

Ecosystem resistance in the face of climate change: a case study from the freshwater marshes of the Florida Everglades

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Abstract. Shaped by the hydrology of the Kissimmee-Okeechobee-Everglades watershed, the Florida Everglades is composed of a conglomerate of wetland ecosystems that have varying capacities to sequester and store carbon. Hydrology, which is a product of the region's precipitation and temperature patterns combined with water management policy, drives community composition and productivity. As shifts in both precipitation and air temperature are expected over the next 100 years as a consequence of climate change, CO₂ dynamics in the greater Everglades are expected to change. To reduce uncertainties associated with climate change and to explore how projected changes in atmospheric CO₂ concentration and climate can alter current CO₂ exchange rates in Everglades freshwater marsh ecosystems, we simulated fluxes of carbon among the atmosphere, vegetation, and soil using the DAYCENT model. We explored the effects of low, moderate, and high scenarios for atmospheric CO₂ (550, 850, and 950 ppm), mean annual air temperature (+1, +2.5, and +4.2°C) and precipitation (−2, +7, and +14%), as predicted by the IPCC for the year 2100 for the region, on CO₂ exchange rates in short- and long-hydroperiod wetland ecosystems. Under 100 years of current climate and atmospheric CO₂ concentration, Everglades freshwater marsh ecosystems were estimated to be CO₂-neutral. As atmospheric CO₂ concentration increased and under climate change projections, there were slight shifts in the start and length of the wet season (−1 to +7 days) and a small enhancement in the sink capacity (by −169 to −573 g C m^{−2} century^{−1}) occurred at both short- and long-hydroperiod ecosystems compared to CO₂ dynamics under the current climate regime. Over 100 years, rising temperatures increased net CO₂ exchange rates (+1 to 13 g C m^{−2} century^{−1}) and shifts in precipitation patterns altered cumulative net carbon uptake by +13 to −46 g C m^{−2} century^{−1}. While changes in ecosystem structure, species composition, and disturbance regimes were beyond the scope of this research, results do indicate that climate change will produce small changes in CO₂ dynamics in Everglades freshwater marsh ecosystems and suggest that the hydrologic regime and oligotrophic conditions of Everglades freshwater marshes lowers the ecosystem sensitivity to climate change.

Key words: climate change; CO₂ exchange rates; DAYCENT; ecosystem resistance; eddy covariance; Florida Everglades.

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INTRODUCTION

The Florida Everglades is composed of a conglomerate of wetland ecosystems that have been shaped by the complex hydrology of south Florida (Davis and Ogden 1994). Hydrology drives wetland community composition, structure, productivity, soil development, and influences decomposition rates across these ecosystems (Davis and Ogden 1994, Mitsch and Gosslink 2007). The mosaic of seasonally fluctuating hydrologic patterns has led to a range of capacities to sequester and store carbon (C), and may be important for ecosystem sensitivity. We refer to ecosystem sensitivity as the magnitude of a response to change, where low sensitivity indicates that a response to an environmental perturbation is small. Climate change projections suggest shifts in both air temperature and precipitation over the next 50 to 100 years (Christensen et al. 2007, Stanton and Ackerman 2007, IPCC 2013), and when coupled with water management decisions and human population expansion in south Florida, these shifts may have serious implications for Everglades hydrology and ultimately the region's C dynamics (Stanton and Ackerman 2007).

The Everglades is expected to be vulnerable to the impacts of climate change that, along with anthropogenic controls, will initiate additional alterations in water levels and inundation periods (Stanton and Ackerman 2007, IPCC 2013). Future climate is dependent on atmospheric CO₂ concentration, which is predicted to increase in the range of 540 to 970 ppm by 2100 (Houghton et al. 2001, Stanton and Ackerman 2007). In combination, wet season precipitation is projected to decrease by 5–10% (Christensen et al. 2007) while annual precipitation may be altered by –2 to +14% (IPCC 2013) and temperatures may warm 1 to 4.2°C (IPCC 2013). The change will likely include larger convective storms and greater intensity hurricanes (Allan and Soden 2008). The uncertainty and confidence in climate change projections depends on the quantity, quality, consistency of evidence (e.g., mechanistic understanding, theory, data, and models) and the degree of agreement among models (IPCC 2013). Although climate change is expected to alter vegetative communities and C dynamics within the Everglades (Davis and Ogden 1994, Bush et

al. 1998, Todd et al. 2010), the range in climate projections is wide, thus making estimates of future C dynamics for the region even less certain.

Anthropogenic activities have been shown to reduce the capacity of ecosystems to cope with disturbance and change (Jackson et al. 2001, Scheffer et al. 2001, Elmqvist et al. 2003), which could have significant implications for ecosystem sensitivity to climate change and ultimately the system's C dynamics and sequestration capacity (Cao and Woodward 1998, Riedo et al. 2000). The greater Everglades system is highly modified by water control structures that disconnect hydrological dynamics from precipitation patterns throughout the Kissimmee-Okeechobee-Everglades watershed (Perry 2004). Efforts are currently underway to improve water flows throughout Everglades National Park in areas suffering from chronically low water levels (Perry 2004). Fluctuations in hydric conditions that alter ecosystem C storage or emission rates might occur slowly, but can have a significant long lasting effect on C pools. Using the ecosystem model DAYCENT (Del Grosso et al. 2001), we aim to explore the effects of increasing atmospheric CO₂ concentration, temperature and altered precipitation, independently and in combination, to determine the relative impact of each on current ecosystem CO₂ exchange rates.

Limited experimental capabilities exist to evaluate the complicated interactive controls on ecosystem responses to multifactor drivers (Fuhner 2003, Luo et al. 2008), although these effects are critical to understand how climate change impacts terrestrial ecosystems (Luo et al. 2008). Ultimately, time and financial constraints limit multifactor experiments (Luo et al. 2008), and thus simulation models have been a useful tool to investigate the effects of rising atmospheric CO₂ concentration and climate change scenarios on terrestrial ecosystems (Abdalla et al. 2010). Ideally, models that simulate long-term changes in C dynamics should link plant, soil and atmospheric processes, and account for interactions among effects (Riedo et al. 2000). The DAYCENT model (Del Grosso et al. 2001) meets these requirements, simulating ecosystem water, C and nutrient dynamics (Parton et al. 1987, Parton et al. 1988) for various native and managed ecosystems (Del Grosso et al. 2002,

Del Grosso et al. 2009, Abdalla et al. 2010).

DAYCENT simulates changes in C and nutrient dynamics within and through the soil-plant-atmosphere continuum in response to changes in environmental conditions (i.e., air temperature, precipitation and atmospheric CO₂ concentration) and management practices (grazing, harvesting, burning, fertilizing, and irrigation; Del Grosso et al. 2000). DAYCENT has been used to successfully simulate ecosystem responses to changes in climate (Parton et al. 1995, Luo et al. 2008, Savage et al. 2013), and to model gas fluxes (CO₂, CH₄, N₂O, NO_x, N₂). It has also been used to model C and nutrient dynamics (N, P, S) in shrublands (Li et al. 2006), forest (Hartman et al. 2007, Parton et al. 2010), crops (Del Grosso et al. 2002, Stehfest et al. 2007, Del Grosso et al. 2009, Chang et al. 2013, Duval et al. 2013), and temperate wetlands and grasslands (Luo et al. 2008, Morgan et al. 2004, Parton et al. 2007). By capturing patterns in soil hydrology, soil thermal regimes, and C dynamics (Chimner et al. 2002, Cheng et al. 2013, Cheng et al. 2014), DAYCENT has been used to effectively model C dynamics in wetland ecosystems, which provides a strong basis for using DAYCENT in Everglades freshwater marsh ecosystems.

Alterations to the Everglades hydrologic cycle are expected with climate change, leaving C pools and sequestration potential highly uncertain. *The goal of these model simulations is to determine how CO₂ exchange rates in Everglades freshwater wetland ecosystems will change as a result of rising atmospheric CO₂ concentration and associated climate projections.* The model projections are important for understanding Everglades vulnerability to climate change, and to indicate how factors interact to influence the CO₂ sequestering capacity of Everglades ecosystems. Wetland ecosystem sensitivity to climate change will have a significant impact on the global C cycle, considering that 535 Gt C are stored in wetland soils as peat (Mitsch and Gosslink 2007) and this sequestered C is vulnerable to changes in hydrologic cycles.

Ecosystem sensitivity to “future” conditions can be used as an indication of the vulnerability of Everglades C pools. Increased atmospheric CO₂ concentration should enhance ecosystem productivity (Nowak et al. 2004, Ainsworth and Long 2005) by reducing nutrient limitations

(Hocking and Meyer 1991, Drake and González-Meler 1997, Ainsworth and Long 2005) and photorespiration in C₃ species (Bowes 1993). Holding atmospheric CO₂ concentration constant, wetland ecosystem productivity and CO₂ exchange rates are driven largely by hydrology (Schedlbauer et al. 2010), nutrient dynamics, light and temperature (Schedlbauer et al. 2010). Precipitation drives hydrological patterns (e.g., water levels) and the onset and start of seasons (Malone et al. 2014b). Water levels above the soil surface influence soil temperature, oxygen availability and respiratory processes, often leading to a decline in ecosystem respiration. Productivity increases with higher water availability until water levels interfere with exposed leaf area and oxygen availability in the soil. Low ecosystem sensitivity would suggest that C pools are less vulnerable to climate change and the future structure and function of ecosystems would be more heavily influenced by changes in disturbance regimes and sea level rise.

