Effects of simulated drought on the carbon balance of Everglades short-hydroperiod marsh

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Abstract

Hydrology drives the carbon balance of wetlands by controlling the uptake and release of CO_2 and CH_4. Longer dry periods in between heavier precipitation events predicted for the Everglades region, may alter the stability of large carbon pools in this wetland's ecosystems. To determine the effects of drought on CO_2 fluxes and CH_4 emissions, we simulated changes in hydroperiod with three scenarios that differed in the onset rate of drought (gradual, intermediate, and rapid transition into drought) on 18 freshwater wetland monoliths collected from an Everglades short-hydroperiod marsh. Simulated drought, regardless of the onset rate, resulted in higher net CO_2 losses net ecosystem exchange (NEE) over the 22-week manipulation. Drought caused extensive vegetation dieback, increased ecosystem respiration (R_{eco}), and reduced carbon uptake gross ecosystem exchange (GEE). Photosynthetic potential measured by reflective indices (photochemical reflectance index, water index, normalized phaeophytinization index, and the normalized difference vegetation index) indicated that water stress limited GEE and inhibited R_{eco}. As a result of drought-induced dieback, NEE did not offset methane production during periods of inundation. The average ratio of net CH_4 to NEE over the study period was 0.06, surpassing the 100-year greenhouse warming compensation point for CH_4 (0.04). Drought-induced diebacks of sawgrass (C_3) led to the establishment of the invasive species torpedo-grass (C_4) when water was resupplied. These changes in the structure and function indicate that freshwater marsh ecosystems can become a net source of CO_2 and CH_4 to the atmosphere, even following an extended drought. Future changes in precipitation patterns and drought occurrence/duration can change the carbon storage capacity of freshwater marshes from sinks to sources of carbon to the atmosphere. Therefore, climate change will impact the carbon storage capacity of freshwater marshes by influencing water availability and the potential for positive feedbacks on radiative forcing.

Keywords: carbon cycling, climate change, Everglades, freshwater marsh, greenhouse carbon balance, greenhouse warming potential

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Introduction

Wetlands have a great potential for carbon sequestration and storage as hydric conditions slow decomposition in the soil, and carbon accumulates over long time periods at rates higher than other ecosystems (Whiting & Chanton, 2001; Brevik & Homburg, 2004; Choi & Wang, 2004). Globally, there is more carbon stored in soil (1672 Gt) than in the atmosphere (738.2 Gt) and plant biomass (850 Gt; living and dead) combined (Reddy & DeLaune, 2008). Representing just 5–8% of global land cover, wetlands are one of the largest components of the terrestrial carbon pool, storing 535 Gt of carbon below ground, which is 32% of all soil carbon (Whiting & Chanton, 1993; Zedler & Kercher, 2005; Mitsch & Gosselink, 2007; Adhikari *et al.*, 2009). The

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stability of this large pool of carbon is uncertain due to human influence and changes in climate.

Globally, wetlands have been reduced as a result of land cover change (Armentano, 1980). Agriculture, development, and changes in hydrology caused 50% of wetland loss in the United States since the 1900s (Dugan, 1993). One of the largest wetland ecosystems in the United States, the Everglades, has had considerable human influence on its hydrological regime. Over the last 130 years, the hydrologic regime in this subtropical system has been altered by 2500 km of spillways, levees, and canals that were designed for flood protection and to provide water to south Florida. Due to the adverse effects of reduced water flow, current water management is being modified again under the Comprehensive Everglades Restoration Plan (CERP) (Perry, 2004). As part of CERP, water resources will be redistributed, changing the

current water levels and hydroperiods to levels closer to natural values in many areas of Everglades National Park (Perry, 2004).

Driving the greenhouse carbon balance, hydrology is an extremely important factor in carbon cycling (Bubier *et al.*, 2003a, b; Smith *et al.*, 2003; Heinsch, 2004; Webster *et al.*, 2013). Hydroperiods directly impact productivity (Childers, 2006; Hao *et al.*, 2011; Schedlbauer *et al.*, 2012), decomposition rates, CH_4 production and oxidation (King *et al.*, 1990; Bachoon & Jones, 1992; Torn & Chapin, 1993; Smith *et al.*, 2003; Whalen, 2005), $CaCO_3$ precipitation (Davis & Ogden, 1994), and CO_2 sequestration (Jimenez *et al.*, 2012). Although wetland ecosystems have large carbon pools, under certain conditions they can become a source of carbon to the atmosphere (Jimenez *et al.*, 2012; Webster *et al.*, 2013). As water levels decrease, oxygen availability increases aerobic respiration rates, decomposing the carbon stored in the soil and causing losses to the atmosphere as CO_2 (Webster *et al.*, 2013). Wetlands also become a source of carbon when low redox potentials initiate other greenhouse gas production, such as CH_4 and N_2O (Smith *et al.*, 2003; Webster *et al.*, 2013).

The ratio of CH_4 emissions to net CO_2 uptake is an index for an ecosystem's greenhouse gas (carbon) exchange balance with the atmosphere (Whiting & Chanton, 2001). In wetland ecosystems, the greenhouse gas (carbon) exchange balance is dependent on interactions between physical conditions, microbial processes in the soil, and vegetation characteristics (King *et al.*, 1990; Bachoon & Jones, 1992; Whiting & Chanton, 2001; Smith *et al.*, 2003). Through heterotrophic respiration and decomposition of organic matter, CO_2 is released from soil, increasing exponentially with higher temperatures (Bubier *et al.*, 2003a; Heinsch, 2004; Aurela *et al.*, 2007; Pearlstine *et al.*, 2010; Jimenez *et al.*, 2012) and decreasing with soil saturation (Torn & Chapin, 1993; Whiting & Chanton, 2001; Smith *et al.*, 2003; Heinsch, 2004; Schedlbauer *et al.*, 2010; Jimenez *et al.*, 2012; Webster *et al.*, 2013). Inundated conditions promote carbon storage from biomass produced by photosynthesis and stimulate losses as a result of low redox potentials that lead to the production of the more potent greenhouse gas CH_4 (Mitsch & Gosselink, 2007; Hao *et al.*, 2011). Although wetlands contribute more than 10% of the annual global emissions of CH_4, previous studies have shown that NEE can mitigate the impact of CH_4 efflux (Whiting & Chanton, 2001; Mitra *et al.*, 2005; Mitsch *et al.*, 2012). However, due to changes in climate, the future greenhouse gas (carbon) exchange balance of wetlands is uncertain (Whiting & Chanton, 2001).

The goal of this study was to use simulated drought to determine how the greenhouse carbon balance of short-hydroperiod freshwater ecosystems respond to changes in hydroperiod. We used the Everglades as our study site, as its hydrologic cycle is not only expected to change with CERP, but with future predictions of climate change. For the south Florida region, the IPCC (2007) projects increased occurrence of large single day rain events with higher drought frequency and rising air temperatures. The increase in drought frequency and higher temperatures will cause lower water availability, which will significantly influence the greenhouse carbon balance of Everglades ecosystems (Davis & Ogden, 1994; Todd *et al.*, 2010). Understanding the complex relationships between carbon cycling in the Everglades freshwater marshes and environmental controls is important in determining the future carbon dynamics of wetland ecosystems.

We hypothesize that the increased frequency and duration of droughts will increase CO_2 and decrease CH_4 emissions from freshwater marshes of the Everglades' through a reduction in soil water availability. Reductions in water availability will result in increased soil oxygenation, lower rates of methanogenesis, and higher CO_2 production via methane oxidation and increased aerobic respiration (Bachoon & Jones, 1992). The effects of water stress will also cause a reduction in the water content of the vegetation, light use efficiency, and chlorophyll content, while chlorophyll degradation should increase. We also hypothesize that the speed of drought onset will influence photosynthetic potentials and net exchange rates for both CO_2 and CH_4. A more gradual transition to drought will produce lower net ecosystem exchange (NEE) rates (more carbon uptake) and higher ecosystem CH_4 fluxes than intermediate and rapid transition into drought, due to the length of water availability. Drought simulation will likely decrease carbon storage and increase atmospheric forcing. As changes in hydrology due to climate and management are the issues for wetlands globally, results from this study can add to our understanding of potential changes in the structure and function of these ecosystems, as well as their contributions to the global carbon cycle and values as reservoirs for carbon.

