Large interannual CO$_2$ and energy exchange variability in a freshwater marsh under consistent environmental conditions
Large interannual CO₂ and energy exchange variability in a freshwater marsh under consistent environmental conditions

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[1] We analyzed a 5-year record of the CO₂ and energy exchange, Aboveground Net Primary Production (ANPP), maximum Leaf Area Index (LAI_max), and Enhanced Vegetation Index (EVI) for a Typha marsh in Southern California. The marsh was a net source of carbon over the study, despite high rates of ANPP. Interannual Net Ecosystem Production (NEP) variability was the largest that has been reported for any terrestrial ecosystem and was attributed to changes in maximum photosynthetic rates (GEE_max). The variation in energy and mass exchange was coupled between years; years with higher than average rates of carbon uptake were associated with lower than average sensible heat fluxes. Remotely sensed measures of surface greenness (EVI) were closely related to GEE_max variation, providing further evidence of interannual variability. We were unable to attribute the fluctuations in GEE_max to the direct effects of weather on ecosystem physiology, or to interannual variation in LAI_max. GEE did not vary systematically with air temperature or the presence of standing water in the marsh; GEE_max did not vary with LAI_max between years. Rather, interannual variation in carbon exchange at the SJFM resulted from shifts in the marsh’s production efficiency (the rates of gross or net CO₂ exchange per LAI) that were not caused by changes in the weather. Our findings challenge the assumptions that interannual variation of land-atmosphere exchange is universally caused by the direct effect of weather on ecosystem physiology, and that an ecosystem’s physiological response to the physical environment is consistent from year-to-year.


1. Introduction

[2] Long-term records of whole ecosystem CO₂, water and energy exchanges have provided valuable insight into the interannual dynamics of ecosystem function. These records have demonstrated that exchanges of energy and mass are tightly coupled [Law et al., 2002] and that ecosystems are dynamic in their ability to capture and store carbon from year to year [cf. Goulden et al., 1996; Chen et al., 1999; Barford et al., 2001; Flanagan et al., 2002; Dunn et al., 2007]. Most work has attributed interannual energy and mass exchange variability solely to weather. However, statistical attribution of interannual variability in Net Ecosystem Exchange of CO₂ (NEE) to climatic factors has been difficult [Hollinger et al., 2004] and attempts to model interannual NEE variability using process based ecosystem models have achieved moderate to low success [Joiner et al., 1999; Kelly et al., 2000; Griffis and Rouse, 2001; Thornton et al., 2002; Hanson et al., 2004; Urbanski et al., 2007].

[3] Our inability to model and attribute interannual ecosystem variability may reflect the simplicity with which we view and represent ecosystems in models. Most models assume that ecosystems respond to the environment passively and that this response is constant over time [Hanson et al., 2004; Urbanski et al., 2007]. Most models are highly parameterized such that ecosystem respiration is represented as a simple Q₁₀ response with temperature, and photosynthesis is represented with a constant light use efficiency and carboxylation capacity [Hanson et al., 2004]. These model parameterizations do not allow for temporal changes in biological factors associated with interannual changes in light use efficiency, carbon allocation, or substrate induced respiration [Davidson et al., 2006]. However, interannual ecosystem variability almost certainly involves internal biological controls, which can change the response of an ecosystem to the environment [Hui et al., 2003; Richardson et al., 2007]. The core question, therefore, involves the relative importance of these internal biological dynamics in controlling interannual variability.

[4] In this study, we describe the interannual dynamics of CO₂ and energy exchanges, Aboveground Net Primary Production (ANPP), maximum Leaf Area Index (LAI_max), and remotely sensed vegetation indices at the Typha-dominated San Joaquin Freshwater Marsh (SJFM) located in Southern California. The SJFM is a freshwater marsh located in a maritime Mediterranean climate. Interannual
weather variability at the SJFM is small and water input to the SJFM is managed and consistent from year to year. *Typha* wetlands are known for their high productivity [Bradbury and Grace, 1983] and abundance of nutrient resources compared to other terrestrial systems [LeBauer and Treseder, 2008]. We hypothesized that interannual variability in energy and mass exchanges would be small, and that the high productivity of the SJFM would result in a strong carbon sink. We address these hypotheses by documenting a long-term record of whole ecosystem CO2 and energy exchange, assessing the ability of the SJFM to sequester carbon, determining the relationships between interannual weather and ecosystem function, and comparing the interannual SJFM ecosystem function variability to that reported for other ecosystem types.

