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ARTICLE

Controls on Ecosystem Carbon Dioxide Exchange in Short- and Long-Hydroperiod Florida Everglades Freshwater Marshes

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Abstract Although freshwater wetlands are among the most productive ecosystems on Earth, little is known of carbon dioxide (CO_2) exchange in low latitude wetlands. The Everglades is an extensive, oligotrophic wetland in south Florida characterized by short- and long-hydroperiod marshes. Chamber-based CO_2 exchange measurements were made to compare the marshes and examine the roles of primary producers, seasonality, and environmental drivers in determining exchange rates. Low rates of CO_2 exchange were observed in both marshes with net ecosystem production reaching maxima of 3.77 and 4.28 μmol CO_2 m^{-2} s^{-1} in short- and long-hydroperiod marshes, respectively. Fluxes of CO_2 were affected by seasonality only in the short-hydroperiod marsh, where flux rates were significantly lower in the wet season than in the dry season. Emergent macrophytes dominated fluxes at both sites, though this was not the case for the short-hydroperiod marsh in the wet season. Water depth, a factor partly under human control, significantly affected gross ecosystem production at the short-hydroperiod marsh. As Everglades ecosystem restoration proceeds, leading to deeper water and longer hydroperiods, productivity in short-hydroperiod marshes will likely be more negatively affected than in long-hydroperiod marshes. The Everglades stand in contrast to many freshwater wetlands because of ecosystem-wide low productivity rates.

Keywords Carbon dioxide exchange · Everglades · Productivity · Water management · Wetland

Introduction

Freshwater wetlands are unique ecosystems that provide important ecosystem services including regulation of biogeochemical cycling, provision of habitat for distinctive species, and flood control (Gopal et al. 2000; Zedler and Kercher 2005; Keddy et al. 2009). Globally, wetlands are threatened by human activities such as residential and urban development, as well as agricultural expansion (Dugan 1993; Dahl 2011). In the conterminous United States, approximately half of all wetlands were lost by the 1970s (Mitsch and Gosselink 2007). As increased attention has focused on wetland conservation and research in recent decades, carbon cycling and storage have emerged as areas of particular interest. Wetlands are among the most productive ecosystems in the world, responsible for approximately 6.3 % of terrestrial net primary production (Houghton and Skole 1990; Neue et al. 1997; Keddy 2000).

Most knowledge of wetland carbon dioxide (CO_2) exchange in non-agricultural, freshwater systems is focused on mid- and high-latitude regions of the world (e.g. Bubier et

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al. 1998; Hirota et al. 2006; Roulet et al. 2007; Rocha and Goulden 2008; Dusek et al. 2009). Research over the course of the past decade has begun to explore CO_2 exchange in the tropics and sub-tropics (e.g. Morison et al. 2000; Jones and Humphries 2002; Jauhiainen et al. 2005; Schedlbauer et al. 2010; Wright et al. 2011), but our knowledge of exchange rates and their controls remains limited. There is much to be learned about carbon dynamics in low latitude wetlands with year-round growing seasons and seasonality defined by wet and dry periods.

The Everglades is a large (>6,000 km^2) subtropical wetland located in south Florida (Davis et al. 1994). The Everglades landscape has been subject to hydrologic management for more than a century, and water flows are regulated by canals, levees, and flow control structures (USACE and SFWMD 1999). As a result of anthropogenic alterations, the Everglades now occupies half of its former spatial extent (Light and Dineen 1994). In addition, hydrologic modification has reduced water levels and hydroperiods (i.e., the duration of inundation) relative to historical levels (Light and Dineen 1994). Current construction proceeding under the Comprehensive Everglades Restoration Plan (CERP) is intended, in part, to reverse these patterns. It is likely that plant community composition and productivity will change in response to these alterations in the timing and quantity of water delivery (Armentano et al. 2006; Childers et al. 2006a).

Short- and long-hydroperiod marshes are the two principal freshwater wetlands found in the Everglades, and both are oligotrophic (Noe et al. 2001; Lodge 2005; Childers et al. 2006b). Short-hydroperiod marshes experience annual dry periods during which the water table falls below the soil surface, while long-hydroperiod marshes are typically inundated year-round. As such, the soils and communities of primary producers in these marshes are quite different. Short-hydroperiod marshes are characterized by marl (calcium carbonate) soils, and the plant community is dominated by a relatively uniform grass-sedge canopy (Davis et al. 2005). In contrast, long-hydroperiod marshes have peat soils and topography typified by sparsely vegetated sloughs and densely vegetated ridges (Ogden 2005). Both types of marshes contain an additional group of primary producers, periphyton, though biomass is much higher in short-hydroperiod marshes than in long-hydroperiod marshes (Gottlieb et al. 2006).

Despite ecosystem oligotrophy, high rates of ecosystem productivity have been reported in both short- and long-hydroperiod Everglades freshwater marshes (Ewe et al. 2006). However, prior studies have not directly compared rates of CO_2 exchange between these contrasting ecosystems, nor have they evaluated the roles of primary producers and climatic factors in driving rates of CO_2 exchange. It is essential to understand these factors, particularly in light of Everglades ecosystem restoration activities currently underway. Three principal research questions were addressed in the present study: (1) How are net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production (GEP) affected by both seasonality and the experimental removal of a primary producer group (i.e., macrophytes or periphyton) in short- and long-hydroperiod marshes? (2) How do ecosystem CO_2 exchange rates vary between short- and long-hydroperiod marshes? (3) What environmental factors are the key drivers of NEP, ER, and GEP, and do these factors vary between short- and long-hydroperiod marshes?

Methods

Study Sites

This research was conducted at two study sites (Fig. 1), a short-hydroperiod marsh located within Taylor Slough at 25 °26′16.50″N 80 °35′40.68″W (a site hereafter referred to as TS) and a long-hydroperiod marsh located within Shark River Slough at 25 °33′6.72″N 80 °46′57.36″W (a site hereafter referred to as SRS). Taylor and Shark River Sloughs are the two major drainages of Everglades National Park, and the research described in the present study was conducted prior to the initiation of any CERP-related restoration activities. Mean annual temperature is 23.9°C and average rainfall is 143 cm per year (NCDC 2009). Climate in south Florida is best characterized by wet and dry seasons (Beck et al. 2006; Kottek et al. 2006) with the majority of the annual precipitation falling between May and October. Wet season precipitation is delivered via convectively formed clouds or during the passage of tropical storms and hurricanes (Duever et al. 1994). Dry season precipitation typically coincides with the passage of cold fronts over the Florida peninsula.