Materials and methods

Study site

Intact monoliths ($30 \times 60 \times 20$ cm; $n = 18$) of short-hydroperiod marsh (marl soils) were collected just outside Everglades National Park ($25°25'33.55''$N, $80°28'7.37''$W). Collection occurred on sites dominated (>90%) by sawgrass on March 18th 2011. Monoliths were cut out of the ecosystem with their physical structure maintained (soil and roots approximately 20 cm deep collected, down to the bedrock). Following

collection, monoliths were placed in transportation tanks to prevent desiccation and transported by truck to the University of Alabama. Monoliths were removed from travel tanks and transplanted into permanent containers at the University's flow-controlled mesocosm facility (http://www.as.ua.edu/biolaqua/cfs/cfsmeso.htm) within 3 days of collection, and allowed 8 weeks to recover from harvesting, travel, and transplanting. Preliminary studies showed that at least 4 weeks was sufficient recovery time from both travel and transplantation (G. Starr and S. Oberbauer, unpublished results). During recovery, water levels were maintained 20 cm above the soil surface to simulate inundated conditions regularly seen in the short-hydroperiod marshes around Taylor Slough during the wet season (Schedlbauer et al., 2010, 2011; Jimenez et al., 2012).

The short-hydroperiod freshwater marsh ecosystems in the Everglades region are oligotrophic, subtropical wetlands with a year round growing season. Receiving approximately 1430 mm of precipitation annually, the majority of rainfall occurs during the wet season (May–October) with only 25% of annual precipitation falling during the dry season (November–April) (National Climatic Data Center, http://www.ncdc.noaa.gov/). Severe drought occurs every 4–6 years with La Niña events (Abtew et al., 2007). These wetlands are dominated by the C_3 species sawgrass (Cladium jamaicense) and by the C_4 species muhly grass (Muhlenbergia capillaris).

Experimental design

Using a randomized complete block design, each monolith ($n = 18$) was randomly assigned to one of two large flow tanks, then to a treatment (drought scenario: gradual, intermediate, and rapid transition to simulated drought). The study was limited to two flow tanks so that all monoliths were contained within one bay of the flow-controlled mesocosm facility to isolate blocking variation. At the beginning of the experiment (following the 8-week recovery period), water levels were maintained at the soil surface for 4 weeks to simulate inundated conditions. Since water levels at Taylor Slough were approximately 20 cm below the surface at the peak of the dry season in 2008 and 2010 (average years; G. Starr and S. Oberbauer, unpublished results), all drought scenarios targeted this water level. Within each tank, drought was simulated by changing hydroperiods (raising monoliths above the water level) at three rates: gradual (20 cm change in 4 weeks), intermediate (20 cm change in 2 weeks), and rapid (20 cm change in 1 week). There were three replicates of each treatment in each tank ($n = 6$ per drought scenario). Once all monoliths were elevated to 20 cm above the water level, blocks were maintained at this height for 3 weeks to simulate moderate dry-season conditions (Jimenez et al., 2012). Following the dry period, monoliths were reinundated for 3 weeks to allow recovery from drought, and the manipulation began again. Successive dry-downs were performed to test the additive effect of drought, a scenario observed at Taylor Slough (2010 dry season) and a scenario likely to occur frequently in the region as a result of climate change. The entire experiment occurred over a 22-week period from June to October 2011.

Carbon dynamic measurements

CO$_2$ fluxes. Net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}) were measured each week of the study with an infrared gas analyzer using a closed path chamber (LI-6200; LI-COR Inc., Lincoln, NE, USA) (Poorter, 1993; Vourlitis et al., 1993; Oberbauer et al., 1998). Chamber temperature and photosynthetically active radiation (PAR) were recorded using a Type-T, fine wire thermocouple and a LI-COR LI-190S-1 quantum sensor attached to the LI-COR 6200 cuvette head. Measurements were taken three times a day (sunrise: 6:00 to 10:00 hours; noon: 11:00 to 3:00 hours, and dusk: 4:00 to 8:00 hours) at ambient light (NEE), and each measurement of NEE was followed by a dark measurement (R_{eco}) (Oberbauer et al., 1998). Gross ecosystem exchange (GEE) was calculated as:

$$GEE = NEE - R_{eco} \qquad (1)$$

CH$_4$ fluxes. Net methane flux was measured using the static chamber method (Whalen & Reeburgh, 1988; Vourlitis et al., 1993; Tsuyuzaki et al., 2001). Four static chambers ($58.72 \times 37.47 \times 126.15$ cm) were used to measure methane fluxes on the 18 monoliths each week, with two chambers randomly assigned to each tank. Headspace samples were drawn from each chamber every 15 min for 45 min, using 3 ml syringes with needles permanently attached with epoxy cement (Whalen & Reeburgh, 1988). At each time point, duplicate samples were collected. Data collection occurred during a 5-h period (9:00 to 2:00 hours) when we would expect to see maximum CH$_4$ fluxes (McDermitt et al., 2011). A SRI-310C (SRI International, Menlo Park, CA, USA) FID gas chromatograph was used to analyze samples. CH$_4$ flux was calculated as the rate of concentration change over the sampling period (Vourlitis et al., 1993).

Greenhouse carbon balance. To determine the greenhouse carbon balance of the short-hydroperiod marsh in relation to simulated drought, we used the greenhouse gas (carbon) exchange balance, the ratio of CH$_4$ emissions to net CO$_2$ (mol mol^{-1}), and the greenhouse warming potential (GWP) of methane for a 100-year time frame (GWP = 25) (IPCC, 2007). Ratios were calculated using maximum midday CH$_4$ emissions and midday NEE. The greenhouse carbon compensation point for a 100-year time frame is 0.04 (1/GWP). Ratios of CH$_4$ to CO$_2$ greater than this value indicate that CH$_4$ emissions are not offset by ecosystem productivity over a 100-year period, reducing the amount of carbon stored in the ecosystem. We examined weekly changes in ratios over the study period for each drought scenario.

Physiological potential

Canopy reflectance measurements were taken 30 cm above the canopy in the center of each monolith on the same day that CO$_2$ flux measurements were conducted, near solar noon, using a UNI007 UniSpec-SC single-channel spectrometer (PP Systems, Amesbury, MA, USA). Reflective indices such as the

photochemical reflectance index (PRI; Gamon & Peñuelas, 1992), water index (WI; Peñuelas *et al.*, 1993, 1997), normalized phaeophytinization index (NPQI; Barnes *et al.*, 1992), and the normalized difference vegetation index (NDVI; modified from Tucker, 1979; Fuentes *et al.*, 2006; Claudio *et al.*, 2006) were used to detect changes in physiological potential and stress levels of the monoliths. PRI is generally used to estimate light use efficiency, WI is associated with water content of the vegetation (Claudio *et al.*, 2006; Fuentes *et al.*, 2006), NPQI is an estimate of chlorophyll degradation (Peñuelas & Filella, 1998), and NDVI is an estimate of chlorophyll content and energy absorption (Fuentes *et al.*, 2006; Ollinger, 2011).

Environmental conditions. In addition to reflectance indices, we monitored additional environmental parameters within the facility bay that are known to be relevant to carbon fluxes. Environmental conditions were monitored continuously and data recorded half hourly with a CR1000 data logger and multiplexer (Campbell Scientific, Logan, UT, USA). Air and soil temperature at 5 cm (type T, copper–constantan), PAR (LI 190; LI-COR Inc.), relative humidity (HMP-45C Vaisala), temperature and relative humidity sensor (Campbell Scientific), and barometric pressure (CS106; Campbell Scientific) were measured using sensors attached to the data logger. We also measured soil volumetric water content (VWC) (CS 615; Campbell Scientific), in one monolith in each treatment per tank during the weeks 7–22. Measurements were made once every 10 s and averaged over 30 min.

Biomass, leaf area, and species composition

All aboveground biomass was harvested at the end of the experiment to examine dieback and changes in species composition in response to drought simulation. Measurements of total fresh and dry weight and total leaf area by species were made for each monolith. Initial fresh weight was measured immediately following harvesting. Following fresh weights, leaf area was measured by species using an LI-3000 (LI-COR Inc.). All live vegetation was separated by species to determine changes in dominant species composition as compared to the initial composition of monoliths that were dominated by sawgrass (>90%). All aboveground vegetation was dried for 48 h at 60°C in a Fisher Scientific Isotemp drying oven (Fisher Scientific, Waltham, MA, USA). Dry weights were recorded directly following removal from the drying oven to prevent moisture absorption.

Data analysis

As a preliminary step, we examined the effect of microclimatic variables on midday carbon fluxes via correlation analysis. Pearson's correlation coefficients were calculated for carbon fluxes, as well as air temperature, PAR, relative humidity, and soil volumetric water content via the SAS procedure PROC CORR (SAS Institute Inc., Cary, NC, USA).