2. Methods

2.1. Site Description

[5] The study was conducted at the San Joaquin Freshwater Marsh Reserve (SJFM) located on the University of California’s Irvine campus [Goulden et al., 2007]. The SJFM is in coastal Orange County, 3 m above sea level and 8 km northeast of the Pacific Ocean (33° 39’ 44.4”N, 117° 51’ 6.1”W). The climate is Mediterranean with a mean annual temperature (1975–2005) of 17.7°C and a mean annual precipitation of 350 mm. The SJFM is dominated by *Cattail (Typha latifolia L.)* with a minor component (~20% percent cover) of Bullrush (*Scirpus californicus* C.A. Mey. Steud.) and willows (*Salix spp.*) around the periphery. The hydrology of the SJFM has been altered and water input is now managed. The SJFM is flooded to a depth of ~1 m above the mineral soil in the winter of most years. Natural precipitation is the only additional source of water after initial flooding and the SJFM dries by evapotranspiration and subsurface drainage through the spring and summer. Standing water disappears by midsummer in most years.

2.2. Micrometeorological Observations

[6] Meteorological data and the NEE of CO2 were calculated at half hourly intervals from December 1998 to December 2003 [Goulden et al., 2007] (http://www.ess.uci.edu/~marsh). The eddy covariance tower was mounted on a floating platform that was unaffected by lateral or vertical wind movement and remained level throughout the year. Instruments at 5.5 m above the platform surface recorded the environmental conditions at 0.5 Hz. Radiation measurements included incoming and reflected Photosynthetic Active Radiation (PAR, and PARs) measured with quantum sensors (Model LI-190, LI-COR Inc., Lincoln, NE) and incoming and reflected shortwave radiation (Ks and K) measured with thermopile pyranometers (Kipp & Zonen CM3, Delft, Netherlands). Vapor pressure deficit (VPD) was calculated from the measured water vapor concentration and air temperature, using the Clausius-Clapeyron equation to derive the saturation vapor pressure. Midday PAR albedo (PARalbedo) was calculated by dividing midday values of PAR by PAR. Air temperature, precipitation, and humidity were recorded at the tower, but we opted to use a more continuous data set from the nearby Santa Ana John Wayne Airport (2 km to the north; data from the U.S. National Climatic Data Center, http://www.ncdc.noaa.gov, see Goulden et al. [2007] for further details). The John Wayne Airport data set contained hourly air temperature, precipitation and relative humidity for 1999–2003.

[7] The NEE of CO2 was calculated as the 30-min covariance of the vertical wind velocity measured with a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and the CO2 mixing ratio measured with a closed path infrared gas analyzer (IRGA: Model 7000 or 6262, LI-COR Inc., Lincoln, NE). Adequate turbulent mixing and energy budget closure are key factors determining the quality of NEE data [Goulden et al., 1997]. Adequate turbulent mixing at the SJFM, as determined from plots of NEE versus friction velocity (u*), occurred for u* > 0.20 m s⁻¹. The eddy covariance technique samples the flux from a few hectare patch of vegetation that is upwind of the tower. Daytime winds at the SJFM almost always originate from the southwest, and we located the tower near the eastern side of the SJFM, in an area where *Typha* marsh extended 500- to 900-m to the southwest. The marsh extended less than 100 m to the northeast of the tower, and the eddy covariance measurements during periods with wind from this direction did not provide a valid measure of marsh exchange. NEE data during periods with either wind from 315° to 145° or u* < 0.20 m s⁻¹ were excluded from the analysis. We referred to the remaining flux data as “un-filled” tower data.

2.3. Separating NEE Into Component Fluxes and Gap Filling

[8] NEE is the sum of three component fluxes: Gross Ecosystem Exchange (GEE), autotrophic respiration (Rc), and heterotrophic respiration (Rh). Eddy covariance determines NEE, which can be partitioned into GEE and Total Ecosystem Respiration (TER) by separately considering the day and night observations [Goulden et al., 1997]. The further partitioning of TER into Rc and Rh is difficult and cannot be done accurately from eddy covariance data alone:

\[
\text{NEE} = (R_a + R_h) + \text{GEE} = \text{TER} + \text{GEE} \tag{1}
\]

Eddy covariance observations are commonly reported using the meteorological sign convention, where a downward movement of CO2 is considered a negative flux. The meteorological GEE always has a negative sign. A more negative meteorological GEE indicates an increase in photosynthesis and a more positive TER indicates an increase in respiration. NEE is negative when photosynthesis is greater than respiration and positive when photosynthesis is less than respiration.

