Seasonal differences in the CO_2 exchange of a short-hydroperiod Florida Everglades marsh

Jessica L. Schedlbauer [a,*], Steven F. Oberbauer [a,b], Gregory Starr [c], Kristine L. Jimenez [c]

[a] 11200 SW 8th St., Department of Biological Sciences, Florida International University, Miami, FL 33199, USA
[b] Fairchild Tropical Botanic Garden, 10901 Old Cutler Rd., Coral Gables, FL 33156, USA
[c] Box 870206, Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, USA

ABSTRACT

Although wetlands are among the world's most productive ecosystems, little is known of long-term CO_2 exchange in tropical and subtropical wetlands. The Everglades is a highly managed wetlands complex occupying >6000 km^2 in south Florida. This ecosystem is oligotrophic, but extremely high rates of productivity have been previously reported. To evaluate CO_2 exchange and its response to seasonality (dry vs. wet season) in the Everglades, an eddy covariance tower was established in a short-hydroperiod marl marsh. Rates of net ecosystem exchange and ecosystem respiration were small year-round and declined in the wet season relative to the dry season. Inundation reduced macrophyte CO_2 uptake, substantially limiting gross ecosystem production. While light and air temperature exerted the primary controls on net ecosystem exchange and ecosystem respiration in the dry season, inundation weakened these relationships. The ecosystem shifted from a CO_2 sink in the dry season to a CO_2 source in the wet season; however, the marsh was a small carbon sink on an annual basis. Net ecosystem production, ecosystem respiration, and gross ecosystem production were −49.9, 446.1 and 496.0 g C m^{-2} year^{-1}, respectively. Unexpectedly low CO_2 flux rates and annual production distinguish the Everglades from many other wetlands. Nonetheless, impending changes in water management are likely to alter the CO_2 balance of this wetland and may increase the source strength of these extensive short-hydroperiod wetlands.

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1. Introduction

Wetlands occupy 5–8% of the earth's land area and are among the most productive ecosystems in the world, accounting for ~6.3% of terrestrial net primary production (NPP) (Houghton and Skole, 1990; Neue et al., 1997; Keddy, 2000; Mitsch and Gosselink, 2007). These ecosystems are characterized by unique habitats and biodiversity and play central roles in water supply, flood control, and biogeochemical cycling (Zedler and Kercher, 2005). The extent of natural wetlands has been greatly reduced through human activity, posing a threat to both ecosystem services and functions (MES, 2005). As human pressure on wetlands increases and climate change proceeds, there is a growing need to increase our knowledge of wetland ecosystem function. In particular, studies of long-term CO_2 exchange could greatly improve our understanding of wetland ecosystem productivity.

To date eddy covariance (EC) studies of CO_2 exchange in wetlands have focused largely on peatlands and other temperate wetlands (e.g. Bonneville et al., 2008; Rocha and Goulden, 2008; Dusek et al., 2009). These studies reinforce that wetlands are highly productive and important in global carbon cycling, but provide limited insight into wetland CO_2 exchange dynamics at lower latitudes. Wetlands of the tropics and subtropics often have year-round growing seasons and may respond differently to seasonality, typically characterized by wet and dry seasons, relative to temperate systems. One such wetland, the Florida Everglades, is reported to have very high rates of NPP (Ewe et al., 2006), though nothing is known about the annual patterns of CO_2 exchange or the role of environmental factors, including hydroperiod (i.e., the duration of inundation), in driving these patterns.

The Everglades is an extensive complex of freshwater wetlands currently occupying >6000 km^2 in south Florida (Davis et al., 1994). Although the Everglades is an oligotrophic ecosystem limited by phosphorus, high rates of aboveground NPP are reportedly maintained in marsh areas through periphyton and aquatic macrophyte growth. Aboveground NPP has been found to reach >10,000 g C m^{-2} year^{-1} in some Everglades marl (calcium carbonate soil) marshes, though rates of 1000–2000 g C m^{-2} year^{-1} are more common (Ewe et al., 2006). Hydroperiod is of central importance in determining productivity in the Everglades and is the product of both active water management and climate (Busch et al., 1998; Childers et al., 2006).

Humans have profoundly modified the Everglades for over a century, reducing the ecosystem's spatial extent by nearly half (Light and Dineen, 1994). Transformation of this landscape has shifted it from one that was characterized by unimpeded, slow sheet flow of water to one that is highly managed. Much of the historical extent of the Everglades has been drained or impounded, and water flow now is controlled by a system that includes ~3000 km of canals and levees, as well as >150 flow control structures (USACE and SFWMD, 1999). Everglades National Park (ENP) is the only remaining portion of the Everglades with unrestricted water flow.

Water management activities have reduced water levels and hydroperiod throughout the Everglades (Light and Dineen, 1994). These changes have had many ecological consequences, including alterations in nutrient concentration and distribution, plant community composition, aboveground net primary production, and periphyton dynamics (Newman et al., 1996; Ross et al., 2000; Armentano et al., 2006; Childers et al., 2006; Iwaniec et al., 2006). In an effort to reverse these alterations, significant Everglades restoration activities began in the 1970s (Lodge, 2005), and now fall under the Comprehensive Everglades Restoration Plan (CERP). In 2000, nearly US$12 billion was designated by CERP for restoration, and the Plan's goals include increased hydroperiods, deeper water, and increased water flows throughout the Everglades.

The potential effects of CERP are far-reaching and are likely to interact with the consequences of a changing climate. In south Florida, temperature is projected to increase by ~2 °C over the next century, and summer months may become 5–10% drier (Christensen et al., 2007). This is significant given that south Florida's wet season and maximum water levels in the Everglades occur in the summer. As the Everglades face further modification and a changing climate, CO_2 exchange in these wetlands will be affected. Because this wetland has shown high potential for carbon storage, it is essential that we better understand CO_2 exchange and its central environmental drivers so that ecosystem responses to future change can be better anticipated.

Toward this end, we established an EC and meteorological tower in a short-hydroperiod Everglades marsh to continuously measure CO_2 exchange. We addressed four central research questions: (1) Is the ecosystem a net sink or source for CO_2? (2) Do the dynamics of CO_2 exchange vary seasonally? (3) What environmental factors exert dominant controls on CO_2 exchange, and do these factors vary seasonally? (4) How may the dynamics of CO_2 exchange be altered with proposed modifications in water management and climate change?

2. Methods

2.1. Site description and climate

An EC and meteorological tower is situated at 25°26′16.5″N, 80°35′40.68″W in ENP, Florida, USA (Fig. 1). The tower is part of the AmeriFlux network and is co-located with a long-term monitoring site managed by the Florida Coastal Everglades Long Term Ecological Research (FCE-LTER) program. This site is in the southern Everglades within Taylor Slough, one of the primary drainage basins in ENP.

A short-hydroperiod marsh surrounds the tower and extends for several kilometers in all directions but east. Approximately 450 m
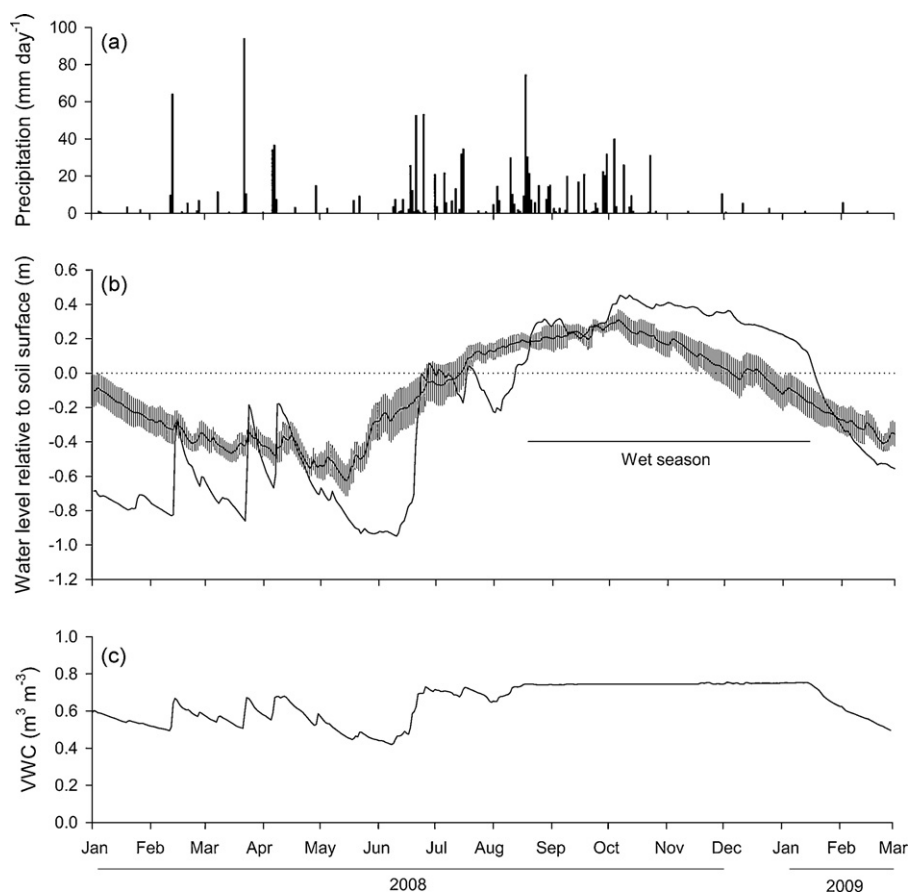

Fig. 1. Total daily precipitation (a), mean daily water level and mean historical water level (b), and soil volumetric water content (VWC) (c) data for the Taylor Slough site. Water level data are shown for the study period, January 2008 to February 2009 (solid black line), and as a daily mean ±1 SE calculated for the period from January 2000 to May 2009 (NPS, 2009). Historical data are from the current water management period only, when flows into Taylor Slough were regulated by the S332D structure. A horizontal bar on the water level figure marks the 2008 wet season, as determined by water level at the site.

to the east is ENP's boundary, comprised of a canal and levee road. The tower site has shallow ($\sim$0.14 m), marl soils overlying limestone bedrock. The soil surface is gently undulating though there is little variation in canopy height, which averages 0.73 ± 0.01 m. The sedge, sawgrass (*Cladium jamaicense*), and the C_4 muhly grass (*Muhlenbergia capillaris*) are the dominant plant species. Periphyton mats, composed of algae, fungi, and bacteria, are also present at the site.

