

Drought legacies influence the long-term carbon balance of a freshwater marsh

Adrian V. Rocha¹ and Michael L. Goulden²

Received 16 November 2009; revised 19 May 2010; accepted 1 June 2010; published 30 September 2010.

[1] Experimental manipulations provide a powerful tool for understanding an ecosystem's response to environmental perturbation. We combined paired eddy covariance towers with an experimental manipulation of water availability to determine the response of marsh carbon balance to drought. We monitored the Net Ecosystem Exchange of CO₂ (NEE) in two ponds from 2004 to 2009 at the San Joaquin Freshwater Marsh (SJFM), and subjected one of the ponds to a yearlong drought treatment in 2007. The two ponds experienced similar flooding and environmental regimes before and after the drought, ensuring that differences between ponds were largely attributable to the 2007 drought. Drought substantially reduced surface greenness, as measured by the Enhanced Vegetation Index (EVI) and photosynthetic carbon sequestration, primarily by inhibiting leaf area development. Respiratory carbon losses were less influenced by drought than photosynthetic carbon gains. The effect of the drought lasted several years, with delayed leaf area development and peak carbon uptake rates during the subsequent year, and reduced leaf area for a couple of years. The combined effect of the drought and legacy effects created an overall loss of carbon that was equivalent to 4 years of the maximum annual carbon sequestration observed over a decade. Our results indicate that drought can have long-term impacts on ecosystem carbon balance and that future projected drought increases in Southern California will have a negative impact on marsh carbon sequestration.

Citation: Rocha, A. V., and M. L. Goulden (2010), Drought legacies influence the long-term carbon balance of a freshwater marsh, *J. Geophys. Res.*, 115, G00H02, doi:10.1029/2009JG001215.

1. Introduction

[2] Droughts are prolonged periods of decreased water availability that play important roles in the carbon cycling of terrestrial ecosystems. Droughts generally induce a net decline in the terrestrial carbon sink, though the response differs among ecosystem types, and the carbon sink of some ecosystems may increase or remain constant during drought [Schwalm *et al.*, 2010]. Long-term (i.e., years to decades) impacts of drought on ecosystem carbon cycling are less understood than short-term (i.e., hours to weeks) impacts due to the lack of long-term records and the difficulty in separating changes caused by drought from other sources of ecosystem variability [Sierra *et al.*, 2009]. Long-term ecosystem responses to drought may include large changes in nutrient cycling, plant mortality or species composition, which result in irreversible changes in ecosystem function [Schwinning *et al.*, 2004; Arnone *et al.*, 2008; Sherry *et al.*, 2008]. Climate projections forecast a higher frequency of droughts for many parts of the world [IPCC, 2007], indicating

a need to understand interactions between water availability and ecosystem carbon cycling at a variety of timescales.

[3] The response of an ecosystem's carbon balance to drought depends on both biotic and abiotic factors that operate at a variety of spatial and temporal scales [Hui *et al.*, 2003; Richardson *et al.*, 2007; Yuan *et al.*, 2009]. Biotic controls are regulated by organisms within an ecosystem and include, but are not limited to, factors such as canopy nitrogen concentration, carbohydrate reserves, species composition, plant mortality, and leaf area. Abiotic controls are the environmental factors that drive biotic responses and include, but are not limited to, factors such as light, water availability, and temperature. Biotic controls can buffer or amplify environmental variability [Rocha and Goulden, 2008; Stoy *et al.*, 2009], and make attribution of changes in fluxes to abiotic factors difficult even with long time series [Sierra *et al.*, 2009]. For example, the impact of a multiyear drought on the carbon cycling of a ponderosa pine forest differed from that of a single-year drought because of carry-over effects associated with soil water and plant carbohydrate reserves [Thomas *et al.*, 2009]. Consequently, understanding interactions between biotic and abiotic factors may yield important insights into the short- and long-term effects of drought on ecosystem function.

[4] Experimental manipulations provide ecologists with a powerful tool for understanding an ecosystem's response to environmental perturbation. Experimental manipulations can be used to isolate the response of an ecosystem to a pertur-

¹Marine Biological Laboratory Ecosystems Center, Woods Hole, Massachusetts, USA.

²Department of Earth System Science, University of California, Irvine, California, USA.



Figure 1. Aerial photograph of the SJFM on April 1, 2007. Stars denote location of eddy covariance towers and arrows indicate location of culverts where water flows between ponds. Note the lack of a green canopy and water at the Experimental Pond. Image purchased from Terraserver (<https://www.terraserver.com>).

bation by comparing the experimental treatment with an unmanipulated control. Unfortunately, experimental manipulations are often limited in both spatial scale and sampling frequency [Englund and Cooper, 2003], and long-term (multiple years) large (1 to 10 ha) experimental manipulations are rare (but see Likens *et al.* [1970] and Schindler *et al.* [1971]). The eddy covariance technique can be used to resolve sampling limitations in large-scale manipulations because it accurately monitors ecosystem carbon fluxes over large spatial (1 to 10 ha) and a range of temporal (half-hourly to decadal) scales [Baldocchi, 2003]. The combination of paired eddy covariance towers with large-scale ecosystem manipulations provides an especially promising tool for analyzing ecosystem response to perturbations.