The TS site is a seasonally inundated freshwater marsh with a typical hydroperiod of ~5 months per year (Schedlbauer et al. 2010). This site is characterized by shallow (0.14 m), marl soils, and the vegetation is dominated by sawgrass (*Cladium jamaicense*) and muhly grass (*Muhlenbergia capillaris*). Vegetation is short-statured, reaching only 0.73 m above the soil surface. There is no seasonal variation in leaf area index (1.8 m^2 m^{-2}), or in the aboveground biomass of one of the co-dominant plant species, *C. jamaicense* (Schedlbauer et al. 2010). Periphyton is present at the site, and mats of periphyton begin to grow substantially ~2 months into the wet season, forming dense "sweaters" around submerged vegetation. When the site is dry, the periphyton exists as a desiccated mat, often suspended in strands between individual plants and sometimes covering the soil surface. Together, periphyton and submerged macrophytes contribute to the geochemical fixation of CO_2 as calcium carbonate during periods when the site is inundated. Seasonality at TS is best defined by

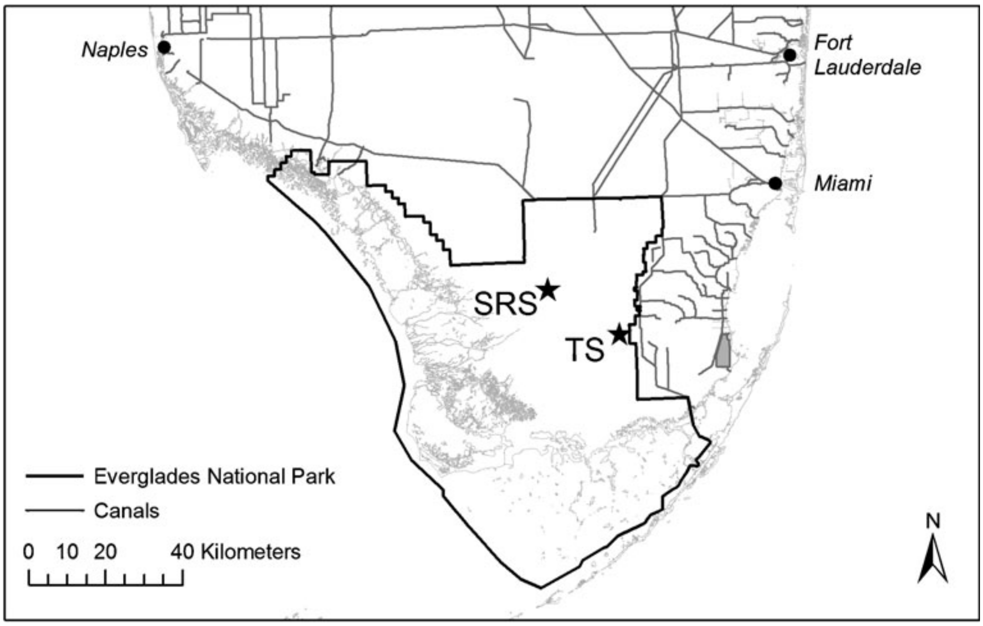


Fig. 1 Map showing the location of the study sites Taylor Slough (TS) and Shark River Slough (SRS) within Everglades National Park

whether or not the site is inundated rather than climatic seasonality because the two do not always coincide (Schedlbauer et al. 2010).

The SRS site is also a freshwater marsh, but is usually inundated year-round and is characterized by ridge and slough topography (Ogden 2005). Soils are composed of peat deposits that are 0.73 m deep within ridges and 0.66 m deep within sloughs. The vegetation at SRS is different from that found at TS. *C. jamaicense* is dominant in ridge areas, and a mixture of emergent spikerush (*Eleocharis* sp.), emergent panic grass (*Panicum* sp.), and submerged bladderwort (*Utricularia* sp.) species dominate the sloughs. Vegetation height on ridges averages 1.34 m above the soil surface, while slough vegetation is approximately 0.70 m above the soil. Periphyton is also present at SRS, floating at or beneath the water surface, often in association with submerged vegetation. Seasonality at this long-hydroperiod marsh is best defined by south Florida's climatic seasonality because the site is typically inundated year-round. As such, there are slight mismatches in seasonality between TS and SRS (Fig. 2a).

The TS and SRS sites are the locations of eddy covariance towers that are part of the AmeriFlux network. At the towers, measurements of air temperature (T_{air}), relative humidity (HMP45C, Vaisala, Helsinki, Finland), and photosynthetically active radiation (PAR, PAR Lite, Kipp and Zonen, Delft, Netherlands) were made every 15 s and averaged at 30 min intervals. Measurements were logged using both CR1000 and CR10X data loggers (Campbell Scientific, Logan, UT). Measurements of water depth were made at both sites with water level recorders installed in PVC wells (HOBO U20-001-01).

Field Measurements

Monthly chamber measurements of ecosystem CO_2 exchange were made at both sites for a period of approximately 1 year. Measurements of NEP and ER were made with custom-made polycarbonate chambers. The chamber used at TS was 0.208 m^3 (50.8 cm × 50.8 cm × 80.6 cm), while that used at SRS was 0.310 m^3 (50.8 cm × 50.8 cm × 120.0 cm). Chamber height varied to accommodate differences in vegetation height at the two sites. Each chamber was fitted with a 4+ m vent tube, a capped vent to aid in pressure equilibration while seating the chamber, and an aluminum angle bar base covered with closed-cell foam. Two box fans were affixed to the inside top of each chamber and were run constantly during measurement periods to ensure that air within the chambers was well mixed. Chambers were configured for non-steady state, flow-through measurements.