Since 2000, managed water flows in Taylor Slough have been regulated by a pumping station (S332D) located $\sim$6 km northeast of the tower. This station was brought online as part of a plan to restore sheet flow and increase water levels in the northern portion of Taylor Slough where the tower is located (Armentano et al., 2006). Pumped water flows through a canal and into the slough primarily by canal overflow. Modeling efforts indicate that both rainfall and the volume of water pumped through the S332D station are important in determining water levels within Taylor Slough (Armentano et al., 2006; J.P. Sah, unpublished manuscript). The portion of Taylor Slough that includes the tower site is usually inundated for 4–5 months per year, and water releases are timed to coincide with historical hydroperiod and rainfall events (Light and Dineen, 1994; Abtew et al., 2009).

Although located in subtropical latitudes, the climate of the Everglades is classified as tropical (Beck et al., 2006; Kottek et al., 2006) with wet summers and dry winters. Long-term data indicate a mean annual temperature of 23.9 °C in the southern Everglades, with an average minimum of 18.1 °C and an average maximum of 29.4 °C (NCDC, 2009). Precipitation in south Florida is dominated by the passage of cold fronts associated with polar air masses in the dry season and by tropical air masses that produce frequent localized thunderstorms, as well as tropical storms and hurricanes, in the wet season. Mean annual precipitation is 1.43 m (NCDC, 2009) with $\sim$60% of rainfall occurring at the height of the wet season (June to September) and $\sim$25% in the dry season (November to April) (Duever et al., 1994).

2.2. Eddy covariance and meteorological measurements

Continuous measurements of EC and meteorological data reported here began in January 2008 and continued through the end of the wet season in February 2009. EC data were collected at 10 Hz on a CR1000 datalogger (Campbell Scientific, Logan, UT) and stored on 2 GB CompactFlash cards. CO_2 concentration was measured with an open-path infrared gas analyzer (IRGA) (LI-7500, LI-COR Inc., Lincoln, NE). Three-dimensional wind speed data and sonic temperature were measured with a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT). The IRGA was mounted 0.09 m from the sonic anemometer head and the center of both sensors was 3.30 m above the ground. The IRGA was calibrated monthly per the manufacturer's instructions using N_2 gas scrubbed with soda lime and Drierite, CO_2 calibration gas ($\pm$1% at 450 ppm), and a dewpoint generator (LI-610, LI-COR Inc., Lincoln, NE).

Barometric pressure was measured and recorded by the CR1000 (PTB110, Vaisala, Helsinki, Finland), as were air temperature (T_{air}) and relative humidity (HMP45C, Vaisala, Helsinki, Finland). The temperature and relative humidity sensor was housed in an aspirated shield (43502, R.M. Young, Traverse City, MI) mounted 2.5 m above the ground.

A CR10X datalogger and AM16/32A Relay Multiplexer (Campbell Scientific, Logan, UT) were used to collect meteorological data. Variables measured every 15 s and averaged every 30 min included photosynthetically active radiation (PAR) (PAR Lite, Kipp and Zonen, Delft, Netherlands), horizontal wind speed and direction (05103, R.M. Young, Traverse City, MI), and soil temperature at 10 cm depth ($n = 2$, Type-T thermocouples, Omega Engineering, Inc., Stamford, CT). Measurements of precipitation (TE525, Texas

Electronics, Dallas, TX) and soil volumetric water content (VWC) in the top 20 cm of soil ($n = 2$, CS616, Campbell Scientific, Logan, UT) were also recorded. A site-specific equation for marl soils was generated to calculate VWC from sensor period (Veldkamp and O'Brien, 2000). Water level at the site was recorded with a water level data logger (HOBO U20-001-01, Onset, Bourne, MA) installed in a solution-hole well.

2.3. Eddy covariance data processing and gap-filling

Raw EC data were processed with EdiRe (v.1.4.3.1184, Clement, 1999) to determine net ecosystem exchange of CO_2 (NEE, μmol CO_2 m^{-2} s^{-1}) over 30 min time intervals. Data processing followed standard methods and included despiking, coordinate rotation, and air density corrections (Webb et al., 1980; Baldocchi et al., 1988; Aubinet et al., 2000). As an input variable, canopy height was adjusted with changing water level in the wet season. A CO_2 storage term was estimated from half-hourly changes in CO_2 concentration measured by the EC system IRGA and added to half-hourly NEE values (Hollinger et al., 1994).

Processed data were corrected to ambient atmospheric pressure and the half-hourly data were then filtered to remove periods with (1) precipitation or condensation on the IRGA or sonic anemometer, (2) friction velocity (u^*) < 0.15 m s^{-1}, (3) wind vectors with SD > 4, (4) IRGA and sonic anemometer flags, and (5) biologically impossible values of NEE (> or <30 μmol m^{-2} s^{-1}). To determine the u^* threshold, half-hourly nighttime NEE data were sorted into u^* bins of 0.05 m s^{-1}. Raw NEE was positively correlated with u^* when u^* was $\leq$0.15 m s^{-1}, suggesting an under-measurement of CO_2 exchange, so all half-hourly NEE data with $u^* \leq 0.15$ m s^{-1} were excluded from the dataset.

Gap-filling of filtered half-hourly data was performed separately for daytime and nighttime data. Of the daytime data, 26% of the half-hourly data were gap-filled, while this was true for 79% of the nighttime data. Coefficients for the following equation were generated monthly, with one exception, using filtered half-hourly NEE data (Appendix A). At the onset of the wet season in August 2008, two sets of coefficients were generated to treat data from the dry and wet seasons separately. This division was found to be unnecessary at the end of the wet season in January 2009. When PAR was $\geq$5 μmol m^{-2} s^{-1}, daytime NEE data were gap-filled with the function,

$$NEE = \left(\frac{-\alpha\,PPFD\,NEE_{max}}{\alpha\,PPFD + NEE_{max}} \right) + ER \qquad (1)$$

where the coefficient α is apparent quantum yield, NEE_{max} is light-saturated net CO_2 exchange, and ER is ecosystem respiration determined as NEE when photosynthetic photon flux density (PPFD) equals 0 μmol m^{-2} s^{-1} (Ruimy et al., 1995). PPFD was approximated from half-hourly PAR data.

When PAR was <5 μmol m^{-2} s^{-1}, nighttime NEE (i.e., ecosystem respiration, ER) data were gap filled with the exponential function,

$$ER = a\,\exp(b\,T_{air}) \qquad (2)$$

where a and b are coefficients determined bi-monthly and T_{air} is air temperature determined from half-hourly data (Appendix B, Lloyd and Taylor, 1994). Bi-monthly timeframes encompassed periods with similar climatic conditions and provided sufficiently large datasets upon which to fit eq. (2). Months during which seasonal transitions occurred (August 2008, January 2009) were divided by season and ER data from early in each month were grouped with the preceding bi-monthly period. T_{air} was chosen as a predictor variable over soil temperature because it was not directly affected by the large volume of water at the site during the wet season. A robust predictive relationship between ER and T_{air} did not exist for the July–August transition period when water

levels increased toward wet season conditions. During this time period, water level was more important than T_{air} in predicting ER, so a linear function relating ER to water level was used to gap-fill these data (Appendix B). Daytime ER was determined using the predictive relationships developed for nighttime periods under the assumption that daytime ER was of similar magnitude and responsiveness as nighttime ER.

In keeping with micrometeorological conventions, negative fluxes represent CO_2 uptake by the ecosystem and a loss of CO_2 from the atmosphere, while positive fluxes represent CO_2 efflux from the ecosystem and into the atmosphere.

Half-hourly NEE and ER data were each summed to determine daily net ecosystem production (NEP, $g\,C\,m^{-2}\,day^{-1}$) and daily ecosystem respiration (ER, $g\,C\,m^{-2}\,day^{-1}$), respectively. Daily gross ecosystem production (GEP, $g\,C\,m^{-2}\,day^{-1}$) was calculated as the sum of -NEP and ER and is expressed as a positive value. Daily NEP, ER, and GEP values were summed to generate monthly, seasonal, and annual values.