[5] We combined a paired tower experimental design with an ecosystem manipulation of water availability to determine the response of NEE, maximum Leaf Area Index (LAI_{max}), and the Enhanced Vegetation Index (EVI; a measure of surface greenness) of a Southern Californian freshwater marsh (i.e., the San Joaquin Freshwater Marsh; SJFM) to a yearlong drought (Figure 1). The SJFM is a managed marsh with two distinct ponds (i.e., the Control and Experimental Ponds) that are hydrologically separated by a series of dikes and culverts, allowing for easy manipulation of water availability. The SJFM is usually flooded during the winter with standing water evaporating or draining into the subsurface by mid-summer. We subjected the two ponds to similar hydrological regimes from 2004 to 2009 with the exception of 2007 when the culverts entering the Experimental Pond were plugged to prevent flooding. Observations prior to the 2007 drought were used to determine how well the two ponds were mat-

ched, while observations after 2007 were used to determine the effect of drought on the marsh carbon balance.

[6] The SJFM is a particularly useful experimental system in which to understand the biotic and abiotic controls on ecosystem carbon cycling. The system experiences large seasonal and interannual fluctuations in water level, is dominated by a single highly productive species (*Typha* spp.) that is adapted to flooded soils, and has been shown to have strong biotic controls that include belowground carbohydrate reserves [Rocha and Goulden, 2009]. Marsh plants are not very resistant to drought in the short term [Li *et al.*, 2004], but may be resilient to drought in the long term by utilizing their large belowground carbohydrate reserves to buffer against prolonged drought [Biesboer, 1984]. We hypothesized that drought causes both an immediate effect through the tight physiological coupling between water availability and ecosystem function [Pereira *et al.*, 2007], and a long-term effect through changes in plant carbohydrate reserves [Rocha and Goulden, 2009].

2. Methods

2.1. Site Description and Experimental Setup

[7] The study was conducted at the San Joaquin Freshwater Marsh Reserve (SJFM) located on the University of California's Irvine campus [Goulden *et al.*, 2007] (Figure 1). The SJFM is dominated by Cattail (*Typha latifolia* L.) with a minor component (~20% percent cover) of Bullrush (*Scirpus californicus* C.A. Mey. Steud.) and willows (*Salix* spp.) around the periphery. Water flow in the SJFM was controlled by a series of dikes and culverts. Water originates from the Irvine Ranch Water District (IRWD) located to the northeast of the SJFM and passes through a series of culverts on the southern side of the Control Pond to flood the Experimental Pond (Figure 1). We recorded the date of the appearance and disappearance of surface water at each tower in each year, and the water level (i.e., depth of water above the soil surface) from a staff gauge located next to each tower from 2006 to 2009. Water was not delivered to the SJFM in 2004 because of a management decision to reduce mosquito habitat, and we utilized flux observations in 2004 to corroborate ecosystem responses to the 2007 drought treatment.

2.2. Eddy Covariance Towers and Data Analysis

[8] We used paired eddy covariance towers with similar instrumentation to monitor carbon exchanges from the Control and Experimental Ponds (see Goulden *et al.* [2007] and Rocha and Goulden [2008] for further details). The tower in the Control Pond was operated since December 1998, and the tower in the Experimental Pond was operated since May 2003. The eddy covariance system was installed on a 6.5 m tower that was attached to a stationary floating platform. Instruments included a closed path InfraRed Gas Analyzer (IRGA; Model 7000 or 6262, Li-Cor Inc., Lincoln, NE) that measured CO_2 and H_2O mole fractions, and a 3-D sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) that measured horizontal and vertical wind speeds at 4 Hz. A data logger (Campbell Scientific CR10 \times or 23 \times Logan, UT) connected to a laptop computer controlled data collection. The high frequency data were downloaded from the computer at weekly to monthly intervals, and fluxes were subsequently calculated using a series of Matlab programs. The Net Eco-

system Exchange of CO₂ (NEE) was calculated as the 30 min covariance of the vertical wind velocity and CO₂ mixing ratio. Fluxes were rotated to the plane with no mean vertical wind, and the underestimation of high frequency flux due to tube attenuation and instrument response were corrected separately for CO₂ and H₂O assuming similarity in transport between sensible heat and gas flux [Goulden *et al.*, 1997]. Half-hour eddy covariance fluxes are presented in the atmospheric sign convention, where a positive flux indicates the net transfer of carbon from the ecosystem to the atmosphere. The data sets are available from the authors (<http://www.ess.uci.edu/~marsh/>).

