Biology Faculty Publications

Biology

4-17-2015

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

Sparkle L. Malone
University of Alabama - Tuscaloosa

Cynthia Keough
Colorado State University - Fort Collins

Christina L. Staudhammer
University of Alabama - Tuscaloosa

Michael G. Ryan
Colorado State University - Fort Collins

William J. Parton
Colorado State University - Fort Collins

See next page for additional authors

Follow this and additional works at: http://digitalcommons.wcupa.edu/bio_facpub

Part of the Terrestrial and Aquatic Ecology Commons

Recommended Citation

Authors

Sparkle L. Malone, Cynthia Keough, Christina L. Staudhammer, Michael G. Ryan, William J. Parton, Paulo Olivas, Steven F. Overbauer, Jessica L. Schedlbauer, and Gregory Starr

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

SPARKLE L. MALONE,[1,2,†] CYNTHIA KEOUGH,[3] CHRISTINA L. STAUDHAMMER,[1] MICHAEL G. RYAN,[2,3] WILLIAM J. PARTON,[3] PAULO OLIVAS,[4] STEVEN F. OBERBAUER,[4] JESSICA SCHEDLBAUER,[4,5] AND GREGORY STARR[1]

[1]Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487 USA
[2]Rocky Mountain Research Station, United States Forest Service, Fort Collins, Colorado 80526 USA
[3]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523 USA
[4]Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA
[5]Department of Biology, West Chester University, West Chester, Pennsylvania 19383 USA

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, CO_2 dynamics in the greater Everglades are expected to change. To reduce uncertainties associated with climate change and to explore how projected changes in atmospheric CO_2 concentration and climate can alter current CO_2 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 CO_2 (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 CO_2 exchange rates in short- and long-hydroperiod wetland ecosystems. Under 100 years of current climate and atmospheric CO_2 concentration, Everglades freshwater marsh ecosystems were estimated to be CO_2-neutral. As atmospheric CO_2 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 CO_2 dynamics under the current climate regime. Over 100 years, rising temperatures increased net CO_2 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 CO_2 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; CO_2 exchange rates; DAYCENT; ecosystem resistance; eddy covariance; Florida Everglades.

† **E-mail:** sparklelmalone@fs.fed.us

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 CO_2 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 CO_2 concentration, temperature and altered precipitation, independently and in combination, to determine the relative impact of each on current ecosystem CO_2 exchange rates.

Limited experimental capabilities exist to evaluate the complicated interactive controls on ecosystem responses to multifactor drivers (Fuhrer 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 CO_2 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 CO_2 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 (CO_2, CH_4, N_2O, NO_x, N_2). 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 CO_2 exchange rates in Everglades freshwater wetland ecosystems will change as a result of rising atmospheric CO_2 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 CO_2 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 CO_2 concentration should enhance ecosystem productivity (Nowak et al. 2004, Ainsworth and Long 2005) by reducing nutrient limitations

(Hocking and Meyer 1991, Drake and Gonzàlez-Meler 1997, Ainsworth and Long 2005) and photorespiration in C_3 species (Bowes 1993). Holding atmospheric CO_2 concentration constant, wetland ecosystem productivity and CO_2 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 CO_2 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 CH_4 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
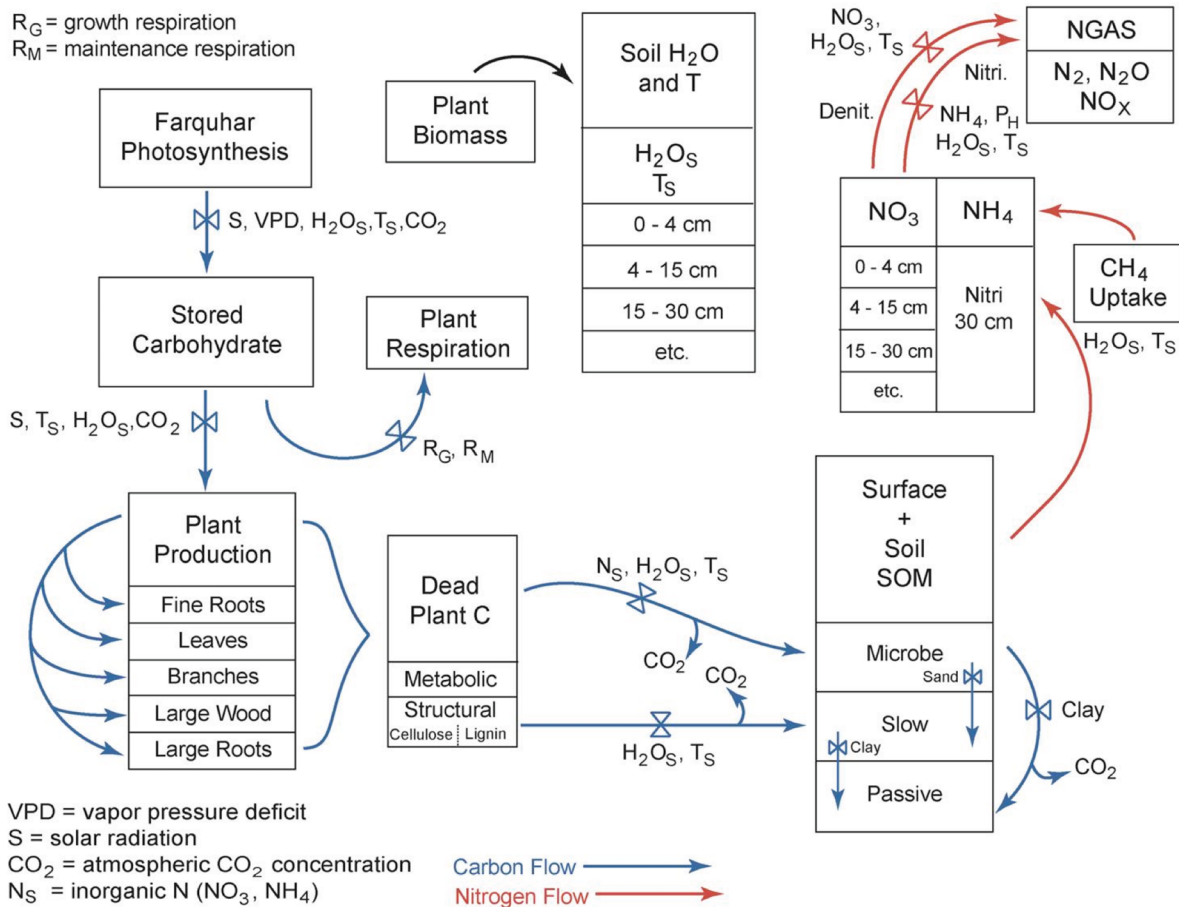
Fig. 1. Conceptual diagram of the DAYCENT_Photosyn ecosystem model. DAYCENT incorporates a soil organic matter (SOM), net primary productivity (NPP) and land surface sub-model. In the SOM sub-model, decomposition is microbially mediated with an associated microbial respiration CO_2 loss that depends 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 C$_3$ sedge (Cladium jamaicense Crantz.) and a C$_4$ 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 micro-topography (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 Research (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.