MATERIALS AND METHODS

Model description

To determine the effect of projected climate change on Everglades freshwater marshes we used DAYCENT_Photosyn (Savage et al. 2013), a modified version of the DAYCENT model (www.nrel.colostate.edu/projects/daycent/). DAYCENT_Photosyn models key processes for evaluating wetland ecosystem CO₂ exchange rates by simulating soil water and thermal dynamics, plant production and allocation of net primary production (NPP), decomposition of litter and soil organic matter, mineralization/immobilization and plant uptake of nutrients, and CH₄ oxidation and methanogenesis. DAYCENT_Photosyn contains the SIPNET photosynthesis model (Braswell et al. 2005, Sacks et al. 2006, 2007), which is a simplified Farquhar photosynthesis and respiration submodel. In DAYCENT, C allocation in the NPP submodel is a function of plant phenology, water and nutrient stress (Parton et al. 2010), soil C and nutrient dynamics (Parton et al. 2001), trace gas flux (Del Grosso et al. 2000), and soil water and temperature (Parton et al. 1998, Eitzinger et al. 2000; Fig. 1). The key process influencing soil C dynamics is soil organic matter decomposition, which is controlled by soil

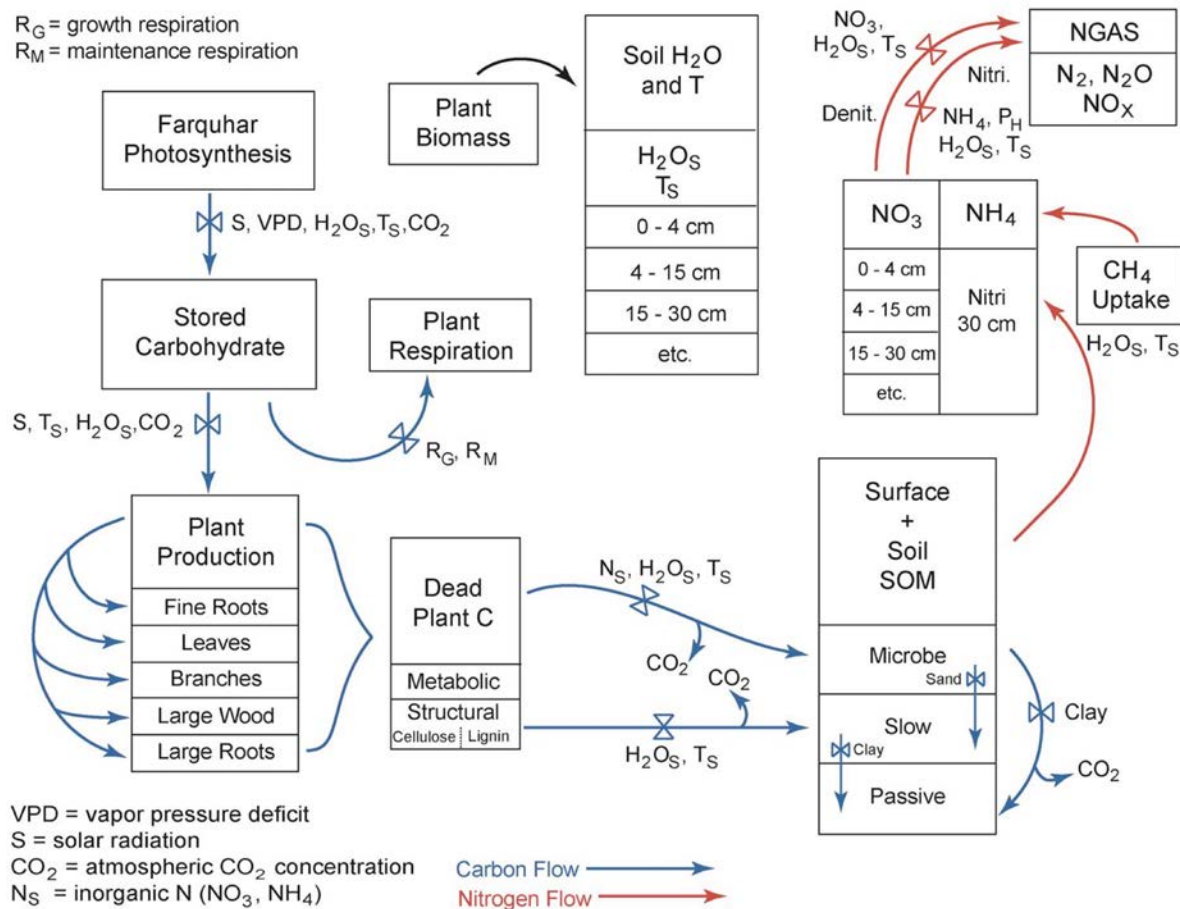


Fig. 1. Conceptual diagram of the DAYCENT_Photosyn ecosystem model. DAYCENT incorporates a soil organic matter (SOM), net primary productivity (NPP) and land surface sub-model. In the SOM sub-model, decomposition is microbially mediated with an associated microbial respiration CO_2 loss that depends on soil texture. The NPP sub-model uses relationships between climatic factors and available soil nutrients to calculate plant production and allocation of nutrients to live aboveground and belowground vegetation. The land surface sub-model simulates water flow through the plant canopy, litter, and soil profile (Parton et al. 1998, Eitzinger et al. 2000).

moisture/oxygen concentrations, temperature and pH. DAYCENT assumes that NPP and organic matter decomposition rates increase as soil water content increases until optimum water content is reached, with the optimum higher for NPP than for decomposition. Analogously, NPP and decomposition are influenced by temperature, and the sensitivity of the temperature response is different for each process. Optimum, minimum, and maximum temperatures for NPP vary with vegetation type whereas no minimum or maximum temperatures for decomposition are assumed, although the rate at which decompo-

sition increases declines as temperature increases. Both NPP and decomposition are also limited by mineral N availability. As CO_2 concentrations increase, DAYCENT allows water-use efficiency to increase by reducing transpiration, so that water savings are immediately reflected in soil moisture. Increases in NPP under rising atmospheric CO_2 concentration using DAYCENT arise from the combined direct effect of CO_2 on NPP, indirect effects of soil moisture on NPP, and reduced N-limitation to NPP due to enhanced soil-N mineralization on moister soils.

Table 1. DAYCENT site characteristics for Taylor Slough (TS) and Shark River Slough (SRS). Site data was obtained from the Florida coastal Everglades Long-term Ecological Research (FCE LTER sites TS-1 and SRS-2), AmeriFlux and the literature.

Parameters (units)	TS	SRS	Source
Site latitude	25°26'16.5" N	25°33'6.72" N	http://ameriflux.ornl.gov
Site Longitude	80°35'40.68" W	80°46'57.36" W	http://ameriflux.ornl.gov
C:N ratio (AG/BG)	39.2 AG/46.8 BG	39.2 AG/46.8 BG	Childers and Troxler 2011a, b, c, d, 2013a, b, Reddy et al. 1999
Root: shoot ratio	60:40	60:40	Schedlbauer et al. 2010, Miao and Sklar 1998
Lignin content (AG/BG; %)	13% AG	34% soil	Reddy et al. 1999
Sand, silt, and clay (%)	80–15–5	80–15–5	Sandy loam (Dade County Soil Survey 1996)
Bulk density (g/cm ³)	0.56	0.066	White and Reddy 2001
Rooting depth (cm)	15	30	
N deposition (wet/dry; mg/l N)	0.73 (wet)/ 0.07–0.25 (dry)	0.73 (wet)/ 0.07–0.25 (dry)	Steward 1975
C in SOM (mg C/g soil)	166	409	Childers 2006 (TS), White and Reddy 2001 (SRS)
N in SOM (mg N/g soil)	5.81	25.3	Childers 2006 (TS), White and Reddy 2001 (SRS)

DAYCENT parameterization

DAYCENT was parameterized for two subtropical Everglades ecosystems with contrasting hydroperiods, Taylor Slough (TS) and Shark River Slough (SRS). The short-hydroperiod marsh, TS, is inundated 4 to 6 months each year (June to November) and is characterized by shallow marl soils (~0.14 m; Duever et al. 1978) and relatively uniform vegetation co-dominated by a *C₃* sedge (*Cladium jamaicense* Crantz.) and a *C₄* grass (*Muhlenbergia capillaris* Lam.). The long-hydroperiod marsh, SRS, is inundated ~12 months each year and is characterized by peat soils (~1 m thick) with ridge and slough microtopography (Duever et al. 1978). Ridges are dominated by *C. jamaicense* and sloughs are dominated by *Eliocharis cellulosa* and *Nymphaea odorata*. Periphyton also exists on submerged structures at both sites and as floating mats at SRS. Both sites are also P limited, have year-round growing seasons and experience wet and dry seasons that are produced by precipitation patterns in the south Florida region (Davis and Ogden 1994). Taylor Slough occupies ~14,398 ha while Shark River Slough covers 88,811 ha of the 609,447 ha Everglades National Park. It is important to note that freshwater marsh ecosystems do not dominate the entire area of TS and SRS. For a more detailed site description, see Davis and Ogden (1994). Vegetation and soil data used in the model were measured at Florida Coastal Everglades Long Term Ecological Re-

search (FCE-LTER) sites TS-1b (25°26'16.5" N, 80°35'40.68" W) and SRS-2 (25°33'6.72" N, 80°46'57.36" W) and made available through the FCE-LTER data portal (<http://fcelter.fiu.edu/data/>) (Table 1).

Long-term weather data were obtained from the nearest weather station, NCDC Royal Palm Ranger Station, where NOAA Daily Surface Meteorological Data were available from 1963 to 2011 (Fig. 2). Data from TS and SRS in 2012 was added to the weather file to aid model validation, creating a 50-year weather file for each site. In the Everglades, complex annual, seasonal, and intra-seasonal precipitation patterns exist, which are caused by global climate cycles (Davis and Ogden 1994). In order to maintain the natural variability in observed weather data and prevent unrealistic patterns in precipitation, weather data variability in climate change simulations (2000 to 2100) was based on observed weather data 1963 to 2012.

To parameterize DAYCENT, vegetation and water dynamics were simplified. The DAYCENT model requires a representative species that is used to characterize the vegetative components of the model. In terms of biomass and density, *C. jamaicense* dominates both TS and SRS (Davis and Ogden 1994), and thus *C. jamaicense* was used to characterize the vegetation parameters. Current site leaf area and P conditions were also used in the model and assumed constant.