Error estimation for NEP, ER, and GEP was performed with Monte Carlo simulations. The standard errors of monthly parameter estimates (Appendix A and Appendix B) were used to generate uniform distributions for each of the model parameters used in gap-filling. Each distribution was randomly sampled 100 times and resulting parameter values were used to calculate NEP, ER, and GEP. Monthly, seasonal, and annual "sampling uncertainty" (cf. Stoy et al., 2006) for NEP, ER, and GEP was determined as the standard error of the 100 model simulations. These estimates of sampling uncertainty reflect only the error associated with gap-filling.

2.4. Tower footprint

The tower footprint area was estimated with a parameterized backward Lagrangian stochastic particle dispersion model (Kljun et al., 2002, 2004) with site-specific inputs including sensor measurement height, roughness length, surface friction velocity (u^*), and the standard deviation of vertical wind velocity (σ_w). Lagrangian models are among the most widely used footprint models (Vesala et al., 2008) and the model by Kljun et al. (2002, 2004) provides a footprint estimate for homogenous terrain that varies with the ratio of σ_w to u^*.

The model indicated that 90% of measured fluxes occurred within 125 m of the tower, given mean raw (filtered) u^* and σ_w values (0.36 m s^{-1} and 0.41 m s^{-1}, respectively). Under rarely observed wind conditions at the site (e.g. $u^* = 0.52$ m s^{-1} and $\sigma_w = 0.33$ m s^{-1}), 90% of the footprint fell within 200 m of the tower. These model outputs indicate that flux measurements provide an accurate representation of the short-hydroperiod marsh immediately surrounding the tower, with minimal influence from the canal and disturbed marsh area located ≥ 450 m to the east, beyond the ENP boundary.

2.5. Leaf area index and aboveground biomass

Indirect measurements of leaf area index (LAI) were made with a LAI-2000 (LI-COR, Inc., Lincoln, NE) at 20 cm intervals from the soil surface to the top of the canopy during the 2009 dry season. A total of 64 measurements were made at 10 m intervals along a transect located east of the tower. For comparison, a set of five indirect LAI measurements and an accompanying set of direct LAI measurements were made in the wet season. Wet season indirect measurements were made at 10 cm intervals from the water surface to the top of the canopy beginning at 20 cm to avoid standing water. Each measurement location was used as the midpoint for a complete leaf area harvest. A 58 cm × 58 cm plot frame was placed at each location and all biomass was harvested at intervals of 10 cm beginning at the top of the canopy (90–100 cm above the soil sur-

face) and ending at 20 cm. Harvested tissue was returned to the lab, divided into living and dead tissue, and cleaned of all attached periphyton. Leaf area within each height interval was determined separately for living and dead tissue with an image analysis system (AgVision, Decagon Devices, Inc., Pullman, WA).

Aboveground biomass of *C. jamaicense*, the most abundant macrophyte at the site, was determined bimonthly by FCE-LTER personnel. Measurements began in January 2000 and continued through January 2009. Biomass was estimated with an allometric relationship developed for Everglades *C. jamaicense* that relates leaf basal diameter and length to biomass (Daoust and Childers, 1998). *C. jamaicense* aboveground carbon content was estimated from these data and *C. jamaicense* leaf carbon content at the site (0.49 g C g biomass^{-1}) (Childers, 2008).

2.6. Data analyses

SigmaPlot (v.11.0, Systat Software, Inc.) was used for all analyses described below. The vertical distribution of LAI was modeled with the two-parameter exponential decay model,

$$LAI = a\,\exp(-bz) \tag{3}$$

where a and b are coefficients and z is height above the soil surface. This model was fit separately to dry and wet season indirect LAI measurement data, as well as direct LAI measurement data. The dry season model derived from indirect LAI measurements was used in conjunction with water depth data to estimate above-water LAI during periods of inundation.

Raw flux data (i.e., non-gap-filled data, referred to as NEE$_{raw}$ and ER$_{raw}$) were used to examine the relationships between daytime NEE$_{raw}$ and PAR (eq. (1)) and nighttime ER$_{raw}$ and T_{air} (eq. (2)) during both the dry and wet seasons. 95% confidence intervals were computed for fitted curves to determine whether these relationships varied seasonally. The Q_{10} of ER in each season was calculated as,

$$Q_{10} = \exp(b\,10) \tag{4}$$

where b is the coefficient determined in eq. (2) above.

Residuals from the NEE$_{raw}$ vs. PAR and ER$_{raw}$ vs. T_{air} relationships were examined for correlations with other environmental and meteorological variables. NEE residuals for each season were compared against half-hourly wind velocity, wind direction, T_{air}, VPD, and water depth. ER residuals were compared with wind velocity, wind direction, and water depth.

Daily NEP and ER values were examined in relation to daily GEP during both the dry and wet seasons with linear regression. The influence of water level on daily GEP values was also examined using linear regression.

3. Results

3.1. Climate and seasonality

Total annual precipitation for 2008 was 1206 mm, slightly lower than the long-term mean. Most rain fell between June and October 2008 during south Florida's wet season (Fig. 1a). There were a few significant rainfall events in the 2008 dry season, but very little rain after mid-October 2008.

Seasonality (i.e., dry and wet seasons) at the Taylor Slough site did not closely coincide with climatic seasonality in south Florida, given the role of active water management in the Everglades. For the analyses presented here, seasonality was determined with water level data where water levels were <10 cm above the soil surface during the dry season and ≥ 10 cm above the soil surface during the wet season. A threshold of 10 cm was chosen because, given the undulating nature of the soil surface, the site was not
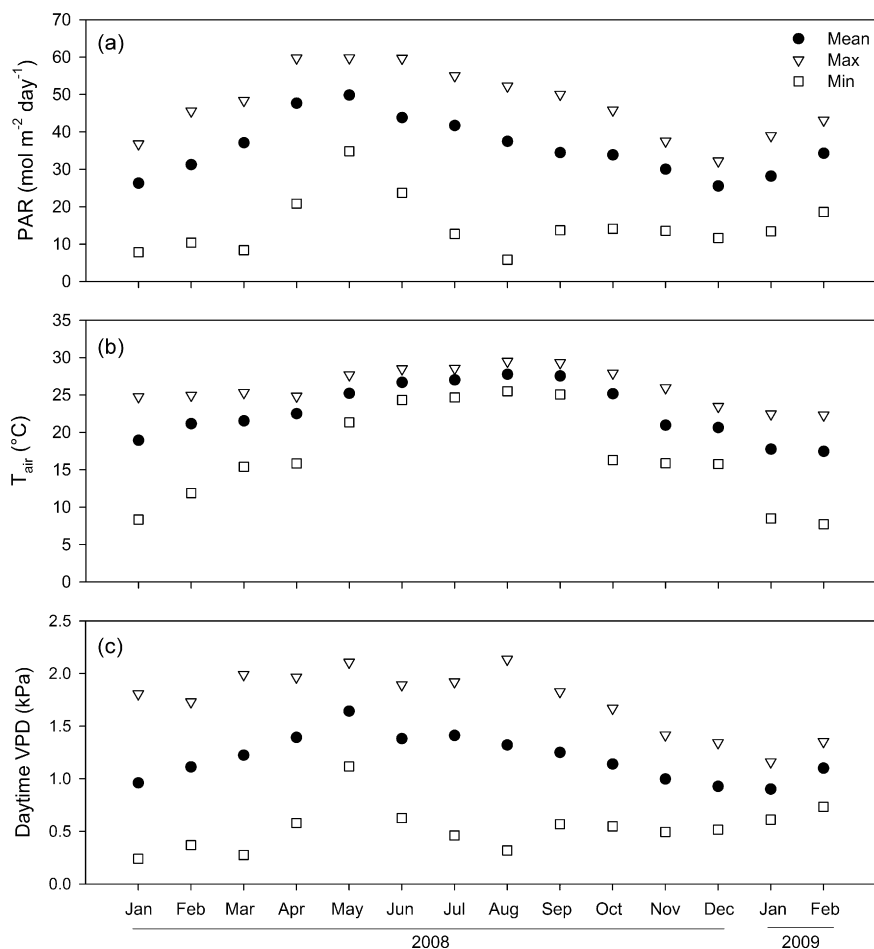
Fig. 2. Monthly mean, minimum, and maximum values of photosynthetically active radiation (PAR) (a), air temperature (T_{air}) (b), and daytime vapor pressure deficit (VPD) (c) during the study period. PAR values were calculated from daily sums, T_{air} data were calculated from daily means, and VPD was calculated from daily means during daylight hours only.

fully inundated until water reached this level. Dry season conditions occurred from January 1, 2008 to August 17, 2008 and from January 15, 2009 to the end of the study period, while wet season conditions occurred from August 18, 2008 to January 14, 2009 (Fig. 1b). The site was partially inundated for 22 days of the 14 month period, with water levels above the soil surface but <10 cm deep. Nineteen of these days occurred intermittently before onset of wet season and the remaining three days were at end of wet season when water levels dropped rapidly (Fig. 1b).