[9] Quality of NEE data depended on adequate turbulent mixing ($u^* > 0.20 \text{ m s}^{-1}$), the location of the sampled fluxes, and instrument functioning [Rocha and Goulden, 2008]. We conducted a footprint analysis [Hsieh *et al.*, 2000] to determine the maximum upwind distance required to capture 85% of the observed half hourly flux. We restricted the analysis to periods with adequate turbulent mixing, and to periods with winds originating from the south (i.e., 145° to 310°) where the marsh extended more than 100 m from the tower. Winds originated from the southern sector 65% of the time. The footprint analysis demonstrated that a majority of the half hourly periods integrated fluxes within the boundary of the Control (86%) and Experimental (94%) Ponds, while the remaining half hourly periods integrated fluxes over a much larger area. We subsequently rejected all observations that included significant areas outside of the ponds, and only included fluxes that integrated within the boundary of each pond and also excluded periods with inadequate turbulent mixing ($u^* < 0.20 \text{ m s}^{-1}$), and instrument malfunction in our analyses. The remaining flux data set was referred to as the “unfilled” NEE data set, and provided the highest quality data for comparing ecosystem function between the Control and Experimental Ponds.

[10] Cumulative sums of annual Gross Ecosystem Exchange (GEE), Total Ecosystem Respiration (TER), and Net Ecosystem Exchange (NEE) were determined using gap filling methods described by Rocha and Goulden [2008]. Short gaps (half hourly to daily) were filled by separately considering day and night NEE; longer gaps (weekly to monthly) were filled using empirical relationships derived from annual correlations between NEE at the Control and Experimental Ponds. Half hourly NEE variations between ponds in each year the marsh was flooded were highly coherent, with Pearson correlation coefficients greater than 0.80. Missing NEE_{night} observations were filled using the average NEE_{night} during the previous 25 days. Average NEE_{night} was then used to estimate the daytime ecosystem respiration rates and to separate Gross Ecosystem Exchange (GEE) from NEE (i.e., $GEE = (NEE_{\text{day}} - NEE_{\text{night}})$). Gaps in the GEE record were filled using a Michaelis-Menten hyperbolic regression with incoming shortwave radiation [Ruimy *et al.*, 1995]. Our selections of gap filling method had less than a 20% effect on the cumulative estimates [Rocha and Goulden, 2008], indicating that our conclusions were minimally influenced by the gap filling technique.

2.3. Biomass Measurements and Calculation of Maximum LAI

[11] Peak biomass harvests were conducted in the Control Pond from 2004 to 2009, and in the Experimental Pond from 2006 to 2009. All living plants were sampled within thirty

0.25 m² quadrants along a 91.5 m transect that radiated to the southwest of each eddy covariance tower in September of each year. Plants were pulled from the ground, clipped below the crown, returned to the lab, oven-dried at 65°C for two to three days and weighed. Maximum Leaf Area Index (LAI_{max}) was calculated from the specific leaf area determined on a subsample of leaves [Rocha and Goulden, 2008].

2.4. Remote Sensing Observations

[12] We obtained at least one midsummer (end of June to mid-August) Landsat TM or ETM+ image for each year from 2004 to 2009, and a more continuous biweekly to monthly record from the 2008 growing season, to assess temporal differences in surface reflectance between ponds. The images had a 30 m spatial resolution and were obtained from the USGS’s Global Visualization Viewer (GLOVIS; <http://glovis.usgs.gov/>). Images were corrected for sensor differences and drift [Chander *et al.*, 2007], and intercalibrated using the temporally invariant surface target method against a LEDAPS surface reflectance image (http://ledaps.nascom.nasa.gov/ledaps/ledaps_NorthAmerica.html) [Hall *et al.*, 1991]. Surface reflectance was extracted from a 90 by 90 m area immediately southwest of each eddy covariance tower and used to calculate the Enhanced Vegetation Index (EVI) [Huete *et al.*, 2002]. We used EVI rather than the more commonly used Normalized Vegetation Index (NDVI) because EVI does not saturate at high leaf area [Huete *et al.*, 2002], and is less sensitive to background reflectance than NDVI [Rocha and Shaver, 2009].

2.5. Statistical Analysis

[13] We screened the unfilled NEE record for anomalous values prior to conducting statistical analysis. We observed small rates ($< -8 \mu\text{mol m}^{-2} \text{ s}^{-1}$) of carbon uptake during periods when the marsh canopy was dormant (<1% of the time) and attribute these values to measurement error [Richardson *et al.*, 2006]. Consequently, these values were excluded from any statistical analysis of the data and gap filled in the cumulative sums, but are included in the presentation of the unfilled NEE record (see Figure 3). The exclusion of these data do not affect the overall conclusions, as we only report those ecosystem responses to drought that are corroborated by multiple independent measures of ecosystem function, or drought responses that are consistent between ponds and years.