[9] At night, GEE is zero and NEE (NEE_night) is equal to total ecosystem respiration. The difference between NEE_day and NEE_night can be used to calculate GEE provided that a realistic approach is adopted for extrapolating nocturnal respiration (NEE_night) to daytime periods. Many researchers have used an exponential fit with temperature to extrapolate NEE_night to daytime conditions (GEE_expcomplex TER) [cf. Goulden et al., 1997]. However, this approach is not without its weaknesses, because the respiration model is parameterized with cool nocturnal temperatures and extrapolated to warmer daytime temperatures, and because the result often depends on whether air or soil temperature is used [Richardson et al., 2006]. An alternative, more con-
serves to air approaches infinity, and Hall et al. Twine et al. record. Chander and Markham NEE and errors in the exponential model /C0 night for /C0, NEE data were filled, 2000; 10 [ ] gap-filling approach will from the prior 25 days. Missing K 10 [61x467] compared to the simple gap-filling approach. From this period to derive Q 10 respiration functions because Q 10 functions based on monthly to seasonal time scales had little to no predictive value. Rates of respiration in equation (3) were determined from unfiltered averaged NEE night from the prior 25 days. Our analysis found that the magnitudes of the fluxes changed, but the patterns of interannual variability remained similar among gap filling techniques (data not shown). On average, -GEE was 17% higher and TER was 16% higher for the annual Q 10 gap-filling approach as compared to the simple gap-filling approach. From this analysis, we conclude that the Q 10 gap-filling approach will overestimate TER and GEE because temperature poorly predicted NEE night and errors in the exponential model increase with increases in temperature. Nonetheless, we emphasize that our conclusions are independent of gap filling technique. We believe that the simple gap filling technique (equation (3)) provides a more conservative and robust estimate of the SJFM annual carbon budget, and we therefore used this approach for our subsequent analyses.

Missing data due to sensor malfunction, periods of low turbulence, and inappropriate wind direction were filled using empirical relationships to calculate the daily and annual sums. Twenty five percent of the data had to be filled for 1999–2003 period. GEE was filled using a Michaelis-Menten hyperbolic regression with K [Ruxeny et al., 1995]. Fitted coefficients for the light curve described the potential maximum GEE as K approaches infinity, and the quantum efficiency of GEE. A combination of the Michaelis-Menten fit and an estimate of leaf phenology derived from a statistical relationship between NEE and reflected radiation during the 2000 growing season was used to fill a two and a half month gap in the early 2000 growing season. Respiration data were filled using averaged NEE night from the prior 25 days. Missing K i data were filled using a lookup table that listed half houry average K i for each period during the entire K i record.

An analysis of the energy budget closure at the SJFM indicated that the raw turbulent energy flux measurements underestimated the true energy flux by \( \sim 20\% \) [Goulden et al., 2007]. This percentage of unaccounted flux is similar to that observed in many other eddy covariance studies, and is presumably caused by transport in low-frequency circulations that are underestimated by a 30-min averaging interval [Twine et al., 2000]. We therefore forced our energy budget to close by multiplying latent and sensible heat fluxes by correction coefficients so that the long-term sum of turbulent fluxes equaled net radiation [Twine et al., 2000; Goulden et al., 2007].

3. Biomass Harvests

Cattails senesce and produce aboveground material annually, and so measurements of peak aboveground biomass were used as a measure of Aboveground Net Primary Production (ANPP). We sampled all living plants within thirty 0.25-m² quadrats along a 91.5 m transect that radiated to the southwest of the eddy covariance tower during the month of peak biomass (September) from 1999 to 2003. Plants were pulled from the ground, clipped below the crown to remove rhizomes and roots, taken back to the lab, oven-dried at 65°C for 2 to 3 days and weighed. We partitioned growth into leaves, stems, flowers, and the crown base by sorting a subsample of plants.

