estimate above ground production over small areas (0.0625 m^2) (Morris and Haskin 1990, Morris *et al* 2002). Further, these productivity estimates take into account carbon burial which is a predominant process in coastal salt marshes and is not reflected in the eddy covariance measurements. However, our growing season NEE estimates compare well with chamber based estimates (77–169 gC m^{-2}) conducted in similar ecosystems (Miller *et al* 2001).

Our research provides evidence of reductions in CO_2 assimilation in response to flooding of salt marshes. Although daily flooding of the marsh is essential to flush out toxic metabolites and reduce interstitial salinity (Mitsch and Gosselink 2007), tidal inundation also reduced measured CO_2 fluxes to near zero. However, flooding has been shown to increase NEE over tropical freshwater wetland ecosystems (Morison *et al* 2000). *In situ* photosynthetic measurements indicated *S. alterniflora* plants continued to photosynthesize throughout the tidal flooding event, albeit at reduced rates (figure 4). The 66% reduction in photosynthesis during inundation was coupled with a reduction in quantum efficiency (α), and lowering of the light requirement, E_k. This observation suggests that tidal flooding imposes a physiological stress upon plants living in inter-tidal marshes. Light limitation of the canopy was determined not to be a factor since ambient light levels were sufficient to sustain light saturating rates of photosynthesis (E_k values of 124 µmol photons m^{-2} s^{-1}). Other measurements (data not shown) found that the degree of foliar inundation directly affects *S. alterniflora* photosynthesis. Partially submerged leaves had greater carbon assimilation than completely submerged leaves, suggesting that CO_2 diffusion from the water column to the plant may be limiting underwater photosynthesis.

Our results suggest that ecosystem-level CO_2 assimilation during tidal inundation can be different than zero because *S. alterniflora* plants photosynthesize while submerged. However, the eddy covariance system could not detect such carbon assimilation because CO_2 molecules diffuse 10 000 times slower in water than in air. This suggests that our estimates of NEE are conservative since our flux measurements do not include underwater photosynthesis. Our study also reveals the complexity of estimating NEE in tidally influenced wetlands. For example, it is

not known whether salt marsh plants recycle CO_2 internally, however, this is a common feature in submerged aquatic vegetation such as sea grasses (Grice *et al* 1996). It is possible that the CO_2 used by *S. alterniflora* while submerged is internally recycled within its aerenchyma system. However, this hypothesis needs to be verified experimentally.

Even partial canopy submergence resulted in substantial decreases in carbon fluxes (figure 2). While ecosystem-level (vertical) carbon fluxes were close to zero during flooded conditions *S. alterniflora* plants assimilated substantial amounts of carbon. Such discrepancies between plant- and ecosystem-level carbon assimilation could be ascribed to the aerenchymatous gas transport observed in *S. alterniflora* (Maricle and Lee 2002). This internal carbon cycling within *S. alterniflora* plants cannot be detected by the eddy covariance. Furthermore, submergence of marshes can change the aerodynamic characteristics of the exchange surface thereby minimizing the turbulent transport of trace gases. While it is possible that tidal activity can also bring in pelagic algae over the marsh surface altering the assimilation patterns, water column chlorophyll, a proxy for pelagic algae, is typically low at our study site (McGlathery *et al* 2001), suggesting that pelagic algae should not be a significant factor in this study.

Although the reduction in marsh–atmosphere carbon exchanges caused by tidal flooding during the 2007 were modest, the results should be considered in the context of expected rates of sea-level rise. The projected sea-level rise by the end of 21st century is expected to range between 18 and 59 cm (IPCC 2007). Predicted changes in sea-level rise may increase the frequency and duration of inundation (Boesch *et al* 1994), leading to decreased CO_2 assimilation from inter-tidal salt marshes provided all other factors remain constant. This study estimates that tidal activity can lead to reductions (3–91% compared to non-flooded conditions) in midday CO_2 assimilation, with an average loss of $46 \pm 26\%$. In marshes where surface elevation is less than optimal, plants are very susceptible to small changes in relative sea level (Morris *et al* 2002). In this instance, it is possible that marsh habitat may be lost to less productive mud flats attributed to longer periods of tidal inundation, resulting in greater physiological stresses and lower CO_2 assimilation. Loss in CO_2 assimilation capability may be expected from coastal wetlands in a scenario of rapid sea-level rise, particularly if marshes cannot accrete sediment to increase surface elevation or migrate landward due to anthropogenic physical barriers such as building structures.

Acknowledgment

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