[14] We used growing season unfilled NEEs along with a Michaelis-Menten light response function to determine how carbon uptake and loss differed between the Experimental and Control Ponds (equation (1)).

$$NEE = R - \frac{GEE_{\text{max}} PAR_i}{K_o + PAR_i} \quad (1)$$

Least squares regression determined ecosystem respiration (R) as the y-intercept of the light response curve, the photosynthetic compensation point (K_o), and maximum canopy photosynthesis as the light saturated GEE (GEE_{max}) in each pond every two weeks during the growing season. Periods when regression statistics indicated a poor fit (i.e., there was no light response of NEE or $GEE = 0$) were evaluated for R by using average nighttime unfilled NEE, and GEE_{max} was set to 0. T-tests were used to determine statistical differences

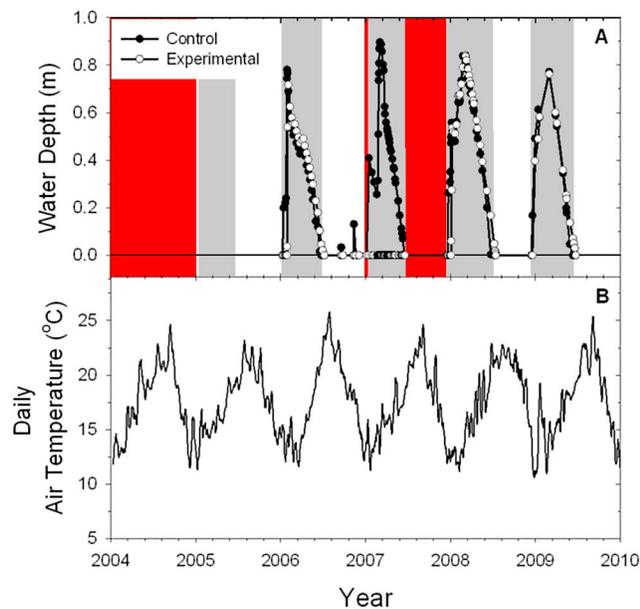


Figure 2. Environmental conditions at the SJFM from 2004 to 2009. (a) Water depths at the Control (closed circles) and Experimental (open circles) Ponds from 2006 to 2009 and the length of the hydroperiod at the Control Pond (gray bars) from 2004 to 2009. The red bars indicate drought at both ponds in 2004 and in the Experimental Pond in 2007. (b) Daily air temperatures from 2004 to 2009.

in LAI_{max} , EVI , GEE_{max} , and R between ponds. LAI_{max} and EVI utilized spatial variability (i.e., variability within sampled area) as a replicate, whereas GEE_{max} and R utilized spatial (i.e., changes in flux footprint) and temporal (i.e., seasonal) variability as a replicate. We are aware of the potential problems with pseudoreplication in our experimental design [Hurlbert, 1984], but use statistical tests to determine if the means for each pond can be distinguished given the observed within pond variability associated with each measure [Oksanen, 2001]. Statistical tests were conducted at the 95% confidence level.

3. Results

3.1. Environmental Conditions

[15] The hydroperiod varied markedly between years, but differed by less than 2 weeks between ponds (Figure 2a). Water was not delivered to either pond in 2004, and to the Experimental Pond in 2007. During flooded years, water levels quickly rose to their maximum in the winter, gradually declined after water input ceased, and was negligible by the summer. Daily air temperatures were high in the summer and low in the winter (Figure 2b). Average annual temperatures were similar between years, ranging from 17.4°C in 2007 to 17.8°C in 2006.

3.2. Pre-Experimental Drought Marsh Comparison

[16] The ponds were well matched and had similar patterns and rates of half hour NEE before the 2007 drought (Figure 3). The absolute rates of NEE exhibited marked interannual variability before the 2007 drought, which was generally parallel at both ponds. Positive daytime NEE's

were observed at both ponds throughout the 2004 drought, with slightly higher carbon loss in the Control Pond (also see Figure 6). Both ponds exhibited similar seasonal patterns during flooded years, with carbon loss during the autumn and winter and carbon uptake during spring and summer. Peak carbon uptake was slightly higher in the Experimental Pond in 2006, and roughly similar to the Control Pond in 2005 (also see Figures 5 and 6).

3.3. Post-Experimental Drought Marsh Comparison

[17] The 2007 drought resulted in a large divergence in NEE between the two ponds (Figure 3). Drought suppressed daytime carbon uptake at the Experimental Pond in 2007, and daytime carbon loss occurred throughout 2007. The Experimental Pond continued to exhibit reduced carbon uptake during 2008 and 2009, despite similar hydroperiods between ponds. Differences in peak carbon uptake were larger in the year following the 2007 drought (2008) than in the second year (2009) (also see Figures 5 and 6). The cumulative carbon loss through 2009 was 44% higher at the Experimental Pond than the Control Pond (Figure 3).