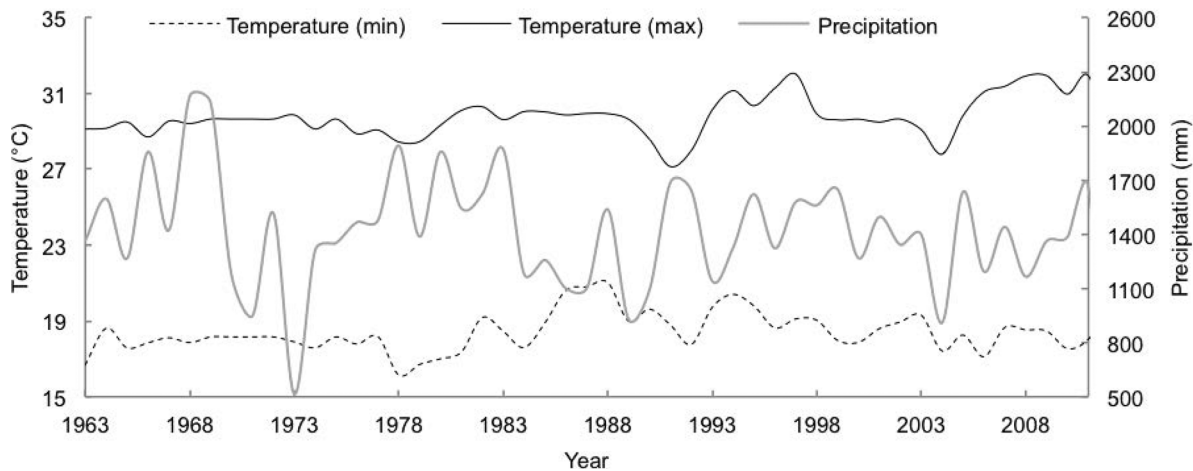To capture the effects of inundation in the

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
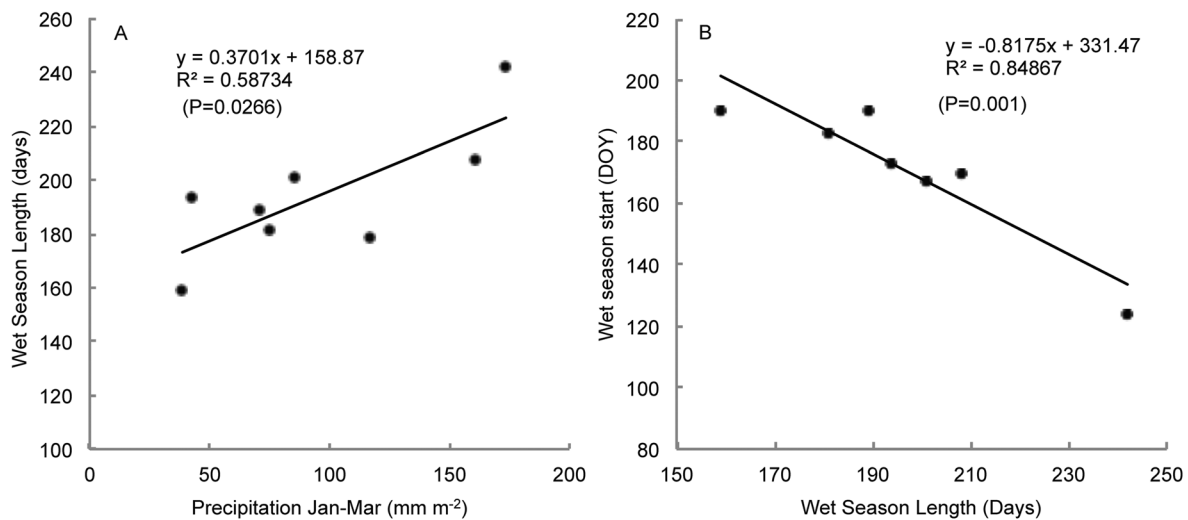
Fig. 3. Wet season length and the start of the wet season at TS and SRS were estimated with data from 2009 to 2012. First, the linear relationship between (A) wet season length and precipitation (mm m^{-2}) January to March was estimated, and then the relationship between (B) wet season length and the 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 (g C m^{-2} 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 ~37.5°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$_{soil}$, °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$_{soil}$, °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 CO_2, 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 CO_2 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 CO_2 concentration and climate change projections we simulated climate change projections by increasing atmospheric CO_2 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 CO_2 concentration and temperature and scalar multipliers to adjust precipitation seasonally and annually to simulate climate change (Fig. 4). Atmospheric CO_2 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 CO_2 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 CO_2 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 CO_2 concentration and altered weather by comparing cumulative CO_2 exchange rates (NEE, R_{eco}, 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 ($R^2 = 0.98$) and at SRS ($R^2 = 0.99$), 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.

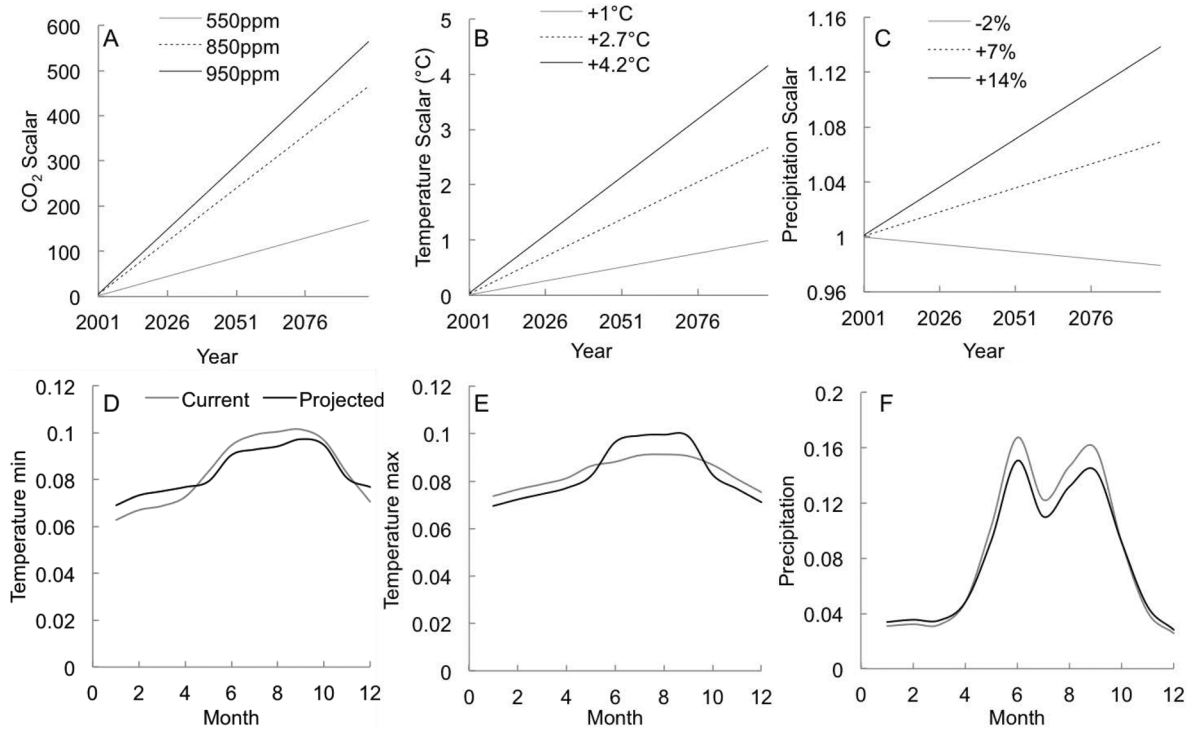DAYCENT weakly captured fluctuations in

Fig. 4. Climate change scalars for (A) elevated atmospheric CO_2 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 CO_2 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 CO_2 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 DAY-CENT captured fluctuation in GEE and NEE much better than it did R_{eco}.

Under recent atmospheric CO_2 concentration and climate, NEE fluctuated around a null balance with a range of ± 100 g C m^{-2} yr^{-1} at both sites. R_{eco} ranged from ~200 to 500 g C m^{-2} yr^{-1} at TS and SRS, whereas GEE ranged from

-200 to -500 g C m^{-2} yr^{-1}, though rates at TS were higher on average. Cumulatively at 100 years, both TS (-30 g C m^{-2} century^{-1}) and SRS (-5 g C m^{-2} century^{-1}) were very small sinks for CO_2, and represent a potential accumulation of 0.33 tons C ha^{-1} century^{-1} at TS and 0.05 tons C ha^{-1} century^{-1} at SRS. These results suggest freshwater marsh ecosystems are near neutral for CO_2 loss versus gain over 100 years.