The dry season of 2008 was characterized by four abrupt increases in water level before water reached the soil surface (Fig. 1b). These spikes in water level coincided with precipitation events of 64, 94, 71, and 91 mm (Fig. 1a). Half-hourly data indicate that on the first two of these occasions, water levels increased by 50 cm over two hour periods. The onset of the 2008 wet season was later than in the past and coincided with the passage of a tropical storm over Florida. The 2008 wet season (148 days) was longer than the average over the last decade (121 days) and greater water depths were maintained throughout the season (Fig. 1b, NPS, 2009).

Daily changes in VWC mirrored changes in water level at the site (Fig. 1b, c) except during inundation, during which soils were saturated with a VWC of 0.75 m^3 m^{-3}. VWC reached its lowest point toward the end of the 2008 dry season (mid-May to mid-June) with levels approaching a minimum of 0.4 m^3 m^{-3}.

Seasonality, as defined by water levels, did not closely correspond with other meteorological variables. These tracked more closely with the climatically-driven seasonality of south Florida. Mean daily PAR varied predictably with time of year, and maxi-

mum light availability coincided with the end of south Florida's dry season and the early wet season (Fig. 2a). Mean monthly T_{air} ranged from 17.4 to 27.8 °C, with the lowest temperatures in January and February of 2008 and 2009, and the highest temperatures from June to September 2008 (Fig. 2b). Daily variation in T_{air} was low from May to September 2008, coinciding with the core of the south Florida wet season. Mean annual T_{air} for 2008 was 23.7 °C, marginally lower than the long-term regional mean. Mean daytime vapor pressure deficit (VPD) varied from 0.90 to 1.64 kPa, reaching a maximum in May 2008 (Fig. 2c). This peak coincided with a period of little rainfall, rising T_{air}, and low water levels (Fig. 1a and b and Fig. 2b and c). VPD was most variable and highest in the dry season, while variation and mean VPD largely declined once there was standing water at the site.

3.2. Environmental drivers of CO_2 exchange

Light response curves used to describe daytime NEE$_{raw}$ as a function of PAR indicate distinct differences in dry and wet season CO_2 uptake by the marsh (Fig. 3a–c). Higher rates of CO_2 uptake were observed in the dry season. Dry season NEE$_{max}$ was −5.54 μmol m^{-2} s^{-1} and was −1.75 μmol m^{-2} s^{-1} in the wet season. Dry season dark respiration was also higher than in the wet season (1.44 and 0.80 μmol m^{-2} s^{-1}, respectively). However, apparent quantum yield was higher in the wet season than the dry season (0.0114 and 0.0107, respectively). Both the dry and wet season models relating NEE$_{raw}$ to PAR were significant ($p < 0.0001$), but greater variance was described by the dry season
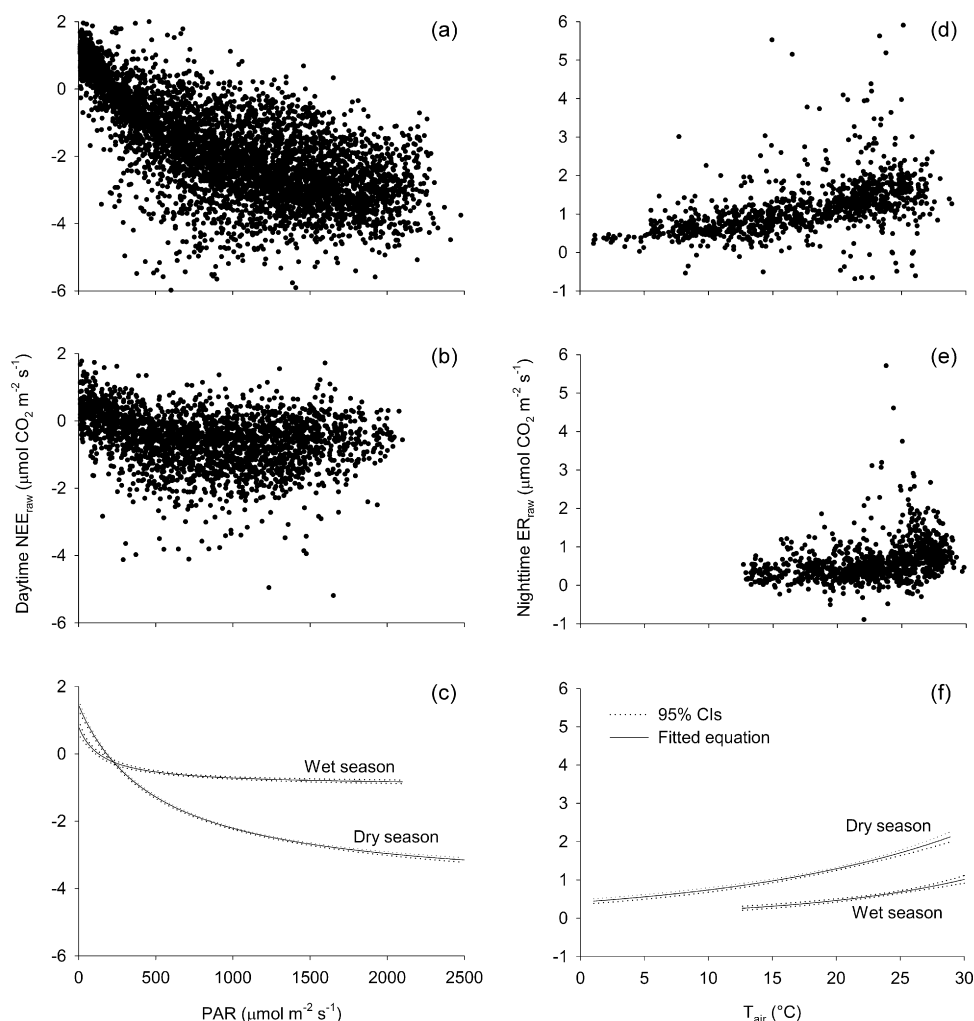
Fig. 3. Daytime raw net ecosystem exchange (NEE_{raw}, μmol CO_2 m^{-2} s^{-1}) in relation to photosynthetically active radiation (PAR) and nighttime raw ecosystem respiration (ER_{raw}, μmol CO_2 m^{-2} s^{-1}) in relation to air temperature (T_{air}). NEE_{raw} vs. PAR data are shown for the dry (a) and wet (b) seasons. The fitted models describing these relationships and 95% confidence intervals are also shown (c). The dry season model was $NEE_{raw} = ((-0.0107 \times PAR \times 5.54)/(0.0107 \times PAR + 5.54)) + 1.44$ ($R^2_{adj} = 0.53$, $p < 0.0001$) and the wet season model was $NEE_{raw} = ((-0.0114 \times PAR \times 1.75)/(0.0114 \times PAR + 1.75)) + 0.80$ ($R^2_{adj} = 0.16$, $p < 0.0001$). ER_{raw} vs. T_{air} data are shown for the dry (d) and wet (e) seasons in relation to air temperature (T_{air}). The fitted modes describing these relationships and 95% confidence intervals are also shown (f). The dry season model was $ER_{raw} = 0.4211$ exp $(0.0560 \times T_{air})$ ($R^2_{adj} = 0.24$, $p < 0.0001$) and the wet season model was $ER_{raw} = 0.0967$ exp $(0.0783 \times T_{air})$ ($R^2_{adj} = 0.09$, $p < 0.0001$).

model relative to the wet season model ($R^2_{adj} = 0.53$, 0.16, respectively).

Nighttime ER_{raw} examined as a function of T_{air} also showed that rates of CO_2 efflux were higher during dry season than the wet season (Fig. 3d–f), though the Q_{10} was slightly higher in the wet season (2.2) than in the dry season (1.8). Models for both seasons were significant ($p < 0.0001$), but little variation in ER was explained by T_{air} in either season. A greater temperature range during the dry season likely contributed to the higher explanatory power of the dry season model, relative to that of the wet season ($R^2_{adj} = 0.24$, 0.09, respectively).

Residuals analysis (data not shown) indicated that dry season NEE_{raw} residuals were significantly correlated with wind velocity, wind direction, T_{air}, and VPD ($p < 0.001$), though these relationships were weak (R^2_{adj} from 0.0093 to 0.0294). Wet season NEE_{raw} residuals were significantly correlated with wind velocity, T_{air}, VPD, and water depth ($p < 0.001$), though only water depth had a notable influence ($R^2_{adj} = 0.19$) on NEE_{raw}. Dry season ER_{raw} residuals were significantly correlated with wind direction ($p = 0.002$) and water depth ($p = 0.002$), but with low predictive power ($R^2_{adj} = 0.0074$, 0.0075, respec-

tively). Wet season ER_{raw} residuals were not significantly correlated with any environmental or meteorological variables.