Collected leaf material was also used to determine the peak Leaf Area Index (LAI max) from measurements of specific leaf area. A subset of 25 to 35 plants from each year were weighed, scanned at 150 dpi using a Microtek ScanMaker i900 (Microtek USA, Carson, Calif.), saved as jpeg images and imported into ENVI 4.0 (ITT Visual Information Solutions; Boulder, CO, USA) for determination of leaf area. The determination of leaf area in ENVI was based on pixel counts on the red band that had a threshold luminosity value of greater than 100. This method was tested for accuracy against materials of known area and estimates were found to be in excellent agreement with actual area \( r^2 = 1.0; y = 1.0048x; \) Mean Absolute Error: 0.80 cm²). Specific leaf areas were then scaled to the canopy based on the leaf biomass measurements.

We obtained 5 midsummer (end of June–mid–August) Landsat images (Landsat 5 or 7) that included the SJFM (Path: 40 Row: 37) during 1999–2003. Landsat scenes have a ~30 m spatial resolution and were purchased from the MultiResolution Land Characteristics Consortium (MRLC; http://www.mrlc.gov/). Landsat data were taken after the hydroperiod, and surface water did not affect the calculation of vegetation indices.

Landsat images were cross-calibrated and surface reflectance data from a 90 by 90 m area located immediately upwind of the eddy covariance tower was used to calculate the Enhanced Vegetation Index (EVI). Images were corrected for sensor differences and drift by transforming pixel values into exoatmospheric radiances [Chander and Markham, 2003]. Images were then intercalibrated to remove any atmospheric influences and transformed into surface reflectance using the temporally invariant surface target method against a surface reflectance image that was processed by the LEDAPS project (http://ledaps.nascom.nasa.gov/ledaps/ledaps_NorthAmerica.html) [Huete et al., 1991]. Surface reflectance images were then used to calculate the Enhanced Vegetation Index (EVI) [Huete et al., 2002]. Images were processed with ENVI.

4. Results

4.1. Intra-annual and Interannual Variability in Environmental Conditions

Seasonal variations in environmental conditions at the SJFM reflected the maritime Mediterranean climate
Incoming solar radiation was low in the winter and peaked about a month before the peak in air temperature (Figure 1a). Over the course of a year, daily average air temperature ranged from 8 to 22°C (Figure 1b). The vapor pressure deficit (VPD) usually peaked about a month after the peak in air temperature and was lowest in the winter (Figure 1c). The SJFM was flooded to a depth of ~1 m beginning in December, January, or March of each year (Figure 1 and Table 1). The earliest arrival of water came in late December of 2002, and the latest arrival of water came in March of 1999. The SJFM received water in late January or early February in the other years.

Interannual variability in environmental conditions at the SJFM from 1999 to 2003 was small (Table 1). Average annual air temperature from 1999 to 2003 (17.4°C) was similar to the 30-year average (17.7°C) and ranged 1.3°C. Average minimum air temperatures ranged 1.7°C, while average maximum air temperatures ranged 1.5°C. The interannual range in average temperature was somewhat less than that observed for a temperate forest (1.6°C [Gough et al., 2008]), a tallgrass prairie (1.6°C [Suyker et al., 2003]), and a tropical peat swamp (1.6°C [Hirano et al., 2007]), and much less than that observed for a boreal forest (3.2°C [Dunn et al., 2007]). Annually averaged VPD ranged from 0.53 to 0.64 kPa and averaged 0.56 kPa, while annually integrated incoming solar radiation varied 8% and averaged 6647 MJ m⁻² a⁻¹. The hydroperiod ranged from 87 to 208 days.

4.2. Interannual Variability in Canopy Properties

There was significant interannual variability in plant canopy properties (Figure 2a). Maximum Leaf Area Index (LAI_max) was higher in 2000, 2001 and 2003 and lower in 1999 and 2002 (ANOVA; P < 0.001). There were no significant differences in stand density (ANOVA; p = 0.21) or specific leaf area (ANOVA; p = 0.18) between years, implying that plants were larger (i.e., more leaves or taller) in 2000, 2001 and 2003. We tested this hypothesis and found that average individual plant weight was reduced in 2002 (ANOVA; P < 0.001). Rates of ANPP were similar to other productive wetlands and crops (Figure 2b) [Esser et al., 2000]. ANPP was highest in 2001 and lowest in 1999 and ranged from 580 gC m⁻² a⁻¹ in 1999 to 1018 gC m⁻² a⁻¹ in 2001. Interannual ANPP variability was not significantly related to annual air temperature (p = 0.17), solar radiation (p = 0.44), average VPD (p = 0.78), or the length of the hydroperiod (p = 0.55).