To capture the effects of inundation in the

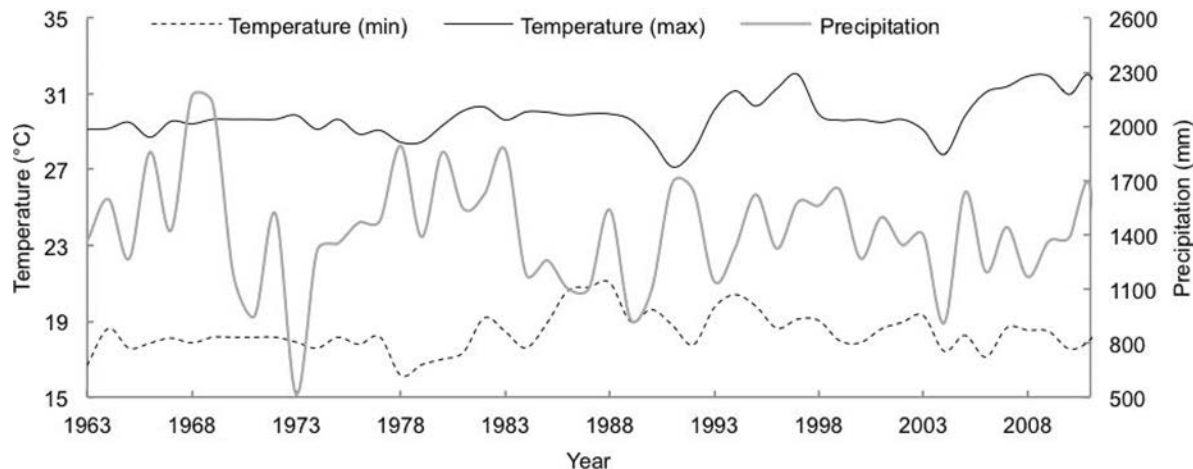


Fig. 2. Long-term daily weather data from the NCDC Royal Palm Ranger Station from 1963 to 2012. In climate change simulations weather data variability during 2000 to 2100 was based on variability at the Royal Palm weather station during 1963 to 2011 and weather data from TS and SRS in 2012.

DAYCENT model we used the program's irrigation option, and indicated when and for how long sites were inundated. Changes in soil water content (available pore space; Kelly et al. 2000) affect O_2 levels, which influence heterotrophic decomposition in the DAYCENT model. Simulations showed that increasing soil water content reduces decomposition rates 10–30% of the maximum rates when soils are saturated. The irrigation option keeps soils saturated, which influences soil oxygen levels, but does not include the effects of standing water on exposed leaf area. To incorporate the effects of standing water on the productivity of emergent vegetation (Jimenez et al. 2012), we adjusted the optimum and maximum temperatures for production and altered the coefficients used to calculate water stress on vegetation production. We matched historical seasonal water levels at each site; at TS, the system was inundated throughout the wet season, while SRS remained inundated during the entire year. The start and duration of the wet season were determined from fluctuations in the Bowen Ratio (β) at TS and SRS (2009–2012; Malone et al. 2014a). The length of the wet season was determined assuming a linear model between cumulative precipitation (January through March) and wet season length derived from β (Fig. 3A) at TS and SRS (separately) using 2009–2012 data (<http://ameriflux.ornl.gov>). We also determined the linear relationship between the

wet season length and the first day of the wet season (Fig. 3B; Malone et al. 2014b). These correlations were then used to incorporate the effect of surface flows on ecosystem productivity and soil water availability. This method was effective in that it allowed seasons to fluctuate with precipitation patterns, and permitted seasons to vary with climate change. However it does not consider the effects of water depth or any changes in water levels that occur as a result of water management activities, and assumes that relationships between precipitation and season length and durations that occurred over a relatively short time frame (2009–2012) were appropriate in the past and in the future under climate change.

Although both TS and SRS experience similar weather, variations in soil water availability and the effect of temperature and moisture on potential productivity resulted in dissimilarities between model parameterization at the two sites. Using observed ecosystem CO_2 exchange rates to parameterize temperature and moisture effects on potential productivity allowed us to account for the presence of co-dominant and subdominant species that also contribute to ecosystem CO_2 exchange. Gross ecosystem exchange (GEE) and net ecosystem exchange (NEE) rates for TS (TS-1b) and SRS (SRS-2) from 2009 to 2011 were used to determine maximum potential production, and the effects of temperature and moisture

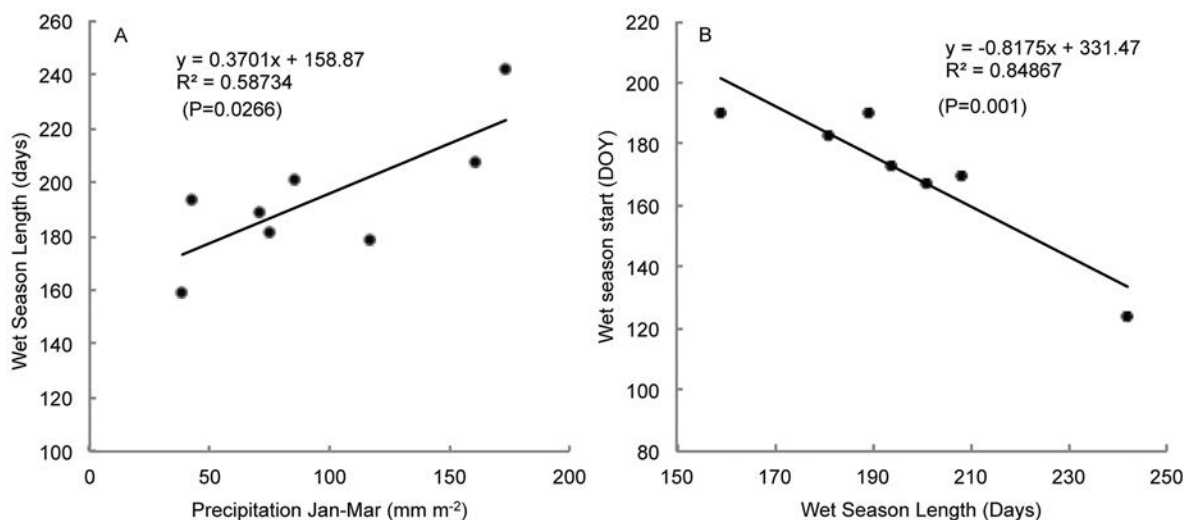


Fig. 3. Wet season length and the start of the wet season at TS and SRS were estimated with data from 2009 to 2012. First, the linear relationship between (A) wet season length and precipitation (mm m^{-2}) January to March was estimated, and then the relationship between (B) wet season length and the start of the wet season was determined.

on production. Maximum potential production, which is a function of solar radiation, was greater in the dry season compared to the wet season and greater for TS compared to SRS. Potential production ($\text{g C m}^{-2} \text{ month}^{-1}$) is a function of the maximum production defined, and the scalars for the effects of temperature, moisture, and shading. In Everglades freshwater marsh ecosystems the effect of temperature on potential production differed by site and seasonally. The optimum temperature for production was higher at SRS than at TS and higher during the summer-wet season (35°C and $\sim 37.5^\circ\text{C}$ at TS and SRS, respectively) than in the winter-dry season (27°C and 30°C at TS and SRS, respectively). The coefficients used to determine the effect of water stress on production were similar for both TS and SRS, though the effect of water stress was slightly greater at TS during the wet season.

DAYCENT validation

To examine the model's ability to adequately characterize the study sites, we ran DAYCENT, parameterized for each site, with weather data collected from TS-1b and SRS-2 in 2012 and compared modeled versus observed soil volumetric water content (VWC), soil temperature (T_{soil} , $^\circ\text{C}$) and CO_2 exchange rates (i.e., NEE,

ecosystem respiration [R_{eco}], and GEE). Using methods similar to Veldkamp and O'Brien (2000), observed soil volumetric water content (VWC, %) was calculated from site-specific equations for soil conditions and from the dielectric constant using two soil moisture sensors (CS616, Campbell Scientific Inc.) buried between 0 and 20 cm soil depth at each site. Observed soil temperature (T_{soil} , $^\circ\text{C}$) was measured at 5 cm depths at two locations within each site using insulated thermocouples (Type-T, Omega Engineering, Stamford, CT). Observed VWC, T_{soil} and CO_2 exchange rates (NEE, R_{eco} , and GEE) were obtained from the eddy covariance tower sites at TS (TS-1b) (Schedlbauer et al. 2010, Schedlbauer et al. 2011, Jimenez et al. 2012) and SRS (SRS-2) (Jimenez et al. 2012). All observed data is available through AmeriFlux (<http://ameriflux.ornl.gov>).

Measured and simulated outputs were evaluated using the coefficient of determination (R^2) and bias. Bias was quantified via a linear regression of simulated versus measured values. Average bias is small when slopes are near 1 and intercepts are near 0, but a thorough examination of modeled values must be made to appropriately evaluate patterns in over- and under-estimation for the range of data.

Climate change simulations

These climate change simulations do not define the future of freshwater marsh ecosystems, but describe how the current system would respond to climate change projections using simplified versions of Everglades short- and long- hydroperiod freshwater marsh ecosystems. A 2000-year equilibrium simulation, under recent climate (380 ppm of CO₂, and using long-term weather data) was conducted before model validation and climate projection simulations so that simulations would start at quasi-equilibrium (Pepper et al. 2005). This approach allowed us to attribute ecosystem responses wholly to climate change and thereby avoid any confounding response from a non-equilibrium state.