3.3. Annual and seasonal patterns of CO_2 exchange

An annual CO_2 budget, determined for 2008, showed that net CO_2 uptake by the ecosystem, NEP, was -49.9 g C m^{-2} year^{-1}, while ER and GEP were 446.1 and 496.0 g C m^{-2} year^{-1}, respectively. Although the ecosystem was a net CO_2 sink over the course of the year, only cumulative dry season measurements showed net ecosystem CO_2 sequestration (Table 1). In the wet season, the

Table 1

Ecosystem carbon exchange at Taylor Slough, with total net ecosystem production (NEP, g C m^{-2}), ecosystem respiration (ER, g C m^{-2}), and gross ecosystem production (GEP, g C m^{-2}) summed for dry and wet periods of 2008 and annually.

	NEP (g C m^{-2})	ER (g C m^{-2})	GEP (g C m^{-2})
2008 Dry Season	−64.9	355.1	420.0
2008 Wet Season	15.0	91.0	76.0
2008 Total	−49.9	446.1	496.0

Table 2
Estimates of sampling uncertainty ($g\,C\,m^{-2}$) for NEP, ER, and GEP at monthly, seasonal, and annual time scales. Uncertainty estimates are the standard error of 100 Monte Carlo simulations and represent the error introduced by gap-filling procedures.

Month	NEP sampling uncertainty ($g\,C\,m^{-2}$)	ER sampling uncertainty ($g\,C\,m^{-2}$)	GEP sampling uncertainty ($g\,C\,m^{-2}$)
January 2008	0.3	0.5	0.3
February 2008	0.3	0.6	0.4
March 2008	0.4	0.5	0.5
April 2008	0.3	0.5	0.5
May 2008	0.5	1.4	1.0
June 2008	0.7	1.4	0.9
July 2008	0.5	0.4	0.5
August 2008	0.5	0.4	0.5
September 2008	0.4	0.7	0.5
October 2008	0.6	0.6	0.5
November 2008	0.2	0.4	0.2
December 2008	0.3	0.4	0.2
January 2009	0.3	0.3	0.3
February 2009	0.3	0.4	0.4
2008 Dry Season	1.5	3.2	2.2
2008 Wet Season	1.0	1.7	1.1
2008 Total	1.7	3.6	2.6

cumulative seasonal NEP indicated that the ecosystem was a CO_2 source to the atmosphere (Table 1). The dynamics of ecosystem CO_2 exchange clearly varied between seasons. ER accounted for 85% of GEP in the dry season and 120% of GEP in the wet season (Table 1). Examination of daily values show that in the dry season, 43% of variation in daily ER was explained by GEP ($p < 0.0001$), while only 12% was explained in the wet season ($p < 0.0001$, data not shown). A similar seasonal change in the relationship between NEP and GEP was found, where 55% and 28% of daily NEP was explained by GEP in the dry and wet seasons, respectively ($p < 0.0001$). Sampling uncertainty associated with NEP, ER, and GEP ranged from ± 1.0 to $\pm 3.6\,g\,C\,m^{-2}$ over these seasonal and annual time scales (Table 2).

The changes in seasonal relationships among NEP, ER, and GEP in the Taylor Slough marsh were most apparent when examined on a monthly basis (Fig. 4). Monthly GEP peaked in the mid to late dry season, between March and June 2008. From August to October 2008, monthly GEP fell substantially as the water level rose above the soil surface, and GEP remained low throughout the wet season. This pattern was driven by a coinciding decrease in ER and increase in NEP (Fig. 4). The wet season decrease in GEP was significantly related to water level ($p < 0.0001$, $R^2_{adj} = 0.3308$), a factor

that was less important in determining GEP during the dry season ($p = 0.0004$, $R^2_{adj} = 0.0409$) (Fig. 5a and b). As the wet season ended, GEP began to increase, a pattern that was dominated by increased ER (Fig. 4). Sampling uncertainty associated with monthly values of NEP, ER, and GEP was typically small ($\leq 0.5\,g\,C\,m^{-2}\,month^{-2}$), but was slightly higher ($0.5–1.4\,g\,C\,m^{-2}\,month^{-2}$) in May and June 2008 (Table 2). NEP and ER sampling uncertainty values were also somewhat elevated in February, September, and October 2008 ($\leq 0.7\,g\,C\,m^{-2}\,month^{-2}$). Higher sampling uncertainty tended to coincide with low predictive power in the NEE or ER gap-filling equations (Appendix A and Appendix B).

The seasonal influence of water level on GEP changed NEP substantially. Throughout the 2008 dry season, the ecosystem was predominantly a CO_2 sink (Fig. 6), but once water levels rose permanently above the soil surface, the ecosystem became a CO_2 source to the atmosphere. Maximum wet season losses of CO_2 occurred in October, with daily NEP reaching $>0.60\,g\,C\,m^{-2}\,day^{-1}$ in the first half of the month. By the middle of the wet season net CO_2 loss to the atmosphere began to decline, and by December the ecosystem was again a CO_2 sink. The ecosystem persisted as a sink through the end of the wet season, at which time another shift from CO_2 sink to source occurred. Early dry season losses of CO_2 reached $0.66\,g\,C\,m^{-2}\,day^{-1}$, but declined steadily through the end of February 2009 as subsurface water level rapidly fell (Fig. 1b, 6).

During the 2008 dry season, days when the ecosystem was a notable CO_2 source to the atmosphere ($>0.4\,g\,C\,m^{-2}$, $n = 4$) always coincided with one or both of the following: a rainfall event and/or low light availability (Fig. 1a, 6). At the beginning of the 2009 dry season there were 10 days in which the ecosystem was a notable CO_2 source, coinciding with a four week period during which VWC dropped from saturation to a point close to the 2008 dry season minimum (Fig. 1c, 6). The magnitude of these 2009 early dry season CO_2 losses to the atmosphere slightly exceeded the maximum wet season rates of NEP.

3.4. Leaf area index and aboveground biomass

Dry season indirect measurements of LAI averaged 1.74 ± 0.10, though this value also included standing dead leaves. LAI, modeled with dry season indirect measurements made at 20 cm intervals above the soil surface, yielded a significant predictive relationship between LAI and height (Fig. 7a, $R^2_{adj} = 0.7439$, $p < 0.0001$). Wet season indirect measurements of LAI, though more limited in scope, also resulted in a significant predictive relationship between LAI and height (Fig. 7a, $R^2_{adj} = 0.6611$, $p < 0.0001$). Equa-

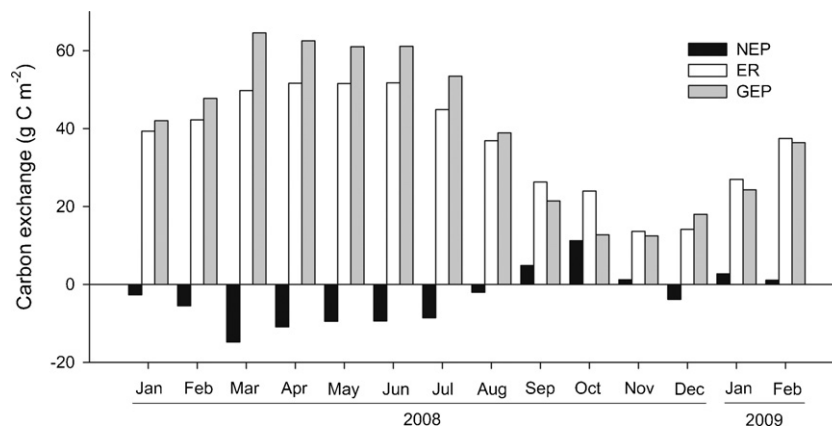**Fig. 4.** Monthly sums of carbon exchange, broken down into net ecosystem production (NEP, $g\,C\,m^{-2}\,month^{-1}$), ecosystem respiration (ER, $g\,C\,m^{-2}\,month^{-1}$), and gross ecosystem production (GEP, $g\,C\,m^{-2}\,month^{-1}$).
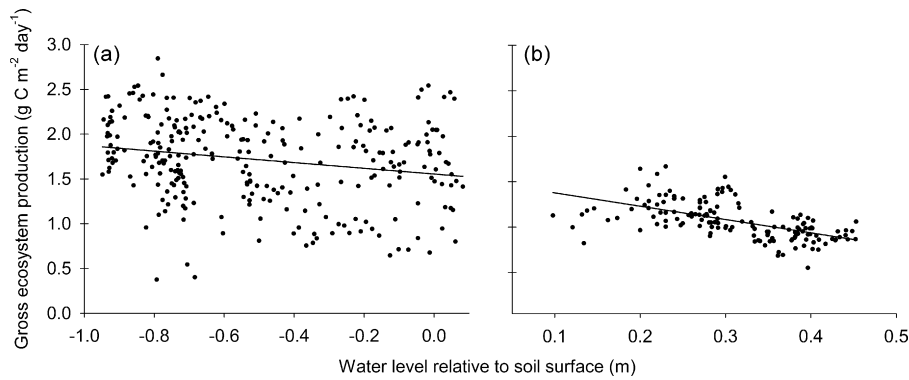
Fig. 5. Daily gross ecosystem production (GEP, g C m^{-2} day^{-1}) in relation to water level during the dry (a) and wet (b) seasons. GEP and water level were weakly related in the dry season (GEP = $-0.3196x + 1.5548$, where x is water level, $p = 0.0004$, $R^2_{adj} = 0.0409$) and more strongly related in the wet season (GEP = $-1.4663x + 1.0239$, $p < 0.0001$, $R^2_{adj} = 0.3308$).