Main effects of climate change scenarios

Rising atmospheric concentration of CO_2 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 CO_2 concentration compared to simulations under current climate (380 ppm). Long-term average annual NEE was -2.0, -4.8 and -5.6 g C m^{-2} yr^{-1} in the low, intermediate and high scenarios, respectively, compared to -0.30 g C m^{-2} yr^{-1} under current climates at TS. Cumulative R_{eco} at TS increased progressively by 1755.2, 7217.8 and 8245.8 g C m^{-2} century^{-1}
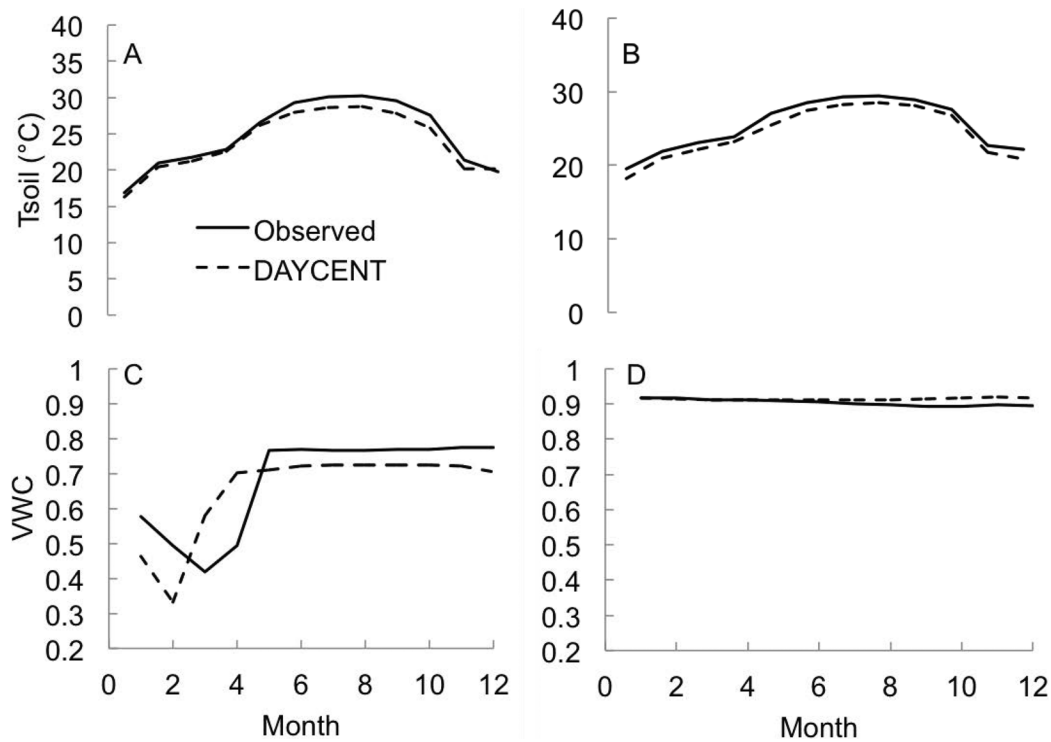
Fig. 5. Observed versus modeled soil temperature at (A) TS and (B) SRS, and soil volumetric water content (VWC) at (C) TS and (D) SRS.

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
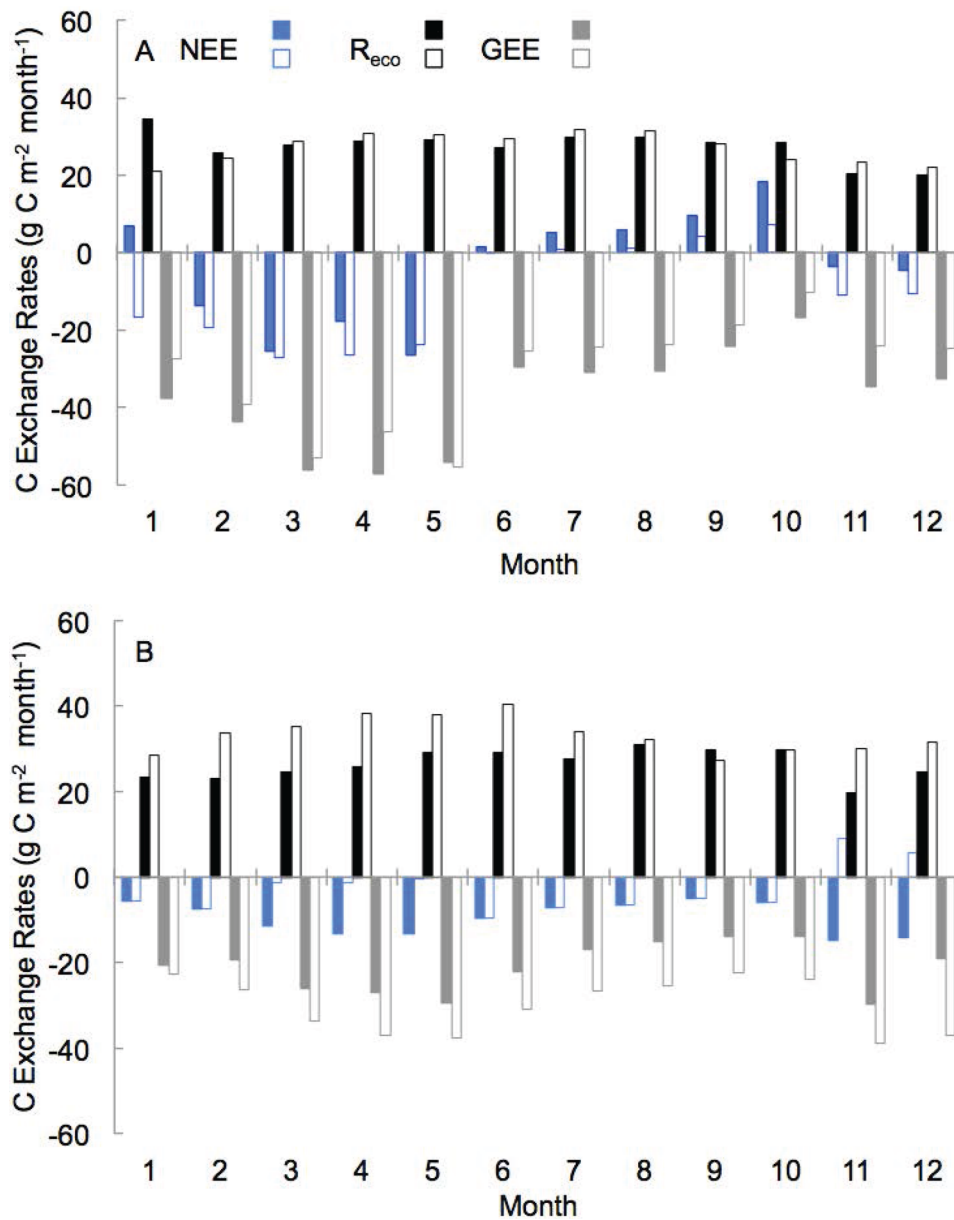
Fig. 6. Observed (solid) versus modeled (hollow) CO_2 exchange rates (NEE, R_{eco} and GEE) at TS (A) and SRS (B). Atmospheric convention is used here and positive numbers indicate a loss of C to the atmosphere.