During measurement periods, the chamber was coupled to a custom-made system to measure chamber CO_2 concentration. This system included a LI-840 CO_2/H_2O infrared gas analyzer (LI-COR, Inc., Lincoln, NE) coupled to a CR10X datalogger (Campbell Scientific, Logan, UT) that recorded CO_2 concentration every second. Air was drawn into the LI-840 with a pump (UNMP 105B, KNF Neuberger, Trenton, NJ) located downstream from the analyzer. The flow rate was maintained at slightly <1 liter per minute with a rotameter (VFA-22-SSV, Dwyer Instruments, Inc.) located upstream from the LI-840. Air was circulated between the chamber and LI-840 through tubing (Bev-A-Line IV, Thermoplastic Processes, Stirling, NJ). Measurements of PAR (LI-210, LI-COR, Inc., Lincoln, NE) were also recorded by the datalogger at 1 s intervals during measurement periods.

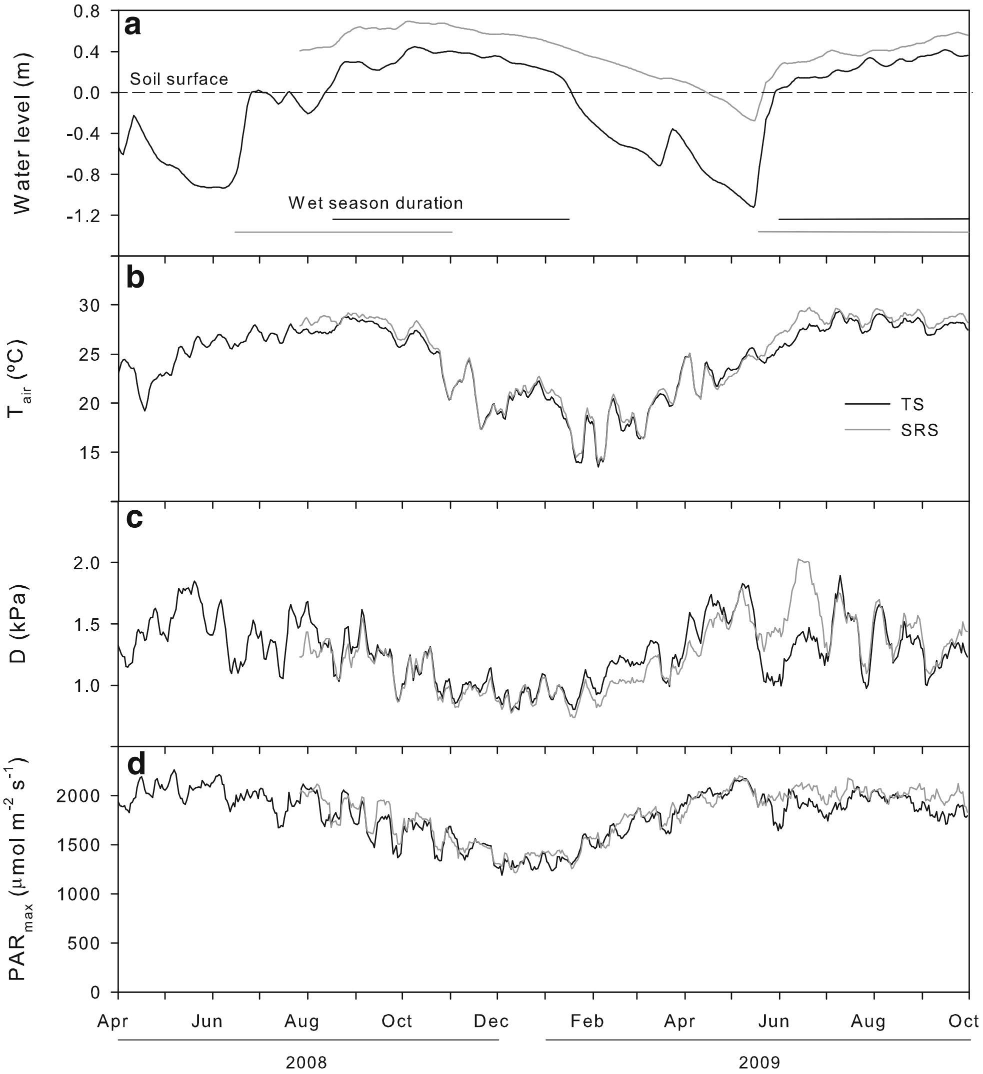


Fig. 2 Micrometeorological data from the short-hydroperiod Taylor Slough (TS) and long-hydroperiod Shark River Slough (SRS) sites. Shown are water level data relative to the soil surface with site specific wet seasons indicated by horizontal bars (A), air temperature (T_{air}, °C, B), vapor pressure deficit (D, kPa, B), and daytime maximum photosynthetically active radiation (PAR_{max}, mol m^{-2} s^{-1}, D). All data are presented as 7-day running means so that seasonal patterns rather than day-to-day variation can be readily observed. Note that micrometeorological measurements did not begin until early July 2008 at SRS

When measurements were made, the chamber was placed over the measurement location and checked to ensure that there was a leak-free seal at the base of the chamber. After a 1 min equilibration period, a 1 min measurement period commenced. Measurements of NEP were made under full-sun conditions and ER was measured with a black nylon cloth placed over the chamber. Chamber measurements were typically made between 10 AM and 1 PM. The chamber was always vented between measurements to ensure that CO_2 concentration, T_{air}, and humidity remained as close to ambient conditions as possible. When water was present at the study sites, water depth was measured at each measurement location so that chamber volume could be adjusted accordingly.

The chamber measurement technique and experimental design varied between study sites. In particular, different manipulative treatments were applied at each site to evaluate the roles of primary producers (i.e., macrophytes and periphyton) in determining CO_2 exchange rates. At TS, a periphyton removal treatment was carried out in the dry season. This treatment did not substantially disturb macrophytes and facilitated repeated measurements over time (see below). However, at SRS the site was continually inundated during measurement periods, and it was not possible to remove submerged periphyton growing in close association with macrophytes. As a result, an above-water macrophyte removal treatment was applied to plots that were first measured in an undisturbed state (see below).