To determine the effect of drought scenarios on carbon exchange, we used repeated measures analysis of variance methods, analyzing weekly flux data (NEE, R_{eco}, GEE),

reflective indices (WI, NDVI, PRI, NPQI), and the ratio of $CH_4 : CO_2$. We utilized mixed modeling methods, with variance–covariance matrices explicitly formulated to appropriately account for both the random effect of blocking (tanks) and the repeated measurement of each experimental unit over time. Variance–covariance parameters were estimated via Restricted Maximum Likelihood using the SAS procedure PROC MIXED. Models included fixed effects for drought scenario and week, and a covariate was included for temperature. We also included a fixed effect to delineate the experimental periods during the manipulation: inundation, manipulation (water level lowering), dry periods (water levels 20 cm below soil surface), and pulse events (1st day of inundation) and drought simulations: simulation 1 (June 1st to August 10th) and simulation 2 (August 17 to October 26th). Random effects were included for tank and plot to appropriately account for the physical design of the experiment, and week to account for the repeated measures nature of the data. An additional analysis was performed for data collected during midday (9:00 to 2:00 hours) (carbon fluxes, reflective indices, temperature, PAR, soil volumetric water content, and relative humidity). Mixed modeling methods were also used to test differences between live and dead vegetation and/or drought scenarios for leaf area and vegetation weight at the end of the experiment. Fixed effects included drought scenario and status (live or dead) and random effects were included for tank and plot.

A modified backward selection method was used to determine the appropriate effects for the final models. First, all parameters were included in the model, including all first-order interactions between parameters. Then, the least significant effects based on the Wald chi-square statistics were dropped one at a time until all remaining in the model were influential ($P < 0.05$). Goodness-of-fit statistics, Akaike's information criteria (AIC) and Bayesian information criteria (BIC), were used to compare models. AIC and BIC are model selection statistics appropriate for non-nested models, which measure how close fitted values are to true values, with a penalty for the number of parameters in the model (Littell *et al.*, 2006). At each step in model selection, the significance of each model parameter was evaluated and we ensured that the final model had the lowest AIC and BIC values. To test for differences among levels of categorical variables, least square means were produced, which are the marginal predicted mean values for the model-dependent variable given all other variables in the model are at their average values. Differences among means were tested with the Tukey–Kramer multiple comparisons test. Assumptions of normality and homoscedasticity were evaluated visually by plotting residuals.

Results

Carbon dioxide

We observed significant changes over the course of the drought experiment in NEE, R_{eco}, and GEE (Fig. 1). Simple two-way Pearson correlations of midday NEE indicated that the chlorophyll content of the vegetation
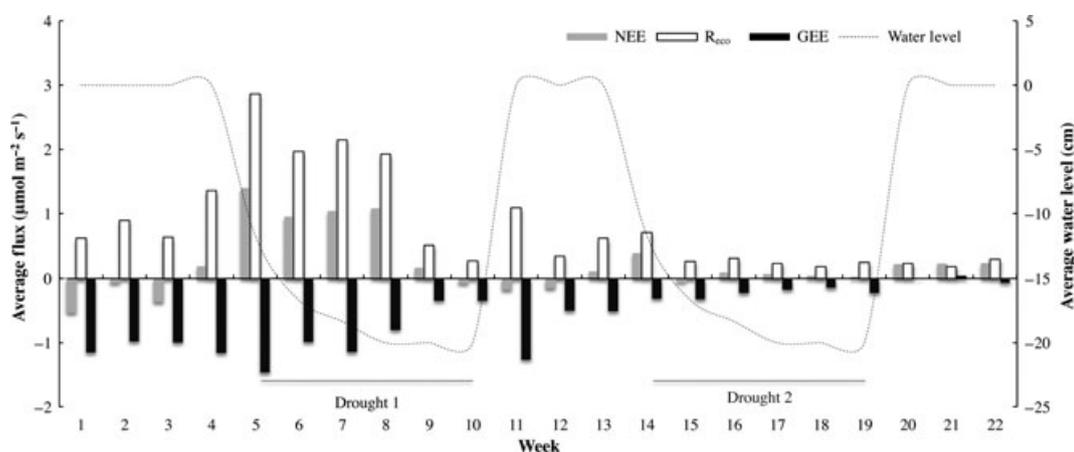
Fig. 1 Changes in average net ecosystem exchange (NEE), R_{eco}, and gross ecosystem exchange (GEE) over the study period in response to changes in water level for all drought scenarios. NEE and GEE were lowest (greater carbon uptake) during periods of inundation and highest (greater carbon release to the atmosphere) during drought simulations. R_{eco} increased during drought simulation up until water began limiting respiration rates.

Table 1 Pearson's correlation coefficients (r) and their associated P-values for midday measurements of CO_2 flux components, reflective indices (NDVI, NPQI, WI), and environmental factors (Air temperature, PAR, barometric pressure, and relative humidity)

r P-value	NEE	R_{eco}	GEE	$CH_4 : CO_2$	NDVI	PRI	NPQI	WI	TEMP	PAR	Pressure	Relative humidity
$CH_4 : CO_2$	0.01	−0.04	0.04									
	0.899	0.409	0.428									
NDVI	−0.13	−0.17	0.04	−0.13								
	0.008	0.001	0.435	0.010								
PRI	−0.02	0.01	−0.07	−0.02	0.26							
	0.729	0.167	0.148	0.074	<0.001							
NPQI	0.002	0.03	−0.03	−0.04	0.35	0.89						
	0.958	0.518	0.577	0.433	<0.001	<0.001						
WI	−0.01	−0.14	0.11	0.04	−0.18	−0.87	−0.89					
	0.785	0.001	0.030	0.451	<0.001	<0.001	<0.001					
TEMP	0.015	0.004	0.002	0.04	0.32	−0.29	−0.41	0.25				
	0.766	0.935	0.961	0.433	<0.001	<0.001	<0.001	<0.001				
PAR	0.08		−0.05	−0.034	−0.10	−0.003	−0.08	−0.06	0.19			
	0.118		0.367	0.504	0.040	0.946	0.114	0.274	<0.001			
Pressure	0.06	−0.07	0.013	−0.03	0.18	−0.21	−0.10	0.17	0.13	−0.02		
	0.261	0.168	0.799	0.508	<0.001	<0.001	0.053	<0.001	0.010	0.699		
Relative humidity	0.02	0.14	−0.12	0.12	−0.27	0.10	0.10	−0.11	−0.03	−0.65	−0.24	
	0.755	0.005	0.013	0.016	<0.001	0.059	0.193	0.023	0.528	<0.001	<0.001	
VWC	0.22	0.08	−0.02	−0.06	0.29	0.29	0.14	−0.03	−0.28	−0.22	−0.24	−0.19
	0.139	0.457	0.888	0.685	0.042	0.050	0.354	0.844	0.058	0.138	0.105	0.203

GEE, gross ecosystem exchange; NDVI, Normalized difference vegetation index; NEE, net ecosystem exchange; NPQI, normalized phaeophytinization index; PAR, photosynthetically active radiation; PRI, photochemical reflectance index; WI, water index.

(NDVI) increased linearly with increasing net carbon uptake ($P = 0.008$; $r = −0.13$) (Table 1). Although temperature did not have a significant correlation with midday NEE, further analysis showed a significant positive correlation with temperature for the entire NEE data set (sunrise, noon, dusk; $P < 0.001$; $r = −0.16$). Repeated measures analysis of net carbon uptake showed that the interaction between the time of day (diurnal: sunrise, noon, or sunset) and experimental period (inundation, manipulation, dry period or pulse; $P < 0.001$), and temperature and the drought simulation (simulation 1: June 1st–August 10th and simulation 2: August 17–October 26th; $P < 0.001$) significantly influenced NEE (Table 2). NEE was

Table 2 Estimated fixed effects, SE, and *P*-values for the repeated measures analysis of net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), gross ecosystem exchange (GEE)