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 CO_2 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 CO_2 concentration, temperature, and precipitation modified ecosys-

Table 2. The change in cumulative NEE, R_{eco}, and GEE (g C m^{-2} 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 g C m^{-2} century^{-1} increase in cumulative NEE, 2092.4 g C m^{-2} century^{-1} increase in cumulative R_{eco} and a 2249.2 g C m^{-2} century^{-1} decrease in GEE at TS. At SRS, cumulative NEE decreased by 160.5 g C m^{-2} century^{-1} (Table 2, Fig. 9B), while cumulative R_{eco} increased 2001.4 g C m^{-2} century^{-1} and GEE declined by 2162.0 g C m^{-2} 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 g C m^{-2} century^{-1}, respectively. At SRS, cumulative NEE, R_{eco} and GEE were enhanced by −509.7, 5666.8, and −6176.5 g C m^{-2} 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 g C m^{-2} 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 g C m^{-2} 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 tons C ha^{-1} century^{-1} at TS and 1.8, 5.6 and 6.1 tons C ha^{-1} 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
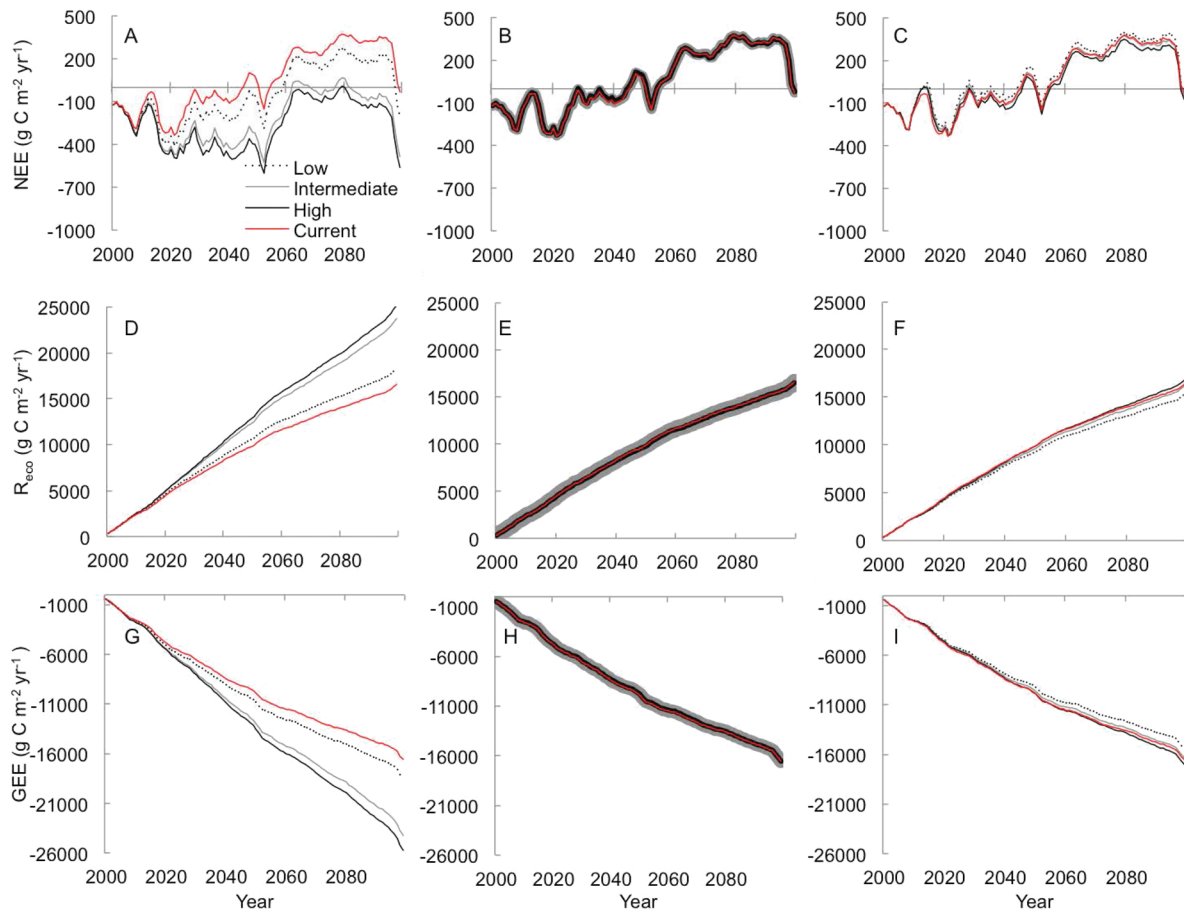
Fig. 7. The effect of elevated atmospheric CO_2 concentration (550 ppm, 850 ppm and 950 ppm) on cumulative (A) NEE, (B) R_{eco} and (G) GEE, at TS. The influence of rising temperatures (1°C, 2.7°C and 4.2°C) on cumulative (B) NEE, (E) R_{eco} and (H) GEE and shifts in seasonal and annual precipitation 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 CO_2 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 CO_2 concentration (Gifford 1980, Ciais et al. 1995,

