Carbon dioxide exchange rates from short- and long-hydroperiod Everglades freshwater marsh

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[1]   Everglades freshwater marshes were once carbon sinks, but human-driven hydrologic changes have led to uncertainty about the current state of their carbon dynamics. To investigate the effect of hydrology on CO_2 exchange, we used eddy covariance measurements for 2 years (2008–2009) in marl (short-hydroperiod) and peat (long-hydroperiod) wetlands in Everglades National Park. The importance of site, season, and environmental drivers was evaluated using linear and nonlinear modeling, and a novel method was used to test for temporally lagged patterns in the data. Unexpectedly, the long-hydroperiod peat marsh was a small CO_2 source (19.9 g C m^{-2} from July to December 2008 and 80.0 g C m^{-2} in 2009), and at no time over the study period was it a strong sink. Contrary to previous research suggesting high productivity rates from a short-hydroperiod marsh, we estimated that the marl site was a small CO_2 sink in 2008 (net ecosystem exchange [NEE] = −78.8 g C m^{-2}) and was near neutral for carbon balance in 2009. In addition, both sites had relatively low gross ecosystem exchange (GEE) over the 2 years of this study. The two sites showed similar responses for NEE versus air temperature, ecosystem respiration (R_{eco}) versus air temperature, and R_{eco} versus water depth, although the magnitude of the responses differed. We saw small lags (30 min in most cases) between carbon fluxes and environmental drivers. This study is foundational for understanding the carbon balance of these ecosystems prior to implementation of the planned Everglades restoration of historical water flow that will likely alter the future trajectory of the carbon dynamics of the Everglades as a whole.

1.   Introduction

[2] Anthropogenic perturbations have caused a massive decrease in the area of wetlands across the world. In the United States alone nearly 50% of wetlands have been lost [*Gibbs*, 2000], while many of the remaining wetlands are degraded and/or under further pressure from anthropogenic disturbance [*Wilen and Frayer*, 1990; *Michener et al.*, 1997; *Zedler and Kercher*, 2004; *Mitsch and Gosselink*, 2007]. The loss of these ecosystems may have considerable effects on regional, continental, and global carbon budgets because wetlands store approximately 225 Pg of carbon globally [*Intergovernmental Panel on Climate Control* (*IPCC*), 2007]. This large carbon pool is ~10% of the total terrestrial soil carbon pool [*Whiting and Chanton*, 2001; *Hadi et al.*, 2005; *Davidson and Janssens*, 2006; *Mitsch and Gosselink*, 2007].

[3] Additional uncertainties surface regarding the future stability of wetland carbon dynamics when climate change and its complex interactions with human management are considered. The Intergovernmental Panel on Climate Change [*IPCC*, 2007] predicts that average global temperatures will rise approximately 1.8°C by the year 2099, accompanied by increases in evaporative demand and precipitation extremes [*Bates et al.*, 2008]. Changes in rainfall frequency and intensity along with evaporation rates will significantly change wetland hydrology, i.e., water table depths and periods of

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inundation, which will strongly affect carbon dynamics in these ecosystems [*Bubier et al.*, 2003; *Blodau et al.*, 2004]. To date, studies focused on wetland CO_2 flux in response to varying water levels have produced mixed findings; *Updegraff et al.* [2001] and *Altor and Mitsch* [2008] found no relationship between changing water table depths and CO_2 emissions. In contrast, *Blodau et al.* [2004] showed an increase in CO_2 emissions and a 24–42% decrease in photosynthetic activity (carbon uptake) with lower water tables. However, these studies, and much of the past wetland carbon research has focused on temperate and high-latitude regions [*Chapin et al.*, 2000; *Zhuang et al.*, 2006; *Riutta et al.*, 2007; *Bonneville et al.*, 2008; *Sulman et al.*, 2009]. Wetlands of the subtropical and tropical regions have been largely unstudied, but are also facing similar fates in the near future.

[4] One such subtropical wetland, the Florida Everglades, is the largest subtropical wetland in the United States (>6000 km^2). As a result of urbanization and agricultural expansion, the Everglades system has been reduced to half of its historical size [*Gunderson*, 1994]. Although the greater Everglades ecosystem is oligotrophic and geologically young, historically large accumulations of peat once occurred in marshes with long hydroperiods, which attests to the high productivity that can occur in the dominant emergent vegetation [*Stephens and Johnson*, 1951; *Gleason and Stone*, 1994]. In other Everglades marshes where hydroperiods are too short to support peat formation, calcium carbonate precipitated during photosynthesis by submerged periphyton microalgae and macrophytes is a dominant component of the marl soils [*Gleason*, 1972; *Gleason and Spackman*, 1974; *Browder et al.*, 1994]. This variation in substrate formation in conjunction with inundation periods in the Everglades has lead to the development of two primary types of marsh systems, those with marl soils under short hydroperiods (inundation less than 6 months per year) and those with peat soils under long hydroperiods. In conjunction with their development these two marsh systems have been shown to have unique and important carbon dynamics.

[5] Understanding the carbon dynamics of Everglade wetlands becomes increasingly important with the implementation of the Comprehensive Everglades Restoration Plan (CERP, http://www.evergladesplan.org/). One of the aims of the CERP is to reestablish more natural water flow patterns into the Everglades by eliminating or moving water control structures which will have an influence on the structure and function of these ecosystems (CERP, 2000, http://www.evergladesplan.org). Previous studies have shown that alterations in hydroperiod can cause rapid changes in Everglade plant communities [*Armentano et al.*, 2006] and thus significantly alter carbon dynamics. Given these impending changes to hydroperiod, the CO_2 exchange of Everglades wetlands will change in the near future, adding to the uncertainty in the magnitude, timing, and sign of their carbon balance.

[6] To date, studies of carbon dynamics in the Everglades have shown mixed results. Net primary production of benthic and free floating algal mat communities (periphyton) are extremely variable over time and space, with some sites having aboveground net primary production (ANPP) rates >600 g C m^{-2} yr^{-1} [*Ewe et al.*, 2006]. *Daoust and Childers*

[1998] reported sawgrass ANPP of 1495 $\pm$ 445 g C m^{-2} yr^{-1} while *Davis* [1989] observed ANPP between 401 and 1517g C m^{-2} yr^{-1}. Based on these high ANPP values, one might expect high net ecosystem C storage in the Everglades. However, a 1 year eddy covariance study by *Schedlbauer et al.* [2010] showed that a short-hydroperiod freshwater marsh was a small CO_2 sink, -49.9 g C m^{-2} yr^{-1}. However, there are no comparative, multiyear carbon exchange studies in Everglades freshwater ecosystems, which makes evaluation of interannual variability in carbon dynamics difficult.

[7] To investigate the drivers and rates of carbon exchange in Everglades freshwater marshes, a 2 year field study (January 2008 to December 2009) was conducted at two sites with contrasting hydroperiods using the eddy covariance (EC) technique. Through the comparison of these two ecosystems we evaluated the overall effects of long and short hydroperiods on CO_2 exchange rates in Everglades freshwater marshes. Our objective was to provide an initial assessment of CO_2 exchange between the atmosphere and the land surface, prior to the implementation of CERP.

[8] In this study we hypothesized that (1) long-hydroperiod marshes would be greater CO_2 sinks compared to short-hydroperiod marshes as a result of reduced respiratory losses with long periods of inundation and (2) effects of seasonality on ecosystem carbon dynamics will be greatest at the short-hydroperiod marsh because of the large differences in soil aeration, hydrology, and thermal regimes that accompany the wet and dry seasons.

2. Methods

2.1. Study Site

[9] Although the Everglades are located in a subtropical region, the climate is classified as tropical with distinct annual wet and dry seasons during the summer and winter, respectively [*Duever et al.*, 1994; *Beck et al.*, 2006; *Rohli and Vega*, 2008]. Water inputs are naturally delivered through precipitation and are 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, tropical storms, and hurricanes in the wet season [*Duever et al.*, 1994]. Mean annual precipitation is 1430 mm (National Climatic Data Center, NCDC, http://www.ncdc.noaa.gov/) with $\sim$60% of rainfall occurring at the height of the rainy season (June to September) and $\sim$25% in the dry season (November to April) with variability among transitional months [*Duever et al.*, 1994]. Mean annual temperature of the Everglades is 23.9°C, with the mean monthly minimum (18.1°C) in January and monthly maximum (29.4°C) in August [*National Climatic Data Center (NCDC)*, 2010].

[10] We conducted our study in two Everglades freshwater marsh sites with contrasting hydroperiods, Taylor Slough (TS) and Shark River Slough (SRS; Figure 1). Both are oligotrophic marshes located in Everglades National Park (ENP) and are part of the Florida Coastal Everglades (FCE) Long Term Ecological Research (LTER) program (Taylor Slough/ Panhandle site 1b and Shark River Slough site 2, respectively). The TS site (25°26′16.5″N, 80°35′40.68″W) is a short-hydroperiod marsh that is flooded for 4–6 months each year, typically from June to November. The site is characterized by shallow marl soils (mostly fine particles of calcium
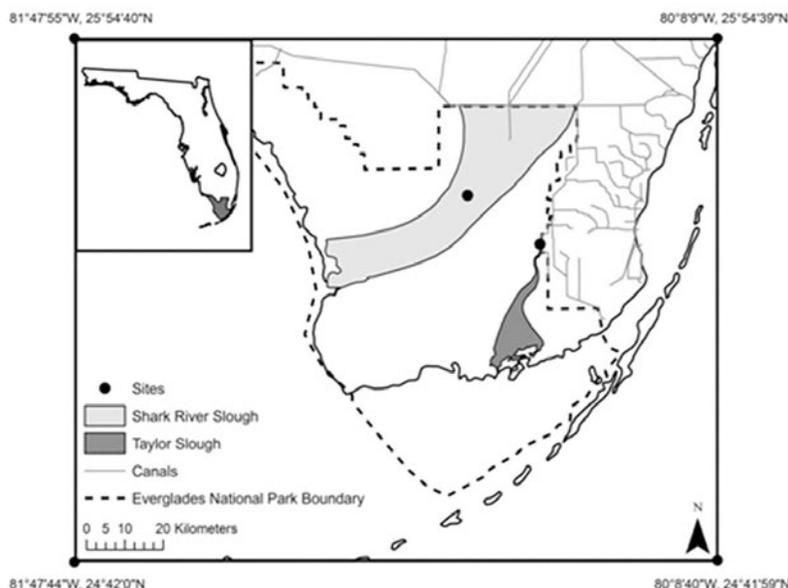
Figure 1. Map of tower sites (denoted by solid circles) at Shark River Slough (shaded light gray) and Taylor Slough (shaded dark gray) in Everglades National Park, southern Florida.

carbonate as calcite, $\sim$0.14 m deep) overlying limestone bedrock (FCE-LTER, http://fcelter.fiu.edu/research/sites/). The site is codominated by the C_3 macrophyte *Cladium jamaicense* Crantz [*Clementz et al.*, 2007], commonly known as sawgrass, with the C_4 grass *Muhlenbergia capillaris* Lam (Muhly grass). Abundant periphyton mats are present during the inundation period [*Gaiser et al.*, 2006; *Gottlieb et al.*, 2006; *Iwaniec et al.*, 2006]. Mean canopy height (Z) and surface roughness (d) for this site are 0.73 and $\sim$0.3 m, respectively. The site is accessible on foot.