Following parameterization and validation, we ran the model for 100 years (1) under climate change projections, and (2) maintaining recent CO₂ concentration (380 ppm) and observed air temperature and precipitation patterns (1963 to 2012; NOAA Daily Surface Meteorological Data) in the Everglades region, for comparison. To examine the effects of rising atmospheric CO₂ concentration and climate change projections we simulated climate change projections by increasing atmospheric CO₂ concentration and temperature and altering precipitation patterns individually and in combination for each of the two sites. The same weather data used for the present-day simulation were altered by applying additive scalars to adjust atmospheric CO₂ concentration and temperature and scalar multipliers to adjust precipitation seasonally and annually to simulate climate change (Fig. 4). Atmospheric CO₂ concentration, temperature, and precipitation were altered gradually while conserving daily (high frequency) variability (Parton et al. 1995, McMurtrie et al. 2001). We explored a low, moderate, and high scenario for atmospheric CO₂ concentration (550, 850, and 950 ppm, respectively: EPA and IPCC 2007) and each climate driver: mean annual air temperature (+1, +2.5, and +4.2°C; IPCC 2013) and precipitation (−2, +7, and +14%; IPCC 2013) (Fig. 4). We also incorporated the seasonal shifts in temperature and precipitation that are expected for this region (Christensen et al. 2007, Stanton and Ackerman 2007). Projected temperature change was applied to the daily minimum temperatures in the dry season (winter months), while tem-

perature increases were applied to maximum temperatures in the wet season (Fig. 4D, E) (Christensen et al. 2007). The annual distribution of precipitation was altered by reducing wet season precipitation by 10% (Fig. 4D–F). When applied together, atmospheric CO₂ concentration, temperature, and altered precipitation patterns approximate the IPCC 2100 climate change projections for the Everglades region. While climate projections also suggest increased hurricane intensity (IPCC 2013) and more frequent heat waves (Stanton and Ackerman 2007), including these potentially important changes was beyond the scope of this study. We examined the effect of elevated atmospheric CO₂ concentration and altered weather by comparing cumulative CO₂ exchange rates (NEE, R_{ecor}, and GEE) over 100 years (2001 to 2100) to cumulative rates under current conditions.

RESULTS

DAYCENT validation

DAYCENT simulated daily T_{soil} and VWC values did not closely match that of the observed data, although monthly average DAYCENT values were comparable to observed average values at TS and SRS (Fig. 5). At both sites the average difference between daily observed and modeled T_{soil} and VWC was less than 0.97°C and 0.007, respectively. Monthly average fluctuations in T_{soil} were slightly underestimated at both TS (R² = 0.98) and at SRS (R² = 0.99), likely the result of increasing water levels at each site. The soil VWC was underestimated at TS once the site was inundated (~0.025% on average), and slightly over-estimated at SRS in the wet season (~0.03% on average). Discrepancies in VWC at TS were a result of differences between observed and modeled inundation. Determined by precipitation patterns, simulated inundation occurred before the site was actually inundated at TS, resulting in higher simulated VWC than observed (Fig. 5C). Once the site actually became inundated, model performance improved. Discrepancies in VWC and T_{soil} suggest that DAYCENT could be improved in wetland ecosystems by incorporating water depth above the soil surface and the effect of water depth on soil water content and temperature.

DAYCENT weakly captured fluctuations in

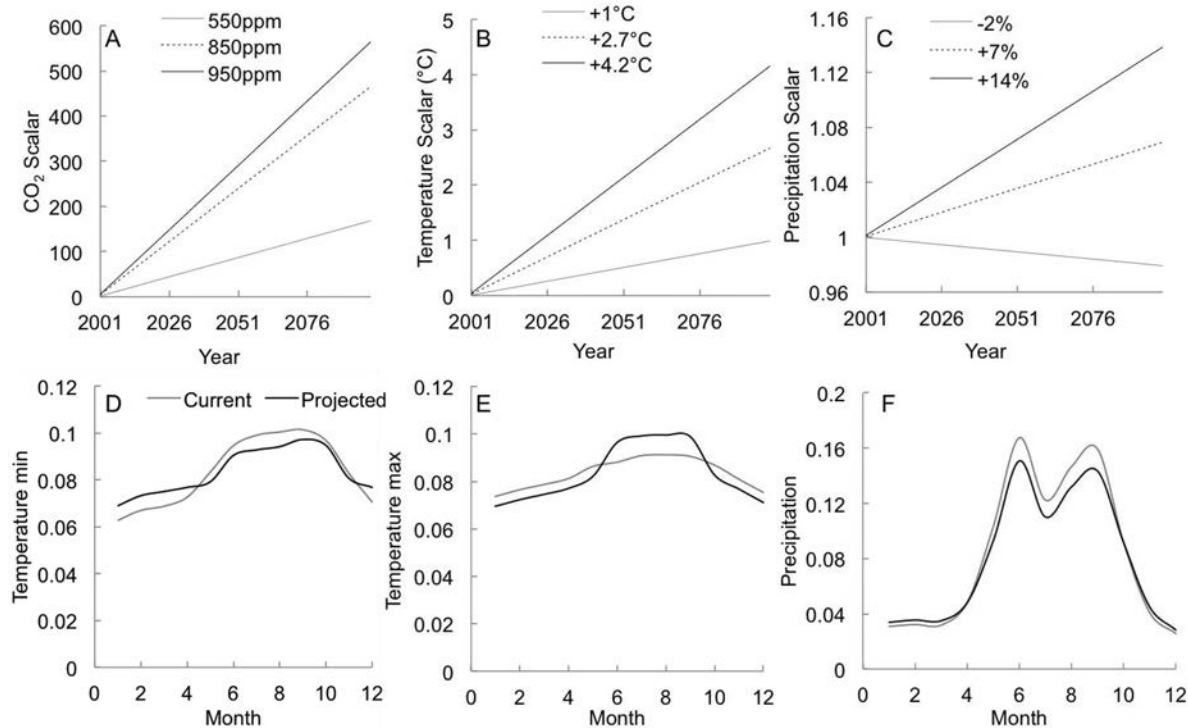


Fig. 4. Climate change scalars for (A) elevated atmospheric CO₂ concentration, (B) air temperature, and (C) precipitation. The distributions for (D) minimum temperature, (E) maximum temperature and (F) precipitation were modified to match projected seasonal change.

daily CO₂ exchange rates, though monthly estimates were very similar to those observed and previously reported for NEE, R_{eco} and GEE at TS and SRS for 2008 to 2009 (Jimenez et al. 2012). Atmospheric convention is used for CO₂ exchange rates, where a positive value denotes a loss of C from the ecosystem. At TS, DAYCENT captured fluctuations in NEE ($R^2 = 0.80$) and GEE ($R^2 = 0.94$), though daily fluctuations in R_{eco} ($R^2 = 0.65$) were often slightly over-estimated (Fig. 6A). At SRS, NEE was over estimated in the dry season and during transition periods as a result of small overestimations in both R_{eco} ($R^2 = 0.68$; Fig. 6B) and GEE ($R^2 = 0.70$; Fig. 6C). On a monthly basis, DAYCENT simulated NEE, R_{eco} and GEE were realistic at both sites and DAYCENT captured fluctuation in GEE and NEE much better than it did R_{eco}.

Under recent atmospheric CO₂ concentration and climate, NEE fluctuated around a null balance with a range of $\pm 100 \text{ g C m}^{-2} \text{ yr}^{-1}$ at both sites. R_{eco} ranged from ~ 200 to $500 \text{ g C m}^{-2} \text{ yr}^{-1}$ at TS and SRS, whereas GEE ranged from

-200 to $-500 \text{ g C m}^{-2} \text{ yr}^{-1}$, though rates at TS were higher on average. Cumulatively at 100 years, both TS ($-30 \text{ g C m}^{-2} \text{ century}^{-1}$) and SRS ($-5 \text{ g C m}^{-2} \text{ century}^{-1}$) were very small sinks for CO₂, and represent a potential accumulation of $0.33 \text{ tons C ha}^{-1} \text{ century}^{-1}$ at TS and $0.05 \text{ tons C ha}^{-1} \text{ century}^{-1}$ at SRS. These results suggest freshwater marsh ecosystems are near neutral for CO₂ loss versus gain over 100 years.

Main effects of climate change scenarios

Rising atmospheric concentration of CO₂ resulted in the greatest change in NEE, R_{eco}, and GEE at both TS and SRS (Table 2, Figs. 7 and 8). At TS cumulative NEE declined substantially with elevated CO₂ concentration compared to simulations under current climate (380 ppm). Long-term average annual NEE was -2.0 , -4.8 and $-5.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the low, intermediate and high scenarios, respectively, compared to $-0.30 \text{ g C m}^{-2} \text{ yr}^{-1}$ under current climates at TS. Cumulative R_{eco} at TS increased progressively by 1755.2, 7217.8 and 8245.8 $\text{g C m}^{-2} \text{ century}^{-1}$