Parameters	NEE Estimate	SE	*P*-value	R_{eco} Estimate	SE	*P*-value	GEE Estimate	SE	*P*-value
Intercept	0.2978	0.2304	0.197	0.5254	0.116	<0.001	−0.1539	0.2385	0.519
Drought scenario									
Gradual vs. rapid	−0.0725	0.084	0.403	−0.0588		0.668	−0.0115	0.1421	0.937
Intermediate vs. rapid	0.0013	0.084	0.988	−0.1195		0.388	0.1299	0.1421	0.375
Diurnal									
Sunrise vs. sunset	0.3265	0.1612	0.043				0.0183	0.0875	0.834
Noon vs. sunset	−0.2332	0.1564	0.136				−0.5321	0.078	<0.001
Experimental period									
Inundation vs. pulse	0.3181	0.1728	0.066	0.3217	0.1537	0.037	−0.5227	0.1503	0.001
Manipulation vs. pulse	1.1727	0.1896	<0.001	0.996	0.1861	<0.001	−0.2495	0.1802	0.17
Dry period vs. pulse	−0.2332	0.1564	0.687	0.1528	0.1176	0.195	−0.2225	0.1123	0.048
Diurnal*experimental period									
Sunrise vs. sunset Inundation vs. pulse	−0.7019	0.2017	0.001						
Sunrise vs. sunset Manipulation vs. pulse	−0.7821	0.2121	<0.001						
Sunrise vs. sunset Dry period vs. Pulse	−0.2555	0.2112	0.227						
Noon vs. sunset Inundation vs. pulse	−0.7198	0.2012	<0.001						
Noon vs. sunset Manipulation vs. pulse	−0.3231	0.2075	0.120						
Noon vs. sunset Dry period vs. pulse	0.3226	0.2089	0.123						
Drought (first vs. second)	1.3475	0.4011	0.001	−0.1282	0.2791	0.646	0.2362	0.3595	0.511
Temperature	−0.0632	0.1566	0.506	−0.0008	0.0004	0.048	0.0008	0.0007	0.244
Temperature*Drought									
First vs. second	−0.0474	0.0118	<0.001	0.0169	0.0007	0.020	−0.0251	0.0103	0.015

highest (lower net carbon uptake) during periods of manipulation at sunrise and sunset when temperatures were lower (Fig. 2d) and lowest during periods of inundation at midday (Fig. 2d). The interaction between drought and temperature indicated that net carbon uptake increased with temperature during the first drought simulation whereas NEE remained constant as temperature increased throughout the second drought simulation (Fig. 2a).

Ecosystem respiration rates (R_{eco}) were positively correlated with relative humidity ($P = 0.005$; $r = 0.14$), and negatively correlated with water stress (WI: $P = 0.001$; $r = −0.14$) and NDVI ($P = 0.001$, $r = −0.17$) (Table 1). Repeated measures analysis of ecosystem respiration (R_{eco}) showed that experimental period ($P < 0.001$) and the interaction between temperature and the drought simulation ($P = 0.020$) were significant indicators of ecosystem respiration (Table 2; Fig. 2b). Drawdowns caused an increase in respiration and rates were highest during dry periods (Fig. 1) until water stress limited respiration. R_{eco} increased slightly when temperatures increased during the first drought, but decreased slightly when temperatures increased during the second drought period (Table 2; Fig. 2b).

Time of day (diurnal; $P < 0.001$), experimental period ($P < 0.001$), and the interaction between temperature and drought ($P = 0.015$) were all significant predictors of GEE (Table 2). GEE followed the same pattern as NEE with greater carbon uptake occurring at noon ($P < 0.001$) and during periods of inundation ($P < 0.001$). Following the same pattern as R_{eco}, during the first drought there was a slight decrease in GEE (greater carbon uptake) as temperature increased, while during the second drought there was a slight increase as temperature increased (Fig. 2c). All CO_2 fluxes were significantly lower following the first drought simulation (Fig. 2a–c), and on average all drought scenarios were a net source of CO_2 to the atmosphere (approximately 0.20 μmol m^{-2} s^{-1}).

Greenhouse carbon balance

Changes in the greenhouse carbon balance occurred as a result of drought simulation. Relative humidity was positively correlated with the $CH_4 : CO_2$ ratio ($P = 0.016$; $r = 0.12$; Table 1), more methane was emitted than net carbon uptake could offset as relative humidity increased. And, as NDVI decreased due to higher water levels, methane levels rose ($P = 0.010$; $r = −0.13$). Repeated measures analysis showed that there were no differences among drought scenarios ($P = 0.497$) and that NDVI was the only significant indicator of
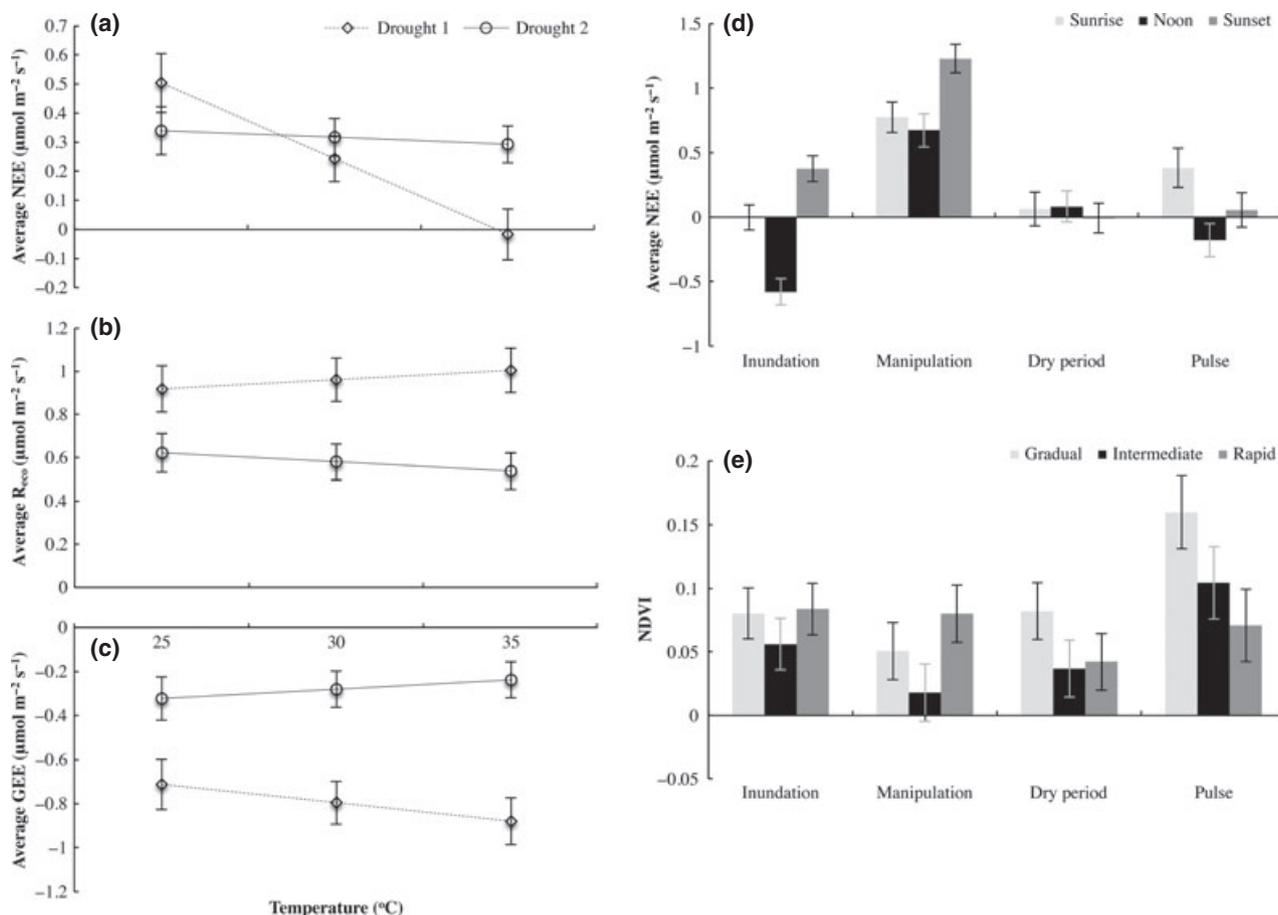
Fig. 2 Least square mean predicted values of the interactions between: (a) temperature and drought simulation for net ecosystem exchange (NEE), (b) R_{eco}, (c) gross ecosystem exchange (GEE), and (d) diurnal (sunrise, noon, and sunset) and experimental period (Inundation, manipulation, dry period, and pulse events) for NEE and (e) Normalized difference vegetation index (NDVI). Increasing temperatures resulted in higher fluxes in drought simulation 1 compared to drought simulation 2 (a–c). Net carbon uptake was greatest during midday measurement when monoliths were inundated and carbon release was greatest during manipulations (d–e). The chlorophyll content of the vegetation was highest for the gradual drought scenario during pulse events (d).

$CH_4 : CO_2$ ($P = 0.010$; Table 3). During periods of inundation, methane flux rates recovered faster than net carbon uptake causing the system to become a source of carbon to the atmosphere (Fig. 3). Although not significantly higher, the gradual simulation scenario had the highest ratio of $CH_4 : CO_2$ on average.