[11] The SRS site (25°33′6.72″N, 80°46′57.36″W) is a long-hydroperiod marsh that is inundated $\sim$12 months yr^{-1}. The SRS site is characterized by peat soils (0.6 to 1.0 m thick) overlying limestone bedrock with ridge and slough micro-topography [*Duever et al.*, 1978; FCE-LTER, 2010, http://fcelter.fiu.edu/research/sites/]. The dominant macrophyte present on ridges is *Cladium jamaicense* with spike rush (*Eleocharis cellulosa* Torr) and periphyton mats in sloughs. For this site, Z and d are 1.02 and $\sim$0.4 m, respectively. The site is accessible only by airboat or helicopter.

[12] Hydroperiods in the Everglades are a combination of both natural and water management controls, and as such are only partially influenced by seasonal precipitation patterns. Saltwater intrusion or tidal processes currently do not influence the sites since both are located in the interior of Everglades National Park [*Childers et al.*, 2006] (Figure 1).

2.2. Eddy Covariance Methodology

[13] Net ecosystem exchange (NEE) of CO_2 was measured using open path eddy covariance methods [*Moncrieff et al.*, 1996; *Ocheltree and Loescher*, 2007]. NEE is commonly estimated through simplification of the continuity equation by applying a control volume approach, where the integrals in equation (1) are the vertical rate of change of mean molar CO_2 concentration and the vertical scalar flux divergence,

respectively, from the ground level to the top measurement height (z, m) [*Loescher et al.*, 2006]:

$$NEE = \underbrace{\int_0^z \overline{\frac{\partial \rho C}{\partial t}} \partial z}_{I} + \underbrace{\int_0^z \overline{\frac{\partial \rho C'w'}{\partial t}} \partial z}_{II} \qquad (1)$$

where the CO_2 concentration (C, mmol CO_2 m^{-3}), density of air (ρ), and vertical wind velocities (w, m s^{-1}) are measured at a fixed plane above the plant canopy. In equation (1), NEE is estimated by both the covariance of the turbulent fluctuations of C and w, where the turbulent fluctuations are the instantaneous deviation (at 10 Hz) from the mean block average (over 30 min, term II), and the storage flux, term I. Primes denote the fluctuations; overbar denotes the mean from the averaging period. Carbon dioxide stored directly below the tower was calculated as a function of measurement height and mean molar CO_2 concentration. Micrometeorological convention is used here, where negative NEE values indicate ecosystem uptake of CO_2.

[14] Eddy covariance instruments were installed in December 2007 and July 2008 at Taylor Slough and Shark River Slough, respectively, and maintained continuously. Tower installation at SRS was delayed as a result of low water levels that prevented airboat access to the site.

[15] The measurement systems consisted of a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, Utah) and an open-path infrared gas analyzer (IRGA; LI-7500, LI-COR Inc., Lincoln, Nebraska) mounted at $\sim$3.3 m above the soil surface. To minimize flow distortion between sensors, the IRGA and sonic anemometer were placed 0.09 and 0.23 m apart at TS and SRS, respectively, such that the open optical path of the IRGA was vertically aligned to match the sonic volume of the CSAT. Digital

signals from sonic anemometer and the gas analyzer (with factory 230 ms delay) were collected by a data logger (CR1000, Campbell Scientific Inc.) at 10 Hz. The IRGAs were calibrated every 20–30 days using a trace gas standard for CO_2 in air (+1.0%), a dew point generator for H_2O (LI-610, LI-COR Inc.), and CO_2 free air scrubbed with soda lime and Drierite, according to the protocols outlined by AmeriFlux [*Loescher and Munger*, 2006].

2.3. Meteorological Instrumentation

[16] The data logger collecting flux measurements also recorded barometric pressure (Vaisala PTB110, Campbell Scientific, Logan, Utah), temperature (T_{air}), and relative humidity (RH; Model HMP45C, Campbell Scientific, Logan, Utah). The temperature and relative humidity probe was housed in an aspirated shield (Model 43502, R.M. Young Company Inc., Traverse City, Michigan) mounted 2.5 m and 2.45 m above the soil surface at TS and SRS, respectively. Vapor pressure deficit (VPD) was calculated using the Clausius-Clapeyron equation as a function of air temperature.

[17] Other meteorological measurements were collected on a second independently powered data logger and relay multiplexer (models CR10X and AM16/32A, respectively, Campbell Scientific Inc., Logan, UT) and included wind direction and velocity (Model 05103-5, R.M. Young Company Inc., Traverse City, Michigan), PAR (PARlite quantum sensor, Kipp & Zonen, Delft, Netherlands), net radiation (R_n; CNR2, Kipp & Zonen, Delft, Netherlands), precipitation (TE525 Tipping Bucket Rain Gage, Texas Electronics Inc., Dallas, Texas), and two sets of soil temperature thermocouples installed 5, 10, and 20 cm below the soil surface (Type-T copper, constantan thermocouples, Omega Engineering, Inc., Stamford, Connecticut). The aforementioned variables were measured every 15 s and averaged every 30 min. Three soil heat flux plates per site (2 Models HFP01 and 1 Model HFP01SC, Hukseflux Thermal Sensors) were buried at 5 cm below the soil surface. Water level at the sites was recorded with a water level data logger (HOBO U20-001-01, Onset Inc., Bourne, Massachusetts) placed in a polyvinyl chloride (PVC) sleeve installed in a nearby solution hole at TS and in the peat at SRS.

2.4. Data Processing

[18] Raw EC data were processed using EdiRe (version 1.4.3.1184, available at http://www.geos.ed.ac.uk/abs/research/micromet/EdiRe), which carried out a 2-D coordinate rotation of the horizontal wind velocities to obtain turbulence statistics perpendicular to the local streamline. The covariance between turbulence and scalar concentrations was maximized through the examination of the time series at 0.1 s intervals on both sides of a fixed lag time (in this case, ~0.3 s). Because of the relatively short roughness lengths and uniform canopy structure at these sites, we assumed that the influence of coherent structures and low-frequency effects were captured by this approach. Fluxes were calculated for half-hour intervals and then corrected for the mass transfer resulting from changes in density not accounted for by the IRGA [*Massman*, 2004; *Webb et al.*, 1980]. Barometric pressure data were used to correct the fluxes to standard atmospheric pressure.

[19] Flux data screening was applied to eliminate half-hourly fluxes resulting from systematic errors such as

(1) rainfall, condensation, or bird fouling in the sampling path, (2) incomplete half-hour data sets during system calibration or maintenance, (3) poor coupling of the canopy with the external atmospheric conditions, as defined by the friction velocity, u*, using a threshold <0.15 m s^{-1} [*Goulden et al.*, 1996; *Clark et al.*, 1999], and (4) excessive variation from the half-hourly mean based on an analysis of standard deviations for u, v, and w wind and CO_2 statistics. We determined the u* threshold using the method described by *Loescher et al.* [2003]. Because this system had low above water biomass (relative to forested ecosystems) and its vertical structure did not change during the year, the threshold also did not change due to changes in seasonal phenology (data not shown). Moreover, this threshold is well within the range of other short stature ecosystems [*Loescher et al.*, 2006]. Quality assurance of the flux data was also maintained by examining plausibility tests (i.e., NEE < −30 and >30 μmol m^{-2} s^{-1}), stationarity criteria, and integral turbulent statistics [*Foken and Wichura*, 1996; *Foken and Leclerc*, 2004].

[20] Eddy covariance measurements of CO_2 estimate net ecosystem exchange at a time resolution of 1 h or less [*Baldocchi*, 2003, *Loescher et al.*, 2006], such that

$$NEP \approx -\,NEE \qquad (2a)$$

$$GPP \approx GEE = -NEE + R_{eco} \qquad (2b)$$

where GPP is gross primary production, GEE is gross ecosystem exchange, and R_{eco} is ecosystem respiration. Gross primary production cannot be measured directly, but rather is estimated from the right hand terms in equation (2b). Half-hourly fluxes of NEE (μmol m^{-2} s^{-1}) were used to calculate GEE and R_{eco} in g C m^{-2} s^{-1} from equations (2a) and (2b) based on the logic provided by *Randerson et al.* [2002], *Campbell et al.* [2004], and *Loescher et al.* [2006].

[21] Missing half-hourly data were gap filled using separate functions for day and night (NEE$_{day}$, NEE$_{night}$). When photosynthetically active radiation (PAR) was ≥10 μmol m^{-2} s^{-1}, daytime NEE data were gap filled using a Michaelis-Menton approach,

$$NEE_{day} = R_{eco} - \frac{\alpha\phi P_{\max}}{\alpha\phi + P_{\max}} \qquad (3)$$

and, when PAR was <10 μmol m^{-2} s^{-1}, nighttime NEE data were gap filled using an Arrhenius approach,

$$NEE_{night} = R_{eco} = R_0\,\exp^{b\cdot T_{air}} \qquad (4)$$

where α is the apparent quantum efficiency ($\partial CO_2/\partial\phi$), ϕ is PAR, R_{eco} is ecosystem respiration (μmol CO_2 m^{-2} s^{-1}), $P_{\max}$ is the maximum ecosystem CO_2 uptake rate (μmol CO_2 m^{-2} s^{-1}), R_0 is the base respiration rate when air temperature is 0°C, and b is an empirical coefficient. These functional relationships were calculated on a monthly basis to gap fill the data where enough data were available. Where too few observations were available to produce stable and biologically reasonable parameter estimates, annual data were used to gap fill data by site. Half-hourly NEE, GEE, and R_{eco} values were used to generate daily, weekly, monthly, and annual values that were evaluated to determine the best time scale for statistical analyses. Gap-filled data accounted for

25% and 30% of daytime and 63% and 78% of nighttime values for TS and SRS, respectively. During the spring of 2009, ~80% of all data for the months of March–May was gap filled when access to SRS was severely limited by low water tables and we could not routinely clean bird fouling of the IRGA. However, our error estimates for gap filling indicate that we were able to produce stable and biologically reasonable parameter estimates for this period, which allowed us to include these values in annual carbon balances for the site (Tables A1 and A2).