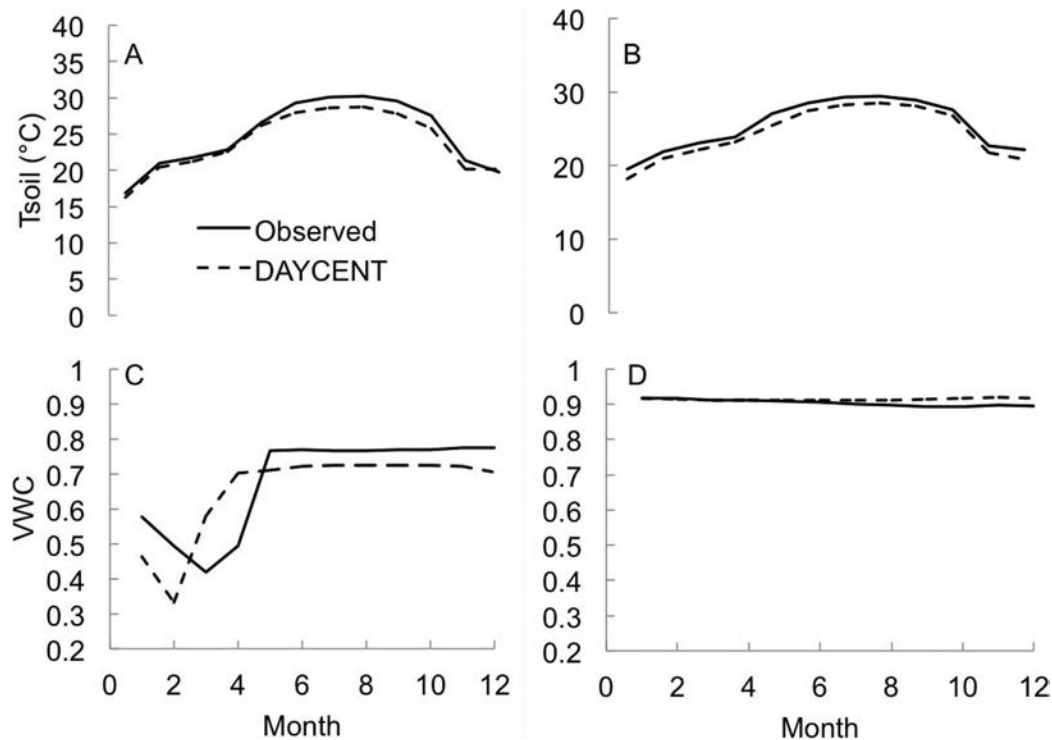


Fig. 5. Observed versus modeled soil temperature at (A) TS and (B) SRS, and soil volumetric water content (VWC) at (C) TS and (D) SRS.

under the low, moderate and high scenarios, and similar to R_{eco} , cumulative GEE at TS declined (higher CO_2 uptake) relative to current conditions by approximately equal and opposite amounts.

At SRS elevated atmospheric concentration also enhanced net CO_2 uptake. At 550, 850 and 950 ppm of CO_2 , cumulative NEE decreased by 176.3, 502.1 and 573.3 $g\ C\ m^{-2}\ century^{-1}$, respectively, compared to cumulative NEE at 380 ppm of CO_2 over 100 years (Table 2, Fig. 8A). Under these scenarios, the long-term average annual NEE was -1.8 , -5.0 and $-5.7\ g\ C\ m^{-2}\ yr^{-1}$ at low, medium, and high, respectively. Similar to TS, at SRS cumulative R_{eco} increased under the low, medium, and high scenarios while GEE decreased by nearly equal and opposite amounts.

Changes in temperature alone resulted in very small changes in CO_2 exchange rates of Everglades ecosystems by causing slight shifts in the ratio of GEE: R_{eco} . At TS, a 1, 2.5 and 4.2°C increase in mean annual temperature led to increased NEE (lower CO_2 uptake) by 1.3, 3.7 and 6.6 $g\ C\ m^{-2}\ century^{-1}$ (Table 2; Fig. 7B).

Cumulative R_{eco} decreased progressively by 2.5, 6.7 and 11.7 $g\ C\ m^{-2}\ century^{-1}$ with increased temperatures, while GEE increased by 3.8 to 18.3 $g\ C\ m^{-2}\ century^{-1}$. At SRS, NEE decreased by 3.1 to 13.0 $g\ C\ m^{-2}\ century^{-1}$ as a mean annual temperature increased by 1, 2.5 and 4.2°C, respectively (Table 2, Fig. 8A). Cumulative R_{eco} decreased by 17.2 to 73.9 $g\ C\ m^{-2}\ century^{-1}$, and GEE increased by 20.3 to 86.9 $g\ C\ m^{-2}\ century^{-1}$ as a mean annual temperature increased at SRS.

Changes in precipitation of -2 , $+7$, and $+14\%$ altered the length of seasons by -1 , 4, and 7 days on average, respectively. A 2% decrease in annual precipitation, which was weighted to reduce wet season precipitation more than in the dry season, increased cumulative NEE by 13.0 $g\ C\ m^{-2}\ century^{-1}$ at TS, while no change in cumulative NEE was found at SRS (Table 2). As mean annual precipitation increased by 7 and 14%, net stored CO_2 increased by 20.3 and 41.8 $g\ C\ m^{-2}\ century^{-1}$, respectively, at TS (Fig. 7C). A change in precipitation of -2 , $+7$ and $+14\%$ at TS altered cumulative R_{eco} by -1105.0 , -220.1 , and 432.9 $g\ C\ m^{-2}\ century^{-1}$, respectively. At TS, cumulative

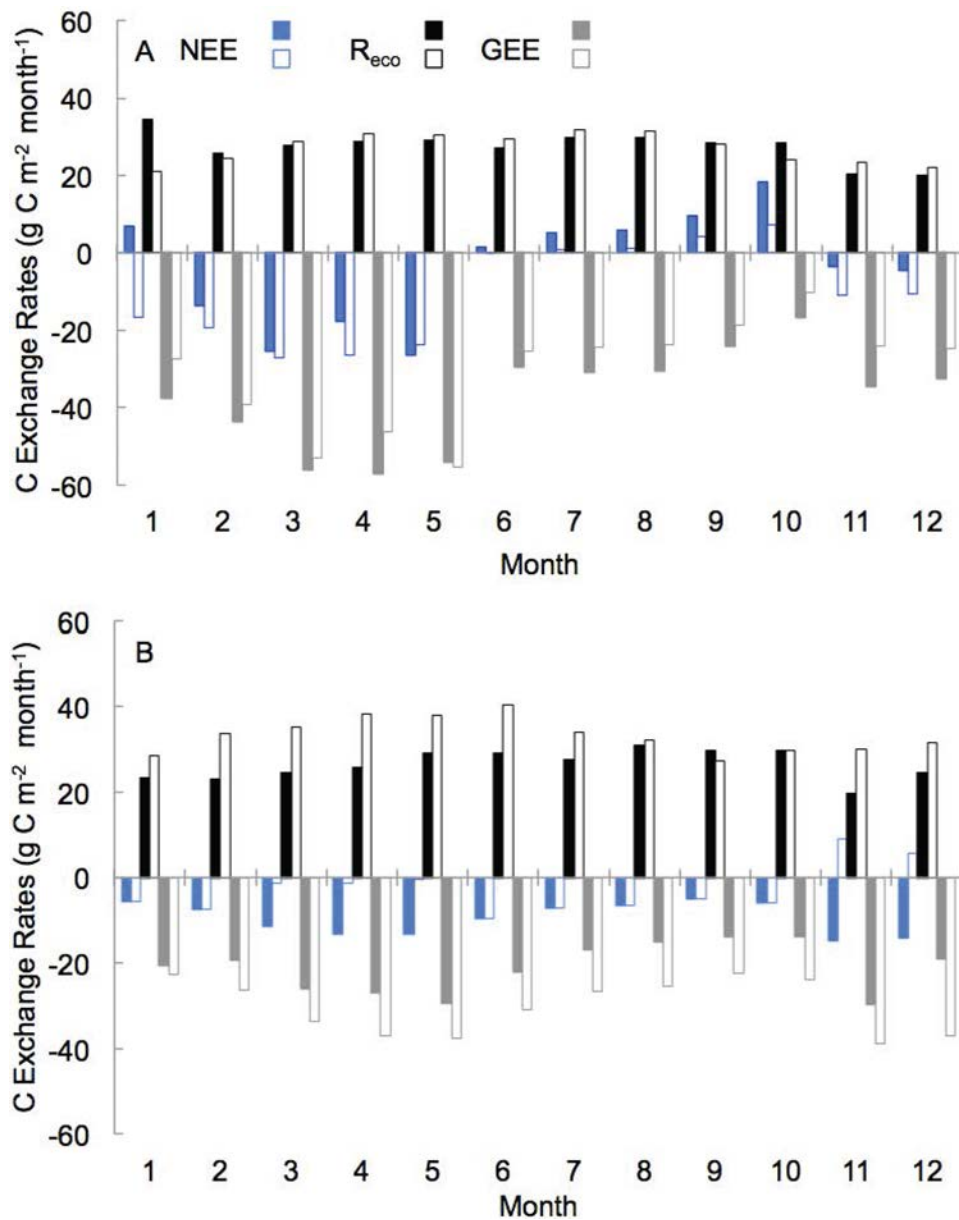


Fig. 6. Observed (solid) versus modeled (hollow) CO₂ exchange rates (NEE, R_{eco} and GEE) at TS (A) and SRS (B). Atmospheric convention is used here and positive numbers indicate a loss of C to the atmosphere.

GEE was altered by -1105.0 , -220.1 , and 432.9 g C m⁻² with a -2 and $+7$ and $+14\%$ change in mean annual precipitation. At SRS, changes in mean annual precipitation had a smaller impact on CO₂ exchange rates. A change in mean annual precipitation of -2 , 7 and 14% shifted NEE by 0 , -21.03 , and -46.1 g C m⁻² century⁻¹, respectively. R_{eco} at SRS increased by 5.4 , 147.6 , and 423.3 g

C m⁻² century⁻¹, and GEE shifted by 5.4 , -115.8 , and -469.4 g C m⁻² century⁻¹ with a -2 , $+7$ and $+14\%$ increase in annual precipitation, respectively.

Interactive effects of climate change scenarios

Simultaneous changes in CO₂ concentration, temperature, and precipitation modified ecosys-

Table 2. The change in cumulative NEE, R_{eco} , and GEE ($\text{g C m}^{-2} \text{ century}^{-1}$) as a result of rising atmospheric CO_2 concentration, increasing mean annual temperature, and variations in annual precipitation individually and in combination (IPCC 2013 projects).