At TS, ten polyethylene bases (50.8 cm×50.8 cm×15.2 cm) were constructed and seated in marl soil at the outset of the experiment. Bases were inserted an average of 3.8 cm into the soil and were allowed to settle for at least 2 weeks prior to the start of the experiment. Five bases served as controls and were not manipulated in any way. Five additional bases were the treatment bases, subjected to the periphyton removal treatment. During the dry season, periphyton was carefully removed from plants and the soil surface by hand. Periphyton was removed only to the extent that it did not disturb the soil surface or vegetation within each base. As such, a small amount of periphyton remained within each of the treatment bases. No attempt was made to remove periphyton from within the bases during periods of inundation or immediately after the water level dropped below the soil surface. Periphyton grew in such close association with the vegetation and soil that removal would have led to a high degree of disturbance.

During measurements at SRS, the site was constantly inundated with water, often reaching 40+ cm above the soil surface (Fig. 2a). As a result, no bases were seated in the soil. Instead, a float was constructed from a piece of foamboard and the chamber was placed over a 50.8 cm × 50.8 cm hole in the board. This allowed the chamber to float above the area of marsh that was to be measured. Chamber measurement plots were randomly selected on each visit to the site and control (i.e., unmanipulated) measurements of NEP and ER were made at each plot. Subsequent to these measurements, all emergent macrophytes within the plot were clipped just beneath the water surface so that NEP and ER could then be measured in treated plots. Clipped macrophytes were returned to the lab, dried at 70°C for 48 h, and weighed.

Chamber measurements were made regularly at TS over the period from April 2008 through August 2009. Measurements at SRS began later and occurred on fewer dates because of limited site access during periods with low water levels. The SRS site is remote and chamber measurements could be made only when the site was accessible by airboat.

Data Processing and Statistical Analyses

Measurements of CO_2 concentration within the chamber during a measurement period were plotted as a function of time, and linear regression was used to determine the rate of change in CO_2 concentration over each 1 min measurement period (i.e., the slope of the relationship). These data were then used to determine CO_2 flux rates in μmol m^{-2} s^{-1} as,

$$CO_2\ \mathrm{flux} = (dC/dt)((p_aV)/(TRA))$$

where dC/dt is the slope described above, p_a is atmospheric pressure (Pa), V is chamber volume (m^3), T is temperature (K), R is the gas constant (8.3143 $Jmol^{-1}$ K^{-1}), and A is chamber area (m^2). Chamber volume was allowed to vary with water level at each measurement location.

Individual measurements of NEP and ER at each base or plot location were used to determine gross ecosystem production (GEP) as,

$$GEP = NEP - ER$$

where positive values indicate CO_2 uptake by the ecosystem and negative values indicate CO_2 release from the ecosystem.

The statistical analyses described below were performed with R (version 2.13.0, The R Foundation for Statistical Computing, 2011). The effects of the experimental treatments and seasonality on NEP, ER, and GEP at both sites were examined with linear mixed-effects models (Schabenberger and Pierce 2002). The fixed effects at both sites were treatment (at TS: periphyton removal and control, at SRS: macrophyte removal and control), season (wet and dry), and the treatment by season interaction term. The random effect at both sites was measurement location (at TS: base location, at SRS: measurement plot). At TS, periphyton removal treatment measurements were eliminated from the dataset for all dates more than 2 months into the wet season. As described above, it was not possible to remove periphyton from within the bases after this time. Therefore, the analysis of the experimental treatment at TS was only for the mid to late dry season and early wet season. The mixed-effects statistical design accommodated an unbalanced study design. In addition to the late-wet season and early dry season data that were eliminated at TS, the weather occasionally made it impossible to complete a full set of chamber measurements.

Analysis of variance (ANOVA) was used to examine whether NEP, ER, and GEP varied between the short- and long-hydroperiod marshes. Specifically, dry and wet season data from the control treatments at TS were compared with seasonally-pooled control treatment data from SRS. Data were analyzed in this manner because of the findings from the mixed effects model analysis, as discussed below. To meet the ANOVA assumptions of normality and equal variances, it was necessary to apply a square root transformation to the GEP data in the TS wet season vs. SRS comparison and to remove three outliers (residuals >2 standard deviations from the mean) from the ER TS dry season vs. SRS comparison.

Multiple linear regressions were used to determine the effect of various environmental factors on rates of CO_2 exchange at each study site. Regressions were performed on control treatment NEP, ER, and GEP values expressed as means for each measurement date. Forward and backward stepwise multiple regressions were performed using the Akaike Information Criterion (AIC) to select predictor variables for the final models (R Package MASS, stepAIC function). Full models for NEP and GEP included water depth relative to the soil surface, T_{air}, vapor pressure deficit (D, as the vapor pressure difference between saturated and ambient air at T_{air}), and PAR as predictor variables. In the ER analysis, PAR was not used as a predictor variable because measurements were made in the dark. Potential predictor variables such as soil temperature, water temperature, and soil volumetric water content were excluded from the analysis because of multicollinearity with the selected variables. Most environmental data used in the models were drawn from the half-hourly micrometeorological dataset and were averaged across the time period during which chamber measurements were made (i.e., from 10AM to 1PM). The one exception was the PAR data, which was calculated as a mean of the PAR measurements made during each 1 min chamber measurement period.

Results

Micrometeorological Site Comparison

Water levels varied seasonally at both TS and SRS with the highest water levels in the wet season and the lowest levels in the dry season (Fig. 2a). Climatically-defined seasonality did not coincide well with site-specific seasonality at TS in 2008, though it matched well in 2009 (Fig. 2a). Measurements of T_{air}, D, and maximum daily PAR (PAR_{max}) were similar between study sites and exhibited expected seasonal patterns (Fig. 2b, c, d).

Treatment and Seasonal Effects on NEP, ER, and GEP

At the short-hydroperiod TS marsh, the periphyton removal treatment had no significant effect on NEP, ER, or GEP ($p>0.05$, Table 1, Fig. 3). It should be noted that this treatment was effectually applied only during the mid to late dry season and early wet season. Seasonality did have an effect on all three parameters, with significantly higher rates of NEP, ER, and GEP observed in the dry season ($p<0.001$, Table 1, Fig. 3). For all analyses at TS, the treatment by season interaction was not significant ($p>0.05$).