3.4. Short-Term Effects of Drought on Ecosystem Physiology and C Balance

[18] Drought influenced the mean diel NEE cycle (Figure 4). Carbon losses occurred throughout the day at the dry Experimental Pond, while carbon uptake occurred at the flooded Control Pond in 2007. NEE varied by 66% at the Experimental Pond and by 247% at the Control Pond over

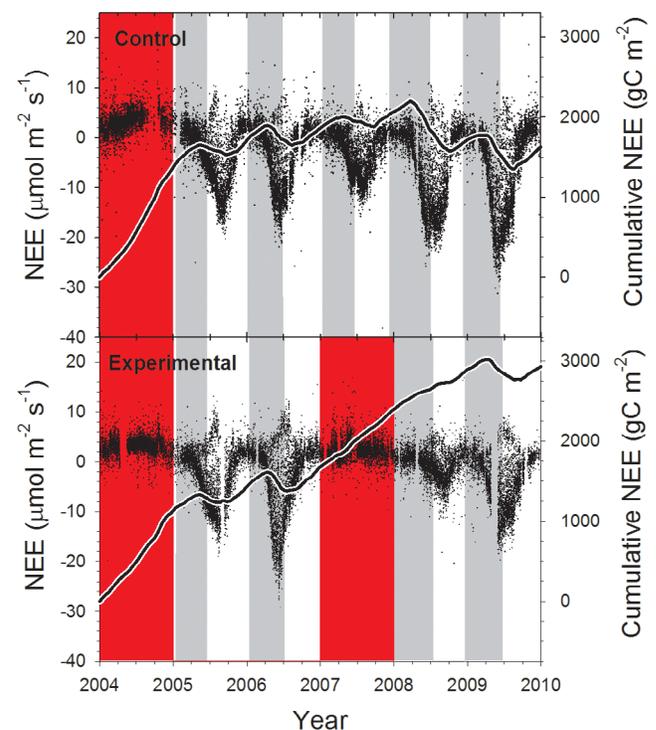


Figure 3. Unfilled half hourly Net Ecosystem Exchange of CO_2 (NEE) (dots) and cumulative NEE (dark line) at the (top) Control and (bottom) Experimental Ponds from 2004 to 2009. Width of the gray bars indicates length of the hydroperiod and red bars indicate yearlong droughts.

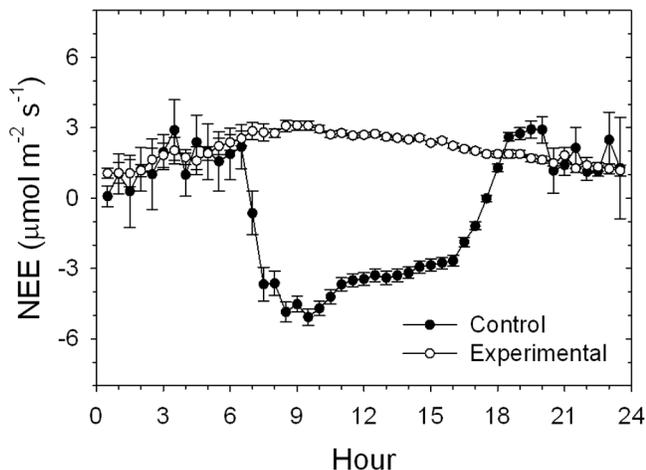


Figure 4. Annual mean diel NEE cycles at the Control (closed circles) and Experimental (open circles) Ponds during the 2007 drought. Error bars represent standard errors.

the course of the day. Differences in the timing of maximum NEE also occurred between the two ponds. Maximum rates of NEE were observed late at night at the Control Pond, and early in the morning at the Experimental Pond. A weak diel NEE cycle also occurred at both ponds during the 2004 drought (data not shown).

[19] The 2007 drought impacted the relationship between daily NEE in the two ponds (Figure 5). Between pond differences in daily NEE were largest during the “active” growing season (i.e., May to September). Daily carbon uptake during the 2006 active season was similar or slightly

larger (i.e., more negative NEE) in the Experimental Pond, but never exceeded the Control Pond after the 2007 drought. NEE’s were positive at the Experimental Pond in 2007 and mostly positive in 2008, as photosynthetic carbon gains did not offset respiratory losses. Active season daily NEE ranged from -2 to $2 \text{ gC m}^{-2} \text{ d}^{-1}$ in 2007 and from -6 to $1 \text{ gC m}^{-2} \text{ d}^{-1}$ in 2008 at the Control Pond. The impact of the 2007 drought continued into the 2009 growing season with a $\sim 33\%$ reduction in daily NEE at the Experimental Pond.