Scenario	TS			SRS		
	Δ NEE	Δ Reco	Δ GEE	Δ NEE	Δ Reco	Δ GEE
CO ₂ only (ppm)						
Low (550)	-169	1755	-1925	-176	2271	-2447
Moderate (850)	-454	7218	-7672	-502	5485	-5987
High (950)	-530	8646	-9176	-573	6464	-7037
Temperature only (°C)						
Low (1)	1.3	-2.5	3.8	3.1	-17.3	20.4
Moderate (2.5)	3.7	-6.7	10.4	7.8	-43.5	51.3
High (4.5)	6.6	-11.7	18.3	13.0	-73.9	86.9
Precipitation only (%)						
Low (-2)	13.0	-1105	-1105	0.0	5.4	5.4
Moderate (7)	-20.3	-220	-220	-21.0	148	-116
High (14)	-42	433	433	-46	423	-469
IPCC						
Low	-157	2092	-2093	-161	2001	-2162
Moderate	-468	7324	-7324	-510	5667	-6177
High	-544	9279	-9279	-558	6776	-7334

tem CO_2 exchange rates (Table 2, Fig. 9). An increase in CO_2 concentration (550 ppm), combined with a 1°C rise in annual temperature and 2% decrease in annual precipitation led to $156.8 \text{ g C m}^{-2} \text{ century}^{-1}$ increase in cumulative NEE, $2092.4 \text{ g C m}^{-2} \text{ century}^{-1}$ increase in cumulative R_{eco} and a $2249.2 \text{ g C m}^{-2} \text{ century}^{-1}$ decrease in GEE at TS. At SRS, cumulative NEE decreased by $160.5 \text{ g C m}^{-2} \text{ century}^{-1}$ (Table 2, Fig. 9B), while cumulative R_{eco} increased $2001.4 \text{ g C m}^{-2} \text{ century}^{-1}$ and GEE declined by $2162.0 \text{ g C m}^{-2} \text{ century}^{-1}$. In the second scenario, atmospheric CO_2 concentration rose to 850 ppm, mean annual temperatures increased by 2.5°C , and mean annual precipitation increased by 7%. At TS cumulative NEE, R_{eco} , and GEE changed by -468.1 , 7323.5 , and $-7323.5 \text{ g C m}^{-2} \text{ century}^{-1}$, respectively. At SRS, cumulative NEE, R_{eco} and GEE were enhanced by -509.7 , 5666.8 , and $-6176.5 \text{ g C m}^{-2} \text{ century}^{-1}$, respectively. The most extreme scenario explored included an atmospheric CO_2 concentration of 950 ppm, a 4.2°C increase in mean annual temperature, and a 14% increase in annual precipitation. At TS, this high scenario led to a -544.4 , 9279.4 , and $-9279.4 \text{ g C m}^{-2} \text{ century}^{-1}$ change in cumulative NEE, GEE, and R_{eco} respectively. At SRS, this high scenario led to a -557.7 , 6776.4 , and $-7334.0 \text{ g C m}^{-2} \text{ century}^{-1}$ change in cumulative NEE, GEE, and R_{eco} respectively. Climate change projections led to a change in potential C sequestration of

1.7 , 5.2 and $6.0 \text{ tons C ha}^{-1} \text{ century}^{-1}$ at TS and 1.8 , 5.6 and $6.1 \text{ tons C ha}^{-1} \text{ century}^{-1}$ with the low, intermediate and high scenarios, respectively.

DISCUSSION

Climate change is considered a major threat to species survival and ecosystem integrity (Hulme 2005, Erwin 2009). Occurring within the transition zone between aquatic and terrestrial environments, wetlands ecosystems are considered to be among the most vulnerable ecosystems to climate change (Burkett and Kusler 2000) as a result of its effects on wetland hydrology and temperature (Ferrati et al. 2005, Erwin 2009). Everglades ecosystems are projected to experience large shifts in ecosystem structure and function by 2100 (Stanton and Ackerman 2007). While projections for temperature and precipitation are within the natural range of conditions observed in the region, ecosystem CO_2 exchange rates were modified by higher winter minimum and summer temperatures, and by greater dry season precipitation. At both sites, increasing atmospheric CO_2 concentration caused the greatest changes in GEE and R_{eco} rates; however, because increases in these fluxes were of similar magnitude but opposite in sign, the effect on net CO_2 exchange was very small. These results suggest that climate change will lessen seasonal

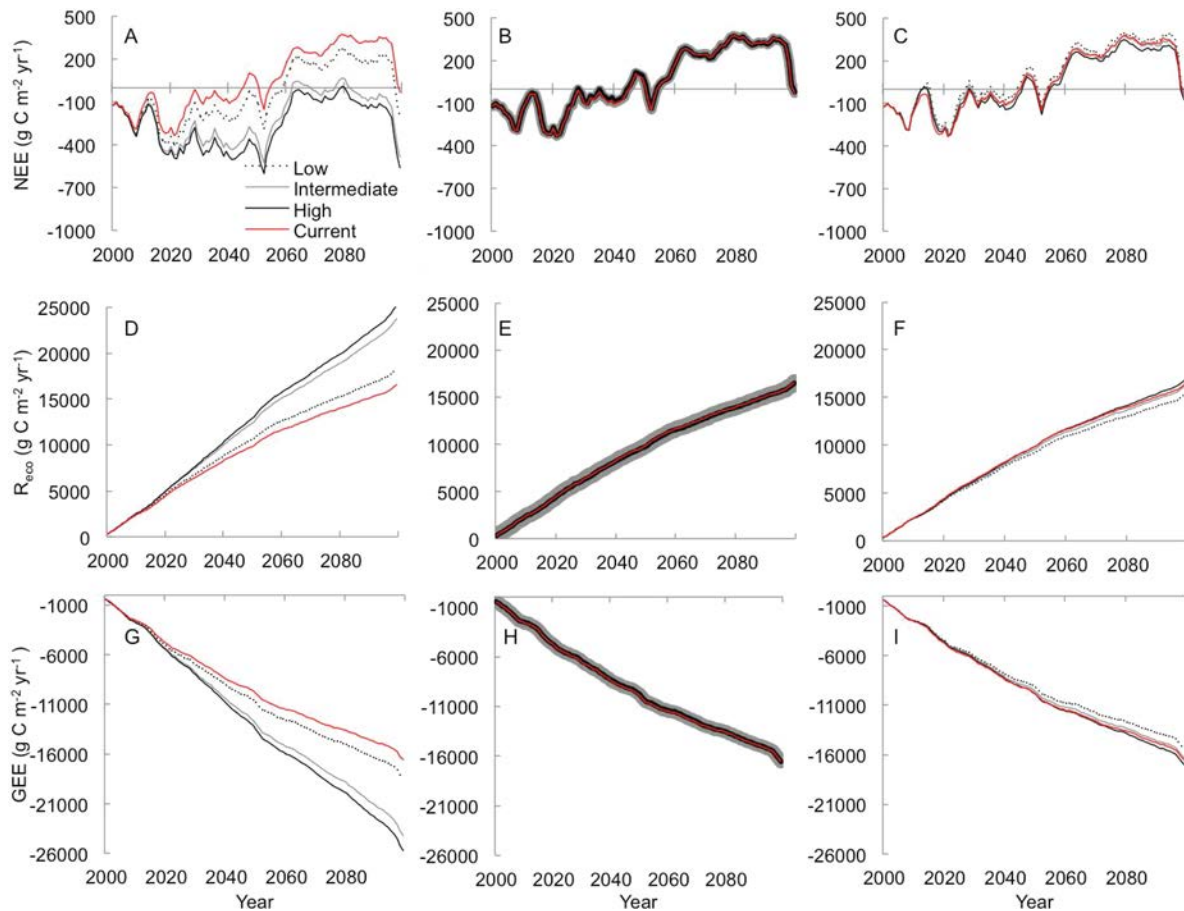


Fig. 7. The effect of elevated atmospheric CO₂ concentration (550 ppm, 850 ppm and 950 ppm) on cumulative (A) NEE, (B) R_{eco} and (G) GEE, at TS. The influence of rising temperatures (1°C, 2.7°C and 4.2°C) on cumulative (B) NEE, (E) R_{eco} and (H) GEE and shifts in seasonal and annual precipitation patterns (−2%, +7% and +14%) on cumulative (C) NEE, (F) R_{eco} and (I) GEE. Atmospheric convention is used here and positive numbers indicate a loss of C to the atmosphere. All simulations were compared to current weather and atmospheric CO₂ concentration (red line)

differences in precipitation patterns by reducing wet and increasing dry season precipitation and results suggest that Everglades ecosystems are more resilient to change than previously thought. This low ecosystem sensitivity is likely the result of hydrology and nutrient limitations.

Main and interactive effects of multifactor climate change

As an important limiting factor for the growth and productivity of many species (Vu et al. 1997), terrestrial ecosystems are currently and have been responding to rising atmospheric CO₂ concentration (Gifford 1980, Ciais et al. 1995,

Keeling et al. 1995, Drake and González-Meler 1997). The biochemical basis of this response is well established (Farquhar et al. 1980) and indicates that below 600 ppm atmospheric CO₂ is generally limiting (Nowak et al. 2004), and many ecosystems will respond to higher concentrations. This was the case for TS and SRS and led to greater C uptake and release rates. Photosynthesis (Long and Drake 1992) and transpiration (Heath 1948, Drake and González-Meler 1997) have long been known to respond to changes in atmospheric CO₂ concentration. Elevated CO₂ concentration reduces photorespiration rates (Bowes 1993) in C₃ species and enhances light