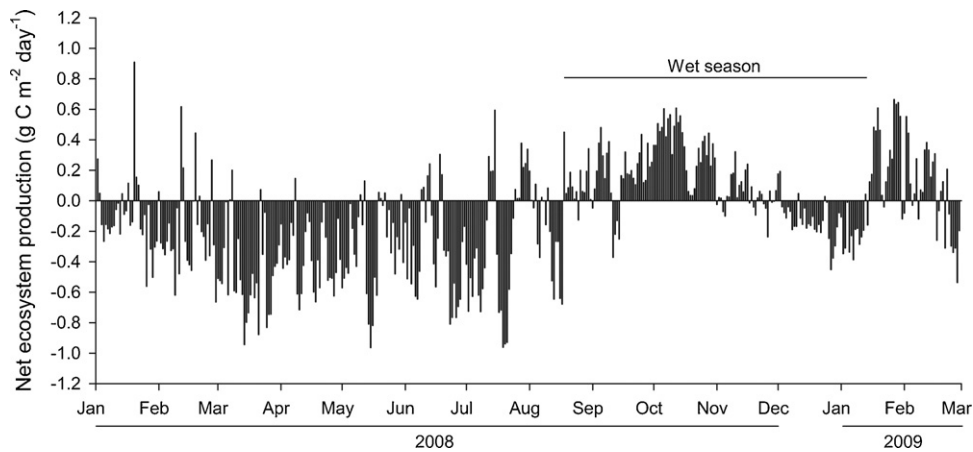**Fig. 6.** Daily sums of net ecosystem production (NEP, g C m^{-2} day^{-1}) during the study period. The 2008 wet season is depicted with a horizontal bar.
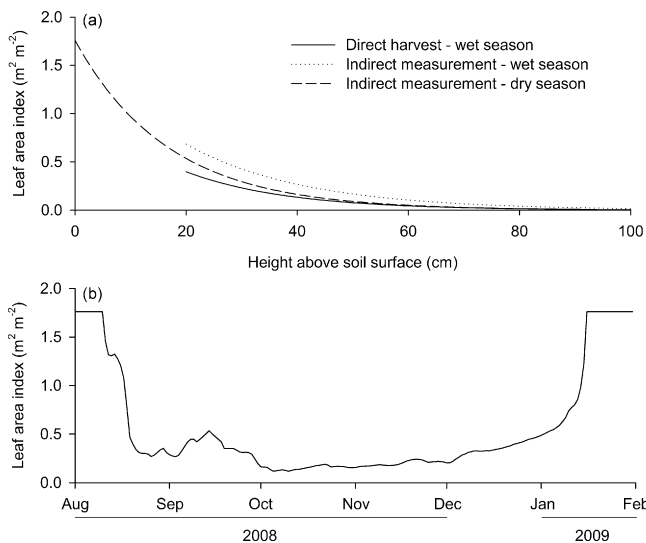

Fig. 7. Exponential decay functions relating leaf area index (LAI, m^2 m^{-2}) to height above the soil surface (a) and modeled LAI during the 2008 wet season (b). Plotted curves (a) reflect data from direct leaf area harvests in the wet season (solid line, LAI = $1.1890 \exp(-0.0547z)$, where z is height above the soil surface, $p < 0.0001$, $R^2_{adj} = 0.8472$) as well as indirect measurements made with a LAI-2000 in both the wet (dotted line, LAI = $1.7456 \exp(-0.0469z)$, $p < 0.0001$, $R^2_{adj} = 0.6611$) and dry (dashed line, LAI = $1.7611 \exp(-0.0596z)$, $p < 0.0001$, $R^2_{adj} = 0.7439$) seasons. The dry season indirect measurement decay function was used to model above-water LAI (b) during the 2008 wet season using water depth data.

tion parameters for both the dry and wet seasons were similar, yielding comparable estimates of total LAI (1.76 and 1.75, respectively). Direct harvest data indicated that indirect measurements slightly overestimated true LAI at all canopy heights (Fig. 7a). Further, these data showed that only $54 \pm 3\%$ of the leaf area was comprised of living tissue at a height of 20 cm above the soil surface. The proportion of living tissue increased with height (data not shown).

The dry season predictive relationship between LAI and height above the soil surface was selected to estimate LAI when there was standing water at the site. This model was chosen because it had the largest sample size and was very similar to the wet season indirect measurement model. Estimated above-water LAI decreased rapidly with the onset of the wet season and was <0.4 for most of the wet season (Fig. 7b). However, this is likely an overestimate of wet season above-water LAI, given the large amount of standing dead leaf area and tendency for indirect measurements to underestimate true LAI in this ecosystem (Fig. 7a).

C. jamaicense aboveground biomass did not vary significantly among months over the nine year period from January 2000 to January 2009 (Table 3). Variation in biomass among years was relatively high and during the study period bi-monthly variation was also high. Mean annual aboveground biomass was slightly higher during the study period than in the preceding eight years $(206.63 \pm 16.02 \, \text{g m}^{-2}$ vs. $171.35 \pm 7.19 \, \text{g m}^{-2})$. The long-term mean for total *C. jamaicense* aboveground carbon content was $83.58 \pm 3.51 \, \text{g C m}^{-2}$ and was $100.80 \pm 7.82 \, \text{g C m}^{-2}$ during our study period.

Table 3
Mean ±1 SE *C. jamaicense* aboveground biomass (g m^{-2}) at the Taylor Slough site from January 2000 to January 2009 and the study period. No significant seasonal differences in aboveground biomass were found over the nine year period.

Time period	Mean *C. jamaicense* aboveground biomass (g m^{-2})					
	January	March	May	July	September	November
2000–2009	181.27 ± 22.92	158.29 ± 13.71	160.81 ± 13.27	201.81 ± 10.66	174.69 ± 13.32	177.58 ± 20.25
2008	263.72	168.43	154.47	237.69	246.39	194.65
2009	181.06					

4. Discussion

4.1. Environmental drivers of CO_2 exchange

Significant seasonal differences were found in light and temperature responses for daytime NEE_{raw} and nighttime ER_{raw}, respectively (Fig. 3c and f). Both NEE_{raw} and ER_{raw} were depressed in the wet season relative to the dry season, and this pattern is opposite that found in other wetlands characterized by dry and wet seasons (Morison et al., 2000; Jones and Humphries, 2002). NEE_{raw} and ER_{raw} were well correlated with PAR and T_{air}, respectively, during the dry season, but these relationships were weaker in the wet season.

Residuals analysis indicated that water level was of central importance in determining NEE_{raw} in the wet season, but not the dry season. The increased influence of water level on NEE_{raw} explains the poor wet season relationship between NEE_{raw} and PAR. Other environmental variables related to NEE_{raw}, including wind velocity and direction, explained little variation (0.1 to 3%) in the data. Water level was marginally related to ER_{raw} in the dry season and unrelated in the wet season. Beyond T_{air}, ER_{raw} was only weakly influenced by the environmental variables measured in both the dry and wet seasons, likely due to the low within-season variance of ER_{raw} (Fig. 3d and e).

A decrease in the predictive power of the NEP–GEP relationship from 55% to 28% between the dry and wet seasons highlights the moderating influence of inundation on relationships that are usually highly predictable. Similar declines in predictive power were found for the light and temperature response curves described above and for the ER–GEP relationship. The onset of the wet season in this short-hydroperiod marsh clearly influences the relationships among NEP, ER, and GEP. Of particular note, are the seasonal changes in the ER–GEP relationship.

Dry season daily ER was significantly positively related to GEP, indicating that photosynthetic activity was as important as T_{air} in determining ER. The dry season ratio of ER to GEP (0.85) was similar to the annual average (0.83) reported by Law et al. (2002) across a wide range of terrestrial ecosystems. Although the magnitude of annual ER and GEP in the Everglades was far lower than that reported in many other ecosystems, the ratio of ER to GEP was preserved. However, with the onset of the wet season this ratio increased to 1.20, a value more consistent with that observed in high-latitude forests (Law et al., 2002). The unexpected nature of wet-season ecosystem CO_2 exchange dynamics can be best understood by examining the roles of various short-hydroperiod marsh ecosystem components.

4.2. The role of water in ecosystem CO_2 exchange

Water level clearly had a significant effect on the dynamics of CO_2 exchange, as the ecosystem shifted from CO_2 sink to source when water rose above the soil surface (Table 1, Fig. 1b, 4). This shift, highlighted by the strong negative relationship between GEP and water level in the wet season (Fig. 5b), has been reported in few wetland ecosystems (e.g. Dusek et al., 2009). Wet seasons in most temperate wetlands coincide with the growing season, thus periods of maximum CO_2 uptake (Roulet et al., 2007; Bonneville et al.,

2008; Rocha and Goulden, 2008). In the Everglades, aboveground NPP in the dominant macrophyte, *C. jamaicense*, is relatively aseasonal (Table 3, Childers et al., 2006) and only minor changes in LAI were found between seasons (Fig. 7), so it is unlikely that seasonal variation in CO_2 exchange is related to vegetative growth cycles.