[20] Between pond comparisons of GEE_{max} , ecosystem respiration, and surface greenness (EVI) revealed how drought influenced ecosystem function (Figure 6). Both ponds had similar EVI, GEE_{max} , and ecosystem respiration rates prior to the experimental drought, except in 2004 when respiratory losses were higher at the Control Pond. The 2007 drought reduced carbon uptake (i.e., less negative GEE_{max}), ecosystem respiration, and EVI from 2007 to 2009. Differences in GEE_{max} between ponds were larger than observed for ecosystem respiration after the 2007 drought. EVI differences between ponds generally tracked differences observed for GEE_{max} with a higher EVI occurring in the pond with a lower GEE_{max} .

3.5. Long-Term Effects of Droughts on Ecosystem Physiology and C Balance

[21] Maximum Leaf Area Index (LAI_{max}) was reduced during and after drought (Figure 7). Species composition in each pond did not change over time and LAI_{max} was comprised entirely of Cattail (*Typha* spp.). LAI_{max} was similar at both ponds in 2006. Drought inhibited leaf area development and resulted in negligible carbon uptake in 2004 at both ponds, and in 2007 at the Experimental Pond (Figures 3, 4, 5, and 6). The 2007 drought resulted in a 74% decrease in

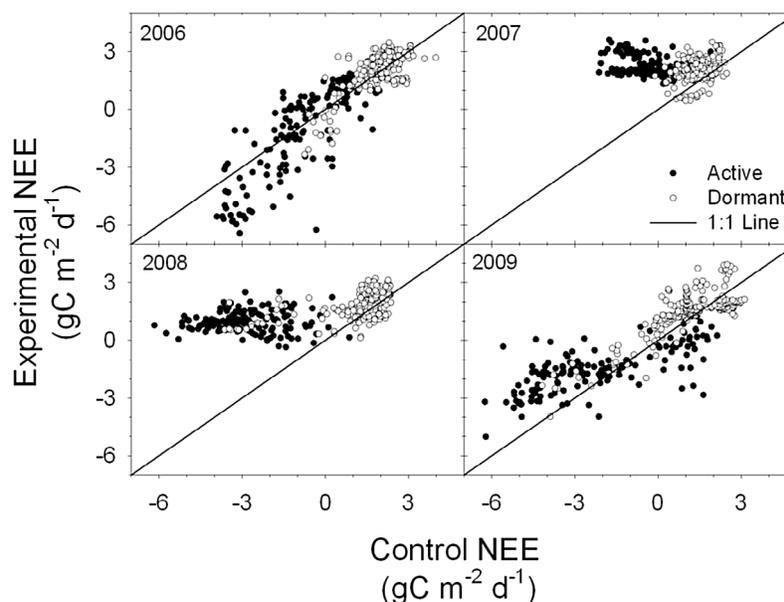


Figure 5. One to one plots of daily NEE in the Control and Experimental Ponds from 2006 to 2009. Closed circles (“Active” growing season) are daily NEEs from May 1st to September 31st, while open circles (“Dormant” season) are daily NEEs for the rest of the year. Lines represent one to one relationship between the two ponds.

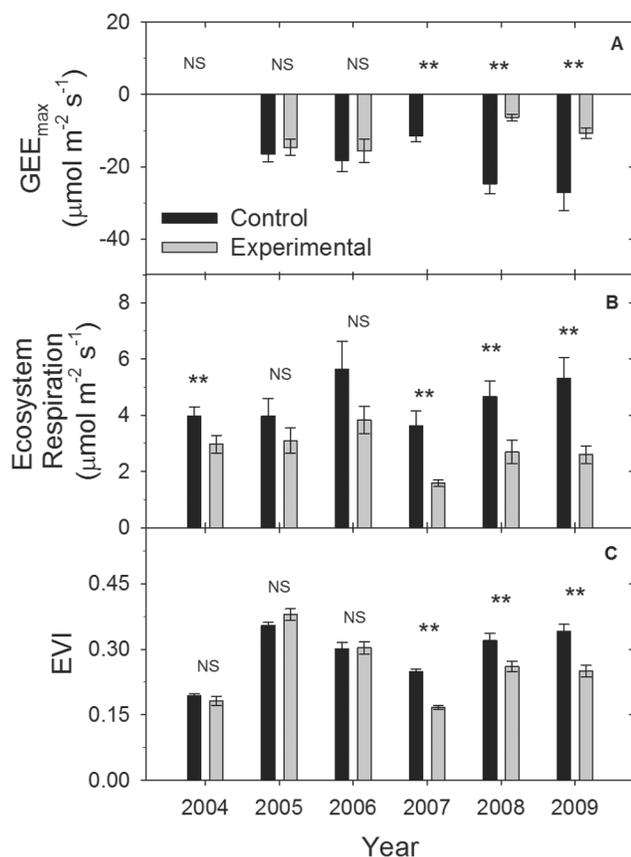


Figure 6. (a) GEE_{max} , (b) Ecosystem Respiration, and (c) the Enhanced Vegetation Index (EVI) at the Control (dark bars) and Experimental (gray bars) Ponds from 2004 to 2009. Asterisks (**) indicate significant differences between ponds, and NS indicates no significant difference at the 95% confidence level.