[22] Error estimation from gap-filled values of NEE was performed via bootstrap methods. Although Monte Carlo methods have been widely used in this context [e.g., *Braswell et al.*, 2005; *Reichstein et al.*, 2007], synthetic data generation and determination of parameter distribution via bootstrap methods are more efficient when the distribution of the measurement error is unknown [*Press et al.*, 1993; *Richardson and Hollinger*, 2005]. For an original data set of size n, synthetic data sets are generated by randomly selecting n observations with replacement from the original data. We generated 1000 synthetic data sets for each estimated gap-filling model (day and night models in equations (3) and (4), respectively, on a monthly or annual basis where appropriate), and constructed the distribution of each model parameter. These distributions were then checked to ensure that the model parameters derived from the original data were contained within a 95% confidence region. Bootstrap procedures were performed monthly for gap-filling models to estimate missing daytime NEE data, and for 23 of the 42 months for estimating missing NEE data during the night. The remaining 19 months had too few usable observations to estimate monthly nighttime NEE, i.e., equation (4). Therefore, we generated bootstrap samples for four annual equations (two sites and 2 years). In all cases, parameter estimates from the original data were within the 95% confidence region constructed from the bootstrap samples (Tables A1 and A2).

2.5. Horizontal Carbon Flows

[23] Dissolved organic and inorganic carbon (DOC and DIC) and particulate organic matter (POM) move through the marsh flux footprints in the slow flow of water during periods of inundation. Because the area surrounding the footprints in both sites is continuous marsh, however, inflows and outflows of DIC, DOC, and POM in the footprint area are likely equal and unlikely to affect the overall CO_2 balance of these marshes [*Schedlbauer et al.*, 2010].

2.6. NDVI and LAI

[24] We obtained normalized difference vegetation indices (NDVI) and leaf area index (LAI) data for TS and SRS over the study period from NASA's MODIS (Moderate Resolution Imaging Spectroradiometer) instruments (http://modis-atmos. gsfc.nasa.gov/, accessed 8 July 2011). NDVI (Level 3 product, MOD13Q1) is expressed as a function of the red (band 1) and near infrared (band 2) wavelengths, and is available at 250 m resolution on 16 day composites. LAI (Level 4 product, MOD15A2) is one-sided green leaf area in square meters per square meter ground area in broadleaf canopies and is available at a 1 km resolution on an 8 day composite basis.

2.7. Statistical Analysis

[25] We first formulated models to investigate the light and temperature responses of NEE by site and season. We estimated the parameters of the nonlinear relationships in equations (3) and (4) via the SAS procedure PROC NLIN (version 9.2, SAS Institute Inc., Cary, North Carolina), adding effects for site and wet versus dry season differences. Because of the high degree of autocorrelation inherent in the NEE data, statistical tests of parameter estimates are artificially sensitive. Therefore, this analysis is presented in a descriptive context.

[26] To examine the relationship between LAI and NDVI versus NEE, we first summarized the data to 8 day intervals and 16 day intervals to correspond to the MODIS data sets, respectively. We used the SAS procedure PROC GLM to model NEE, separately as a function of LAI and NDVI, adding effects for site, season, and their interaction. Because water table depth may strongly influence LAI and NDVI we also investigated the nature of their relationship in the same manner.

[27] Since microclimate may affect CO_2 fluxes at varying time lags, we also examined the sample cross correlation between NEE and each key environmental variable and R_{eco} and each key environmental variable by site. These variables included PAR, precipitation, T_{air}, water table depth, and VPD. The cross correlation, which is used to determine the delay in one signal versus another, was computed with the SAS procedure PROC ARIMA. Since the direct cross-correlation function between the input and response series can be misleading if the input series is autocorrelated or nonstationary [*SAS Institute Inc.*, 2008], we first prewhitened each data series and tested for stationarity. Nonstationary series have statistical properties (e.g., mean, variance) that are nonconstant over time, but often stationarity can be achieved via a transformation to the first differenced series (i.e., the series of changes between adjacent observations). The process of prewhitening reduced each series to an uncorrelated "white noise" residual series, which could then be examined for cross-correlation patterns with NEE and R_{eco} using lags up to 8 weeks.

[28] General linear models (GLMs) were used to model NEE, GEE, and R_{eco} as a function of key environmental variables using the procedure PROC GLM. Though half-hourly data were collected, data were grouped into monthly means for our analyses because high levels of autocorrelation were found in data sets from shorter time scales (Durbin-Watson statistic, $d < 1$) [*Wooldridge*, 2009]. This grouping of data may have limited our ability to examine transitions between wet and dry seasons; however, it facilitates statistical analyses, enabling the use of general linear modeling techniques. Pearson correlation coefficients were initially computed for all explanatory variables to assess correlations and to avoid statistical issues related to multicollinearity among explanatory variables in the models estimated (data not shown). Explanatory variables in the model included site, season, PAR, precipitation, T_{air}, VPD, water table height, and each variable's interaction with site and season, where appropriate. We used a combination of p values and the small-sample corrected value of the Akaike information criteria (AIC_C) to select models. Variables that showed no significant effect ($\alpha \geq 0.05$) on NEE, GEE, and R_{eco} and those whose inclusion increased the AIC_C were removed from the models. Simple effects whose interactions
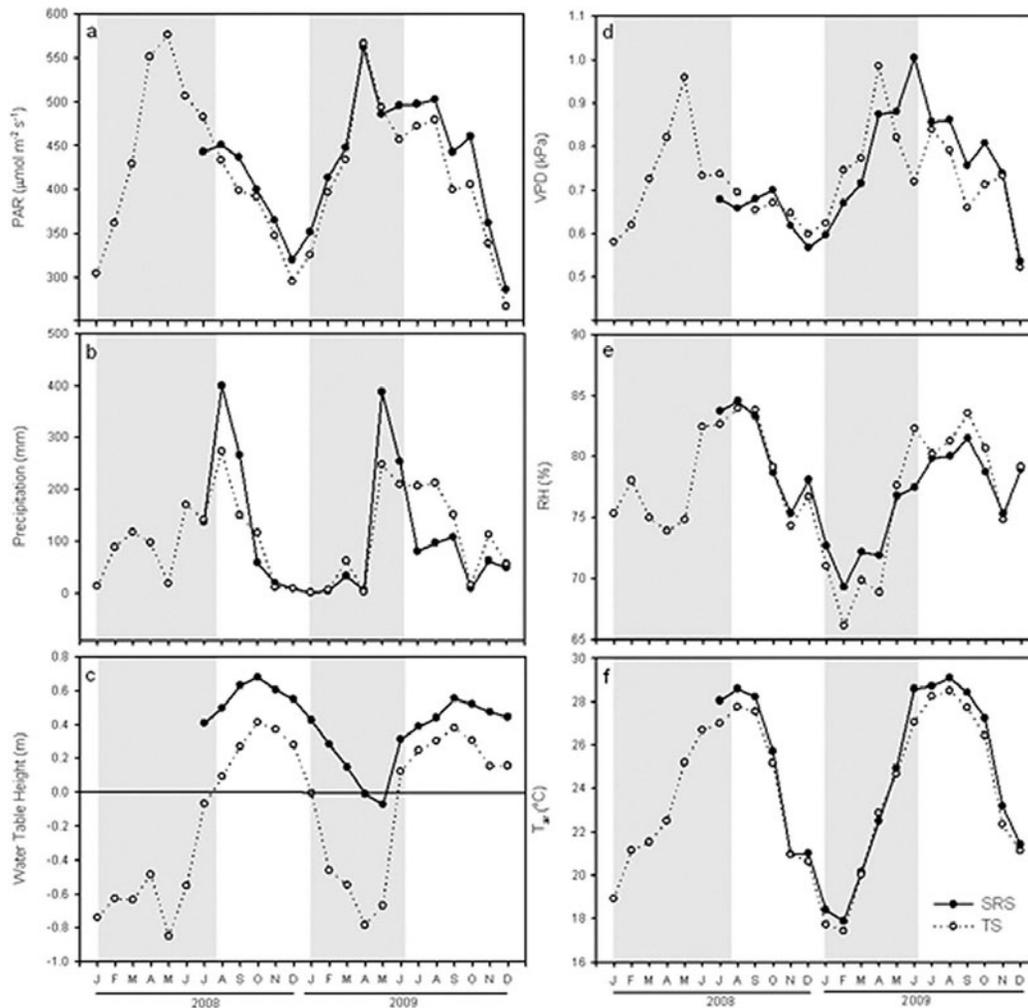
Figure 2. Environmental variables measured at Taylor Slough (TS) and Shark River Slough (SRS) from January 2008 to December 2009. Monthly means were calculated for (a) photosynthetically active radiation (PAR), (c) water table height relative to the soil surface, (d) vapor pressure deficit (VPD), (e) relative humidity (RH), and (f) air temperature (T_{air}). (b) Monthly sums were calculated for precipitation. Gray shaded areas indicate dry season periods.

were significant were kept in the models. When variables had significant interactions with site or season, we used a least squares mean approach that incorporated all model effects to determine the specific roles these environmental variables had on the two sites and if these roles were similar or different. Residuals from the final model were tested for autocorrelation using the Durbin-Watson statistic and plotted to ensure that assumptions of normality and homoscedasticity were met [*Aguinas*, 2004].

3. Results

3.1. Environmental Variables and Climate

[29] Most environmental variables exhibited similar patterns over time for both Taylor Slough and Shark River Slough (Figure 2). Mean monthly T_{air} ranged from 17.4 to 29.1°C during the measurement period, with the lowest temperatures occurring in January and February and the highest temperatures occurring in August for both sites (Figure 2f). The mean T_{air} during the period of this study was 23.7 and 24.6°C for TS and SRS, respectively. Although, mean T_{air} for TS was lower than that of SRS, it was representative of the long-term average of 23.9°C [*NCDC*, 2010]. The higher mean temperature at SRS may be partially attributed to the lack of winter 2008 data.

[30] Rainfall during the measurement period at TS was 1206 mm in 2008 and 1284 mm in 2009, which is below the long-term average of 1430 mm [*NCDC*, 2010]. Rainfall during the measurement period at SRS was 889 mm from July to December 2008 and 1090 mm in 2009.