4.3. Intra-annual and Interannual Variability in Surface Fluxes

Half-hour fluxes of energy and mass at the SJFM displayed marked intra and interannual variability (Figure 3). Latent and sensible heat fluxes were closely tied to the intensity of sunlight and canopy phenology over the season. Sensible heat fluxes were lowest from October to December and were often negative during winter nights and early mornings.
mornings. Sensible heat fluxes decreased in the middle of the summer as more energy was partitioned to latent heat. Peak rates of latent heat lagged peak rates of sensible heat by 3 to 4 months (Figures 3a and 3b). High rates of sensible heat flux occurred during the 2001 and 2002 growing seasons, and low rates during 1999, 2000 and 2003. Peak rates of sensible heat fluxes ranged from 375 W m$^{-2}$ in 2000 to 550 W m$^{-2}$ in 2002. Although peak rates of sensible heat were usually associated with the middle of the hydroperiod, the presence or absence of standing water at the SJFM had little direct effect on the sensible heat flux. [21] Latent heat flux also demonstrated large intra and interannual variability (Figure 3b). Latent heat peaked during midsummer and was lowest in the winter as the canopy senesced. Intraannual latent heat fluxes were more related to canopy development than to the presence or absence of standing water. Goulden et al. [2007] demonstrated that plant transpiration was more important than evaporation for controlling fluxes of latent heat at the SJFM, because a thick litter layer keeps water temperatures cool and rates of evaporation low. Interannual variability in latent heat fluxes was large, with peak midsummer rates of latent heat ranging from 150 W m$^{-2}$ in 2002 to 325 W m$^{-2}$ in 2000. Years with low latent heat flux (2001 and 2002) were coincident with years with high sensible heat flux, as required by conservation of energy. [22] The NEE of CO$_2$ also demonstrated large intra and interannual variability (Figure 3c). The seasonal cycle of NEE was closely correlated with the seasonal cycle of latent heat, underscoring the importance of canopy development in controlling both fluxes. Positive NEE occurred at night and during the winter, whereas negative NEE occurred during spring and summer days. There was large interannual variability in daytime as well as nighttime NEE. Peak rates of daytime NEE ranged from $-11 \mu$mol m$^{-2}$ s$^{-1}$ in 2001 to $-26 \mu$mol m$^{-2}$ s$^{-1}$ in 2003. Peak rates of nighttime NEE ranged from $4.5 \mu$mol m$^{-2}$ s$^{-1}$ in 1999 to $8.5 \mu$mol m$^{-2}$ s$^{-1}$ in 2001 and 2002. Nighttime NEE values indicate that respiration was highest in 2001 and 2002, and lowest in 1999, 2000, and 2003. Daytime NEE values indicate that net carbon uptake was highest in 2000 and 2003 and lowest in 2001 and 2002. [23] Interannual variability in the monthly averages of midday Bowen ratio, daily gross carbon uptake (GEE) and
daily carbon loss (TER) reflected the variability observed in the half hourly data (Figure 4). The midday Bowen ratio was highest in the winter months (Figure 4a), indicating that most of the energy was dissipated as sensible heat during this period. There was some interannual variability in the winter (Jan–Mar) midday Bowen ratios, but the data during this period had a high variance. Growing season midday Bowen ratios during 2001 and 2002 were significantly higher than in 1999, 2000, and 2003. Average daily GEE was highest during 2000 and 2003 (Figure 4b). Peak rates of average daily TER usually lagged peak rates of photosynthesis by a month and were highest during the 2001 and 2002 growing season (Figure 4c).