LAI_{max} in 2008, and a 45% decrease in LAI_{max} in 2009 at the Experimental Pond. LAI_{max} differences between ponds generally paralleled surface greenness (EVI), with higher EVI occurring in the pond with higher LAI_{max} (Figure 6c).

[22] Drought impacted the annual carbon balance by inhibiting photosynthetic carbon uptake (Table 1). The responses of annual GEE and NEE to drought were consistent across droughts with respiration dominating the carbon balance at both ponds in 2004 and in 2007 at the Experimental Pond. Although both ponds were sources of carbon to the atmosphere in 2007, the drought caused the Experimental Pond to lose ~3 times more carbon than the Control Pond. The Control Pond was a carbon sink a year after the 2007 drought, whereas the Experimental Pond was a carbon source. Lower respiration slightly compensated for lower carbon uptake at the Experimental Pond in 2009, and resulted in the smallest difference in carbon balance between the two ponds since 2007.

3.6. Drought Legacies

[23] Droughts imposed legacy effects on the seasonal timing of carbon uptake and surface greenness in the year after the drought. The onset of the growing season occurred

~60 days later, and peak uptake occurred ~90 days later at the Control Pond the year following the 2007 drought (Figure 8a). A similar pattern was observed in both ponds a year after the 2004 drought, with the onset of the growing season occurring one to two weeks later, and the peak rates occurring a month later, relative to previous years (Figure 8b). Differences in the timing of carbon uptake were not apparent two years after drought (i.e., 2009) (Figure 3).

[24] Differences in the 2008 seasonal NEE cycle were reflected in the seasonality of GEE and EVI (Figure 9). Daily GEE's were normalized by the annual minimum (GEE_{norm}) to highlight the seasonal timing of peak GEE in each pond. GEE_{norm} increased and peaked earlier at the Control Pond than at the Experimental Pond, indicating that between pond differences in the seasonal NEE cycle were driven by photosynthesis rather than respiration (Figure 9a). EVI tracked the greening of the ponds and the seasonal pattern of GEE_{norm} with peak EVI occurring later and longer at the Experimental Pond (Figure 9b).

4. Discussion

[25] This is the first study we are aware of that combined a water manipulation with paired eddy covariance towers to determine the short- and long-term impacts of drought on a wetland. The two ponds were well matched with similar hydrological regimes and environmental conditions prior to the 2007 experiment (Figures 2, 3, and 6), though NEE differed by as much as 25% prior to the 2007 drought (Figures 3 and 6). NEE differences between the ponds were slightly larger than the spatial variability observed for a spruce stand in Maine [Hollinger *et al.*, 2004], and may be attributed to the greater dependence of this system on internal biotic ecosystem dynamics, which include carbohydrate translocation [Rocha and Goulden, 2009] and shading from standing litter [Rocha *et al.*, 2008]. We encourage future studies that adopt this approach to monitor conditions at both the Experimental

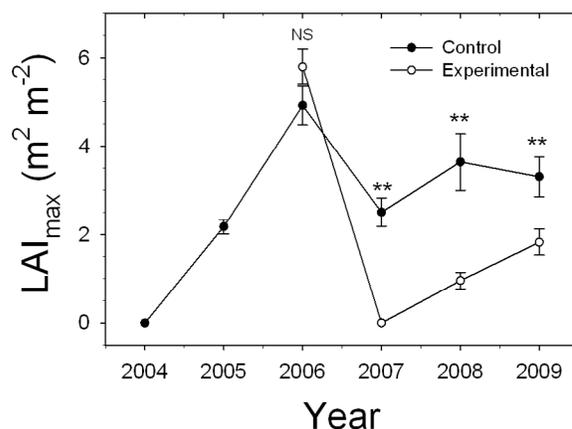


Figure 7. Maximum Leaf Area Index (LAI_{max}) at the Control (closed circles) and Experimental (open circles) Ponds. LAI_{max} 's for the Experimental are not available prior to 2006 and error bars represent standard errors. Asterisks (**) indicate significant differences between ponds, and NS indicates no significant difference at the 95% confidence level.

Table 1. Annual Sums of Gross Ecosystem Exchange, Total Ecosystem Respiration, and Net Ecosystem Exchange From the Control and Experimental Ponds From 2004 to 2009^a

Year	GEE ($\text{gC m}^{-2} \text{y}^{-1}$)		TER ($\text{gC m}^{-2} \text{y}^{-1}$)		NEE ($\text{gC m}^{-2} \text{y}^{-1}$)	
	Control	Experimental	Control	Experimental	Control	Experimental
2004	0	0	1377	1107	1377	1107
2005	-972	-889	1312	1208	340	318
2006	-927	-1043	1103	1305	176	261
2007	-824	0	1042	676	218	676
2008	-1410	-423	1069	961	-341	539
2009	-1419	-910	1466	1171	47	261

^aThe pond with the higher carbon sink in each year is noted in bold.

and Control locations for several years prior to the treatment in order to document any baseline differences.