[31] Water levels ranged from 0.9 m below to 0.4 m above the surface at TS and 0.05 m below to 0.7 m above the surface at SRS (Figure 2c). Although the temporal patterns of water levels at the two sites were similar, the duration of water above the surface was very different. Water level was below the surface only 2 of 18 months at SRS, but 12 of 24 months

Table 1. Annual and Seasonal Estimates (g C m^{-2}) of NEE, GEE, and R$_{eco}$[a]

Year	NEE	R$_{eco}$	GEE	R$_{eco}$/GEE (%)
		Site TS		
2008 dry	−86.6 (10.7)	253.7 (12.3)	−340.3 (8.2)	75 (5)
2008 wet	7.9 (4.6)	135.7 (5.2)	−127.8 (5.6)	106 (9)
2008 all	−78.8(15.3)	389.4 (17.5)	−468.2 (13.8)	83 (6)
2009 dry	−27.9 (9.0)	236.4 (10.0)	−264.3 (4.8)	89 (5)
2009 wet	16.8 (5.5)	208.6 (6.8)	−191.8 (5.3)	109 (7)
2009 all	−11.0 (14.5)	445.1 (16.8)	−456.1 (10.1)	98 (6)
		Site SRS		
2008 dry[b]	1.6 (0.1)	11.2 (0.1)	−9.5 (0.2)	117 (4)
2008 wet	18.3 (0.8)	127.1 (1.6)	−108.6 (2.0)	117 (4)
2008 all[b]	19.9 (0.8)	138.3 (1.7)	−118.2 (2.2)	117 (4)
2009 dry	8.1 (10.8)	192.3 (4.9)	−184.0 (11.7)	105 (10)
2009 wet	71.9 (3.9)	249.3 (4.8)	−177.2 (5.6)	141 (7)
2009 all	80.0 (14.7)	441.6 (9.6)	−361.3 (17.3)	122 (9)

[a]Standard errors shown in parentheses. Negative values indicate ecosystem uptake of CO_2.
[b]Data during the 2008 dry season at SRS were incomplete.

at TS. Water level and flooding duration in these wetlands was a function of both precipitation and water management. As a result, the increase of water table height did not always correlate with precipitation events, and there was a lag between precipitation and water table increases (Figures 2b and 2c). Because monthly water table values at SRS were less variable than at TS, we based our analyses of seasonal differences (wet versus dry) on the period of time TS was not inundated with water. This categorization of water table height and seasonality allowed for an equal time frame to make comparisons between TS and SRS. We classified the "wet" and "dry" seasons by the monthly average water table height

being above or below the soil surface. Based on our classification, the dry season occurred from January to July in 2008 and January to June in 2009, respectively. Because this delineation is based solely on TS dynamics, we consider the interpretation of these analyses to be qualitative.

3.2. CO$_2$ Balances

[32] Taylor Slough was a small net CO_2 sink in 2008, with an NEE rate of −78.8 g C m^{-2} yr^{-1} in 2008; however, its sink/source status was indeterminate in 2009, as its NEE rate was smaller than its standard error (−11.0 ± 14.5; Table 1). SRS was a net CO_2 source for the 2008 measurement period (July to December) and the entire year of 2009, releasing 19.9 g C m^{-2} and 80.0 g C m^{-2} yr^{-1}, respectively. Because we did not retrieve a full year of data for 2008 in SRS due to lack of access to the site, the reported values likely underestimate system carbon losses that year. Only 3 of 18 months showed net ecosystem CO_2 uptake at SRS, and during no month was SRS a strong sink. NEE at the two sites tracked similarly during the wet season, but exhibited an opposite pattern during the dry season with SRS releasing more CO_2 (Figure 3). Rates of GEE generally were higher at TS, except during the 2009 wet season, while R$_{eco}$ values were in the same range for both sites except during the 2009 dry season (Table 1 and Figure 3). LAI was in general higher at SRS versus TS, excepting a few months during the wet seasons (Figure 3).

3.3. Light and Temperature Response Curves

[33] Light response curves were formulated to characterize the relationship between NEE and PAR by site and season. Both sites exhibited higher photosynthetic capacity during the dry season versus the wet season (Figure 4), but for SRS the difference was small. In contrast, TS showed
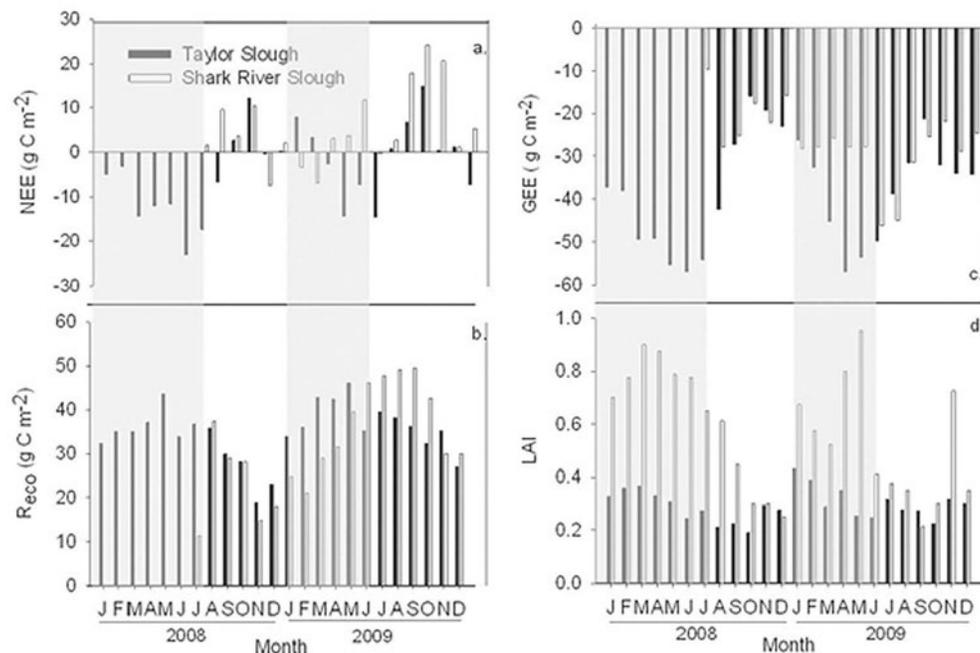

Figure 3. Monthly estimates of components of CO_2 exchange (g C m^{-2}) and leaf area index at Taylor Slough and Shark River Slough: (a) NEE, (b) R$_{eco}$, (c) GEE, and (d) LAI. Negative values indicate ecosystem uptake of CO_2. Gray shaded areas indicate dry season periods.
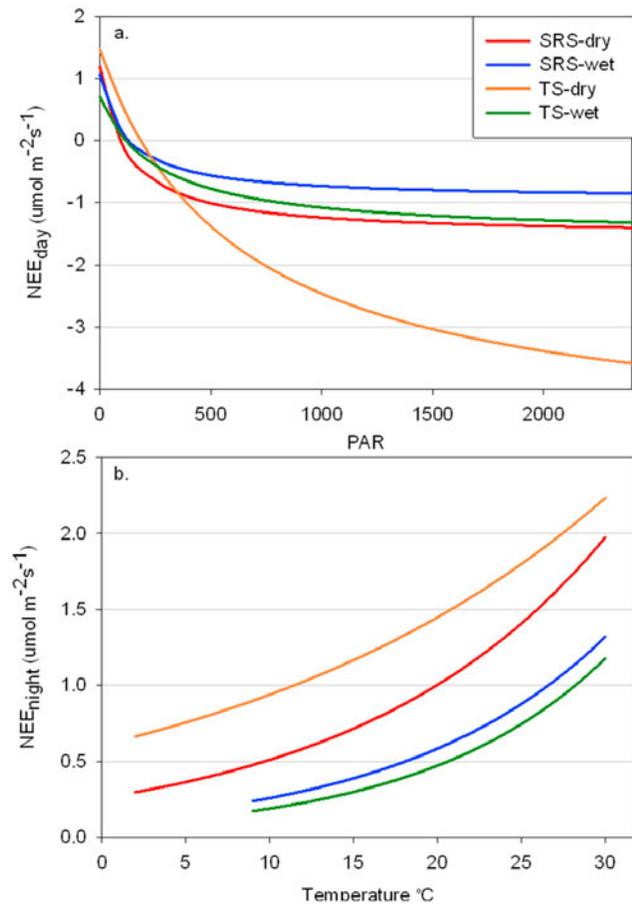
Figure 4. (a) Light and (b) temperature response curves for long- and short-hydroperiod marsh sites (SRS and TS, respectively) by season.

Figure 5. Relationship between LAI and NEE by site (SRS = long-hydroperiod, TS = short-hydroperiod). LAI is significantly affected by NEE, site, and season ($p < 0.05$); however, the relationship between LAI and NEE is not significantly different by site (statistically parallel lines for each pair of sites within season).

3.5. Cross Correlations Between NEE and Environmental Variables

[35] Sample cross correlations (CCFs) were computed with prewhitening of most input variables using daily autoregressive lags over 10 days, as significant temporal autocorrelation patterns were indicated with the original data series. Only one environmental variable required first differencing; half-hourly differencing of water table depth was required to achieve stationarity. The CCFs of T_{air} and VPD with NEE indicated significant but small positive cross correlations in SRS and TS (CCF = 0.050 and 0.102 for T_{air} and CCF = 0.040 and 0.088 for VPD, respectively) with a temporal delay of 30 min. This indicated that in both sites, T_{air}

marked differences, with considerably more uptake in the dry season versus wet season, particularly at high values of PAR (>400 μmol m^{-2} s^{-1}). The temperature pattern associated with R_{eco} showed the opposite response, with a greater release of CO_2 at both sites in the dry season versus the wet season (Figure 4). At SRS, the difference between seasons was small, except at high temperatures (>24°C), while at TS the difference between seasons was consistently large over all temperature values (Figure 4).