Keeling et al. 1995, Drake and Gonzàlez-Meler 1997). The biochemical basis of this response is well established (Farquhar et al. 1980) and indicates that below 600 ppm atmospheric CO_2 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 Gonzàlez-Meler 1997) have long been known to respond to changes in atmospheric CO_2 concentration. Elevated CO_2 concentration reduces photorespiration rates (Bowes 1993) in C_3 species and enhances light
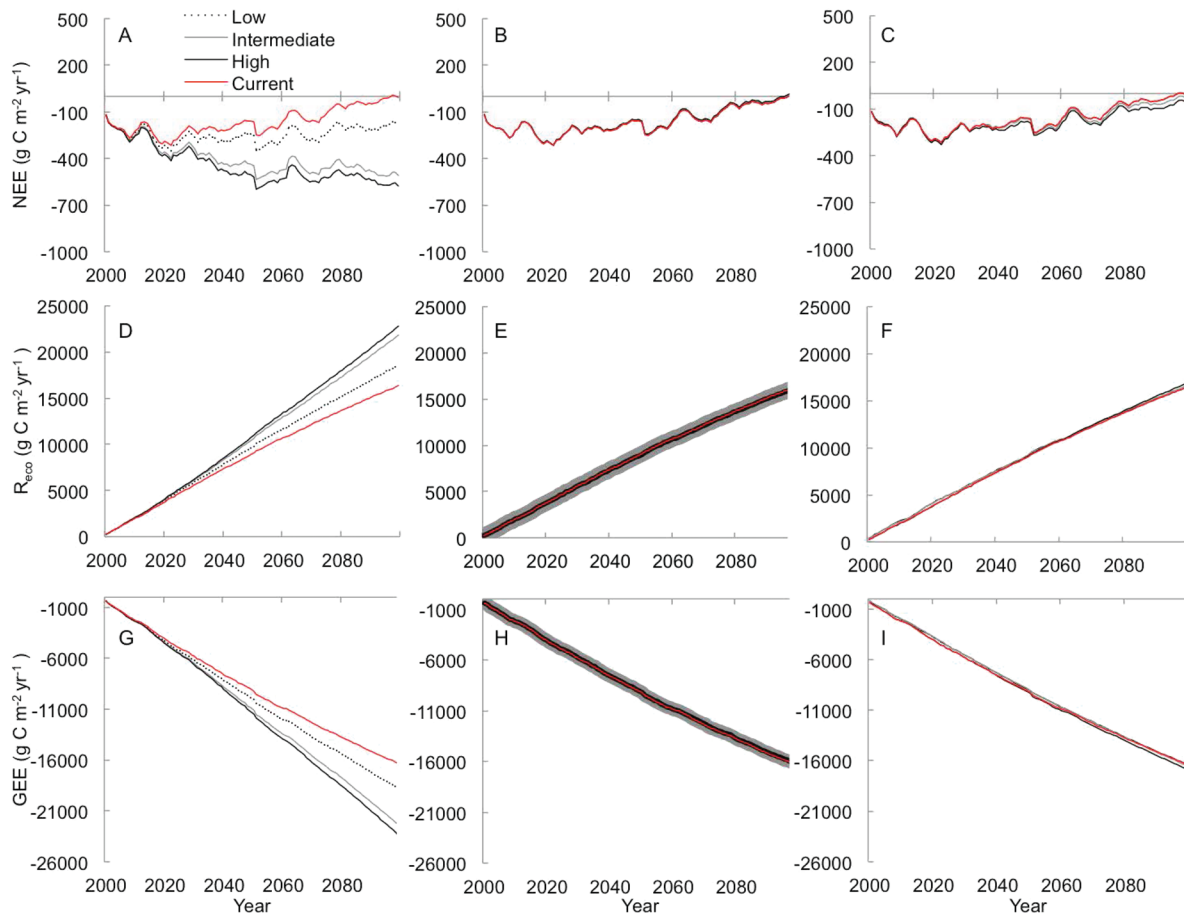
Fig. 8. The effect of elevated atmospheric CO_2 concentration (550 ppm, 850 ppm and 950 ppm) on cumulative (A) NEE, (D) R_{eco} and (G) GEE, at SRS. The influence of rising temperatures (1°C, 2.7°C and 4.2°C) on cumulative (B) NEE, (E) R_{eco} and (H) GEE and shifts in seasonal and annual precipitation patterns (−2%, +7% and +14%) on cumulative (C) NEE, (F) R_{eco} and (I) GEE. Atmospheric convention 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 Gonzàlez-Meler 1997, Ainsworth and Long 2005), nutrient (Hocking and Meyer 1991, Drake and Gonzàlez-Meler 1997) and water use efficiency (Drake and Gonzàlez-Meler 1997) in plants. Ecosystem respiration rates also respond to rising atmospheric CO_2 concentration (Gonzàlez-Meler et al. 1996, Drake and Gonzàlez-Meler 1997) through the direct inhibition of respiratory enzyme activity (e.g., cytochrome c oxidase and succinate dehydrogenase, Drake and Gonzàlez-Meler 1997). Rising atmospheric CO_2 concentration generally reduces dark respiration rates (Drake and Gonza-lez-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 Gonzàlez-Meler 1997). Although both sites fluctuate between being a very small
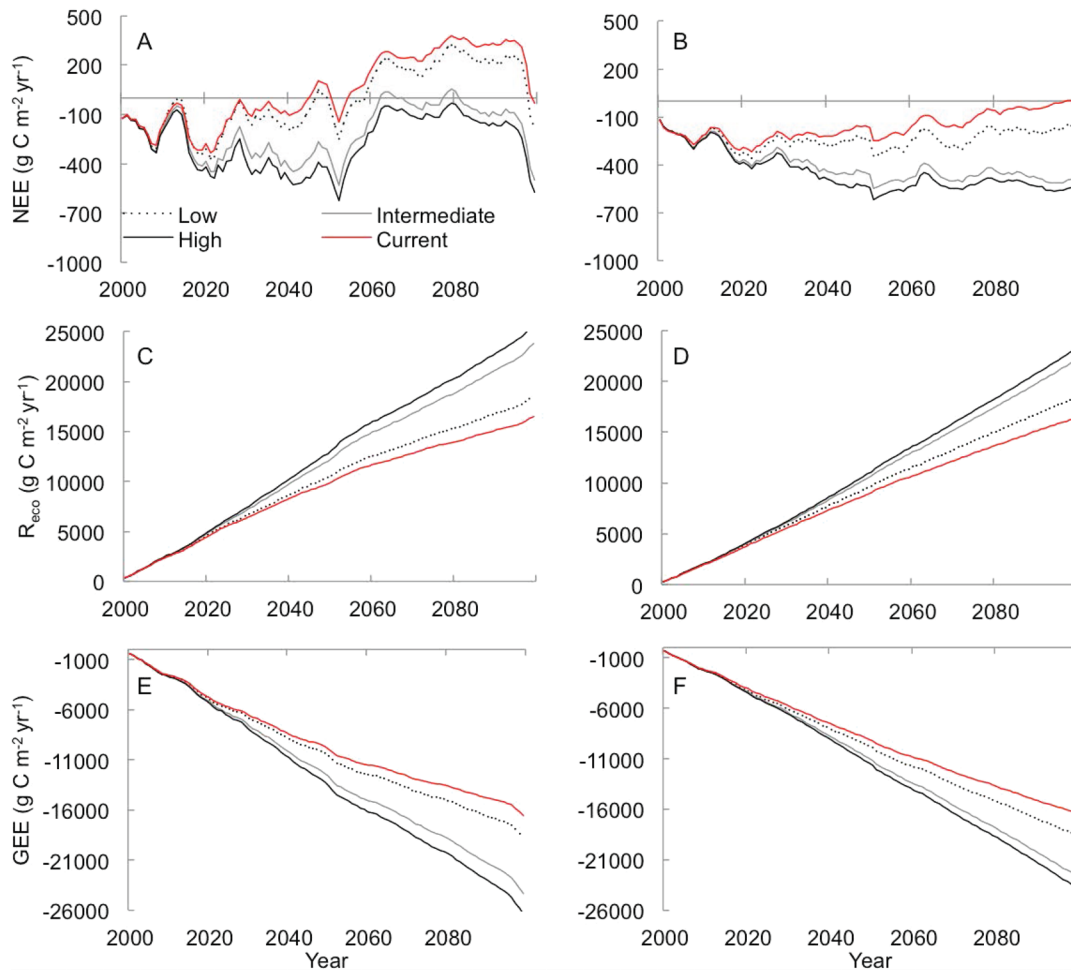
Fig. 9. The effect of climate change projections on cumulative CO_2 exchange rates: (A) NEE, (C) R_{eco} and (E) GEE at TS, and on (B) NEE, (D) R_{eco} and (F) GEE on at SRS. Atmospheric convention is used here and positive numbers indicate a loss of C to the atmosphere.

sink, source, or near neutral annually (Jimenez et al. 2012, Malone et al. 2014b), rising CO_2 concentration may cause an enhancement in the sink potential of Everglades freshwater marsh ecosystems by improving resource use efficiencies, though the response to CO_2 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 C_3 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 CO_2 relative to O_2 (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 CO_2 concentration, changes in temperature had a much smaller impact on CO_2 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 Gonzàlez-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 Gonzàlez-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 CO_2 rarely has reduced photosynthetic capacity enough to completely compensate for stimulated photosynthetic rates (Drake and Gonzàlez-Meler 1997, Ward and Strain 1999). Although in these simulations Everglades freshwater marsh ecosystems exhibit low sensitivity to changes in atmospheric CO_2 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, C_3 vs C_4 plants, and invasive species

To understand Everglades ecosystem vulnerability and resistance to change, future research must consider changes in ecosystem structure, disturbance regimes, C_3 versus C_4 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 CO_2 (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* Flüggé) and torpedo grass (*Panicum repens* L.), exotic species introduced for cattle forage, spread quickly and aggressively. Under current conditions, these C_4 grasses are more metabolically efficient than C_3 species, allowing them to encroach on sawgrass marshes. Invasion may increase in the future if these species are sensitive to elevated atmospheric CO_2 concentration. It has been suggested that elevated CO_2 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 C_4 species respond weakly to elevated CO_2 (Ainsworth and Long 2005), others have found many C_4 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 C_4 photosynthesis is not necessarily saturated at current CO_2 levels (Sionit and Patterson 1984, Imai and Sato 1991). C_4 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 CO_2 concentration. Previous research has also shown that CO_2 saturation levels in C_4 species may be altered by environmental conditions (Wand et al. 1999). Ziska et al. (1990) found that elevated CO_2 concentration stimulated CO_2 assimilation rates in a cordgrass (*Spartina patens* Aiton) dominated salt marsh, though the effect was seasonal. Although enhanced C assimilation rates in C_3 species has been shown to decline when stressed (Wand et al. 1999), C_4 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 CO_2 concentration and climate change on the current ecosystems CO_2 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 CO_2 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 CO_2 exchange rates may enhance the sink strength of Everglades ecosystems. Larger sink strength, albeit small, may be enough to switch these near CO_2 neutral sites to small sinks that negatively feedback to global warming.