[24] The seasonality of CO₂ uptake was consistent from year to year, with a peak in July (Figure 4b). The rates of CO₂ uptake did not change markedly coincident with drying, either between or within years. The rates of CO₂ uptake increased from June to July of each year, even

**Figure 3.** Half hourly surface energy and mass exchanges at the SJFM from 1999 to 2003. Panels represent half hourly fluxes of (a) sensible heat, (b) latent heat, and (c) net ecosystem exchange of CO₂ (NEE). The length of the hydroperiod is denoted by the width of the gray bars.
though the marsh was drying at that point. The increase in CO₂ uptake from June to July was consistent from year to year, even though the marsh was wet during this period in some years (2003) and dry in others (2002). The timing of the onset of CO₂ uptake varied considerably from year to year, with early starts in 2000 and 2003. However, the onset of GEE in spring was not closely related to the presence or absence of water, except possibly for 1999, which was unusually dry. The onset of GEE was rapid in 2000 and 2003 and slow in 2001 and 2002, even though the marsh was flooded throughout the winter and spring of all four years. The presence or absence of standing water after the initial flooding period does not appear to exert a strong direct effect on the interannual variation of CO₂ exchange in midsummer, or on the timing of GEE development in spring.

4.4. Interannual Variability in Annual Carbon Budget

Interannual variability in the annual sums of GEE, TER and NEP were large (Figure 5). NEP ranged from -251 gC m⁻² a⁻¹ in 2000 to 515 gC m⁻² a⁻¹ in 2001. Gross uptake ranged from 1090 gC m⁻² a⁻¹ in 1999 to 1639 gC m⁻² a⁻¹ in 2000, while TER ranged from 1313 gC m⁻² a⁻¹ in 1999 to 1632 gC m⁻² a⁻¹ in 2001. Larger annual GEEs were observed in 2000 and 2003 and were associated with years that resulted in carbon sinks. Years with low GEE were associated with a net annual carbon loss. Interannual variability in annual TER was 73% less than the variability in GEE. NEP was better correlated with annual GEE (r²: 0.87; p = 0.02) than TER (r²: 0.56; p = 0.14), indicating that interannual variability in NEP was strongly controlled by GEE.

The annual sums of GEE, TER, and NEE differed in their relationship to weather and length of the hydroperiod. Interannual variability in TER was unrelated to annual air temperature (p = 0.92), annual precipitation (p = 0.69), or the length of the hydroperiod (p = 0.84), while GEE was unrelated to the average potential growing season temperature (DOY: 100–300) (p = 0.12) and length of the hydroperiod (p = 0.82), but weakly related to average annual air temperature (r²: 0.60; p = 0.05). The effect of warmer temperatures on GEE did not directly translate to interannual differences in carbon storage and NEP was unrelated to annual air temperature (p = 0.21), solar radiation (p = 0.82), or length of the hydroperiod (p = 0.23).

The weak correlation between annual air temperature and GEE possibly reflects the longer growing season brought on by warm spring temperatures in 2000 and 2003 (Figure 1), and we therefore investigated whether air temperature helps to explain the start of the growing season. Since growing degree days are sensitive to the base temperature, we ran a Monte Carlo simulation that changed the base temperature, recalculated growing degree days, and predicted the start of the growing season based on a range of growing degree days, which were constrained by actual observations (Figure 6). The simulation ran 400 correlations and none of the predictions came close to predicting the start of the growing season, indicating that air temperature alone cannot explain the start of the growing season (Figure 6, inset panel).

4.5. Interannual Variability in Vegetation Indices

Midsummer EVI and midday PAR albedo (PAR_alb) recorded changes in surface reflectance during the growing seasons of 1999–2003 (Figure 7). The seasonality of PAR_alb represented the seasonality of green leaves. Interannual midsummer EVI variability followed changes in ecosystem physiology from 1999 to 2003 in predictable ways. EVI was low during years with reduced net and gross CO₂ uptake, and increased midday Bowen ratios (1999, 2001, and 2002); EVI was high during years with increased net
and gross CO$_2$ uptake, and decreased midday Bowen ratios (2000 and 2003). Midsummer EVI was well correlated with $\text{-GEE}_{\text{max}}$ (Figure 7c) ($r^2$: 0.92; $p = 0.01$) and $\text{NEE}_{\text{max}}$ (data not shown) ($r^2$: 0.89; $p = 0.01$) indicating that changes in surface greenness were related to interannual physiological differences at the SJFM. At the same time, $\text{LAI}_{\text{max}}$ was not significantly correlated with EVI (Figure 7b) ($p = 0.62$), $\text{GEE}_{\text{max}}$ ($p = 0.54$) or $\text{NEE}_{\text{max}}$ ($p = 0.63$), implying a change in photosynthetic efficiency between years (the rates of gross or net CO$_2$ exchange per LAI). Midsummer EVI was unrelated to annual air temperature ($p = 0.22$), potential growing season temperature ($p = 0.39$), and length of the hydroperiod ($p = 0.09$).