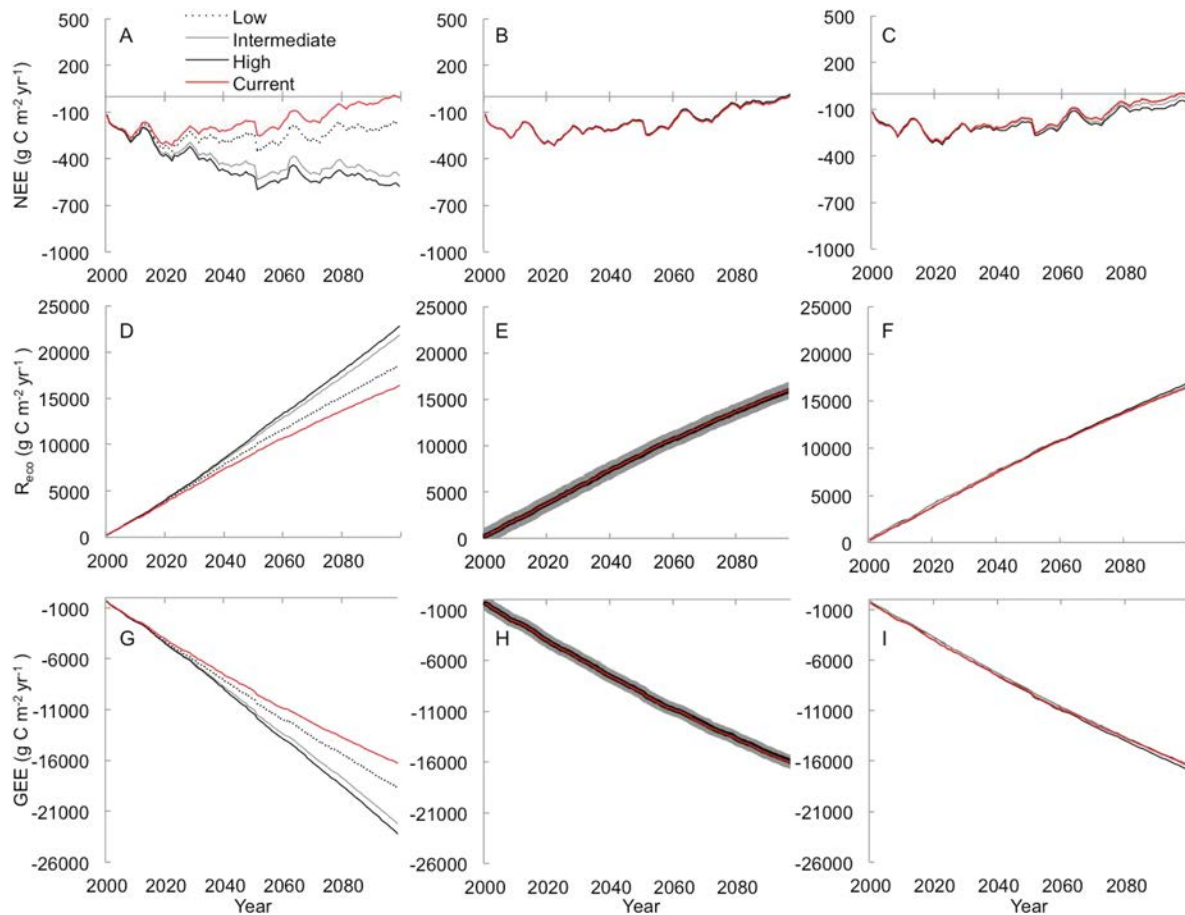


Fig. 8. The effect of elevated atmospheric CO_2 concentration (550 ppm, 850 ppm and 950 ppm) on cumulative (A) NEE, (D) R_{eco} and (G) GEE, at SRS. The influence of rising temperatures (1°C , 2.7°C and 4.2°C) on cumulative (B) NEE, (E) R_{eco} and (H) GEE and shifts in seasonal and annual precipitation patterns (-2% , $+7\%$ and $+14\%$) on cumulative (C) NEE, (F) R_{eco} and (I) GEE. Atmospheric convection is used here and positive numbers indicate a loss of C to the atmosphere. All simulations were compared to current weather and atmospheric CO_2 concentration (red line).

(Drake and González-Meler 1997, Ainsworth and Long 2005), nutrient (Hocking and Meyer 1991, Drake and González-Meler 1997) and water use efficiency (Drake and González-Meler 1997) in plants. Ecosystem respiration rates also respond to rising atmospheric CO_2 concentration (González-Meler et al. 1996, Drake and González-Meler 1997) through the direct inhibition of respiratory enzyme activity (e.g., cytochrome c oxidase and succinate dehydrogenase, Drake and González-Meler 1997). Rising atmospheric CO_2 concentration generally reduces dark respiration rates (Drake and González-Meler 1997) compared to GEE rates.

A small increase in net CO_2 uptake at both

Everglades sites occurred in response to elevated atmospheric CO_2 , suggesting that ecosystem responses at both TS and SRS will provide a negative feedback to global warming and will maintain current soil C pools. Compared to SRS, TS had greater CO_2 uptake rates, although SRS was most sensitive to changes in CO_2 concentration. Variations in site sensitivity were due to differences in leaf area. At SRS, leaf area is greater than at TS, and studies have shown that while rising CO_2 concentration alters productivity rates, leaf area often remains unchanged (Drake and González-Meler 1997). Although both sites fluctuate between being a very small

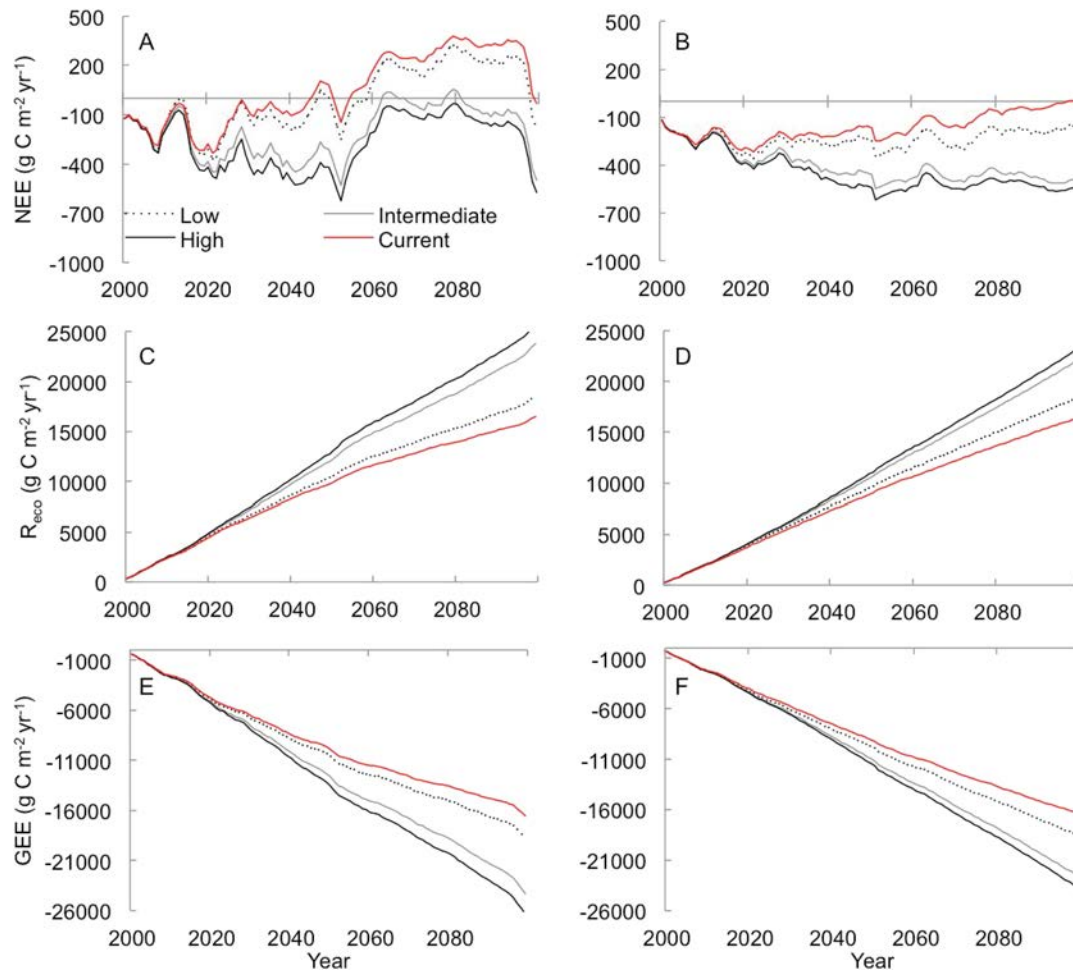


Fig. 9. The effect of climate change projections on cumulative CO₂ exchange rates: (A) NEE, (C) R_{eco} and (E) GEE at TS, and on (B) NEE, (D) R_{eco} and (F) GEE on at SRS. Atmospheric convention is used here and positive numbers indicate a loss of C to the atmosphere.

sink, source, or near neutral annually (Jimenez et al. 2012, Malone et al. 2014b), rising CO₂ concentration may cause an enhancement in the sink potential of Everglades freshwater marsh ecosystems by improving resource use efficiencies, though the response to CO₂ enrichment will be limited by low P levels.

Climate change is expected to have the strongest and most immediate effect on plant phenology (Forrest and Miller-Rushing 2010) and physiology. Significant changes in physiology have been observed in response to higher temperatures, affecting photosynthetic rates of C₃ plants (Long 1991), which is a dominant mode of photosynthesis at both sites. Higher tempera-

tures lower the activation state of Rubisco (Kobza and Edwards 1987, Holaday et al. 1992) and both the solubility and the specificity for CO₂ relative to O₂ (Jordan and Ogren 1984, Brooks and Farquhar 1985, Long 1991). At the ecosystem level, variations of only a few degrees centigrade are sufficient to affect gas fluxes (Hirano et al. 2009). Compared to CO₂ concentration, changes in temperature had a much smaller impact on CO₂ exchange rates at both TS and SRS and sensitivity to changes in temperature was similar at both sites. An increase in temperature, up until optimal conditions, often leads to an increase in metabolic activity (Medlyn et al. 2002, Lambers et al. 2008), although when temperatures rise

beyond optimal growth and activity ranges higher temperatures lead to reductions in productivity (Lambers et al. 2008). Higher temperatures shifted the ratio of GEE to R_{eco} and led to greater C release at TS and SRS, though this effect was very small. In Everglades ecosystems, inundation may buffer the ecosystem response to higher temperatures.