LITERATURE CITED

Abdalla, M., M. Jones, J. Yeluripati, P. Smith, J. Burke, and M. Williams. 2010. Testing DayCent and DNDC model simulations of N2O fluxes and assessing the impacts of climate change on the gas flux and biomass production from a humid pasture. Atmospheric Environment 44(25):2961–2970.

Ainsworth, E. A., and S. P. Long. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytologist 165(2):351–372.

Allan, R. P. R., and B. J. B. Soden. 2008. Atmospheric warming and the amplification of precipitation extremes. Science 321(5895):1481–1484.

Bowes, G. 1993. Facing the Inevitable: Plants and Increasing Atmospheric CO_2. Annual Review of Plant Physiology and Plant Molecular Biology

44(1):309–332.

Braswell, B. H., W. J. Sacks, E. Linder, and D. S. Schimel. 2005. Estimating diurnal to annual ecosystem parameters by synthesis of a carbon flux model with eddy covariance net ecosystem exchange observations. Global Change Biology 11(2):335–355.

Brooks, A., and G. D. Farquhar. 1985. Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light : Estimates from gas-exchange measurements on spinach. Planta 1653):397–406.

Burkett, V., and J. Kusler. 2000. Climate change potential impacts and interactions in wetlands of the United States. Journal of the American Water Resources Association 362:313–320.

Bush, D. E., W. F. Loftus, and W. F. Bass. 1998. Long-term hydrologic effects on marsh plant community structure in the southern Everglades 18(2):230–241.

Cao, M., and F. I. Woodward. 1998. Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. Nature 393(6682):249–252.

Chang, K. H., J. Warland, P. Voroney, P. Bartlett, and C. Wagner-Riddle. 2013. Using DayCENT to simulate carbon dynamics in conventional and no-till agriculture. Soil Science Society of America Journal 77(3):941–950.

Childers, D., and T. Troxler. 2011a. Sawgrass above ground biomass from the Taylor Slough, Everglades National Park (FCE), South Florida from August 1999 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/80f2bb1ab8c4571ba6844b00ffac5eae

Childers, D., and T. Troxler. 2008. Sawgrass above ground biomass from the Taylor Slough, just outside Everglades National Park (FCE), South Florida from October 1997 to December 2006. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/9288a2ace33120f25b749ecc8ce2c776

Childers, D., and T. Troxler. 2011b. Sawgrass above ground biomass from the Shark River Slough, Everglades National Park (FCE), South Florida from November 2000 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/5824e4e14b46de012d44d4b0998c0149

Childers, D., and T. Troxler. 2011c. Sawgrass Above and Below Ground Total Nitrogen and Total Carbon from the Taylor Slough, Everglades National Park (FCE), South Florida for March 2002 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/6381ab64adcf4f68840838950870c194

Childers, D., and T. Troxler. 2013a. Sawgrass above and below ground total phosphorus from the Shark River Slough, Everglades National Park (FCE), from September 2002 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.

6073/pasta/656a5803beeb61f9a513735207e3397e

Childers, D., and T. Troxler. 2011d. Sawgrass above and below ground total nitrogen and total carbon from the Taylor Slough, Everglades National Park (FCE), South Florida for March 2002 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/6381ab64adcf4f68840838950870c194

Childers, D., and T. Troxler. 2013b. Sawgrass above and below ground total nitrogen and total carbon from the Shark River Slough, Everglades National Park (FCE), from September 2002 to Present. Long Term Ecological Research Network. http://dx.doi.org/10.6073/pasta/cfc20b35e784313f86b39a6e92d78c46

Cheng, K., S. M. Ogle, W. J. Parton, and G. Pan. 2013. Predicting methanogenesis from rice paddies using the DAYCENT ecosystem model. Ecological Modelling 261-262:19–31.

Cheng, K., S. M. Ogle, W. J. Parton, and G. Pan. 2014. Simulating greenhouse gas mitigation potentials for Chinese Croplands using the DAYCENT ecosystem model. Global Change Biology 20(3):948–962.

Chimner, R. A., D. J. Cooper, and W. J. Parton. 2002. Modeling carbon accumulation in Rocky Mountain fens. Wetlands 22(1):100–110.

Christensen, J. H., et al. 2007. Regional climate projections. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Ciais, P., P. Tans, M. Trolier, J. White, and R. Francey. 1995. A large northern hemisphere terrestrial CO_2 sink indicated by the C13/C12 ratio of atmospheric CO_2. Science 269:1098–1102.

Craighead, F. C. 1971. The trees of South Florida. Volume I. The natural environments and their succession. University of Miami Press, Coral Gables, Florida, USA.

Curtis, P. S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated CO_2 in situ. Plant, Cell and Environment 19:127–137.

Curtis, P. S., and X. Wang. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113(3):299–313.

Dalrymple, N. K., G. H. Dalrymple, and K. A. Fanning. 1993. Vegetation of restored rock-plowed wetlands of the East Everglades. Restoration Ecology 1(4):220–225.

Davis, S. M., and J. C. Ogden, editors. 1994. Everglades: the ecosystem and its restoration. St. Lucie Press, Boca Raton, Florida, USA.

Del Grosso, S. J., W. J. Parton, A. R. Mosier, M. D. Hartman, L. Brenner, D. S. Ojima, and D. S. Schimel. 2001. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. Pages 303–332 in M. E. A.

Schaffer, editor. Modeling carbon and nitrogen dynamics for soil management. CRC Press, Boca Raton, Florida, USA.

Del Grosso, S. J., W. J. Parton, A. R. Mosier, D. S. Ojima, A. E. Kulmala, and S. Phongpan. 2000. General model for N_2O and N_2 gas emissions from soils due to dentrification. Global Biogeochemical Cycles 14(4):1045–1060.

Del Grosso, S., D. S. Ojima, W. J. Parton, A. Mosier, G. Peterson, and D. Schimel. 2002. Simulated effects of dryland cropping intensification on soil organic matter and greenhouse gas exchanges using the DAYCENT ecosystem model. Environmental Pollution 116 Supplement 1:S75–S83.

Del Grosso, S. J., D. S. Ojima, W. J. Parton, and E. Stehfest. 2009. Global scale DAYCENT model analysis of greenhouse gas emissions and mitigation strategies for cropped soils. Global and Planetary Change 67(1-2):44–50.

Dimitrov, D. D., J. S. Bhatti, and R. F. Grant. 2014. The transition zones (ecotone) between boreal forests and peatlands: Modelling water table along a transition zone between upland black spruce forest and poor forested fen in central Saskatchewan. Ecological Modelling 274:57–70.

Drake, B. G., and M. A. Gonzàles-Meler. 1997. More efficient plants: a consequence of rising atmospheric CO_2? Annual Review of Plant Physiology and Plant Molecular Biology 48(1):609–639.

Duever, M. J., J. E. Carlson, L. A. Riopelle, and L. C. Duever. 1978. Ecosystem analysis at Corkscrew Swamp, in Cypress Wetlands for water management, recycling, and conservation: Fourth annual Report to the National Science Foundation and to the Rockefeller Foundation. University of Florida, Gainesville, Florida, USA.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14(4):135–139.

Duval, B. D., K. J. Anderson-Teixeira, S. C. Davis, C. Keogh, S. P. Long, W. J. Parton, and E. H. DeLucia. 2013. Predicting greenhouse gas emissions and soil carbon from changing pasture to an energy crop. PLoS ONE 8(8):e72019. doi: 10.1371/journal.pone. 0072019

Dykyjová, D., and J. Kvĕt. 1978. Pond littoral ecosystems. Springer-Verlag, New York, New York, USA.

Eitzinger, J., W. J. Parton, and M. Hartman. 2000. Improvement and validation of a daily soil temperature submodel for freezing/thawing periods. Soil Science 165(7):525.