4.6. Long-Term Carbon Budget

[29] The long-term (1999–2003) carbon budget indicates that the SJFM was a source of 680 gC m$^{-2}$ to the atmosphere (Figure 8). The low photosynthetic and high respiration rates in 2001 and 2002 heavily influenced the cumulative sum of carbon and switched the SJFM from a system that was approximately at steady state to one that was losing carbon (Figure 8b).

5. Discussion

[30] Interannual NEP variability at the SJFM, as indicated by the standard deviation of NEP, was the largest that has been reported for any terrestrial ecosystem (Table 2). The large interannual variability in several independent measures of ecosystem function (i.e., NEP, ANPP, EVI) indicates that the eddy covariance observations represented “true” variability, and were not mere methodological artifact. A survey of the literature indicates that Duke Forest’s loblolly pine plantation had the second largest variability, followed by a Southeast Asian tropical peat swamp. The difference between maximum and minimum NEP at the SJFM was 83% larger than at the pine plantation and the standard deviation of NEP for the SJFM was 118% larger than at the pine plantation. The large interannual NEP variability at the SJFM is surprising given that the annual temperature and water variability at the marsh is less than that reported for other eddy covariance sites (Table 1).

5.1. Does High Plant Productivity at the SJFM Result in a Large Carbon Sink?

[31] The SJFM was a source of carbon over five years despite high rates of aboveground NPP, which were typical of other freshwater marshes (Figures 2 and 8). The tower measurements may have underestimated this source somewhat, since additional carbon may have been exported as Dissolved Organic Carbon (DOC) or Particulate Organic Carbon (POC). However, these additional exports were likely minor, since most water is lost from the marsh through evapotranspiration and subsurface flow, and since the closed basin hydrology of the SJFM prevents the lateral

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**Figure 5.** Annual rates of ecosystem respiration [TER] (black bar), gross carbon uptake [-GEE] (light gray bar), and the annual carbon balance [NEP] (dark gray bar) from 1999 to 2003.

**Figure 6.** The relationship between start of the growing season and growing degree days with a base temperature equal to 10°C. The inset plot includes a histogram of Pearson correlation coefficients of modeled and predicted start of the growing season with different base temperatures and growing degree days. The right side of the hatched line represents correlations that would be significant at the 95% confidence level.
movement of large pieces of organic material. For example, if we assume the annual subsurface and lateral outflow was 50 cm and the DOC concentration was equal to the maximum concentration reported for a constructed wetland in Florida [Stern et al., 2007], the DOC export was $10 \text{ gC m}^{-2} \text{ a}^{-1}$, implying that Figure 8 understates the loss of carbon by $10\%$.

The inability of the SJFM to sequester carbon resulted from consistently high respiration rates, and two years with lower than average carbon uptake (i.e., 2001 and 2002). Aerial photographs and personal communication indicate the marsh is approximately fifty years old [Goulden et al., 2007]. It is likely that the ability of seasonally flooded freshwater marshes to sequester carbon diminishes with age due to the accumulation of organic matter and the stimulation of ecosystem respiration by increased substrate. Previous researchers have suggested that the high productivity of freshwater marshes make them ideal ecosystems for carbon

Figure 7. (a) Midsummer EVI (closed dark circles), 1-midday PAR albedo (closed gray circles) and the relationship between (b) EVI and LAI$_{\text{max}}$ and (c) EVI and $-\text{GEE}_{\text{max}}$ for the SJFM from 1999 to 2003. Numbers in inset plots indicate respective years.