Precipitation affects both productivity and ecosystem respiration rates by influencing water and oxygen availability, altering exposed leaf area through its effect on water depth, and enhancing N inputs through wet N deposition. As water levels affect ecosystem CO_2 exchange rates differently at TS and SRS (Malone et al. 2014b), so do changes in precipitation patterns. At TS a 2% decrease in precipitation led to higher net exchange rates via a smaller decrease in ecosystem respiration relative to GEE. SRS was insensitive to the 2% reduction in precipitation, and at both TS and SRS, precipitation increased cumulative GEE more than R_{eco} , leading to greater net C uptakes rates. In the precipitation scenarios, wet season precipitation declined more than in the dry season, and as a result of greater sensitivity to changes in water levels the short hydroperiod site, TS, was more sensitive to changes in precipitation.

Climate change scenarios represent the range in climate that would result from changes in greenhouse gas concentration in the atmosphere. At both sites, NEE, R_{eco} and GEE responded to changes in atmospheric CO_2 concentration, temperature and precipitation, though the magnitudes of change were small, less than a 20% increase in average annual CO_2 exchange rates. Interactive effects of atmospheric CO_2 concentration and climate change on ecosystem CO_2 exchange rates were greater than the sum of the individual effects and this enhancement was likely due to the interaction between rising CO_2 concentration and air temperature. CO_2 enrichment modifies the response to temperature (Drake and González-Meler 1997) in C_3 species, like the dominant species at both sites, sawgrass. Enrichment reduces photorespiration rates, which moderates the adverse effects of high temperature on C_3 photosynthesis and results in greater net photosynthesis as growth temperatures increase (Long 1991, Vu et al. 1997). The amount of Rubisco required also declines with

increasing temperature (Drake and González-Meler 1997) and the degree of C_3 photosynthesis enhancement by higher CO_2 concentration is influenced by the temperature optimum for the species (Vu et al. 1997). Considerable evidence supports the prediction that CO_2 uptake will be greater in warm climates (Long 1991, McMurtrie and Wang 1993), though this may not occur in systems with low sensitivity to climate change.

Ecosystem sensitivity

Ecosystem sensitivity may be an essential factor underlying the sustained C sequestering capacities of Everglades ecosystems. Ecosystem sensitivity to climate change is driven by water, nutrients, and the responses of C_3 species relative to C_4 species. At Both TS and SRS, nutrient limitations should constrain the response to climate change but at TS where hydroperiods are short, changes in water cycling and the response of C_4 co-dominant species could increase the ecosystems sensitivity to climate change. Both TS and SRS exhibit low sensitivity to changes in rising CO_2 concentration and climate change scenarios. Previous studies have indicated that wet systems might be more resilient to change than dry systems (Luo et al. 2008). In the Everglades, hydroperiods may serve as a barrier to climate variation, which links the importance of hydroperiod to ecosystem sensitivity. Water above the soil surface dampens low temperature effects, cools the system when temperatures are high, and reduces the temperature response of soil and macrophyte respiration by slowing gas exchange. In addition to hydroperiods, low nutrient (P) levels may also affect ecosystem sensitivity to change (Steward and Ornes 1975, Curtis and Wang 1998). The Everglades is an oligotrophic system (Craighead 1971), and nutrient limitation can reduce the capacity of ecosystems to respond to rising atmospheric CO_2 concentration (Stitt and Krapp 1999). Interacting environmental stresses can influence the response to elevated CO_2 in plants (Lloyd and Farquhar 1994, Curtis 1996, Curtis and Wang 1998) and environmental stresses tend to reduce the CO_2 response in C_3 species (Wand et al. 1999). Studies have shown that although vegetation may initially respond to elevated CO_2 , acclimation is reported to be more pronounced when plants are N limited (Wong 1979, Oberba-

uer et al. 1986, Bowes 1993, Curtis 1996, Stitt and Krapp 1999, Ward and Strain 1999, Isopp et al. 2000). Studies have also shown that acclimation to elevated CO₂ rarely has reduced photosynthetic capacity enough to completely compensate for stimulated photosynthetic rates (Drake and González-Meler 1997, Ward and Strain 1999). Although in these simulations Everglades freshwater marsh ecosystems exhibit low sensitivity to changes in atmospheric CO₂ concentration and climate change, shifts in disturbance regimes (e.g., fire, tropical storms, drought) are also projected for the region and will significantly influence the future condition of the Everglades.

Disturbance regimes, C₃ vs C₄ plants, and invasive species

To understand Everglades ecosystem vulnerability and resistance to change, future research must consider changes in ecosystem structure, disturbance regimes, C₃ versus C₄ plants, and invasive species risk in the Everglades region. Although not considered in these model simulations, the magnitude and frequency of disturbance events may significantly alter Everglades ecosystem structure and function (Stanton and Ackerman 2007). A rise in hurricane intensity, more frequent heat waves, salt-water intrusion and sea-level rise are all projected for the Everglades region (Stanton and Ackerman 2007). Disturbance and altered hydrologic regimes promote the displacement of native vegetation by introduced or formerly restricted species (Groves and Burdon 1986, Mooney and Drake 1986), and have already led to changes in vegetation community composition in the Everglades (Toth 1987, 1988, Herndon et al. 1991, Urban et al. 1993). Sawgrass communities in the northern Everglades have already been replaced by dense stands of cattail (*Typha domingensis* Pers.; Richardson and Marshall 1990, Rutchey et al. 1994, Jensen et al. 1995, Newman et al. 1998), which invade disturbed and nutrient rich environments (Dykyjová and Květ 1978, Grace and Harrison 1986, Keddy 1990). Marl prairie landscapes comprising the outer regions of Everglades National Park (ENP) have also shown vulnerability to woody plant expansion (Jenkins et al. 2003, Knickerbocker et al. 2009) due to alterations in natural disturbance mechanisms (flood and fire management, Hanan and Ross

2010). Since trees have the greatest response to elevated CO₂ (Ainsworth and Long 2005), woody encroachment in TS may increase.

Soil disturbance has also caused encroachment by exotics (Dalrymple et al. 1993) in the Everglades. Bahia grass (*Paspalum notatum* Flügge) and torpedo grass (*Panicum repens* L.), exotic species introduced for cattle forage, spread quickly and aggressively. Under current conditions, these C₄ grasses are more metabolically efficient than C₃ species, allowing them to encroach on sawgrass marshes. Invasion may increase in the future if these species are sensitive to elevated atmospheric CO₂ concentration. It has been suggested that elevated CO₂ may preferentially increase the abundance of invasive species (Dukes and Mooney 1999, Weltzin et al. 2003), which may have already played a stimulatory role in plant invasions (Ziska 2003) and shifts in dominance. Although some studies have shown C₄ species respond weakly to elevated CO₂ (Ainsworth and Long 2005), others have found many C₄ plants to exhibit enhanced photosynthetic and growth responses (Sionit and Patterson 1984, Ziska et al. 1990, Imai and Sato 1991, Wand et al. 1999). This suggests that C₄ photosynthesis is not necessarily saturated at current CO₂ levels (Sionit and Patterson 1984, Imai and Sato 1991). C₄ grasses have shown significant changes in gas exchange, leaf area development (Wand et al. 1999), and an average growth enhancement of ~22% (Poorter and Oberbauer 1993) following elevated CO₂ concentration. Previous research has also shown that CO₂ saturation levels in C₄ species may be altered by environmental conditions (Wand et al. 1999). Ziska et al. (1990) found that elevated CO₂ concentration stimulated CO₂ assimilation rates in a cordgrass (*Spartina patens* Aiton) dominated salt marsh, though the effect was seasonal. Although enhanced C assimilation rates in C₃ species has been shown to decline when stressed (Wand et al. 1999), C₄ species show less negative impacts of environmental stresses (Wand et al. 1999).

Model limitations

Shifts in disturbance regimes and species dynamics are very important factors that will impact the sensitivity of Everglades ecosystems. Although the DAYCENT model was appropriate

for exploring the multifactor effects of rising atmospheric CO₂ concentration and climate change on the current ecosystems CO₂ exchange rates, to better understand the future condition of Everglades freshwater marsh ecosystems changes in species cover need to be incorporated into the model. In addition, incorporating changes in P dynamics would be a significant improvement in our confidence in model results in these P limited systems. Modeling water table dynamics (Dimitrov et al. 2014), beyond their effects on NPP, soil C dynamics and season length, will also be a very important component to determining how climate change will influence Everglades ecosystems. Furthermore, climate induced alterations to disturbance regimes (i.e., salt water intrusion, sea level rise and the frequency of hurricanes and drought) and the incorporation of data uncertainties into DAYCENT for both data and the model output should also be considered. Comparisons with results from simulations with other ecosystem models (Luo and Reynolds 1999, Sitch et al. 2003, Gerten et al. 2004, Krinner et al. 2005) will be necessary before drawing firm conclusions related to the question of how hydroperiods aid ecosystem resilience and what thresholds for air temperature and precipitation patterns significantly alter ecosystem sensitivity in the Florida Everglades.

CONCLUSION

Climate change projections have created substantial uncertainty about the future structure and function of Everglades ecosystems. As shifts in atmospheric CO₂ concentrations, air temperature, and precipitation are all expected over the next 100 years, exploring these effects is important for determining the current systems' vulnerability, which may be an indication of the potential ecosystem response to changes in sea level rise and disturbance regimes. Our results indicate that the hydrologic regime (timing, length of inundation and water depth) is important for ecosystem vulnerability, aiding Everglades ecosystems in light of climate change. The hydrologic regime may prove vital for reducing vulnerability to invasive species and changes in disturbance regimes as well, suggesting that restoration efforts in the Everglades region will be important for ecosystem resilience. Overall, a

future with greater C sequestration seems likely for the Everglades region, so long as hydroperiods are maintained. As climate change reduces seasonal fluctuations in temperature and precipitation, elevated CO₂ exchange rates may enhance the sink strength of Everglades ecosystems. Larger sink strength, albeit small, may be enough to switch these near CO₂ neutral sites to small sinks that negatively feedback to global warming.

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