Elmqvist, T., C. Folke, and M. Nyström. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology 1(9):488–494.

Erwin, K. L. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. Wetlands Ecology and Management 17(1):71–84.

Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C3 species. Planta 149(1):78–90.

Ferrati, R., G. A. Canziani, and D. R. Moreno. 2005. Esteros del Ibera: hydrometeorological and hydrological characterization. Ecological Modelling 186:3–15.

Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B 365(1555):3101–3112.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change. Agriculture, Ecosystems and Environment 97(1-3):1–20.

Gerten, D., S. Schaphoff, U. Haberlandt, W. Lucht, and S. Sitch. 2004. Terrestrial vegetation and water balance—hydrological evaluation of a dynamic global vegetation model. Journal of Hydrology 286(1-4):249–270.

Gifford, R. M. 1980. Carbon storage by the biosphere. Pages 167–181 *in* Carbon dioxide and climate: Australian research. Australian Academy of Science, Canberra, Australia.

Gonzàles-Meler, M. A., M. Ribas-Carbó, J. N. Siedow, and B. G. Drake. 1996. Direct inhibition of plant mitochondrial respiration by elevated CO_2. Plant Physiology 112(3):1349–1355.

Grace, J. B., and J. S. Harrison. 1986. *Typha latifolia* L., *Typha angustifolia* L., and *Typha glauca* Godr. Canada Journal of Plant Science 66(2):361–379.

Groves, R. H., and J. J. Burdon, editors. 1986. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Hanan, E. J., and M. S. Ross. 2010. Across-scale patterning of plant-soil–water interactions surrounding tree islands in Southern Everglades landscapes. Landscape Ecology 25(3):463–476.

Hartman, M. D., J. S. Baron, and D. S. Ojima. 2007. Application of a coupled ecosystem-chemical equilibrium model, DayCent-Chem, to stream and soil chemistry in a Rocky Mountain watershed. Ecological Modelling 200:493–510.

Heath, O. V. S. 1948. Control of stomatal movement by a reduction in the normal carbon dioxide content of the air. Nature 161(4083):179–181.

Herndon, A., L. Gunderson, and J. Stenberg. 1991. Sawgrass (*Cladium Jamaicense*) survival in a regime of fire and flooding. Wetlands 11(1):12–28.

Hirano, T., J. Jauhiainen, T. Inoue, and H. Takahashi. 2009. Controls on the carbon balance of tropical peatlands. Ecosystems 12(6):873–887.

Hocking, P. J., and C. P. Meyer. 1991. Carbon dioxide enrichment decreases critical nitrate and nitrogen concentrations in wheat. Journal of Plant Nutrition 14(6):571–584.

Holaday, A. S., W. Martindale, R. Alred, A. L. Brooks, and R. C. Leegood. 1992. Changes in activities of enzymes of carbon metabolism in leaves during exposure of plants to low temperature. Plant Physiology 98(3):1105–1114.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiasu, editors. 2001. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK.

Hulme, P. E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42:7840794.

Imai, K., and O. M. Sato. 1991. Effects of temperature on CO_2 dependence of gas exchanges in C_3 and C_4 crop plants. Japanese Journal of Crop Science (Japan) 60:139–145.

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. Cambridge University Press, Cambridge, UK.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Isopp, H., M. Frehner, S. P. Long, and J. Nösberger. 2000. Sucrose-phosphate synthase responds differently to source-sink relations and to photosynthetic rates: *Lolium perenne* L. growing at elevated CO_2 in the field. Plant, Cell and Environment 23(6):597–607.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530):629–637.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass estimators for United States tree species. Forest Science 49(1):12–35.

Jensen, J. R., K. Rutchey, M. S. Koch, and S. Narumalani. 1995. Inland wetland change detection in the Everglades Water Conservation Area 2A using a time series of normalized remotely sensed data. Photogrammetric Engineering and Remote Sensing 61:199–209.

Jimenez, K. L., G. Starr, C. L. Staudhammer, J. L. Schedlbauer, H. W. Loescher, S. L. Malone, and S. F. Oberbauer. 2012. Carbon dioxide exchange rates from short- and long-hydroperiod Everglades freshwater marsh. Journal of Geophysical Research 117(G4):G04009.

Jordan, D. B., and W. L. Ogren. 1984. The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase. Planta 161(4):308–313.

Keddy, P. A. 1990. Competitive hierarchies and centrifugal organization in plant communities.

Pages 265–290 *in* J. B. Grace and D. Ž. Tilman, editors. Perspectives on plant competition. Academic Press, London, UK.

Keeling, C. D., T. P. Whorf, M. Wahlen, and J. van der Plichtt. 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375(6533):666–670.

Kelly, R. H., W. J. Parton, M. D. Hartman, L. K. Stretch, D. S. Ojima, and D. S. Schimel. 2000. Intra-annual and interannual variability of ecosystem processes in shortgrass steppe. Journal of Geophysical Research: Atmospheres (1984–2012) 105(D15):20093–20100.

Knickerbocker, C. M., et al. 2009. Tree encroachment of a sawgrass (*Cladium jamaicense*) marsh within an increasingly urbanized ecosystem. Natural Areas Journal 29(1):15–26.

Kobza, J., and G. E. Edwards. 1987. Influences of leaf temperature on photosynthetic carbon metabolism in wheat. Plant Physiology 83(1):69–74.

Krinner, G., N. Viovy, and N. de Noblet Ducoudré. 2005. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochemical Cycles 19:GB1015.

Lambers, H., F. S. Chapin, and T. L. Pons. 2008. Plant physiological ecology. Springer, New York, New York, USA.

Li, X., T. Meixner, J. O. Sickman, A. E. Miller, J. P. Schimel, and J. M. Melack. 2006. Decadal-scale dynamics of water, carbon and nitrogen in a California chaparral ecosystem: DAYCENT modeling results. Biogeochemistry 77(2):217–245.

Lloyd, J., and G. D. Farquhar. 1994. 13C discrimination during CO_2 assimilation by the terrestrial biosphere. Oecologia 99(3-4):201–215.

Long, S. P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? Plant, Cell and Environment 14(8):729–739.

Long, S. P., and B. G. Drake. 1992. Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. Pages 69–107 *in* N. R. Baker and H. Thomas, editors. Topics in photosynthesis. Volume 2: Crop Photosynthesis Spatial and Temporal Determinants. Elsevier, Amsterdam, The Netherlands.

Luo, Y., and J. F. Reynolds. 1999. Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. Ecology 80:1568–1583.

Luo, Y., et al. 2008. Modeled interactive effects of precipitation, temperature, and CO_2 on ecosystem carbon and water dynamics in different climatic zones. Global Change Biology 14(9):1986–1999.

Malone, S. L., et al. 2014a. Seasonal patterns in energy partitioning of two freshwater marsh ecosystems in

the Florida Everglades. Journal of Geophysical Research: Biogeosciences 119(8):1487–1505.

Malone, S. L., et al. 2014b. El Niño Southern Oscillation (ENSO) enhances CO_2 exchange rates in freshwater marsh ecosystems in the Florida Everglades. PLoS ONE 9(12):e115058.

McMurtrie, R. E., B. E. Medlyn, and R. C. Dewar. 2001. Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years. Tree Physiology 21:831–839.

McMurtrie, R. E., and Y. P. Wang. 1993. Mathematical models of the photosynthetic response of tree stands to rising CO_2 concentrations and temperatures. Plant, Cell and Environment 16(1):1–13.

Medlyn, B. E., et al. 2002. Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. Plant, Cell and Environment 25:1167–1179.

Miao, S. L., and F. H. Sklar. 1998. Biomass and nutrient allocation of sawgrass and cattail along a nutrient gradient in the Florida Everglades. Wetlands Ecology and Management 5(4):245–264.

Mitsch, W. J., and J. G. Gosslink. 2007. Wetlands. Fourth edition. John Wiley and Sons, Hoboken, New Jersey, USA.