3.4. LAI and NDVI Versus NEE and Water Table Height

[34] The model of LAI versus NEE had significant effects for site, season and NEE. There were, however, no significant interactions of NEE with site. In other words, the relationship between LAI and NEE was significant, but it did not differ significantly by site if seasonality was taken into account (Figure 5). Similarly, the model of LAI versus water table depth had significant effects for site, season, and water table, with no significant interactions between water table and site. That is, the relationship between LAI and water table was significant, but it did not differ significantly by site if seasonality was taken into account (Figure 6). The models of NDVI did not show any significant relationship with NEE or water table (data not shown).
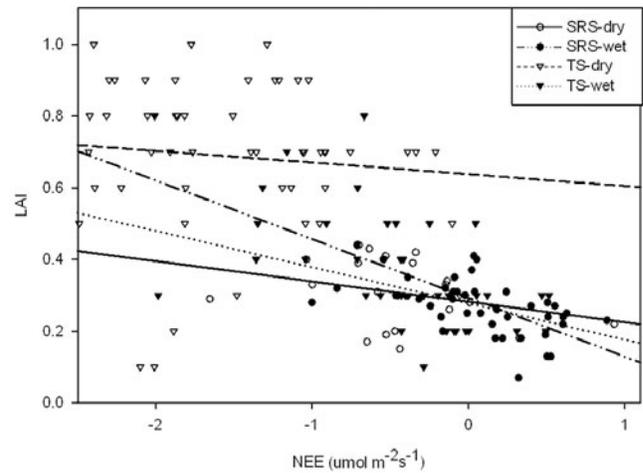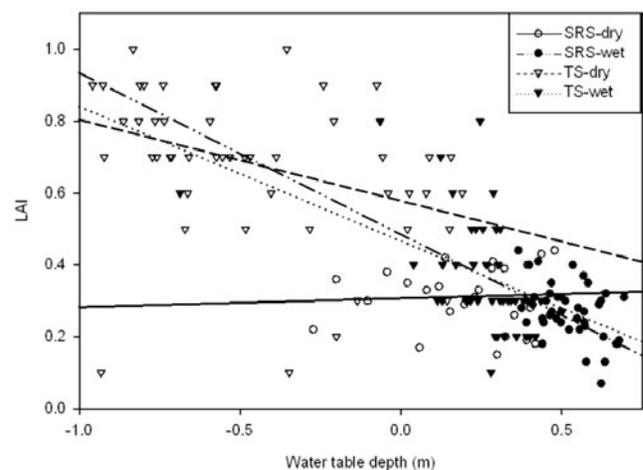

Figure 6. Relationship between LAI and water table by site (SRS = long-hydroperiod, TS = short-hydroperiod). LAI is significantly affected by water table, site, and season ($p < 0.05$); however, the relationship between LAI and water table is not significantly different by site (statistically parallel lines for each pair of sites within season).

Table 2. Type III Tests of Fixed Effects for GLMs of NEE, Reco and GEE[a]

Parameter	Estimate	Standard Error	t Value	Pr>|t|
Model of NEE				
Intercept	−1.237	0.483	−2.56	0.016
Site (SRS)	−0.546	0.440	−1.24	0.224
Season (dry)	2.164	0.456	4.75	<0.0001
PAR	−0.0028	0.0010	−2.67	0.012
VPD	1.184	0.545	2.17	0.038
T_{air}	0.046	0.022	2.11	0.043
T_{air} * Site (SRS)	0.044	0.017	2.54	0.016
T_{air} * Season (dry)	−0.077	0.016	−4.74	<0.0001
Water table	1.487	0.413	3.60	0.001
Water table * Site (SRS)	−1.403	0.307	−4.57	<0.0001
Water table * Season (dry)	−1.229	0.392	−3.13	0.004
Model of R_{eco}				
Intercept	−0.0031	0.0063	−0.50	0.623
Season (Dry)	0.0135	0.0068	1.99	0.055
Site (SRS)	−0.0216	0.0064	−3.39	0.002
T_{air}	0.00063	0.0003	2.49	0.018
T_{air} * Site (SRS)	−0.0011	0.0003	4.18	<0.001
T_{air} * Season (dry)	−0.00071	0.00026	−2.74	0.010
Water table	−0.0205	0.0056	−3.64	0.001
Water table * Season (dry)	0.0180	0.0049	3.65	0.001
VPD	0.0210	0.0055	3.79	<0.001
Model of GEE				
Intercept	−1.900	0.385	−4.93	<0.0001
Site (SRS)	−0.031	0.339	−0.09	0.927
Season (dry)	0.556	0.280	1.99	0.055
Site * Season (SRS dry)	0.885	0.366	2.42	0.021
VPD	−1.750	0.454	−3.85	0.001
Water table depth	4.661	0.739	6.30	<0.0001
Water table * Site (SRS)	−1.700	0.615	−2.76	0.009
Water table * Season (dry)	−4.349	0.753	−5.77	<0.0001

[a]Parameter estimates for site and its interaction reflect the added NEE, R_{eco} and GEE at SRS versus the base site (TS).

and VPD were significantly correlated to half-hourly lagged NEE. PAR and rainfall did not show signal delays with NEE; that is, correlations between these variables and NEE were synchronous. While there was no significant CCF for half-hourly changes in water table depth with NEE at TS, there were significant correlations of 0.044–0.096 at SRS at a lag of ~10 days; NEE was synchronous to half-hourly changes in water table depth at TS, but asynchronous to those changes at SRS. Similar to NEE, the CCF of half-hourly changes in water table depth with R_{eco} indicated that there were small but significant signal synchronies at SRS at a lag of 10 days (CCF = 0.046–0.108); however, there were no significant signal lags at TS. The CCF of rainfall with R_{eco} at SRS also responded similarly, indicating small but significant signal delays of ~10 days (CCF = 0.045–0.077) at that site. VPD, PAR, and T_{air} did not show signal delays with R_{eco}. These results indicate that lagged values of rainfall and water table depth may be significant predictors in modeling R_{eco} and NEE as a function of environmental variables, and therefore should be included in further analyses.

3.6. Environmental Drivers of CO_2 Fluxes

[36] The best (lowest AIC_C) model of NEE had a RMSE of 0.166. Significant effects for site, season, PAR, VPD, T_{air}, and water table height (Table 2) explained 80% of the variation in NEE. NEE was most significantly impacted by the T_{air} and water table depth, but these effects varied by site and season.

At both sites, uptake decreased as temperature increased, while at TS the effect was dampened compared to SRS ($p = 0.016$; Figure 7a). In the wet season, uptake strongly decreased with increasing temperature, but this effect was smaller and opposite in the dry season ($p < 0.001$; Figure 7a). The effect of water table depth was positive at TS (less water, more uptake) and also during the wet season, while the effect was reversed at SRS and during the dry season (more water, less uptake; $p < 0.01$; Figure 7c). In other words, NEE became more positive as water table depth increased either at the short-hydroperiod site or during the wet season, limiting net carbon uptake through a reduction in photosynthetic capacity, not by enhancing aerobic respiration. There was significantly more uptake with increasing PAR and significantly less uptake with increasing VPD, but these effects were smaller in magnitude than those of T_{air}, water table, and season.

[37] The GLM of R_{eco} indicated that similar to NEE, site, season, T_{air}, VPD and water table all significantly affected R_{eco} (Table 2), and explained 84% of the variation in the response (RMSE = 0.00279). T_{air} was the most important predictor in the model, with increased ecosystem respiration and loss of carbon from the two systems as temperatures increased (Figure 7b). R_{eco} however, had a larger response to changes in T_{air} at SRS than at TS and in the wet season versus the dry season (Figure 7b). This result indicates that on average more CO_2 was released from TS than SRS at lower temperatures (<24°C), but at higher temperatures (>24°C), more CO_2 was released from SRS than TS. Similarly, there was more CO_2 released during the dry season versus the wet season at lower temperatures, but at higher temperatures (>24°C), more CO_2 was released during the wet season than during the dry season. The effect of water table was negative on R_{eco} (less carbon loss from the two systems), with a larger response to changes in water table depth during the wet season than during the dry season (Figure 7d). VPD had a smaller, but significant effect on R_{eco}, with more loss of carbon as VPD increased.

[38] GEE was significantly impacted by site, season, VPD, and water table. These predictors explained 84% of the variation in GEE (RMSE = 0.295), and the effect of water table significantly varied by site and by season. There was a positive response of GEE to water table height between sites (lower exchange rates), though the effect was stronger at TS (Figure 8). The strongest predictors of GEE were water table and season, with GEE showing a small negative relationship with water table during the dry season, but a strong positive relationship during the wet season (Figure 8). As water table height increased from below the soil surface to above the soil surface, CO_2 uptake decreased more strongly at TS than at SRS and in the wet season compared to the dry season (Figure 8). There was also a negative effect of VPD on GEE, which did not change by site.

4. Discussion

[39] Contrary to our expectations, the long-hydroperiod, peat soil marsh at SRS was a net CO_2 source over the study period while the short-hydroperiod, marl soil marsh was a small net CO_2 sink. These finding were counter to our hypothesis that the long-hydroperiod marshes of the Everglades would be larger sinks of CO_2 compared to short-hydroperiod marshes. While it is possible that our results are
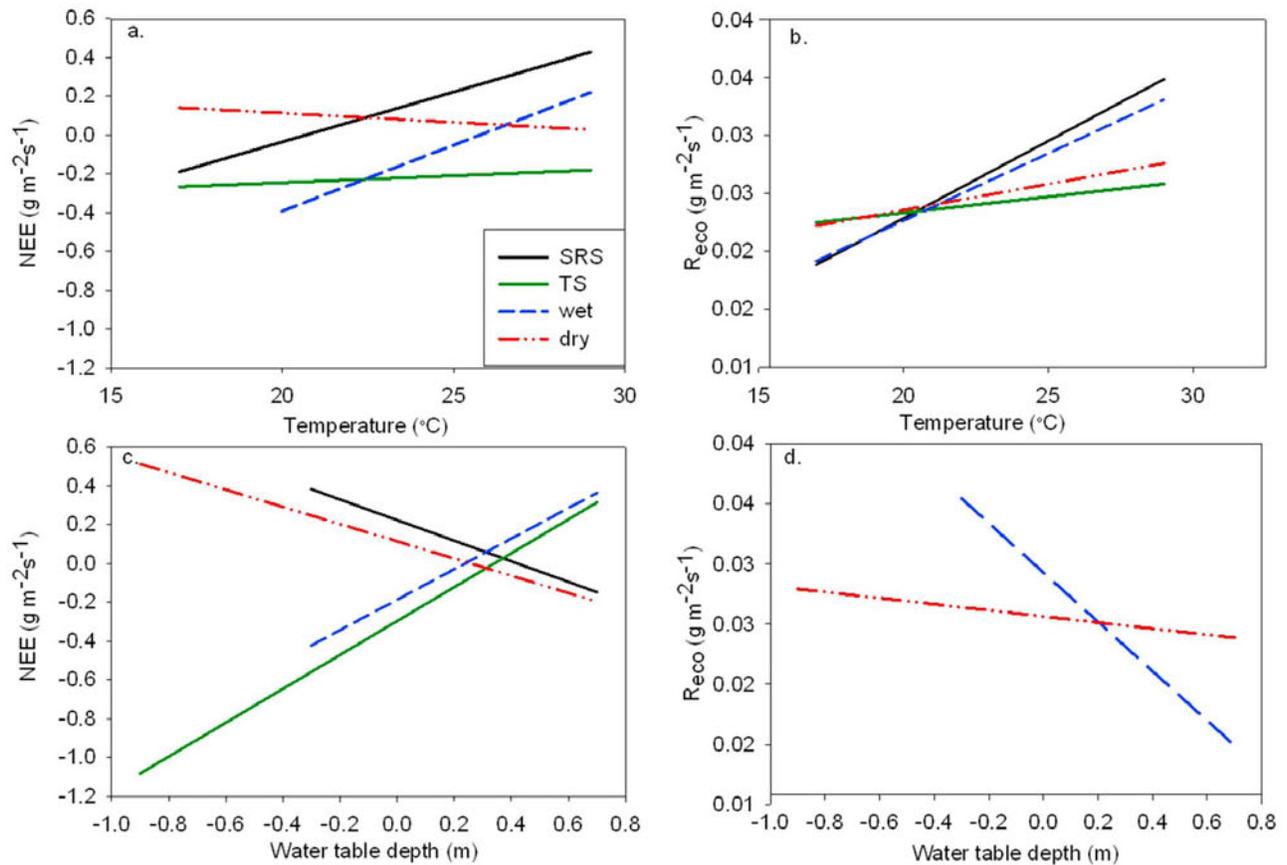
Figure 7. Least squares mean values of NEE in response to (a) air temperature and (c) water table depth by site and season. Least squares mean values of R_{eco} in response to (b) air temperature by site and by season and (d) water table depth by season (SRS = long-hydroperiod, TS = short-hydroperiod).

anomalous to the particular years of study, during most months of the study, SRS was either near neutral or a source with respect to CO_2 exchange, and at no time was a strong sink (Figure 3). Below we consider how the two sites and their controls compare with each other and with other wetlands. We conclude with discussion about how they might currently differ from their state in the past and possible responses to increased flow resulting from Everglades restoration.