Figure 8. (a) Long-term and (b) annual carbon budget for the SJFM from 1999 to 2003. The length of the hydroperiod is denoted by the width of the gray bars in the main plot, while numbers beside Figure 8b designate representative years of annual cumulative sums.
Table 2. Comparison of Interannual NEP Variability Among Different Ecosystems

<table>
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<th>Ecosystem Type</th>
<th>Number of Years</th>
<th>NEP&lt;sub&gt;max&lt;/sub&gt; (gC m&lt;sup&gt;-2&lt;/sup&gt; min&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>HEV</th>
<th>Standard Deviation of NEP</th>
<th>Source</th>
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*The SJFM is in bold, and other values were compiled from the literature.

sequestration [Thom et al., 2002]. However, our results emphasize the need to understand the individual components of an ecosystem’s carbon balance in order to assess its carbon sequestration potential.

5.2. Physiological Characteristics of the SJFM and Their Relationship to Environmental Factors

[35] The SJFM is unusual in that much of the interannual variability in NEP was attributable to changes in GEE, whereas the attribution of NEP variability in other ecosystems has focused more on ecosystem respiration [cf. Valentini et al., 2000; Barford et al., 2001; Hollinger et al., 2004; Dunn et al., 2007]. This indicates that photosynthesis is the key to interpreting SJFM interannual ecosystem function variability. High leaf areas did not translate into high photosynthetic rates in 2001 and 2002, resulting in the poor relationships between LAI<sub>max</sub> and both HEV and the peak rates of photosynthesis (Figure 7). This finding is important because it diverges from previous work that has established LAI as the main factor that connects vegetation indices and canopy gas exchange [Gamon et al., 1995; Rahman et al., 2005]. Our findings imply that changes in the photosynthetic efficiency of the canopy (the rates of gross or net CO<sub>2</sub> exchange per LAI) are the main cause of interannual ecosystem function variability at the SJFM.

5.3. Is the Physical Environment Directly Responsible for Interannual NEP Variability at the SJFM?

[34] Previous work has attributed interannual GEE, TER, and NEP variability to the direct effects of physical factors such as temperature and precipitation on ecosystem physiology [cf. Barford et al., 2001; Flanagan et al., 2002; Dunn et al., 2007]. Ecosystems with the highest interannual variability in temperature or water availability might therefore be expected to have the highest interannual NEP variability. However, we found that the interannual NEP variability at the SJFM was the largest that has been reported for any terrestrial ecosystem, even though the variability in average annual temperature was equal to or less than that observed for many ecosystems (Tables 1 and 2). This finding calls into question the idea of a universal, tight link between weather and interannual GEE, TER, and NEP variability.

[35] The effects of interannual weather variability on ecosystem physiology would be expected to play out in a couple of ways: (1) through strong, direct correlations between specific weather conditions and CO<sub>2</sub> exchange (for example, a decrease in CO<sub>2</sub> uptake coincident with drying soil or unusually warm temperatures), or (2) through a chain of strong correlations between specific weather conditions, the development or loss of LAI, and the effect of LAI on CO<sub>2</sub> exchange (for example, the rapid development of LAI with spring warming, and a subsequent increase in CO<sub>2</sub> uptake). In fact, we were unable to find clear evidence that either of these factors plays an important role at the SJFM.

[36] Many processes at the SJFM were uncorrelated with the immediate physical conditions (Figures 2, 5, and 7 and Table 1). Differences in the start of the growing season were not well correlated with either the presence of standing water (Figure 4) or temperature (Figure 6). The seasonal
patterns of GEE, TER, and midday Bowen ratio were independent of the length of the hydroperiod and the initial timing of flooding. Air temperature was weakly correlated with annual GEE, but the unrealistic sensitivity of annual GEE to temperature indicates that this relationship was more coincident than causative. Attributing interannual GEE variability to temperature would require a temperature sensitivity that is nine times greater than that reported previously [Law et al., 2002]. Finally, LAI_max and land-atmosphere exchange were largely uncorrelated, implying that the causal relationships between weather, LAI development, and exchange were weak.

[37] In conclusion, the interannual variation in carbon exchange at the SJFM resulted from shifts in the marsh’s production efficiency that were not caused by changes in the weather. Our findings challenge the assumption that interannual variation of land-atmosphere exchange is universally caused by the direct effect of weather on ecosystem physiology, and that an ecosystem’s physiological response to the physical environment is consistent from year-to-year. Future work will focus on further understanding the mechanisms behind interannual variability at the SJFM [Rocha et al., 2008; Rocha and Goulden, 2008].

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