Mooney, H. A., and J. A. Ž. Drake, editors. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Morgan, J. A., et al. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140(1):11–25.

Newman, S., J. Schuette, J. B. Grace, and K. Rutchey. 1998. Factors influencing cattail abundance in the northern Everglades. Aquatic Botany 60(3):265–280.

Nowak, R. S., D. S. Ellsworth, and S. D. Smith. 2004. Functional responses of plants to elevated atmospheric CO_2: Do photosynthetic and productivity data from FACE experiments support early predictions? New Phytologist 162(2):253–280.

Oberbauer, S. F., N. Sionit, S. J. Hastings, and W. C. Oechel. 1986. Effects of CO_2 enrichment and nutrition on growth, photosynthesis and nutrient concentration of Alaskan tundra plant species. Canadian Journal of Botany 64:2993–2998.

Parton, W. J., P. J. Hanson, C. Swanston, M. Torn, S. E. Trumbore, W. Riley, and R. Kelly. 2010. ForCent model development and testing using the Enriched Background Isotope Study experiment. Journal of Geophysical Research: Atmospheres (1984–2012) 115(G4):G04001.

Parton, W. J., M. Hartman, D. S. Ojima, and D. S. Schimel. 1998. DAYCENT and its land surface submodel: description and testing. Global and Planetary Change 19:35–48.

Parton, W. J., J. A. Morgan, G. Wang, and S. Del Grosso. 2007. Projected ecosystem impact of the prairie heating and CO_2 enrichment experiment. New Phytologist 174(4):823–834.

Parton, W. J., D. S. Schimel, and C. V. Cole. 1987. Analysis of factors controlling SOM levels in Great Plains grasslands. Soil Science Society of America Journal 51:1173–1179.

Parton, W. J., J. Scurlock, D. S. Ojima, D. S. Schimel, and D. O. Hall. 1995. Impact of climate change on grassland production and soil carbon worldwide. Global Change Biology 1(1):13–22.

Parton, W. J., J. W. B. Stewart, and C. V. Cole. 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5(1):109–131.

Parton, W. J., et al. 2001. Generalized model for NO_x and N_2O emissions from soils. Journal of Geophysical Research: Atmospheres (1984–2012) 106(D15):17403–17419.

Pepper, D. A., S. J. Del Grosso, R. E. McMurtrie, and W. J. Parton. 2005. Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising CO_2, temperature and nitrogen input. Global Biogeochemical Cycles 19(1):GB1004.

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

Poorter, L., and S. F. Oberbauer. 1993. Photosynthetic induction responses of two rainforest tree species in relation to light environment. Oecologia 96(2):193–199.

Reddy, K. R., G. A. O'Connor, and C. L. Schelske. 1999. Phosphorus biogeochemistry of sub-tropical ecosystems. CRC Press, Boca Raton, Florida, USA.

Richardson, J. R., and A. Marshall. 1990. An evaluation of refuge habitats and relationship to water quality, quantity and hydroperiod. A.R.M. Loxahatchee National Wildlife Refuge, Boynton Beach, Florida, USA.

Riedo, M., D. Gyalistras, and J. Fuhrer. 2000. Net primary production and carbon stocks in differently managed grasslands: simulation of site-specific sensitivity to an increase in atmospheric CO_2 and to climate change. Ecological Modelling 134(2):207–227.

Rutchey, K., L. Vilchek, and South Florida Water Management District, Everglades Systems Research Division. 1994. Development of an Everglades vegetation map using a SPOT image and the global positioning system. Photogrammetric Engineering and Remote Sensing 60:767–775.

Sacks, W. J., D. S. Schimel, and R. K. Monson. 2007. Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. Oecologia 151(1):54–68.

Sacks, W. J., D. S. Schimel, R. K. Monson, and B. H.

Braswell. 2006. Model-data synthesis of diurnal and seasonal fluxes at Niwot Ridge, Colorado. Global Change Biology 12(2):240–259.

Savage, K. E., W. J. Parton, E. A. Davidson, S. E. Trumbore, and S. D. Frey. 2013. Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest. Global Change Biology 19(8):2389–2400.

Schedlbauer, J. L., S. F. Oberbauer, G. Starr, and K. L. Jimenez. 2010. Seasonal differences in the CO_2 exchange of a short hydroperiod Florida everglades marsh. Agricultural and Forest Meteorology 150:994–1006.

Schedlbauer, J. L., S. F. Oberbauer, G. Starr, and K. L. Jimenez. 2011. Controls on sensible heat and latent energy fluxes from a short-hydroperiod Florida Everglades marsh. Journal of Hydrology 411(3-4):331–341.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413(6856):591–596.

Sionit, N., and D. T. Patterson. 1984. Responses of C_4 grasses to atmospheric CO_2 enrichment I. Effect of irradiance. Oecologia 65:30–34.

Sitch, S., et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9(2):161–185.

Stanton, E. A., and F. Ackerman. 2007. Florida and climate change: the costs of inaction. Tufts University, Medford, Massachusetts, USA.

Stehfest, E., M. Heistermann, J. A. Priess, D. S. Ojima, and J. Alcamo. 2007. Simulation of global crop production with the ecosystem model DayCent. Ecological Modelling 209(2-4):203–219.

Steward, K. K., and W. H. Ornes. 1975. Assessing a marsh environment for wastewater renovation. Journal Water Pollution Control Federation 47(7):1880–1891.

Stitt, M., and A. Krapp. 1999. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. Plant, Cell & Environment 22:583–621.

Todd, M. J., R. Muneepeerakul, D. Pumo, S. Azaele, F. Miralles-Wilhelm, A. Rinaldo, and I. Rodriguez-Iturbe. 2010. Hydrological drivers of wetland vegetation community distribution within Everglades National Park, Florida. Advances in Water Resources 33(10):1279–1289.

Toth, L. A. 1987. Effects of hydrologic regimes on lifetime production and nutrient dynamics of sawgrass. Technical Publication 87-6. South Florida Water Management District, West Palm Beach, Florida, USA.

Toth, L. A. 1988. Effects of hydrologic regimes on lifetime production and nutrient dynamics of cattail. Technical Publication 88-6. South Florida Water Management District, West Palm Beach, Florida, USA.

Urban, N. H., S. M. Davis, and N. G. Aumen. 1993. Fluctuations in sawgrass and cattail densities in Everglades Water Conservation Area 2A under varying nutrient, hydrologic and fire regimes. Aquatic Botany 46(3-4):203–223.

Veldkamp, E., and J. J. O'Brien. 2000. Calibration of a frequency domain reflectometry sensor for humid tropical soils of volcanic origin. Soil Science Society of America Journal 64(5):1549–1553.

Vu, J., L. H. Allen, K. J. Boote, and G. Bowes. 1997. Effects of elevated CO_2 and temperature on photosynthesis and Rubisco in rice and soybean. Plant, Cell and Environment 20(1):68–76.

Wand, S., G. Y. Midgley, and H. H. Jones. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions. Global Change Biology 5:723–741.

Ward, J. K., and B. R. Strain. 1999. Elevated CO_2 studies: past, present and future. Tree Physiology 19(4-5):211–220.

Weltzin, J. F., S. D. Bridgham, J. Pastor, J. Chen, and C. Harth. 2003. Potential effects of warming and drying on peatland plant community composition. Global Change Biology 9(2):141–151.

Wong, S. C. 1979. Elevated atmospheric partial pressure of CO_2 and plant growth. Oecologia 44(1):68–74.

Ziska, L. H. 2003. Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide. Journal of Experimental Botany 54:395–404.

Ziska, L. H., B. G. Drake, and S. Chamberlain. 1990. Long-term photosynthetic response in single leaves of A C3 and C4 salt marsh species grown at elevated atmospheric CO_2 in situ. Oecologia 83(4):469–472.