4.1. Influence of Vegetation Differences

[40] The vegetation structure at the two sites differed, which in part controlled the surface-atmosphere exchanges. The flux source area of SRS included a matrix of well-vegetated ridges and low leaf area, relatively open sloughs, in which the spatial scales are heterogeneous on the order of a few meters with comparatively larger roughness lengths. In contrast, TS structure is relatively homogeneous at the scale of 10 to >100 m with consistently short roughness lengths, composed of marl prairie with occasional solution holes containing hydric species. MODIS LAI estimates over the study period show higher overall values of LAI at SRS with less intra-annual variation than at TS. Even though estimates were <1 m^2 m^{-2}, maximum values at both sites occurred during the dry season and minimum values during the wet. However, the accuracy with which MODIS can distinguish above versus below water leaf area is uncertain.

[41] The between-site differences in ability to capture carbon were influenced in part by the fraction of total leaf area (and its quantum efficiency) that was directly exposed to light as opposed to being submerged. The amount of exposed leaf area has a large impact on the rates of wetland carbon
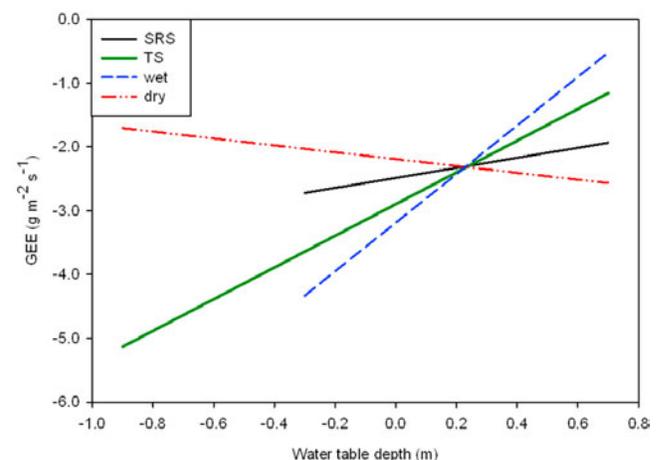

Figure 8. Least squares mean values of GEE in response to water table height by site and season (SRS = long-hydroperiod, TS = short-hydroperiod).

Table 3. Annual Flux Estimates (g C m^{-2}) for Various Wetland Ecosystems Using the EC Technique

Ecosystem Type	Period	NEP/NEE Range	R_{eco} Range	GEE/GPP Range	Citation
Subtropical sawgrass marsh	2008–2009	−47.1–63.7	150.1–408.3[a]	−118.3 to −454.8[a]	This study
Alpine wetland meadow	2004–2006	44 to 173.2	676.8 to 808.2	575.7 to 682.9	*Zhao et al.* [2010]
Temperate cattail marsh	1998–2003	−251 to 515	1313 to 1632	−1090 to −1639	*Rocha and Goulden* [2008]
Temperate cattail marsh	2005–2006	−264	567	831	*Bonneville et al.* [2008]
Temperate reed wetland	2005	−65 (−115 to 75 per month)	-	-	*Zhou et al.* [2009]
Subtropical mangrove forest	2004–2005	−1170	-	-	*Barr et al.* [2010]
Tropical drained peat swamp	2002–2005	296 to 594	-	-	*Hirano et al.* [2007]

[a]An incomplete year that may be an underestimation of annual flux.

exchange [*Olivas et al.*, 2010; *Schedlbauer et al.*, 2010; *Zhao et al.*, 2010]. At SRS, standing water was present for most of the study period (Figure 2c) and at times, only the upper ~31% of the canopy volume was exposed to the atmosphere. At TS, standing water was present during half of the study period (Figure 2c), but at some portions of the year only ~36% of the canopy was exposed. Because LAI decreases with canopy height, a disproportionately large amount of leaf area is low in the canopy and therefore susceptible to inundation. Using direct harvest and indirect measurements of LAI (LAI-2000, LI-COR, Inc, Lincoln, Nebraska), *Schedlbauer et al.* [2010] showed that LAI above water during the wet season at TS was approximately 0.4 m^2 m^{-2}. A similar trend was seen at SRS based on indirect measurements of LAI (S. F. Oberbauer, unpublished data, 2009). The differences in the wet and dry season light response curves for the two systems in part reflect the proportion of leaf area submerged.

[42] Some wetland plants such as *Eleocharis*, which is abundant at SRS but largely absent at TS, are capable of compensatory extension growth in response to rising water levels to maintain above water photosynthetic rates [*Busch et al.*, 2004]. However, measurements of leaf length of *Cladium* and *Muhlenbergia* at TS show no evidence of extension growth in these species (S. F. Oberbauer, unpublished data, 2009). Submerged leaves of some wetland macrophytes are capable of photosynthesis, but macrophyte removal treatments at SRS in combination with chamber-level measurements indicate that the great majority of CO_2 exchange is driven by above water macrophyte tissue [*Schedlbauer et al.*, 2012].

[43] Periphyton might be an important contributor to ecosystem CO_2 flux [*Ewe et al.*, 2006], particularly at TS where it is very abundant during the wet season. *Schedlbauer et al.* [2010] suggested that the distinct rebound of GEE at TS following the wet season minimum in October (at a time of declining PAR) is driven by CO_2 uptake activity associated with the recovery of periphyton biomass. The same pattern was seen again in 2009 (Figure 3). At SRS, periphyton biomass is much lower and not subject to the large seasonal swings seen at TS. The previously mentioned macrophyte removal treatments also indicate that periphyton is not an important contributor to ecosystem CO_2 flux at SRS.

4.2. Components of CO_2 Exchange and Their Controls

[44] Despite similar weather (Figure 2), clear differences in NEE, R_{eco}, and GEE and their controls were observed between these two sites (Tables 1 and 2). These differences are in large part attributable to the amount of time these systems were inundated (90% versus 50% for SRS and TS, respectively). Consequently NEE and R_{eco} at SRS were correlated to water and T_{air} (Figures 4 and 8). The highest CO_2 losses at SRS corresponded to the periods with high air temperatures and lowest water tables, when decomposition is likely to be less oxygen limited (Table 2 and Figure 3). At TS, the importance of T_{air} for NEE and R_{eco} was comparatively low, but that of water table was high (Figures 7 and 8).

[45] PAR was a significant environmental driver of NEE at both sites, as has been well documented in other studies [*Hollinger et al.*, 1994; *Loescher et al.*, 2003; *Barr et al.*, 2010]. Even though the Everglades are subtropical, mean PAR in December was only about half of the peak value that occurs in May just before the onset of the rainy season. Both sites showed strong positive correlations of R_{eco} with PAR and VPD (which covaried at the monthly time scale).

[46] Water table was the dominant control over GEE at TS but of smaller importance at SRS; the seasonal difference in response to changes in hydroperiod for GEE at SRS (~10 g C m^{-2} 2009) was much less than that found at TS (~213 and ~73g C m^{-2} for 2008 and 2009, respectively, Table 1). Alterations in R_{eco} were the primary driver for the seasonal differences in GEE (Table 1).

[47] R_{eco} was always an order of magnitude greater than NEE and often the dominant flux component at both sites (Table 1). The dominance of R_{eco} at SRS is reflected in the strong correlation between monthly R_{eco} and NEE compared to that between GEE and NEE. At TS, monthly NEE was very strongly correlated with GEE (r > 0.90, data not shown) but seasonal R_{eco}:GEE ratios were always >70% and more often >100%. In contrast, *Law et al.* [2002] reported an average ratio of 83% for a wide range of terrestrial ecosystems.

4.3. Productivity

[48] Productivity rates found in this study were lower than expected based on biometric estimates previously reported from other Everglades marsh [*Childers et al.*, 2006; *Ewe et al.*, 2006]. One possible reason is differences in scale of these different types of measurements, both spatially and temporally. *Ewe et al.* [2006] based their values for TS and SRS on biomass surveys that sampled three (1 m^2) plots to make annual estimates. In contrast to the plot studies, our EC footprint encompasses an area of ~6,250 m^2, which encompasses a significantly larger area, which includes more heterogeneity in vegetation and bare areas (under daytime convective conditions) [*Kormann and Meixner*, 2001; *Schedlbauer et al.*, 2010]. High values of Everglades marsh productivity have also been attributed to periphyton [*Ewe et al.*, 2006], which is also very difficult to scale temporally and spatially.

[49] Our NEE estimates were more similar to those found in temperate, northern, and alpine wetlands (Table 3). *Bubier et al.* [1999] reported maximum rates of CO_2 uptake up to

12 μmol m^{-2} s^{-1} and NEP values during the growing season ranging from 0 to -65 g C m^{-2} in a boreal fen of Manitoba. Our maximum NEE rates for both sites spanned *Bubier et al.*'s [1999] estimates and were -11 to -14 μmol m^{-2} s^{-1} (data not shown). What must be considered is that the ecosystems in these studies, unlike the Florida Everglades, are located in climates with much lower air temperatures (implying lower respiratory losses) and shorter growing seasons (less time annually for net carbon capture). Although the Everglades has a longer warm and wet growing period compared to northern wetlands, high water levels, extremely low nutrient levels, and low leaf areas [*Schedlbauer et al.*, 2010] reduced the overall net productivity in the ecosystems studied here.