Physiological potential

Physiological potential had strong correlations with environmental and flux variables (Table 1). The chlorophyll content of the vegetation (NDVI) increased with NPQI ($P < 0.001$; $r = 0.35$), PRI ($P < 0.001$; $r = 0.26$), temperature ($P < 0.001$; $r = 0.32$), pressure ($P = 0.001$; $r = 0.18$), VWC ($P = 0.042$, $r = 0.29$), and net carbon uptake (NEE; $P = 0.008$; $r = -0.13$), and decreased with increasing ecosystem respiration (R_{eco}; $P = 0.001$; $r = -0.17$), $CH_4 : CO_2$ ($P = 0.010$; $r = -0.13$), WI ($P =$

0.001; $r = -0.18$), PAR ($P = 0.040$; $r = -0.10$), and relative humidity ($P < 0.001$; $r = -0.27$) (Table 1). Repeated measures analysis of NDVI showed that changes in physiological potential were significantly different over the times in the study period (Table 3). The interaction of drought scenario and experimental period ($P = 0.023$), NPQI ($P < 0.001$), and WI ($P < 0.001$) were all significant indicators of NDVI (Table 3). NDVI was greatest during pulse events under the gradual drought scenario and lowest during periods of manipulation under the intermediate drought scenario (Fig. 2e).

There were no significant differences between total leaf area at the end of the study for the drought scenarios for all species combined ($P = 0.282$). However, total leaf area for sawgrass was marginally significantly different by drought scenario ($P = 0.157$), with the gradual scenario having the highest predicted least square mean (473.47 $cm^2 \pm$ SE 105.24) vs.

Table 3 Estimated fixed effects, SE, and *P*-values for the repeated measures analysis of the ratio of net CH_4 flux to net CO_2 uptake, and the normalized difference vegetation index (NDVI)

Parameters		$CH_4 : CO_2$			NDVI		
		Estimate	SE	*P*-value	Estimate	SE	*P*-value
Intercept		2.5699	2.9156	0.4266	−0.016	0.0315	0.6155
Drought scenario							
Gradual vs. rapid		2.4586	3.1601	0.4506	0.059	0.0383	0.0224
Intermediate vs. rapid		−1.3962	3.2424	0.673	0.0336	0.0383	0.3835
Experimental period							
Inundation vs. pulse					0.0128	0.0246	0.6019
Manipulation vs. pulse					0.0009	0.0266	0.7325
Dry period vs. pulse					−0.0286	0.0265	0.2798
Drought scenario*experimental period							
Gradual vs. rapid	Inundation vs. pulse				−0.0998	0.035	0.0008
Gradual vs. rapid	Manipulation vs. pulse				−0.1184	0.0376	0.002
Gradual vs. rapid	Dry period vs. pulse				−0.0491	0.0373	0.1895
Intermediate vs. rapid	Inundation vs. pulse				−0.0611	0.0348	0.08
Intermediate vs. rapid	Manipulation vs. pulse				−0.0957	0.0376	0.0114
Intermediate vs. rapid	Dry period vs. pulse				−0.0389	0.0373	0.299
NDVI		−38.19	14.806	0.0104			
NPQI					0.2247	0.0212	<0.0001
WI					0.0998	0.0134	<0.0001

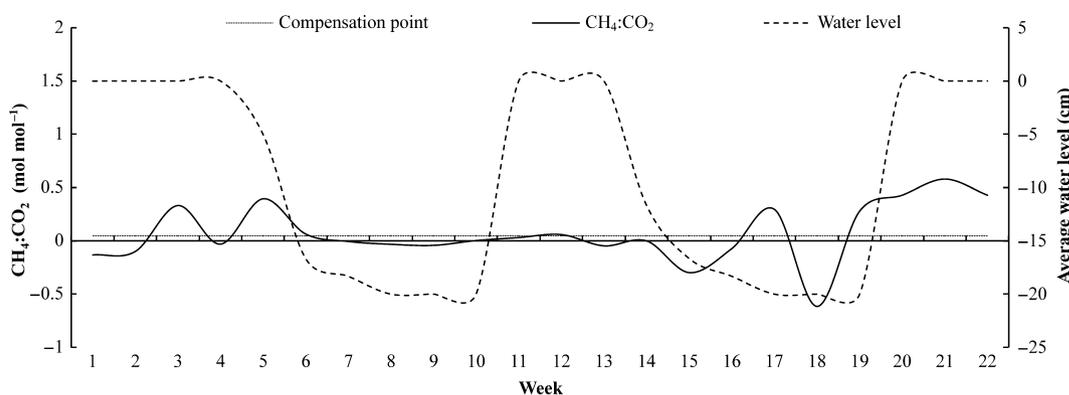NPQI, normalized phaeophytinization index; WI, water index.

Fig. 3 Changes in average CH_4 to net CO_2 exchange over the study period in relation to average changes in water levels and the greenhouse carbon compensation point for 100 years (0.04). This system is a small source of carbon to the atmosphere due to the lack of recovery in net ecosystem exchange (NEE) during periods of inundation.

the intermediate (177.37 cm^2± SE 105.24) and the rapid (263.12 cm^2 ± SE 105.24) scenarios (Fig. 4a). Prior to the start of the study, monoliths were dominated (>90%) by sawgrass. At the end of the study, sawgrass accounted for just 47% of average total leaf area whereas torpedograss accounted for 35% of average total leaf area for the gradual and rapid drought scenarios (Fig. 4a). Die back as a result of drought simulation was observed under all drought scenarios and differences in dry weight of live vegetation differed marginally by drought scenario (*P* = 0.248) (Fig. 4b). The gradual transition to drought had the

greatest predicted least square mean (42.43 g ± SE 10.18), vs. the intermediate (11.29 g ± SE 10.18) and rapid (12.75 g ± SE 10.18) drought scenarios. High variability between plots led to marginal differences among drought scenarios for the amount of vegetation and the species that sprouted following the final simulated drought (Fig. 4a).

Discussion

As expected, drought turned the ecosystem into a source of carbon to the atmosphere by increasing
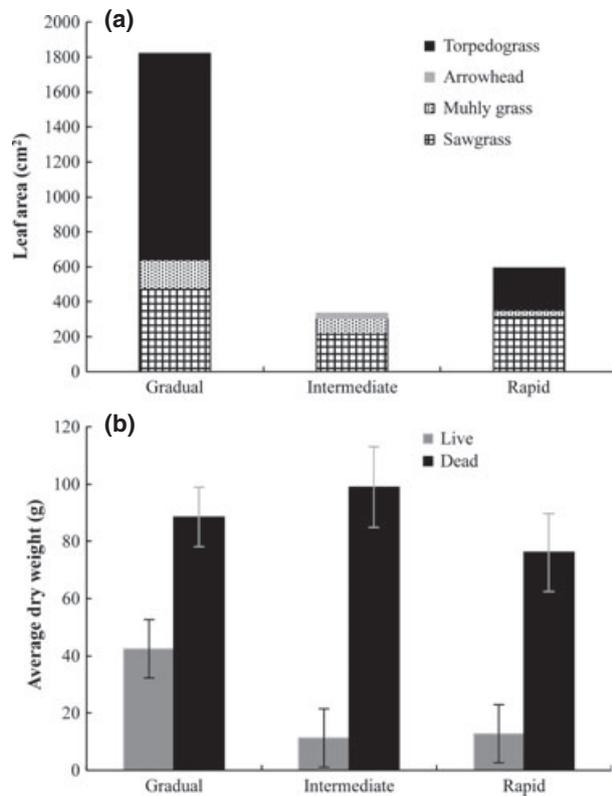
Fig. 4 (a) Average leaf area for each drought scenario by species contribution at the end of the experiment. There were no significant differences in total leaf area, however, sawgrass leaf area had marginal differences for the drought scenarios ($P = 0.157$). The gradual transition to drought had greater average sawgrass leaf area ($473.47 \text{ g} \pm \text{SE } 105.24$) compared to the intermediate ($177.37 \text{ g} \pm \text{SE } 105.24$) and the rapid ($263.11 \text{ g} \pm \text{SE } 105.24$) drought scenarios. (b) Average dry weight of aboveground biomass for each drought scenario at the end of the experiment. There was no significant difference in the amount of dead biomass between drought simulations. However, there was a marginal difference in the amount of live vegetation at the end of the experiment ($P = 0.248$). The gradual drought scenario had the greatest predicted least square mean ($42.43 \text{ g} \pm \text{SE } 10.18$), vs. the intermediate ($11.29 \text{ g} \pm \text{SE } 10.18$) and rapid ($12.75 \text{ g} \pm \text{SE } 10.18$) drought scenarios.

ecosystem respiration rates (R_{eco}) and reducing net carbon exchange rates (NEE). Over the entire study period, changes in NEE relative to recovering net CH_4 emissions during inundation resulted in changes in the greenhouse gas (carbon) exchange balance. These results support our hypothesis that the increased frequency and duration of drought would increase CO_2 and decrease CH_4 emissions, cause a reduction in photosynthetic potential due to water stress, and decrease the carbon storage potential of the ecosystem. Although not *in situ* responses to drought, recent studies that considered the effects of hydrology on CO_2 fluxes in Everglades' freshwater marsh ecosystems

(Schedlbauer *et al.*, 2010; Jimenez *et al.*, 2012) support our results. Below, we evaluate the effects of drought and drought onset on carbon fluxes and determine how these changes impact the greenhouse carbon balance.