At the long-hydroperiod SRS marsh, the macrophyte removal treatment had a significant effect on both NEP and GEP ($p<0.0001$), but not on ER ($p>0.05$, Table 1). Significantly higher rates of NEP and GEP were observed for measurements made prior to macrophyte removal (Fig. 4). In contrast to TS, there was no significant effect of seasonality on any of the CO_2 exchange parameters at SRS. As such, all data from SRS were pooled across seasons for subsequent analyses. The treatment by season interaction was not significant for any of these analyses at SRS ($p>0.05$, Table 1, Fig. 4).

Table 1 F-values from mixed-effects ANOVA analyses of net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production (GEP) measured at Taylor Slough (TS) and Shark River Slough (SRS). All models had the fixed effects treatment, season, and treatment by season interaction. Treatment at TS was the periphyton removal, while at SRS it was the macrophyte removal, and both treatments were compared with control measurements. Season refers to dry or wet season. Asterisks indicate significance at the following levels: $p<0.001$ (***), $0.001\leq p\leq 0.01$ (**), $0.01<p\leq 0.05$ (*)

Site	Variable	Treatment	Season	Treatment × Season
TS	NEP	0.04	27.74***	0.41
	ER	0.59	65.13***	0.08
	GEP	0.21	109.12***	0.88
SRS	NEP	132.44***	2.79	2.88
	ER	11.45**	0.14	3.52
	GEP	117.98***	2.91	3.82

Short- vs. Long-Hydroperiod Comparisons of CO_2 Exchange

Net ecosystem production did not differ significantly between TS in the dry season and SRS ($p>0.05$), though ER and GEP did differ significantly ($p<0.001$, Table 2). Both ER and GEP were significantly greater at TS during the dry season than they were at SRS. These relationships changed when the TS wet season data were compared to the seasonally-pooled data from SRS. In this case, NEP, ER, and GEP were all significantly different ($p<0.001$) between sites with NEP and GEP greater at SRS, while ER remained greater at TS (Table 2).

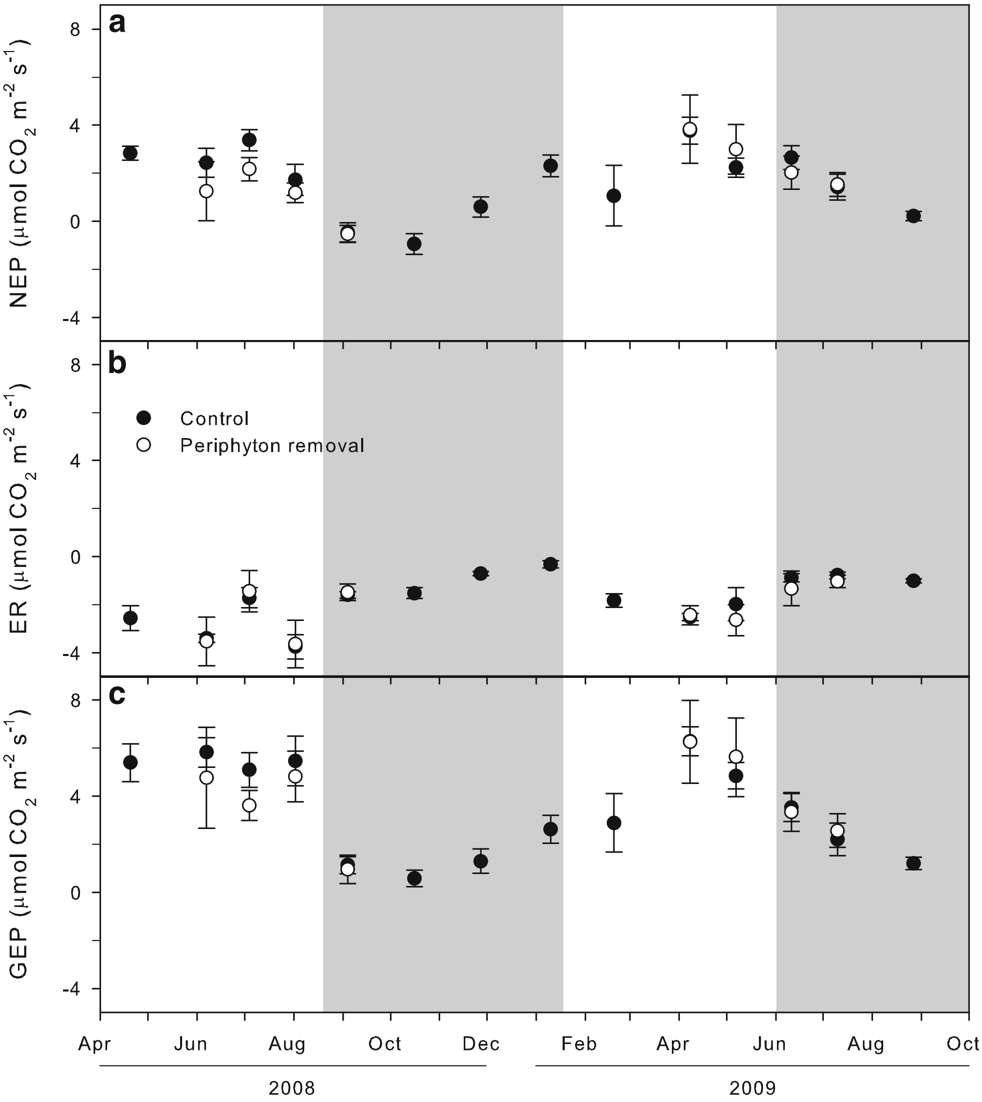
Environmental Drivers of NEP, ER, and GEP

Multiple regression analyses indicated that T_{air} and D best predicted rates of NEP at TS, while at SRS, T_{air} and PAR were the most important predictor variables for NEP. However, neither of these regression equations accounted for much of the variation in the data (R_{adj}^2 of 0.26 and 0.24 for TS and SRS, respectively) and neither equation was significant ($p>0.05$, Table 3). The regression equations used to predict ER were significant at both sites ($p<0.05$) and included the variables water depth and D at TS and T_{air} and D at SRS (Table 3). These equations explained 62 % of the variation in ER rates at TS and 59 % at SRS. Equations for GEP were also significant at both sites ($p<0.05$) and included water depth, T_{air}, and D at TS, but only T_{air} at SRS (Table 3). The explanatory power of the GEP equation was higher at TS than at SRS (R_{adj}^2 of 0.65 and 0.34, respectively).