4.4. Marsh Response to Inundation

[50] Net carbon accumulation in wetland systems with contrasting hydroperiods is a function of above and below water rates of respiration, the ability of above and below water biomass to photosynthetically fix carbon, and seasonal changes in the drivers of both. As soils become waterlogged, oxygen is rapidly depleted [*De Datta*, 1981; *Cronk and Fennessy*, 2001; *Richardson*, 2001]. Under inundated, anaerobic conditions, decomposition occurs slowly allowing carbon to accumulate in wetlands [*Bridgham et al.*, 2006; *Keller et al.*, 2009; *Kayranli et al.*, 2010]. Once saturated soils become aerated, soil gases, including CO_2, diffuse out of solution and oxygen becomes available for rapid aerobic respiration and decomposition [*Richardson*, 2001; *Davidson and Janssens*, 2006]. As wetland soils become very dry, decomposition may be limited by low water availability.

[51] When wetlands are inundated, the effective photosynthetic leaf area may be reduced as macrophyte leaves are submerged. Oxygen depletion has been shown to trigger stomatal closure, epinasty and leaf abscission in some wetlands plants [*Kozlowski*, 1984; *Larcher*, 2003]. *Schedlbauer et al.* [2010] found daytime stomatal closure of *Cladium* and *Muhlenbergia* at TS during inundation conditions that reduced macrophyte photosynthesis. Cladium does not have highly efficient aerenchyma [*Chabbi et al.*, 2000], and *Muhlenbergia* is less flood tolerant than *Cladium* (P. C. Olivas, unpublished data, 2012). Anaerobic respiration is inefficient and in coastal marshes leads to a reduction in productivity compared to aerobic pathways [*DeLaune et al.*, 1987]. Species with aerenchyma and adaptations to deliver oxygen to roots, however, may be capable of continued photosynthesis during periods of inundation. On the other end of the spectrum, wetland dry downs may lead to water stress and reduced photosynthesis.

[52] This conceptual framework would argue for general patterns to emerge in response to seasonality, such as high respiration during the dry season as a result of improved soil aeration and low respiration during the wet season, as was observed at TS (Table 1). Results consistent with this pattern are seen in the Amazon; seasonal precipitation controls the amount and duration of flooding, and higher ecosystem respiration rates during lower water periods were reported from sediments, plant roots, and litter [*Morison et al.*, 2000]. Similarly, Everglades mangrove forests exhibited lower respiration rates during inundation and higher rates of carbon loss to the atmosphere during periods with exposed soil conditions [*Barr et al.*, 2010]. These findings suggests that low seasonal respiration rates during periods of flooding are a combination of reduced diffusion rates and anoxic soils, contrasted with larger conversion of stored labile carbon pools and a larger fraction of aerobic microbial respiration effluxes during periods of low water.

[53] Results from *Hirano et al.* [2009], however, contrast with this pattern and showed a decrease in ecosystem respiration rates from a tropical peatland with declining water levels. Results from our peat site, SRS, were coherent with the pattern of *Hirano et al.* [2009] (Table 1). A third pattern is also present in the literature, where water table does not affect productivity (neither NEE or R_{eco}) in some temperate cattail marshes [*Bonneville et al.*, 2008] and in some northern peatlands [*Bubier et al.*, 1998; *Lafleur et al.*, 2005; *Parmentier et al.*, 2009] but not in tundra landscapes [*Billings et al.*, 1982; *Oberbauer et al.*, 1991; *Olivas et al.*, 2010]. In those cases with no water table response, temperature exhibited strong control on CO_2 fluxes [*Bonneville et al.*, 2008]. If we examine dry season R_{eco} rates at SRS that were a strong a function of temperature, rates match those reported for temperate and northern wetlands. However, patterns at these other sites were mainly driven by the length of growing season, large seasonal differences in temperature, and periods of snow cover/melt [*Bubier et al.*, 1998; *Lafleur et al.*, 2005; *Bonneville et al.*, 2008; *Aurela et al.*, 2009; *Zhou et al.*, 2009; *Zhao et al.*, 2010]. This temperature response can be seen across many different ecosystems and across biome types [*Bond-Lamberty and Thomson*, 2010; *Loescher et al.*, 2003; *Lafleur et al.*, 2005; *Bonneville et al.*, 2008].

[54] The results of our study also show contrasting patterns for the GEE response to water level. The site at TS showed a strong reduction in GEE with higher water tables via submersion of leaf area and reduced uptake driven by stomatal closure, a pattern shared with a temperate sedge-grass marsh [*Dušek et al.*, 2009, 2012] and alpine meadow [*Zhao et al.*, 2010]. In contrast, SRS, with long hydroperiods, showed no trend of GEE versus water level (Figure 8). The smaller range of water tables at SRS and the fact that water level is nearly always above the surface likely contributes to the smaller response, but water table levels ranged over 0.5 m (Figures 2c and 8). Our chamber-level macrophyte removal treatments at SRS suggest that the basis for much of the R_{eco} is emergent macrophyte tissue. The reduction in CO_2 uptake in our short-hydroperiod site (TS) was also consistent with the reported decrease in aboveground net primary productivity (ANPP) from Everglades sawgrass ecosystem in response to increased water levels [*Childers et al.*, 2006].

[55] Clearly, no one process is responsible for R_{eco} and GEE patterns in response to hydroperiod. In the Everglades, the strong responses of R_{eco} and GEE to water level seen at TS is driven by the extreme seasonality of water level and a plant community that includes species intolerant of long-term root submersion (lacking aerenchyma). Some of the reduction in GEE and R_{eco} is likely compensated by annual regrowth of periphyton biomass after inundation. At SRS, water level is above the surface most of the time and the vegetation is composed of species tolerant of inundation, including some that can compensate for submerged photosynthetic surfaces. These factors combine to limit the CO_2 exchange response to changes in water level.

4.5. Past, Present, and Future

[56] Over the past 100 years the Everglades have undergone large changes in hydrology regimes both in terms of amount

and timing of water delivery [*Light and Dineen*, 1994]. Indeed, the aim of the Everglades restoration program is to reestablish the timing and flows of water to historic patterns from long-term reductions and anthropogenic timing of flows (CERP, 2000, http://www.evergladesplan.org). The specific differences between current CO_2 dynamics at SRS versus those of the peat-forming past are not clear, but most likely are a consequence of some aspect of changes in hydrology.

[57] The rate of sink activity needed to accumulate large amounts of peat in the Everglades need not have been particularly great over the estimated 5,000 y of their existence. Based on soil carbon estimates from the Florida Coastal Everglades LTER (http://fcelter.fiu.edu/data/), the current soil carbon at SRS could have built up at an accumulation rate of 6 g C m^{-2} y^{-1}. The 3 m of peat formerly at some sites could have accumulated in 5,000 y at 27 g C m^{-2} y^{-1}, assuming the same bulk density as the LTER sites. Given the soil bulk density and soil organic carbon content at Taylor Slough, the organic carbon at that site could be stored in 530 y at the accumulation rate of 30.7 g C m^{-2} y^{-1}, the average NEE measured at TS over 2009–2010. Note that not all carbon stored as NEE at TS is organic, some is stored as calcite of the marl soil, but the rate of C storage by this mechanism appears to be low [*Schedlbauer et al.*, 2010]. To shift SRS from the current source to the weak sink would not require large changes in GEE or R$_{eco}$. Nevertheless, SRS during the study showed no tendency toward strong sink activity. Striking are the low GEE values at SRS that were lower than those at TS, even during the wet season when TS rates were depressed relative to dry season values.

[58] These low rates of GEE at SRS could be the result of previous drought or other legacy events [*Rocha and Goulden*, 2010]. Though the SRS site is near the center of Shark River Slough, recent dry periods including 2009, one of the driest dry seasons on record, have led to complete dry downs in recent years. Peat storage at the site may have been historically associated with the wetter periods [*Light and Dineen*, 1994], before the Everglades were bisected by the Tamiami canal. Following construction of the Tamiami canal, the marsh to the south in what was to become ENP was subject to increased fire frequency. The fire map database of ENP indicates that since 1948, four fires, including two very large burns, intersected with the current SRS flux tower footprint (J. Redwine, South Florida Caribbean Monitoring Network, personal communication, 2012). Another alternative is that peat may have developed under a different plant community than that present, although the ridge and slough structure of intact marsh is still present at the site.

[59] The Comprehensive Everglades Restoration Plan, which is currently being implemented over the next 30 years (CERP, 2000, http://www.evergladesplan.org), will cause an increase in water levels at our study sites. These increased water levels will lengthen inundation periods in the Everglades, possibly causing an initial decrease in the carbon sequestration capacity of these ecosystems. This scenario is especially likely at TS where longer hydroperiods will reduce photosynthesis until the plant community shifts toward species tolerant of long-term inundation. These shifts can be relatively rapid [*Armentano et al.*, 2006]. Whether longer hydroperiods and possible elimination of dry downs at SRS results in increased CO_2 uptake remains to be seen.

[60] One of the needs from the scientific community is an understanding of the long-term trends that govern processes, controls and potential feedbacks of critical ecological systems. Through the establishment of these long-term studies the scientific community will have greater power in ecological forecasting. We define ecological forecasting as what is the most likely future state of an ecological system and what is the most likely future state of a system given a decision made today? This question is directly relevant to CERP. Ecological forecasting requires continuous observations from a starting point (now) and quantitative information about specific processes (temperature sensitivity, change in function and structure with inundation over time, tipping points, etc.). To apply this technique to ecological research in the Everglades in broad terms, the signal-to-noise ratio (inverse of the coefficient of variation) of our measurement systems has to be the signal-to-noise of the desired phenomenon, e.g., function, driver, feedback mechanism over changing conditions. Using the same technologies and approaches as those used here, *Sierra et al.* [2009] found that ~10 years of observations are needed to detect trends in productivity without making a type II error. Indeed, trend detection and the need for long-term observations are the basis of ecological observatories [*Schimel et al.*, 2009; *National Research Council*, 2001, 2003; P. Ciais et al., A European research infrastructure dedicated to high-precision observations of greenhouse gases fluxes, http://www.icos-infrastructure.eu, 2010]. As such, continuous long-term measurements are needed among sites of different hydroperiods in the Everglades to provide the needed prognostic results on function and structure in view of CERP and long-term planning in southern Florida.

5. Conclusions

[61] This study of the CO_2 balance of Everglades short- and long-hydroperiod marshes revealed that hydroperiod is central to the CO_2 exchange of these wetlands. The two contrasting marshes studied here followed two different patterns of carbon dynamics. R$_{eco}$ was always >NEE and the dominant flux controlling NEE. Yet each site behaved in fundamentally different ways suggesting that under short hydroperiods (TS), seasonal respiration rates were a combination of lower diffusion rates and anoxic soils during periods of flooding versus greater decomposition of stored carbon pools and a greater fraction of aerobic plant respiratory effluxes during dry season. Under long hydroperiods (SRS), there were high rates and a strong temperature dependence of R$_{eco}$ during inundation and a decrease in R$_{eco}$ with declining water levels. During this study, the long-hydroperiod marsh was a net annual CO_2 source while the short-hydroperiod marsh was a net CO_2 sink. Furthermore, these oligotrophic ecosystems had low rates of productivity, contrary to results from some previous Everglades studies. Although trends of decreased carbon sequestration during wet periods were observed, this finding may only reflect the short time frame of this study. Long-term continuous data sets will allow us to assess carbon dynamics and the controls on interannual variability in the Everglades.