Instead, the relatively short stature of the plant canopy and plant physiological flooding responses in this Everglades marsh play important roles in the ecosystem's response to rising water levels. During the wet season, much of the site's leaf area was submerged, and above-water LAI was less than 0.4 (Fig. 7). Reduced above-water leaf area clearly limited wet season gas exchange and, though carbon uptake is possible in submerged aquatic plant leaves, these tissues are often shaded or surrounded by periphyton. Additional photosynthetic and respiratory limitations on the site's dominant macrophytes were imposed by flooding. *C. jamaicense* and *M. capillaris* are flood-tolerant species that contain aereynchyma cells, but soil hypoxia or anoxia can decrease overall plant metabolic activity and force stomatal closure (Chabbi et al., 2000; Jackson, 2002). Wet season gas exchange measurements made on *C. jamaicense* and *M. capillaris* showed a significant reduction ($p \le 0.02$) in the stomatal conductance and photosynthetic rates of submerged plants relative to those growing on adjacent dry ground (S.F. Oberbauer, unpublished data). This indicates that flooding decreased the capacity for CO_2 uptake in these species.

In addition to the role of vegetation in determining CO_2 exchange at this site, periphyton was also important during the wet season. Periphyton in short-hydroperiod Everglades marshes is known to lie dormant for months during the dry season, but exhibits an immediate metabolic response to rewetting (Thomas et al., 2006a). However, a ~2–3 month period of inundation is necessary before substantial periphyton growth is initiated in short-hydroperiod marl marshes (Thomas et al., 2006b; J.L. Schedlbauer, personal observation). This time lag coincides with the pattern observed in daily NEP during the wet season (Fig. 6). Following the ecosystem's shift from CO_2 sink to source with the onset of the wet season, NEP was predominantly positive for the first 2.5 months of the season. After this time, daily NEP declined, and the ecosystem became a CO_2 sink for the final six weeks of the wet season. These negative NEP values at the end of the wet season were likely linked to increased periphyton growth and CO_2 uptake activity. Seasonal peaks in periphyton GPP and photosynthesis have been observed ~2 months into the wet season in short-hydroperiod Everglades marshes (Thomas et al., 2006b). However, the late wet season increase in marsh CO_2 uptake was not large enough to shift cumulative wet season NEP from CO_2 source conditions.

Geochemical fixation of CO_2 as calcium carbonate is another key component of wet season CO_2 exchange in this Everglades marsh. As CO_2 diffuses into the water column it reacts with water to form carbonic acid, which then dissociates to form bicarbonate. These reactions are reversible and vary diurnally with dissolved CO_2 concentration. The production and consumption of hydrogen ions in these reactions causes pH to vary with the predominant form of inorganic carbon in the water column. CO_2 predominates at low pH (<6.5) while bicarbonate predominates at higher pH (6.5–10.5) (Vymazal, 1994). As periphyton and macrophyte photosynthesis proceeds during daylight hours, the concentration of CO_2 in the

water column declines and pH increases. This daytime shift in water chemistry toward bicarbonate leads to the precipitation of calcium carbonate in the calcium-rich waters of short-hydroperiod Everglades marshes. These reactions are reversed at night as respiration increases the dissolved CO_2 concentration and forces calcium carbonate back into solution. The balance between calcium carbonate precipitation and dissolution will affect the overall carbon balance of these marshes.

Gleason and Spackman (1974) found that water pH in a short-hydroperiod Everglades marsh varied diurnally from a low of 7.59 before sunrise to a maximum of 8.22 in the late afternoon. Over the same time period, the partial pressure of CO_2 in the water column declined from 3981 to 692 ppm (Gleason and Spackman, 1974). These patterns suggest considerable diurnal shifts in the carbonate equilibrium reactions influencing calcium carbonate precipitation and dissolution. Given evidence of continuous CO_2 supersaturation in the water column, changes in carbonate equilibrium reactions may not be immediately captured by eddy covariance methods. The degree of equilibration between atmospheric and dissolved CO_2 will be influenced by CO_2 concentrations, as well as wind speed. Future studies of CO_2 exchange dynamics in short-hydroperiod Everglades marshes should include measurements of pH and dissolved CO_2 to clarify the degree of coupling existing between atmospheric and aquatic CO_2 exchange.

The current magnitude of geochemical CO_2 fixation in short-hydroperiod marshes is unknown, though historical marl accretion rates of 0.8 mm year^{-1} have been reported in Everglades wetlands close to the Atlantic coast (Gaiser et al., 2006). These accretion rates are from the period prior to extensive water management in the Everglades and equate to a deposition of 70 g C m^{-2} year^{-1}, given mean bulk density and soil carbon content at the Taylor Slough study site (Childers, 2005; J.L. Schedlbauer, unpublished data). The data presented here suggest that current annual rates of marl accretion are lower than in the past, a finding that may be related to water management activities that have decreased hydroperiods in Everglades marl marshes (Davis et al., 2005).

The slow flow of water through the Taylor Slough marsh introduces potential non-atmospheric sources of carbon to the ecosystem in the forms of dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and particulate organic matter (POM). During the wet season, DIC, DOC, and POM may have moved through the footprint area. However, it is unlikely that lateral movement of carbon in the water column affected the overall CO_2 balance of this marsh. The area surrounding the tower footprint is a continuous marl marsh and surface water flow rates in these marshes are ~0.5 to 0.8 cm s^{-1} (Schaffranek and Ball, 2001). Therefore, inflows and outflows of DIC, DOC, and POM in the footprint area were likely equal.

4.3. CO_2 exchange during seasonal transitions

Seasonal transitions in NEP were notably different at the beginning and end of the wet season (Fig. 6). At the onset of the wet season, water level gradually rose to fully inundated conditions over the course of two months (Fig. 1b), and the marsh fluctuated between CO_2 source and sink conditions as the water level rose and fell from the soil surface. At the end of the wet season when the marsh was a CO_2 sink, the rapid drop in water level below the soil surface coincided with an immediate shift from CO_2 sink to source conditions (Fig. 1b, 6). Source conditions persisted for over a month at the end of the wet season. It is probable that a flooding response by macrophytes dominated changes in daily NEP at the outset of the wet season, while respiring periphyton and respiration from the re-aerated soil dominated NEP at the end of the wet season. Once periphyton was mostly desiccated and decomposition of highly labile carbon produced during the

wet season declined, CO_2 uptake by macrophytes again dominated NEP.

Although dry season conditions (i.e., water level <10 cm above the soil surface) predominated after mid-January 2009, the ecosystem was a strong CO_2 source (NEP > 0.4 g C m^{-2} day^{-1}) to the atmosphere. This period was characterized by rapidly declining VWC (Fig. 1c), in contrast to days during the 2008 dry season when the marsh was a strong source of CO_2 to the atmosphere. In the dry season there were trigger events, principally low light conditions, that coincided with the net loss of CO_2 from the ecosystem. These short-lived, dry season CO_2 source events were of similar magnitude to those observed during seasonal source-sink transitions (Fig. 6), but the mechanisms involved in the induction of these events were different. Daily rates of NEP in this short-hydroperiod Everglades marsh appear to be highly sensitive to environmental changes, and long-term EC data will help to further elucidate these relationships.

4.4. Annual ecosystem CO_2 exchange

Meaningful annual comparisons of Everglades ecosystem CO_2 exchange with other tropical and subtropical wetlands are difficult because most EC studies have been confined to short time periods (weeks) spanning seasonal extremes in water level (e.g. Morison et al., 2000; Jones and Humphries, 2002). However, short-term data from these studies show NEE that is more than four times greater than the maximum values observed in this Everglades marsh (Fig. 3a,b). For example, maximum NEE of 30–35 μmol m^{-2} s^{-1} was recorded in Amazonian floodplains (Morison et al., 2000), while maximum NEE of 24 μmol m^{-2} s^{-1} was found in African papyrus (*Cyperus papyrus*) wetlands (Jones and Humphries, 2002). Further, the highest rates of CO_2 uptake in these tropical wetlands were found during periods with the highest water levels.

In relation to temperate wetlands where year-round measurements of EC are more common, annual values of ecosystem CO_2 exchange in this short-hydroperiod marsh were quite low (Bonneville et al., 2008; Rocha and Goulden, 2008; Dusek et al., 2009). Of particular note was the low GEP (496 g C m^{-2} year^{-1}) in the Everglades, a value that was constrained by the limitation of CO_2 uptake during the wet season (Table 1, Fig. 5b). Recent EC studies of temperate wetlands show GEP values ranging from 831 to 1639 g C m^{-2} year^{-1} at sites in southern California and Ottawa, Ontario (Bonneville et al., 2008; Rocha and Goulden, 2008). GEP in both of these regions was limited by the growing season, yet it was much higher than in the Everglades. Although wetlands are among the most productive ecosystems on earth, short-hydroperiod Everglades marshes appear to be an exception.