Although PAR is an important driver of CO_2 exchange, it was only incorporated as a variable in the multiple regression analyses to account for seasonal variation (Fig. 2b). Measurements of NEP were made under full-sun conditions and were assumed to represent maximum daily rates of NEP. An analysis of PAR recorded during the 1 min NEP measurement intervals revealed that on all but 2 days (at SRS on 10/30/08 and 7/17/09) PAR was greater than or equal to (i.e., within one standard error) mean PAR values recorded by the nearby micrometeorological stations during the measurement period (data not shown).

In addition to environmental drivers, it was possible to explore the relationship between plant biomass and CO_2 exchange at SRS because of the nature of the macrophyte removal treatment. Linear regression analyses indicated that

Fig. 3 Means ± one SE for CO_2 exchange rates (μmol CO_2 m^{-2} s^{-1}) measured at the short-hydroperiod Taylor Slough (TS) site. Shown are values for net ecosystem production (NEP, **a**), ecosystem respiration (ER, **b**), and gross ecosystem production (GEP, **c**) for both control and periphyton removal treatments. Dry and wet seasons are indicated by white and grey shading, respectively



plant dry biomass exhibited a significant positive relationship with both NEP and GEP at SRS (R_{adj}^2=0.71 and 0.58, respectively, $p<0.0001$, data not shown). There was no significant relationship between ER and plant biomass ($p>0.05$, data not shown).

Discussion

Treatment and Seasonal Effects on NEP, ER, and GEP

Contrasting patterns of CO_2 flux responses to experimental treatments and seasons were observed between the short- and long-hydroperiod Everglades marshes. At the short-hydroperiod TS marsh, no significant differences in CO_2 exchange rates were observed in the control vs. periphyton removal treatments. This indicated that during the period in which the treatment was effectively applied (i.e., the mid-dry to early wet season), periphyton did not significantly contribute to CO_2 fluxes at the site. Although periphyton exhibits an immediate metabolic response to rewetting in the wet season (Thomas et al. 2006a), the contribution of periphyton to ecosystem CO_2 exchange was not strong enough to be detected.

Seasonality played a key role in influencing rates of CO_2 exchange at TS, such that exchange rates were significantly lower during periods of inundation. The seasonal patterns of NEP, ER, and GEP mirrored those reported at the nearby eddy covariance tower (Schedlbauer et al. 2010). Flux rates were highest in the dry season, declined through the early part of the wet season, and then increased again as the wet season proceeded. Similarity between the two measurement methods was reflected in a linear regression analysis of mean control chamber derived NEP vs. eddy covariance derived NEP (mean values from 10 AM to 1 PM on the chamber measurement dates). This analysis yielded a significant, positive relationship between the two methods (y=1.10 ×–0.58, R_{adj}^2=0.70, $p<0.001$, data not shown). Chamber measurements indicated

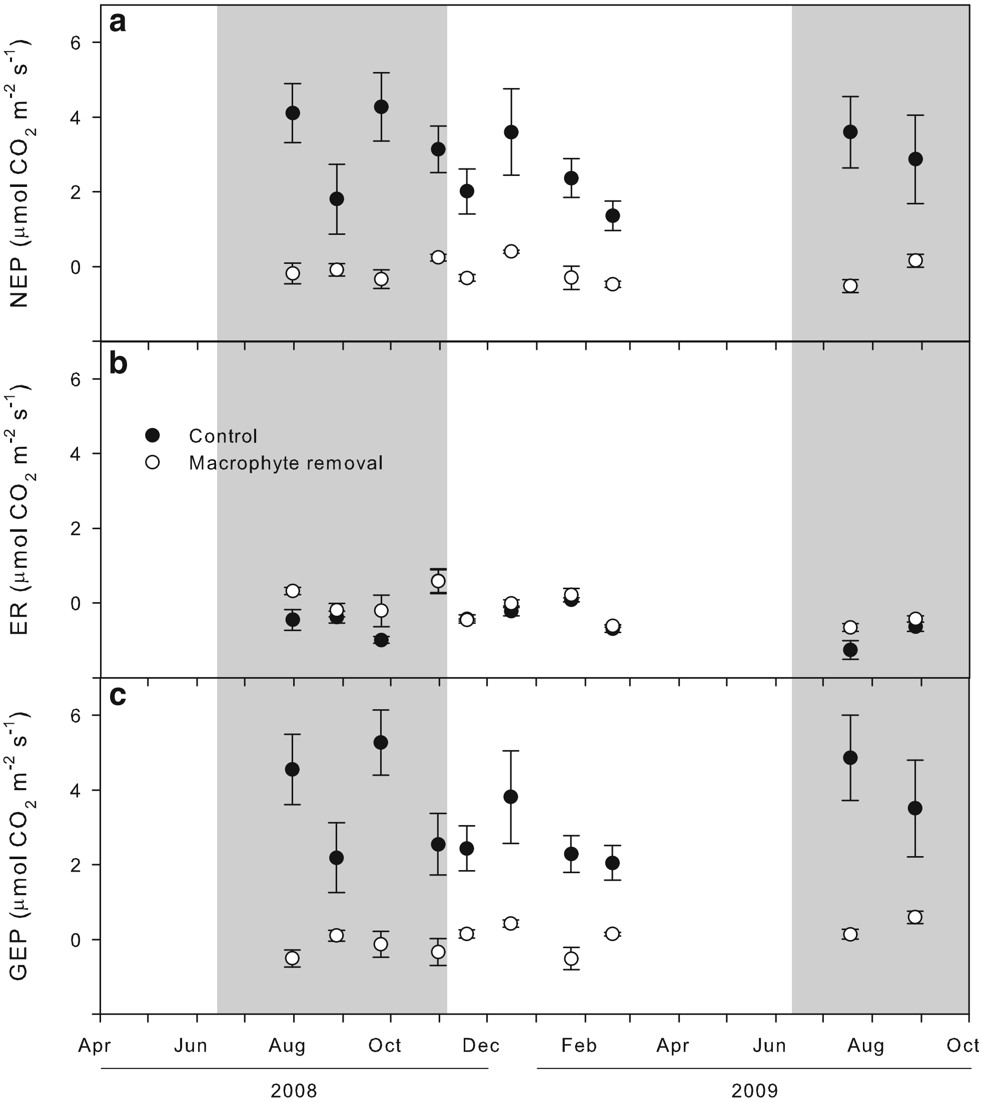


Fig. 4 Means ± one SE for CO_2 exchange rates (μmol CO_2 m^{-2} s^{-1}) measured at the long-hydroperiod Shark River Slough (SRS) site. Shown are values for net ecosystem production (NEP, **a**), ecosystem respiration (ER, **b**), and gross ecosystem production (GEP, **c**) for both control and macrophyte removal treatments. Dry and wet seasons are indicated by white and grey shading, respectively