Effects of drought on CO_2 flux components

CO_2 flux components are controlled by different biological processes, which vary in their response to drought. Ecosystem carbon uptake is controlled by photosynthetic rates whereas ecosystem respiration is the combination of both autotrophic and heterotrophic respiration. Changes in GEE relative to changes in R_{eco} are important for net carbon exchange rates. Although sawgrass marshes in the Everglades region do not generally have very high productivity rates, high carbon storage potential is the result of reduced decomposition rates under anoxic conditions. We found that in this wetland ecosystem, droughts increased CO_2 emissions through a reduction in carbon uptake relative to ecosystem respiration. In response to drought simulation, we observed significant changes in NEE, R_{eco}, GEE, and the greenhouse carbon balance (net CH_4 : NEE) (Fig. 1; Fig. 2a–c; Fig. 3), although drought onset rates had no significant effect. We saw the largest changes in carbon dynamics in maximum photosynthetic rates and during periods of inundation. As expected, there was greater net carbon exchange during the midday measurements while inundated, when photosynthetic activity was greatest and water stress was not limiting photosynthesis and respiration. During inundation, the ratio of R_{eco} to GEE was less than 1 (0.76), indicating that GEE contributed more to net exchange rates. This result is supported by other wetland studies that found, when water was not limited GEE dominated NEE (Alm *et al.*, 1999; Bubier *et al.*, 2003a, b; Heinsch, 2004; Hao *et al.*, 2011; Webster *et al.*, 2013). Because photosynthetic CO_2 fixation can be limited by leaf water potential, GEE is impacted by water stress during prolonged drought (Heinsch, 2004; Rocha & Goulden, 2010; Webster *et al.*, 2013).

In wetland systems, soil respiration (R_s) dominates ecosystem respiration rates accounting for up to 75% of R_{eco} (Law *et al.*, 2002). Our results are consistent with many other wetland ecosystems that show that R_{eco} increases as a result of drought (Kramer & Boyer, 1995; Alm *et al.*, 1999; Morison *et al.*, 2000; Smith *et al.*, 2003; Heinsch, 2004; Rocha & Goulden, 2010; Webster *et al.*, 2013). The increase in oxygen availability causes a rise in heterotrophic respiration rates as the depth of soil oxygenation deepens and the rate of gas diffusion into the atmosphere improves (Kramer & Boyer, 1995; Morison *et al.*, 2000; Law *et al.*, 2002; Bubier *et al.*, 2003a, b; Smith *et al.*, 2003; Heinsch, 2004; Aurela *et al.*, 2007;

Barr *et al.*, 2010; Schedlbauer *et al.*, 2010; Jimenez *et al.*, 2012; Webster *et al.*, 2013). The increase in oxygen availability and diffusion rates caused R_{eco} to dominate net carbon exchange during drought simulation, indicated by a ratio of R_{eco} to GEE greater than 1 (1.39). R_{eco} is the dominant flux component controlling NEE in wetland ecosystems (Jimenez *et al.*, 2012). These results are supported by Jimenez *et al.* (2012), which compared CO_2 fluxes between short- and long-hydroperiod marsh ecosystems in the Everglades and found that during drought, faster diffusion and higher heterotrophic respiration rates increased ecosystem respiration. While inundated, R_{eco} was reduced due to lower diffusion rates out of the soil and anoxic conditions; under drought, limitations on diffusion and oxygen stress are lifted (Jimenez *et al.*, 2012).

Prior to drought, GEE dominated net exchange rates. During the first drought simulation, there were no distinct changes in GEE, but there was an increase in ecosystem respiration (Fig. 1). Drought-depressed NEE values are a result of increased R_{eco} and not a change in GEE (Aurela *et al.*, 2007). However, after the first drought simulation, water availability began to limit photosynthesis, reducing carbon uptake rates and ecosystem respiration. Other wetland studies have observed reductions in carbon uptake as a result of water stress during the dry season and under drought conditions (Heinsch, 2004; Rocha & Goulden, 2010). The relationship between carbon flux, experimental period, and the water index suggests that water stress was reducing the capacity of this system to acquire carbon. Under normal conditions, photosynthesis exceeds respiration in plants. When photosynthesis is inhibited but respiration continues, respiration will proceed as long as photosynthetic reserves are available in drought intolerant plants. In drought-tolerant plants like sawgrass, when photosynthesis declines, so do respiration rates (Kramer & Boyer, 1995). Eventually, dehydration inhibits respiration in all plants since water is required for the hydrolytic reactions associated with respiration. Following the first drought when all fluxes were reduced, water stress likely limited heterotrophic respiration in the soil as well (Smith *et al.*, 2003). As the second drought began, both photosynthesis and respiration rates were impacted and resulted in reduced CO_2 fluxes (Fig. 1). Once water began to limit ecosystem productivity, there was a great reduction in GEE and even during periods of inundation, exchange rates did not recover.

The greenhouse carbon balance

The greenhouse gas (carbon) exchange balance remained relatively constant over the study period, yet spikes (increases in net CH_4 relative to NEE) were observed during periods of inundation. During drought, methane emissions were null. Consequently, NEE offset net CH_4 rates. Following drought, inundation caused an increase in net CH_4 relative to NEE resulting in a reduction in the ratio of $CH_4 : CO_2$. Prior research in wetland ecosystems has found that methane fluxes increase with higher soil moisture levels (King *et al.*, 1990; Bachoon & Jones, 1992; Torn & Chapin, 1993; Smith *et al.*, 2003; Whalen, 2005; Webster *et al.*, 2013). However, as the depth to oxygenation increases, soils become a sink for methane (Bachoon & Jones, 1992; Smith *et al.*, 2003). Even during periods of inundation, sawgrass marshes are only a weak source of methane to the atmosphere (Bachoon & Jones, 1992).

In this ecosystem, methane moves out of the soil through ebullition. Ebullition is difficult to quantify due to its stochastic nature (Tokida *et al.*, 2007; Goodrich *et al.*, 2011), reducing our ability to find a significant difference between drought onset rates and the experimental period. Although no significant difference was detected between drought scenarios, water availability does influence methanogenesis and CH_4 movement out of the soil (Bachoon & Jones, 1992; Torn & Chapin, 1993; Smith *et al.*, 2003; Whalen, 2005; Goodrich *et al.*, 2011; Webster *et al.*, 2013). The rapid transition to drought had the highest average ratio of net CH_4 to NEE (0.16), followed by the gradual transition (0.08), and finally the intermediate (0.03) transition to drought. Under inundation, CH_4 production by methanogens persists, and when conditions become aerobic, both methane oxidation rates and CH_4 diffusion rates increase (Smith *et al.*, 2003). Therefore, the swift reduction in water levels in the rapid drought scenario may have enhanced CH_4 diffusion and ebullition out of the soil while the slow reductions in water levels may have aided greater CH_4 production and increased probabilities of methane oxidation. These results indicate that drought onset rate may actually influence CH_4 diffusion out of the soil so that rapid changes in water levels promote CH_4 emission, whereas more gradual transitions allow for slower diffusion and therefore increased rates of methane oxidation.

The 100-year greenhouse warming compensation point for methane is 0.04, indicating that both the rapid and gradual transition to drought caused the marsh monoliths to be a source of methane to the atmosphere over the long term. Overall the average ratio of net CH_4 to NEE for the study period was 0.06, showing that even under extended drought, freshwater marsh ecosystems can be a source of methane to the atmosphere if inundation periods are sufficient for CH_4 production. Extended drought conditions also promote greater CO_2 release and reductions in CO_2 uptake, further reducing the ratio of $CH_4 : CO_2$.

Changes in photosynthetic potential

The effect of drought on carbon uptake rates can be explained by reductions in photosynthetic potential, an effect of water stress. Although the water content of the vegetation showed no significant differences between drought scenarios, the water index was a good indicator of the onset and persistence of water stress throughout the study. Water content of the vegetation is important in determining the response to rehydration following inundation (Kramer & Boyer, 1995). The ability to recover photosynthetic capacity when water is resupplied is influenced by the extent and duration of dehydration (Kramer & Boyer, 1995; Lambers *et al.*, 2008). As a result of dehydration, vascular blockages occur in the xylem from the cavitation caused by high water tension (Lambers *et al.*, 2008). More severe dehydration results in higher tension and more frequent blockages, which can lead to cell death, further limiting recovery when water is resupplied (Kramer & Boyer, 1995; Lambers *et al.*, 2008). Premature leaf senescence is a common effect of dehydration (Kramer & Boyer, 1995; Lambers *et al.*, 2008). This may have also influenced the patterns observed in NDVI. NDVI showed differences between drought scenarios with the interaction of experimental period (inundation, manipulation, drought, and pulse events) suggesting that there were significant changes in the photosynthetic capacity of the ecosystem in response to changes in water availability. Photosynthesis can also be inhibited by low cellular water potentials through changes in solute concentrations (Kramer & Boyer, 1995; Lambers *et al.*, 2008). Changes in the solute environment around enzymes often lead to reductions in photophosphorylation activity (Lambers *et al.*, 2008).