[62] The Comprehensive Everglades Restoration Plan (CERP, 2000, http://www.evergladesplan.org) will reintroduce historical water flow to the Everglades and will cause an

Table A1. Distribution of Parameters From Daytime NEE Bootstrap Simulations[a]

Year	Month	α				P_{max}				R_{eco}			
		Est	LCL	Median	UCL	Est	LCL	Median	UCL	Est	LCL	Median	UCL
						Site SRS							
2008	7	−0.027	−0.064	−0.028	−0.015	−2.646	−3.319	−2.677	−2.223	1.332	0.934	1.354	1.969
	8	−0.022	−0.050	−0.022	−0.012	−2.409	−2.921	−2.446	−2.019	1.373	0.961	1.390	1.931
	9	−0.013	−0.024	−0.014	−0.008	−1.652	−2.006	−1.668	−1.379	0.746	0.479	0.757	1.094
	10	−0.011	−0.022	−0.011	−0.006	−1.593	−1.962	−1.596	−1.335	0.927	0.648	0.921	1.301
	11	−0.006	−0.009	−0.006	−0.004	−1.904	−2.096	−1.903	−1.724	0.246	0.087	0.238	0.435
	12	−0.006	−0.012	−0.006	−0.003	−1.380	−1.624	−1.396	−1.185	0.415	0.182	0.403	0.679
2009	1	−0.025	−0.052	−0.025	−0.012	−1.986	−2.415	−2.005	−1.669	0.588	0.276	0.598	0.973
	2	−0.011	−0.022	−0.011	−0.006	−1.936	−2.182	−1.953	−1.726	0.296	0.054	0.295	0.561
	3	−0.004	−0.103	−0.005	−0.001	−2.233	−4.383	−2.344	−1.494	0.644	−0.016	0.723	1.866
	4	−0.016	−0.787	−0.017	−0.005	−2.482	−12.12	−2.562	−2.100	1.432	1.003	1.440	10.46
	5	−0.566	−5.210	−0.276	0.000	−8.291	−25.72	−6.645	−0.141	7.583	−0.588	5.879	22.93
	6	−0.026	−0.052	−0.025	−0.015	−4.507	−5.703	−4.460	−3.719	2.011	1.239	1.960	3.232
	7	−0.047	−0.084	−0.046	−0.026	−3.725	−4.498	−3.726	−3.063	2.061	1.425	2.055	2.817
	8	−0.049	−0.136	−0.050	−0.023	−2.524	−3.454	−2.538	−2.110	1.961	1.535	1.968	2.877
	9	−0.012	−0.027	−0.013	−0.006	−1.985	−2.357	−2.028	−1.702	1.508	1.257	1.525	1.843
	10	−0.011	−0.028	−0.011	−0.004	−1.456	−1.849	−1.493	−1.236	1.177	0.905	1.201	1.563
	11	−0.006	−0.012	−0.006	−0.003	−2.166	−2.622	−2.212	−1.821	0.395	0.034	0.411	0.715
	12	−0.027	−0.083	−0.029	−0.012	−2.615	−3.755	−2.691	−2.123	1.427	0.899	1.498	2.559
						Site TS							
2008	1	−0.009	−0.011	−0.010	−0.008	−7.104	−7.948	−7.101	−6.553	1.199	1.037	1.203	1.361
	2	−0.009	−0.011	−0.009	−0.007	−7.607	−8.441	−7.612	−7.046	1.386	1.157	1.394	1.650
	3	−0.013	−0.019	−0.013	−0.008	−5.685	−6.284	−5.741	−5.184	1.113	0.473	1.126	1.710
	4	−0.012	−0.014	−0.012	−0.010	−6.554	−6.935	−6.567	−6.269	1.708	1.528	1.704	1.894
	5	−0.010	−0.012	−0.010	−0.008	−7.161	−7.599	−7.161	−6.826	1.752	1.558	1.754	1.940
	6	−0.016	−0.023	−0.016	−0.012	−7.305	−7.856	−7.340	−6.877	1.985	1.405	1.994	2.693
	7	−0.017	−0.023	−0.017	−0.014	−6.822	−7.238	−6.831	−6.434	2.106	1.706	2.101	2.588
	8	−0.009	−0.013	−0.009	−0.006	−4.654	−5.319	−4.676	−4.133	1.049	0.690	1.059	1.440
	9	−0.011	−0.016	−0.011	−0.007	−2.252	−2.534	−2.270	−2.036	0.975	0.759	0.985	1.249
	10	−0.007	−0.021	−0.007	−0.003	−1.008	−1.432	−1.020	−0.718	0.775	0.494	0.781	1.203
	11	−0.003	−0.006	−0.003	−0.001	−1.078	−1.342	−1.092	−0.900	0.152	−0.018	0.153	0.350
	12	−0.003	−0.010	−0.004	−0.001	−2.168	−3.848	−2.226	−1.794	0.235	−0.077	0.257	0.689
2009	1	−0.010	−0.015	−0.010	−0.007	−3.406	−3.752	−3.437	−3.160	1.350	1.097	1.358	1.700
	2	−0.008	−0.011	−0.008	−0.005	−4.990	−5.868	−5.015	−4.524	1.239	0.976	1.237	1.512
	3	−0.010	−0.012	−0.010	−0.008	−6.525	−6.922	−6.526	−6.194	1.579	1.366	1.585	1.809
	4	−0.013	−0.015	−0.013	−0.011	−6.964	−7.292	−6.984	−6.678	1.785	1.624	1.790	1.973
	5	−0.018	−0.023	−0.018	−0.014	−6.566	−6.900	−6.585	−6.276	2.109	1.745	2.118	2.517
	6	−0.018	−0.023	−0.018	−0.014	−5.069	−5.427	−5.085	−4.767	1.487	1.168	1.490	1.836
	7	−0.015	−0.024	−0.016	−0.010	−2.809	−3.274	−2.840	−2.495	1.058	0.744	1.082	1.501
	8	−0.023	−0.313	−0.021	−0.006	−2.172	−5.269	−2.162	−1.583	1.182	0.524	1.150	4.206
	9	−0.011	−0.022	−0.011	−0.006	−1.744	−2.054	−1.759	−1.511	1.126	0.886	1.131	1.444
	10	−0.008	−0.016	−0.008	−0.004	−1.752	−2.063	−1.780	−1.512	0.380	0.134	0.386	0.690
	11	−0.004	−0.007	−0.004	−0.002	−4.101	−6.825	−4.139	−3.402	0.306	−0.067	0.302	0.720
	12	−0.006	−0.009	−0.007	−0.005	−3.515	−3.946	−3.513	−3.190	0.348	0.157	0.350	0.588

[a]Est = estimated values; LCL = lower limit of 95% confidence region; UCL = upper limit of 95% confidence region.

increase in water levels at our study sites. These increased water levels will lengthen inundation periods in the Everglades, possibly causing a decrease in the carbon sequestration capacity of these ecosystems. The interaction between hydrology and carbon dynamics becomes even more uncertain when one considers the possible alterations in precipitation and evapotranspiration rates with climate change predictions. While we cannot predict the resiliency of these ecosystems, these measurements provide the first step toward understanding the current and future carbon sequestration capacity of these ecosystems.

Appendix A

[63] Table A1 gives estimates of each parameter from equation (3) by month and site, as well as results from 1000 bootstrap estimates from each month and site. The lower and upper confidence regions give an interval in which 95% of all estimates were contained. The median is the 50th percentile of each estimated parameter distribution. Table A2 gives similar information for equation (4), and gives estimates and bootstrap distribution statistics for annual equations as well.

Table A2. Distribution of Parameters From Nighttime NEE Bootstrap Simulations[a]

Year	Month	R_0				b			
		Est	LCL	Median	UCL	Est	LCL	Median	UCL
					Site SRS				
2008	8	0.697	0.257	0.704	1.972	0.019	−0.021	0.019	0.054
	10	0.558	0.391	0.559	0.780	0.018	0.005	0.018	0.032
	11	0.049	0.030	0.049	0.073	0.098	0.079	0.098	0.119
Annual		0.095	0.079	0.094	0.114	0.084	0.077	0.085	0.092
2009	2	0.177	0.128	0.178	0.229	0.075	0.055	0.075	0.100
	9	0.951	0.249	0.923	3.542	0.017	−0.031	0.018	0.063
	12	0.357	0.293	0.360	0.436	0.038	0.027	0.038	0.048
Annual		0.262	0.231	0.262	0.298	0.060	0.055	0.060	0.065
					Site TS				
2008	1	0.445	0.393	0.447	0.509	0.056	0.048	0.056	0.063
	2	0.412	0.290	0.412	0.566	0.064	0.047	0.064	0.082
	3	0.113	0.045	0.116	0.218	0.124	0.095	0.123	0.161
	4	0.486	0.353	0.481	0.650	0.055	0.040	0.055	0.070
	5	0.671	0.314	0.657	1.227	0.041	0.016	0.042	0.072
	7	0.050	0.000	0.047	1.682	0.126	−0.012	0.127	0.322
	9	0.073	0.003	0.088	1.254	0.089	−0.018	0.082	0.202
	10	0.010	0.001	0.010	0.066	0.175	0.095	0.174	0.273
Annual		0.268	0.211	0.268	0.331	0.051	0.042	0.051	0.061
2009	1	0.689	0.529	0.684	0.863	0.025	0.008	0.025	0.043
	2	0.624	0.509	0.623	0.744	0.054	0.042	0.054	0.066
	3	0.473	0.294	0.477	0.673	0.067	0.049	0.066	0.090
	4	0.380	0.193	0.369	0.727	0.072	0.042	0.073	0.101
	5	0.697	0.097	0.698	4.970	0.042	−0.043	0.042	0.121
	6	0.858	0.098	0.948	7.329	0.006	−0.075	0.003	0.081
	9	0.105	0.009	0.101	1.072	0.088	0.000	0.089	0.178
	10	0.506	0.332	0.500	0.775	0.019	0.001	0.019	0.038
	12	0.071	0.033	0.071	0.124	0.105	0.079	0.105	0.138
Annual		0.875	0.789	0.872	0.969	0.012	0.007	0.012	0.017

[a]Est = estimated values; LCL = lower limit of 95% confidence region; UCL = upper limit of 95% confidence region.

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