that dry season fluxes were clearly dominated by contributions from macrophytes, though heterotrophic contributions from the well-aerated soil also played a role in determining ER. In the daytime hours of the dry season, the TS marsh was a net sink for CO_2, and maximum rates of NEP reached 3.77 μmol CO_2 m^{-2} s^{-1}.

Table 2 Mean ± one SE for CO_2 exchange rates (μmol CO_2 m^{-2} s^{-1}) and F-values for the variables net ecosystem production (NEP), ecosystem respiration (ER), and gross ecosystem production (GEP). Means and F-values are reported for one-way ANOVAs performed to compare data from Taylor Slough (TS) during the dry and wet seasons individually with seasonally-pooled data from Shark River Slough (SRS). An asterisk indicates that the TS data for a given variable were significantly different from data from SRS ($p<0.001$)

Variable	TS Dry Season		TS Wet Season		SRS
	Mean ± SE	F-value	Mean ± SE	F-value	Mean ± SE
NEP	2.49±0.27	1.12	0.82±0.26	27.78*	2.92±0.28
ER	−2.53±0.19	181.14*	−0.97±0.09	17.03*	−0.55±0.09
GEP	5.11±0.33	14.40*	1.79±0.24	12.69*	3.35±0.31

Following the onset of the wet season, the TS ecosystem became a net source of CO_2 to the atmosphere during the daytime with NEP rates reaching a minimum of −1.36 μmol CO_2 m^{-2} s^{-1}. The wet season shift from CO_2 sink to source principally reflected the seasonal suppression of photosynthesis by macrophytes following flooding of the site (Schedlbauer et al. 2010). The subsequent transition from low to moderate flux rates during the wet season can be attributed to the growth and development of dense periphyton mats ~2 months into the season (Thomas et al. 2006b; Schedlbauer et al. 2010). It appears that large, metabolically active periphyton mats shifted the ecosystem from net CO_2 source to sink as the wet season proceeded. The contribution of periphyton to primary production at TS was principally confined to the mid to late wet season. Although a prior study indicated that periphyton was responsible for >50 % of aboveground net primary production (ANPP) at TS (Ewe et al. 2006), the present data set suggests a

Table 3 Results from multiple regression analyses in which full models for NEP and GEP included the predictor variables water depth relative to the soil surface, air temperature (T_{air}), vapor pressure deficit (D), and photosynthetically active radiation (PAR). The PAR term was excluded from the full ER models. Missing values indicate that a given predictor variable was not included in the final model. An asterisk next to a predictor variable's coefficient indicates significance at $p<0.10$

	Taylor Slough (TS)			Shark River Slough (SRS)		
	NEP	ER	GEP	NEP	ER	GEP
Intercept	5.68	−0.17	4.83	2.55	1.13	0.29
Water depth	–	1.30	−2.13*	–	–	–
T_{air}	−0.37*	–	−0.27	0.12	−0.10*	0.12*
D	3.56*	−0.81*	3.31	–	0.80*	–
PAR	–	NA	–	−0.002	NA	–
F-statistic	3.29	11.63	9.03	2.42	7.56	5.57
Tolerance	0.63	0.32	0.27	0.59	0.32	0.59
R_{adj}^2	0.26	0.62	0.65	0.24	0.59	0.34
p-value	0.0761	0.0002	0.0034	0.1594	0.0178	0.0460
AIC	8.13	−9.76	8.04	−0.24	−19.54	1.57

smaller role for periphyton in determining site productivity. Scaling errors in the previous study may have contributed to this discrepancy (Schedlbauer et al. 2010). The depressed NEP rates in the wet season also indicate that geochemical fixation of CO_2 and subsequent marl accretion at TS was proceeding slowly.

In contrast to TS, treatment effects were strong and seasonal effects were non-existent at the long-hydroperiod SRS marsh. Rates of CO_2 exchange were strongly driven by contributions from the emergent macrophyte community. In the absence of emergent macrophytes, NEP, ER, and GEP rates significantly decreased and were often close to zero. The effect of macrophyte removal was most dramatic for NEP and GEP, given that rates of ER were low year-round, regardless of treatment. These data indicate that the contribution of periphyton to ecosystem CO_2 exchange was minor in this long-hydroperiod marsh. This finding supports data reported by Ewe et al. (2006) indicating that periphyton contributes only 10 % of the average ANPP at this study site.

As a peat marsh, it was expected that the long-hydroperiod SRS ecosystem would act as a CO_2 sink and, on each measurement date under mid-day, full sun conditions, this was found to be the case. Rates of NEP varied from 1.36 to 4.28 μmol CO_2 m^{-2} s^{-1}. Despite data showing the site as a CO_2 sink during daytime hours, the unusually dry conditions recorded at the site in spring 2009 exposed peat soil at the site (J.L. Schedlbauer, personal observation), and the exposure of these carbon-rich soils likely switched the site from CO_2 sink to source. Unfortunately, chamber measurements were logistically impossible during this time period. The historical occurrence of site dry-downs is unknown, but likely to be rare given the presence of >0.65 m deep peat deposits at the site.

In comparison with other subtropical and tropical freshwater wetlands where CO_2 exchange rates have been measured, the findings reported for these Everglades marshes are notably different. Typically, net rates of CO_2 uptake by tropical wetlands are highest in the wet season and lowest in the dry season (Morison et al. 2000; Jones and Humphries 2002). This pattern was not found in either short- or long-hydroperiod Everglades marshes; the pattern was opposite at TS and there was no pattern at SRS. The seasonal stimulation of primary productivity in many low-latitude wetlands is absent in these oligotrophic Everglades marshes.