Reflective indices supported patterns observed in carbon flux components. Net carbon uptake increased with NDVI and water availability. $CH_4 : CO_2$, which also increased with water levels, had a significant negative relationship with NDVI, indicating that although productivity increased with water availability, CH_4 recovered and produced greater fluxes than NEE could account for. Previous studies have found significant relationships between NEE and CH_4 production in wetland ecosystems (Whiting & Chanton, 1993; Joabsson & Christensen, 2001; Mitsch *et al.*, 2012). Normally, greater productivity relates to higher NDVI and larger methane emissions. The decline in net carbon uptake as water was resupplied and increased methanogenesis caused this negative relationship between $CH_4 : CO_2$ and NDVI. The correlation between NDVI and net methane flux indicates that photosynthetic rates may serve as an indicator of methane flux by integrating environmental variables important in methanogenesis (Whiting & Chanton, 1993; Joabsson & Christensen, 2001).

Although the components of the CO_2 flux did not differ significantly by drought scenario, we saw an effect of drought onset rate on the final biomass. Final biomass harvesting indicated a reduction in the recovery of monoliths experiencing faster transitions and longer drought durations. Drought simulation resulted in dieback in all scenarios, but the amount of sawgrass that resprouted following the final simulated drought was greater for the gradual drought scenario than it was for the intermediate and rapid drought scenarios. Reductions in sawgrass recovery may have also facilitated a community shift in the gradual and rapid transition to drought where torpedograss rhizomes were present. Prior to the start of the study, monoliths were dominated (>90%) by sawgrass. At the end of the study, torpedograss accounted for 35% of average total leaf area for the gradual drought scenario. Torpedograss is an invasive species that has taken over 70% of Florida's public waters (Center for Aquatic and Invasive Plants http://plants.ifas.ufl.edu/node/308). Mechanisms whereby invasive plants suppress other species include dense rhizomes and roots that leave little space for neighbors, strong competition for nutrients (Perry & Galatowitsch, 2004), tall dense canopies that intercept light, and faster establishment following disturbance (Zedler & Kercher, 2004; Herr-Turoff, 2005). The gradual and rapid drought scenario provided conditions that facilitated establishment of torpedograss following sawgrass dieback. Torpedograss culms originate from rhizomes, are drought tolerant, and thrive in well drained to poorly drained soils. The rhizomes are in the short-hydroperiod marsh ecosystem and pose a threat of invasion following disturbance.

Global impacts

These results indicate that fluctuations in hydrology due to climate or water management, an issue of great concern for wetlands globally, could cause significant changes in the structure and function of these ecosystems. Hydrology drives the carbon sequestering capacity of wetlands and has resulted in the accumulation of large belowground pools. This in turn makes wetland contributions to the global carbon cycle much greater than their land area would imply. Climate-induced changes in hydrology could also distort the structure of these ecosystems by stressing local vegetation and enhancing conditions for invasive species establishment. This study demonstrates the complex relationship between hydrology and carbon cycling and how the value of wetlands as reservoirs for carbon might diminish amid changes in climate and water management.

The objective of this experiment was to examine changes in the greenhouse carbon balance of freshwater

marsh ecosystems in response to drought simulation. IPCC (2007) projected climate change for the Everglades predicts that there will be an increased occurrence of drought due to changes in precipitation patterns in the southeastern US. We found that drought resulted in the system being a net source of carbon to the atmosphere. The capacity for the system to serve as a source of CO_2 was influenced by changes in physiological potential of the vegetation due to water stress and changes in ecosystem respiration through enhanced diffusion and higher soil respiration rates. The CH_4 source potential was likely influenced by both CH_4 production during inundation and changes in diffusion rates out of the soil following rapid modifications in water levels. We also observed increased vulnerability to invasive species directly following the second simulated drought with the invasive species torpedograss. This study indicates that although drought occurrence and duration may increase in the future, land managers can influence the way ecosystems respond to drought by preventing abrupt changes in water levels, which would prevent greater gas diffusion out of the soil and delay water stress at the onset of dry periods. The increase in drought frequency and intensity in the future could potentially turn subtropical wetland ecosystems into sources of carbon as ecosystem productivity is reduced by water stress, and stored carbon in the soil becomes oxic for longer periods of time.

Acknowledgments

References

Abtew W, Huebner RS, Pathak C (2007) Hydrology and Hydraulics of South Florida. World Environmental & Water Resources Congress 2007 ASCE Conference in Tampa, Florida, May 15 to 19, 2007.

Adhikari S, Bajracharaya RM, Sitaula BK (2009) A review of carbon dynamics and sequestration in wetlands. *Journal of Wetlands Ecology*, **2**, 42–46, doi: 10.3126/jowe. v2i1.1855

Alm J, Schulman L, Walden J (1999) Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology*, **80**, 161–174, doi: 10.2307/176987

Armentano TV (1980) Drainage of organic soils as a factor in the world carbon cycle. *BioScience*, **30**, 825–830, doi: 10.2307/1308375

Aurela M, Riutta T, Laurila T *et al.* (2007) CO_2 exchange of a sedge fen in southern Finland—the impact of a drought period. *Tellus B*, **59**, 826–837, doi: 10.1111/j.1600-0889.2007.00309.x

Bachoon D, Jones R (1992) Potential Rates of methanogenesis in sawgrass marshes with peat and marl soils in the Everglades. *Soil Biology & Biochemistry*, **24**, 21–27, doi: 10.1016/0038-0717

Barnes JD, Balaguer L, Manrique E, Elvira S, Davidson AW (1992) A reappraisal of the use of Dmso for the extraction and determination of chlorophylls-a and chlorophylls-b in lichens and higher-plants. *Environmental and Experimental Botany*, **32**, 85–100, doi: 10.1016/0098-8472

Barr JG, Engel V, Fuentes JD, Zieman JC, O'Halloran TL, Smith TJ, Anderson GH (2010) Controls on mangrove forest-atmosphere carbon dioxide exchanges in western Everglades National Park. *Journal of Geophysical Research*, **115**, 1–14, doi: 10.1029/2009JG001186

Brevik EC, Homburg JA (2004) A 5000 year record of carbon sequestration from a coastal lagoon and wetland complex. Southern California, USA. *Catena*, **57**, 221–232, doi: 10.1016/j.catena.2003.12.001

Bubier J, Crill P, Mosedale A, Frolking S, Linder E (2003a) Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical Cycles*, **17**, 1066, doi: 10.1029/2002GB001946

Bubier JL, Bhatia G, Moore TR, Roulet NT, Lafleur PM (2003b) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, **6**, 353–367, doi: 10.1007/s10021-003-0125-0

Childers DL (2006) A synthesis of long-term research by the Florida Coastal Everglades LTER Program. *Hydrobiologia*, **569**, 531–544, doi: 10.1007/s10750-006-0154-8

Choi Y, Wang Y (2004) Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Global Biogeochemical Cycles*, **18**, GB4016.

Claudio HC, Cheng Y, Fuentes DA (2006) Monitoring drought effects on vegetation water content and fluxes in chaparral with the 970 nm water band index. *Remote Sensing of Environment*, **103**, 304–311, doi: 10.1016/j.rse.2005.07.015

Davis SM, Ogden JC (1994) (eds) *Everglades, the Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, FL, USA.

Dugan P (ed.) (1993) *Wetlands in Danger in a World Conservation Atlas*. Oxford University Press, New York City, NY.