An additional factor in the overall carbon balance of the Everglades is methane (CH_4) flux, a component beyond the scope of this study. As a wetland that is saturated for 4–5 months per year, CH_4 emission will contribute to wet season carbon losses from the ecosystem. Chamber measurements show that wet season CH_4 fluxes from short-hydroperiod Everglades marshes average 45 mg m^{-2} day^{-1} (Bartlett et al., 1989). Future ecosystem carbon balance research should account for CH_4 fluxes, particularly because seasonal changes have not yet been quantified.

4.5. Productivity in short-hydroperiod Everglades marshes

Previous work in Everglades marshes suggesting high rates of productivity was not substantiated by the EC data collected during the 14 months of the present study. Monthly chamber measurements of NEE and ER at the tower site corroborate the EC data presented here and further call into question prior estimates of productivity (J. Munyon, unpublished manuscript). Though there is undoubtedly annual variation in marsh productivity, important climatic drivers including temperature and precipitation were

within historical bounds during 2008. In general, daily rates of CO_2 exchange and maximum NEE values were small in both the dry and wet seasons. While interannual variation in ecosystem CO_2 exchange is yet to be documented in this ecosystem, existing EC data suggest that this marsh is at the extreme low end of wetland productivity. The classification of the Everglades as an oligotrophic ecosystem is supported by the findings presented here, but is in contrast to previously reported NPP data.

Mean periphyton production in the marsh surrounding the tower site was calculated to be $1276 \, g \, C \, m^{-2} \, year^{-1}$ between 2001 and 2004 (Ewe et al., 2006), while total NEP in 2008 was $50 \, g \, C \, m^{-2} \, year^{-1}$. Climatic variation between these time periods is unlikely to have been great enough to account for such a large discrepancy in productivity. Instead, scaling errors associated with the earlier dataset, based on infrequent (1–3 times during the wet season) biological oxygen demand measurements of periphyton, may be the primary source of this difference. NPP estimates for *C. jamaicense*, the dominant macrophyte at the site, can more easily be reconciled with the EC data. From 2001–2004, *C. jamaicense* aboveground NPP averaged $124 \, g \, C \, year^{-1}$ (Ewe et al., 2006). While this number is relatively large, productivity in this species is dominated by leaf turnover rather than biomass accrual (Childers et al., 2006). Therefore, *C. jamaicense* does not play a major role in carbon accumulation in this ecosystem.

In addition to nutrient limitation in the Everglades, the accumulation of standing dead leaves may be related to low productivity. Evidence of NEE limitation by standing litter has been found in a temperate wetland (Rocha et al., 2008), and could be important at this site during the dry season given the large quantity of standing dead leaves. Approximately 23% of the total canopy height in this marsh is shaded by standing litter. A disturbance event, such as the large fires that occasionally occur in Everglades marl marshes, would be necessary to substantially alter the amount of litter in short-hydroperiod marshes.

5. Conclusions

These findings distinguish the Everglades from most other wetlands where maximum CO_2 uptake occurs in the wet season and annual values of GEP are high. No evidence was found to support prior research indicating extremely high rates of NPP in the Everglades. Although wetlands are among the most productive ecosystems in the world, the short-hydroperiod oligotrophic Everglades prove to be an exception.

During the period of study this Everglades short-hydroperiod marsh was a small CO_2 sink. CO_2 fluxes were of small magnitude throughout the year, but were substantially reduced in the wet season. This led to a seasonal ecosystem shift from CO_2 sink to source with the beginning of the wet season. While light and temperature were key factors in determining ecosystem CO_2 exchange in the dry season, inundation led to a deterioration of these relationships. Water level was of central importance in determining GEP during the wet season, and high water levels substantially reduced macrophyte photosynthetic activity. Future research should focus on quantifying interannual variability in ecosystem CO_2 exchange and on the physiological responses of macrophytes and periphyton to seasonality. These data would improve knowledge of CO_2 exchange dynamics and aid in the prediction of future ecosystem responses to water management and climate change.

As water management in the Everglades is altered by the implementation of CERP, it is expected that hydroperiod will increase and water levels will be deeper. These changes in management may have unintended consequences for short-hydroperiod marshes by decreasing the capacity of these ecosystems to sequester CO_2. A reduction in the length of the dry season, during which the ecosystem is a CO_2 sink, will directly affect the annual balance of NEP. As climate change proceeds, anticipated reductions in south Florida's wet season rainfall could partly counteract the management changes imposed by CERP. Nonetheless, this ecosystem is a small CO_2 sink and CO_2 source-sink dynamics in this marsh are sensitive to environmental changes. Alterations in water management activities should be carefully considered if the CO_2 sequestration capacity of this ecosystem is to be maintained, particularly in light of the large spatial extent of short-hydroperiod Everglades marshes.

Appendix A.

Model parameters (fitted value ± one SE) and statistics for the nonlinear regressions (Eq. (1)) used to gap-fill daytime net ecosystem exchange (NEE) data. August was divided into two periods reflecting dry (early August) and wet (late August) season conditions. Such a division was not found to be necessary for January 2009, the other month spanning dry and wet season conditions. All regressions were significant ($p < 0.0001$).

Month	Model parameters			Statistics			
	α	NEE_{max}	ER	R^2_{adj}	n	Residual mean	Residual SD
January 2008	0.009 ± 0.001	5.68 ± 0.25	1.17 ± 0.14	0.68	535	-3.00×10^{-10}	0.78
February 2008	0.010 ± 0.001	5.86 ± 0.22	1.18 ± 0.15	0.69	521	8.64×10^{-10}	0.75
March 2008	0.021 ± 0.005	5.44 ± 0.26	1.76 ± 0.30	0.53	453	1.48×10^{-9}	0.98
April 2008	0.013 ± 0.002	5.50 ± 0.17	1.64 ± 0.18	0.61	651	4.00×10^{-10}	0.90
May 2008	0.010 ± 0.001	6.05 ± 0.18	1.63 ± 0.17	0.65	683	2.72×10^{-10}	0.84
June 2008	0.015 ± 0.003	6.83 ± 0.25	2.00 ± 0.33	0.57	561	-1.39×10^{-10}	1.10
July 2008	0.018 ± 0.004	6.10 ± 0.30	2.10 ± 0.36	0.46	554	6.69×10^{-9}	1.24
Early August 2008	0.018 ± 0.006	5.90 ± 0.46	1.93 ± 0.57	0.43	264	1.23×10^{-9}	1.20
Late August 2008	0.012 ± 0.009	1.99 ± 0.34	0.85 ± 0.38	0.18	209	1.08×10^{-8}	0.88
September 2008	0.018 ± 0.007	2.42 ± 0.22	1.36 ± 0.25	0.27	520	2.51×10^{-9}	0.78
October 2008	0.009 ± 0.009	1.02 ± 0.27	0.77 ± 0.30	0.06	528	4.26×10^{-9}	0.70
November 2008	0.004 ± 0.002	0.87 ± 0.10	0.21 ± 0.12	0.14	538	-7.29×10^{-10}	0.43
December 2008	0.005 ± 0.001	2.22 ± 0.16	0.35 ± 0.13	0.37	437	2.07×10^{-10}	0.55
January 2009	0.015 ± 0.004	3.19 ± 0.21	1.50 ± 0.25	0.33	559	1.15×10^{-9}	0.85
February 2009	0.007 ± 0.002	4.13 ± 0.23	1.08 ± 0.17	0.47	536	1.94×10^{-10}	0.85

Appendix B.

Model parameters (fitted value ± one SE) and statistics for the regressions used to gap-fill ecosystem respiration (ER) data. Models were fit to bi-monthly datasets, given the limited number of raw half-hourly ER data points. An exponential function relating ER to air temperature (T_{air}) $ER = a \exp(b\, T_{air})$ was fit to data for all months except for July–August 2008 (*). A significant predictive relationship between ER and T_{air} did not exist for the July–August 2008 data, so the linear regression, $ER = a$ water level $+ b$, relating ER to water level was used for this period. Breaks in bi-monthly periods were allowed to vary to accommodate shifts between the dry and wet seasons at the site. Specifically, late August 2008 data was included with the September–October 2008 bi-monthly period and early January 2009 data were included with the November–December 2008 bi-monthly period. All regressions were significant ($p \leq 0.05$).

Month	Model parameters		Statistics			
	a	b	R^2_{adj}	n	Residual mean	Residual SD
January–February 2008	0.31 ± 0.04	0.07 ± 0.01	0.27	364	-1.85×10^{-4}	0.54
March–April 2008	0.28 ± 0.03	0.08 ± 0.01	0.54	250	-2.57×10^{-3}	0.38
May–June 2008	0.88 ± 0.27	0.02 ± 0.01	0.02	130	-1.62×10^{-4}	0.50
*July–August 2008	-4.46 ± 1.86	1.09 ± 0.20	0.10	46	-1.22×10^{-10}	0.96
September–October 2008	0.15 ± 0.05	0.06 ± 0.01	0.05	587	1.89×10^{-4}	0.52
November–December 2008	0.18 ± 0.06	0.04 ± 0.01	0.02	462	-2.52×10^{-4}	0.39
January–February 2009	0.42 ± 0.05	0.06 ± 0.01	0.15	308	-9.43×10^{-4}	0.61

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