Short- vs. Long-Hydroperiod Comparisons of CO_2 Exchange

Both TS and SRS exhibited statistically similar rates of NEP when compared during the TS dry season. This was unexpected given the contrasting primary producer communities and hydroperiods at these sites. However, both GEP and ER were significantly higher at TS, likely reflecting the contributions of the well-aerated soil microbial community to CO_2 fluxes from the site. During the wet season at TS, macrophyte leaf area was submerged and photosynthetic rates declined (Schedlbauer et al. 2010), and this led to rates of NEP and GEP that were significantly lower than at SRS. Despite the fact that both sites share *C. jamaicense* as a dominant plant species, inundation had contrasting effects on site productivity. These data suggest that the *C. jamaicense* population at SRS is better adapted to flooded conditions, an idea supported by ANPP data for the species. *C. jamaicense* ANPP at SRS is nearly double the value reported for TS (606 vs. 304 gC m^{-2} $year^{-1}$, Ewe et al. 2006).

The seasonal and year-round mean values for NEP, ER, and GEP compared favorably with data collected at the eddy covariance towers at each site (Schedlbauer et al. 2010; K.L. Jimenez, unpublished manuscript). Carbon dioxide fluxes determined using chamber measurement methods clearly captured representative data at both sites. However, it should be noted that measurements of ER during inundated periods at both study sites may have underestimated true ER. Although the chamber was darkened for ~1 min before a measurement was recorded, it is probable that lags were present in the system. In sunlight, aquatic photosynthesis will decrease the dissolved CO_2 concentration in the water column and cause a net flux of CO_2 into the water. This flux likely continued following chamber darkening because equilibration of CO_2 in a large volume of water proceeds relatively slowly. Further, because the chamber was placed on a float at SRS, it is possible that water upstream from the darkened chamber flowed under the float during ER measurements. Although water flow at SRS is slow (1.5–4.5 cm s^{-1}, Riscassi and Schaffranek 2002), the introduction of recently sunlit water depleted in dissolved CO_2 may have affected ER measurements. Because of these possibilities, ER may have been underestimated at TS in the wet season and at SRS year-round.

The data collected from these Everglades marshes contrast with other studies of CO_2 exchange in wetlands at low latitudes. Carbon dioxide flux rates in both short- and long-hydroperiod marshes were much lower than values reported elsewhere. For instance, the maximum rates of net CO_2 uptake in a papyrus (*Cyperus papyrus*) wetland were reported to reach 24 μmol CO_2 m^{-2} s^{-1} (Jones and Humphries 2002), while maximum values in an Amazonian floodplain were >40 μmol CO_2 m^{-2} s^{-1} (Morison et al. 2000). Also, in comparison with growing season data from freshwater wetlands at mid to high latitude, these Everglades CO_2 exchange rates were low (Bonneville et al. 2008; Rocha and Goulden 2008; Dusek et al. 2009). The present data strongly reflect the oligotrophic nature of Everglades wetlands, where phosphorous availability is known to limit the productivity of periphyton and macrophytes including *C. jamaicense* and *Eleocharis* sp. (Daoust and Childers 1999; Noe et al. 2001; Iwaniec et al. 2006).

Environmental Drivers of NEP, ER, and GEP

Environmental drivers of CO_2 exchange varied between the short- and long-hydroperiod study sites. Considering the significant multiple regression equations for ER and GEP, the most notable finding is that water level influenced both terms at TS, but had no effect at SRS. This supports the findings reported above showing a significant seasonal effect on CO_2 exchange at TS, but not at SRS. This relationship is important in light of impending changes in Everglades water management as the Comprehensive Everglades Restoration Plan (CERP) proceeds. These data indicate that increased water depths and longer hydroperiods will have a substantial effect on CO_2 exchange in short-hydroperiod marshes, but a limited effect within long-hydroperiod marshes. While other environmental drivers (i.e., T_{air}, D, PAR) influence NEP, ER, and GEP, these factors are largely beyond human control.

The weakness of the relationship between environmental drivers and the NEP and GEP terms at SRS was likely related to heterogeneity in the site's plant community. Both terms were significantly related to plant biomass, a metric that varies substantially from ridge to slough. It seems that variation in the amount of plant material enclosed by the measurement chamber was more important than any environmental variable in determining CO_2 exchange rates. However, the same cannot be said for the weak relationship between environmental drivers and NEP at TS where vegetation is relatively heterogeneous. A longer-term dataset may help to resolve the role of environmental drivers in determining NEP.

Conclusions

Although wetlands are among the world's most productive ecosystems, the freshwater marshes of the Everglades are atypical. In contrast to previous research (Ewe et al. 2006), the data reported here reflect that the Everglades is an oligotrophic ecosystem with low productivity in both short- and long-hydroperiod marshes. Everglades wetlands are also distinguished because seasonal cues, specifically the transition from dry to wet season, do not yield pulses in productivity, as reported in other low-latitude wetland ecosystems.

Despite contrasting plant communities, net ecosystem production was surprisingly similar between short-hydroperiod marshes in the dry season and long-hydroperiod marshes year-round. Further, it is clear that (emergent) macrophytes were the dominant contributors to CO_2 exchange rates during these periods. Whether these similarities will persist in the future, as Everglades restoration under CERP proceeds, is uncertain.

It is likely that productivity in short-hydroperiod marshes, rather than long-hydroperiod marshes, will be most affected by alterations in the timing and quantity of water delivery to the Everglades. The current study shows that rates of CO_2 exchange in short-hydroperiod marshes like TS are highly sensitive to seasonality and water levels. Deeper water and longer hydroperiods are likely to decrease the amount of carbon stored by these ecosystems on an annual basis. Additionally, past research indicates that plant communities in short-hydroperiod Everglades marshes can change rapidly (i.e., within 3–4 years) in response to altered hydrologic regimes (Armentano et al. 2006). As a result, these ecosystems may shift toward more hydrophytic plant communities. The net effect of Everglades restoration activities on productivity in short-hydroperiod marshes is, as yet, unclear, but any alterations will have wide-ranging effects given that these marshes occupy approximately one-third of the Everglades' spatial extent (Davis et al. 2005).

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