Fuentes DA, Gamon JA, Cheng Y (2006) Mapping carbon and water vapor fluxes in a chaparral ecosystem using vegetation indices derived from AVIRIS. *Remote Sensing of Environment*, **103**, 312–323, doi: 10.1016/j.rse.2005.10.028

Gamon JA, Peñuelas J (1992) A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment*, **41**, 35–44, doi: 10.1016/0034-4257(92)90059-S

Goodrich JP, Varner RK, Frolking S, Duncan BN, Crill PM (2011) High-frequency measurements of methane ebullition over a growing season at a temperate peatland site. *Geophysical Research Letters*, **38**, L07404, doi: 10.1029/2011GL046915

Hao YB, Cui XY, Wang YF *et al.* (2011) Predominance of precipitation and temperature controls on ecosystem CO_2 exchange in Zoige alpine wetlands of Southwest China. *Wetlands*, **31**, 413–422, doi: 10.1007/s13157-011-0151-1

Heinsch F (2004) Carbon dioxide exchange in a high marsh on the Texas Gulf Coast: effects of freshwater availability. *Agricultural and Forest Meteorology*, **125**, 159–172, doi: 10.1016/j.agrformet.2004.02.007

Herr-Turoff AM (2005) Responses of an invasive grass, Phalaris arundinacea, to excess resources, PhD Thesis. Department of Botany, University of Wisconsin, Madison, WI.

IPCC (2007) Climate Change 2007: The Physical Science Basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 760–782. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jimenez K, Starr G, Staudhammer C, Schedlbauer J, Loescher H, Malone SL, Oberbauer SF (2012) Carbon dioxide exchange rates from short- and long-hydroperiod Everglades freshwater marsh. *Journal of Geophysical Research*, **117**, 1–17, doi: 10.1029/2012JG002117

Joabsson A, Christensen TR (2001) Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology*, **7**, 919–932, doi: 10.1046/j.1354-1013.2001.00044

King GM, Roslev P, Skovgaard H (1990) Distribution and rate of methane oxidation in sediments of the Florida Everglades. *Applied and Environmental Microbiology*, **56**, 2902–2911.

Kramer PJ, Boyer JS (1995) *Water Relations of Plants and Soils*. Academic Press, San Diego, California.

Lambers H, Chapin FS III, Pons TL (2008) *Plant Physiological Ecology*. Springer-Verlag, New York Inc. ISBN 9780387783413.

Law BE, Falge E, Gu L *et al.* (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, **113**, 97–120.

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) *SAS for Mixed Models*, 2nd edn. SAS Publishing, Caryn, NC, USA.

McDermitt D, Burba G, Xu L *et al.* (2011) A new low-power, open-path instrument for measuring methane flux by eddy covariance. *Applied Physics B-Lasers and Optics*, **102**, 391–405, doi: 10.1007/s00340-010-4307-0

Mitra S, Wassmann R, Vlek PLG (2005) An appraisal of global wetland area and its organic carbon stock. *Current Science*, **88**, 25–35.

Mitsch WJ, Gosselink JG (2007) *Wetlands*, 4th edn. John Wiley & Sons, Inc., Hoboken, New Jersey. ISBN 9781118174487.

Mitsch WJ, Bernal B, Nahlik AM *et al.* (2012) Wetlands, carbon, and climate change. *Landscape Ecology*, doi: 10.1007/s10980-012-9758-8

Morison JIL, Piedade MTF, Muller E, Long SP, Junk WJ, Jones MB (2000) Very high productivity of the C-4 aquatic grass Echinochloa polystachya in the Amazon floodplain confirmed by net ecosystem CO_2 flux measurements. *Oecologia*, **125**, 400–411, doi: 10.1007/s004420000464

Oberbauer S, Starr G, Pop E (1998) Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska. *Journal of Geophysical Research-Atmospheres*, **103**, 29075–29082, doi: 10.1029/98JD00522

Ollinger SV (2011) Sources of variability in canopy reflectance and the convergent properties of plants. *The New Phytologist*, **189**, 375–394, doi: 10.1111/j.1469-8137.2010.03536.x

Pearlstine LG, Pearlstine EV, Aumen NG (2010) A review of the ecological consequences and management implications of climate change for the Everglades. *Journal of the North American Benthological Society*, **29**, 1510–1526, doi: 10.1899/10-045.1

Peñuelas J, Filella I, (1998) Visible and near-infrared reflectance techniques for diagnosing plant physiological status. *Trends in Plant Science*, **3**, 151–156.

Peñuelas J, Filella I, Biel C, Serrano L, Save R (1993) The reflectance at the 950–970 nm region as an indicator of plant water status. *International Journal of Remote Sensing*, **14**, 1887–1905, doi: 10.1080/01431169308954010

Peñuelas J, Pinol J, , Ogaya R (1997) Estimation of plant water concentration by the reflectance water index WI (R900/R970). *International Journal of Remote Sensing*, **18**, 2869–2875.

Perry W (2004) Elements of south Florida's comprehensive Everglades's restoration plan. *Ecotoxicology*, **13**, 185–193.

Perry LG, Galatowitsch SM (2004) Competitive control of invasive vegetation: a native wetland sedge suppresses Phalaris arundinacea in carbon-enriched soil. *Journal of Applied Ecology*, **41**, 151–162, doi: 10.1016/S1360-1385(98)01213-8

Poorter L (1993) Photosynthetic induction responses of two rainforest tree species in relation to light environment. *Oecologia*, **96**, 193–199, doi: 10.1007/BF00317732

Reddy KR, DeLaune RD (2008) *Biogeochemistry of Wetlands*. CRC Press, Boca Raton, FL. ISBN 978-1-56670-678-0.

Rocha AV, Goulden ML (2010) Drought legacies influence the long-term carbon balance of a freshwater marsh. *Journal of Geophysical Research*, **115**, G00H02, doi: 10.1029/2009JG001215

Schedlbauer JL, Oberbauer SF, Starr G, Jimenez KL (2010) Seasonal differences in the CO_2 exchange of a short-hydroperiod Florida Everglades marsh. *Agricultural and Forest Meteorology*, **150**, 994–1006, doi: 10.1016/j.agrformet.2010.03.005

Schedlbauer JL, Oberbauer SF, Starr G, Jimenez KL (2011) Controls on sensible heat and latent energy fluxes from a short-hydroperiod Florida Everglades marsh. *Journal of Hydrology*, **411**, 331–341, doi: 10.1016/j.jhydrol.2011.10.014

Schedlbauer JL, Munyon JW, Oberbauer SF, Gaiser EE, Starr G (2012) Controls on ecosystem carbon dioxide exchange in short- and long-hydroperiod Florida Everglades freshwater marshes. *Wetlands*, **32**, 801–812, doi: 10.1007/s13157-012-0311-y

Smith KA, Ball T, Conen F, Dobbie KE, Massheder J, Rey A (2003) Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *European Journal of Soil Science*, **54**, 779–791, doi: 10.1046/j.1365-2389.2003.00567.x

Todd MJ, Muneepeerakul R, Pumo D, Azaele S, Miralles-Wilhelm F, Rinaldo A, Rodriguez-Iturbe, (2010) Hydrological drivers of wetland vegetation community distribution within Everglades National Park, Florida. *Advances in Water Resources*, **33**, 1279–1289, doi: 10.1016/j.advwatres.2010.04.003

Tokida T, Miyazaki T, Mizoguchi M, Nagata O, Takakai F, Kagemoto A, Hatano R (2007) Falling atmospheric pressure as a trigger for methane ebullition from peatland. *Global Biogeochemical Cycles*, **21**, GB2003, doi: 10.1029/2006GB002790

Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from arctic tundra. *Chemosphere*, **26**, 357–368, doi: 10.1016/0045-6535(93)90431-4

Tsuyuzaki S, Nakano T, Kuniyoshi S, Fukuda M (2001) Methane flux in grassy marshlands near Kolyma River. North-Eastern Siberia. *Soil Biology & Biochemistry*, **33**, 1419–1423, doi: 10.1016/S0038-0717(01)00058-X

Tucker C (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150, doi: 10.1016/0034-4257(79)90013-0

Vourlitis GL, Oechel WC, Hastings SJ, Jenkins MA (1993) A system for measuring in situ CO_2 and CH_4 flux in unmanaged ecosystems: an arctic example. *Functional Ecology*, **7**, 369–379.

Webster KL, McLaughlin JW, Kim Y, Packalen MS, Li CS (2013) Modelling carbon dynamics and response to environmental change along a boreal fen nutrient gradient. *Ecological Modelling*, **248**, 148–164, doi: org/10.1016/j.ecolmodel.2012.10.004

Whalen SC (2005) Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environmental Engineering Science*, **22**, 73–94, doi: 10.1089/ees.2005.22.73

Whalen SC, Reeburgh WS (1988) A methane flux time series for tundra environments. *Global Biogeochemical Cycles*, **2**, 399–409, doi: 10.1029/GB002i004p00399

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. *Nature*, **364**, 794–795, doi: 10.1038/364794a0

Whiting GJ, Chanton JP (2001) Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus Series B-Chemical and Physical Meteorology*, **53**, 521–528, doi: 10.1034/j.1600-0889.2001.530501.x

Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, **23**, 431–452, doi: 10.1080/07352680490514673

Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources*, **30**, 39–74, doi: 10.1146/annurev.energy.30.050504.144248