[26] The response of NEE to drought depended on the sensitivity of canopy photosynthesis and ecosystem respiration. Canopy photosynthesis was the dominant controller of the annual carbon balance, as noted in previous work [Rocha and Goulden, 2009], and was more sensitive to drought than respiration (Figures 5 and 6). Respiration decreases from drought were much smaller than photosynthetic decreases; respiration differed by $2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and GEE_{max} differed by $11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, during the 2007 drought

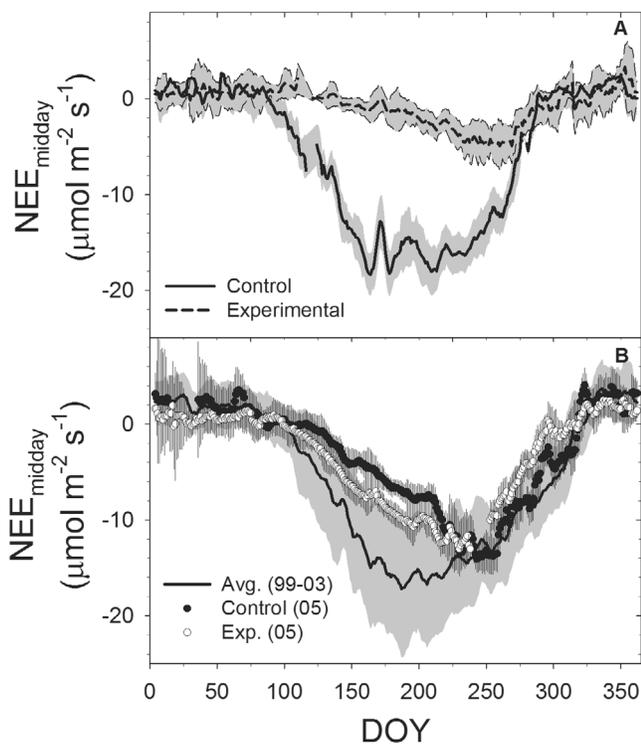


Figure 8. Seasonal midday NEE ($\text{NEE}_{\text{midday}}$) cycle a year following the (a) 2007 and (b) 2004 droughts. The 2008 seasonal $\text{NEE}_{\text{midday}}$ cycle at the Control (solid line) and Experimental (hatched line) Ponds following the 2007 drought (Figure 8a). The 2005 seasonal $\text{NEE}_{\text{midday}}$ cycle at the Control (closed circles) and Experimental (open circles) Ponds were compared to the historical average $\text{NEE}_{\text{midday}}$ cycle from 1999 to 2003 (solid line) (Figure 8b). Gray bars represents 1 standard deviation and lines smoothed with 7 day moving average.

(Figure 6). Consequently, drought resulted in a net carbon loss that rivaled respiratory losses during flooded years (Table 1). A higher sensitivity of photosynthesis to drought has been reported for other ecosystems, and arises from the coupling between carbon uptake and water loss through stomata [Schulze, 1986; Schwalm et al., 2010].

4.1. Short-Term Effects of Drought

[27] Drought inhibited leaf area development (Figure 7), which suppressed photosynthetic carbon uptake (Figures 3, 4, 5, and 6), and altered the diel cycle of NEE (Figure 4). Consequently, marshes exposed to drought were solely controlled by ecosystem respiration and exhibited a weak diel NEE cycle that peaked early in the morning rather than during the middle of the day (Figure 4). Models based on the Q_{10} temperature dependence of respiration would predict highest respiration rates during the middle of the day when temperatures are at their maximum [Davidson et al., 2006]. However, maximum respiration rates were observed in the

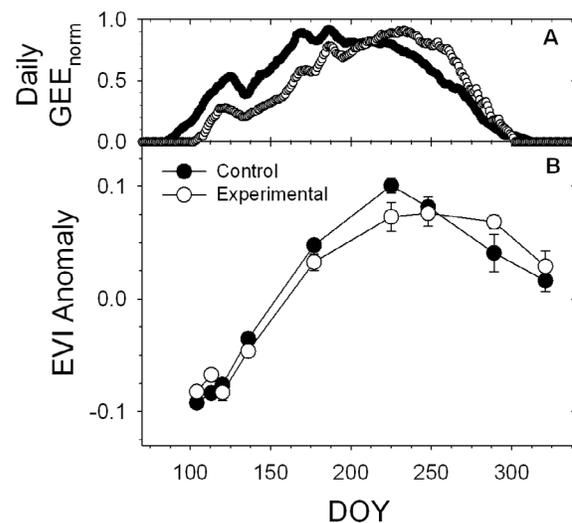


Figure 9. Seasonal cycle of normalized daily Gross Ecosystem Exchange (GEE_{norm}) (a) and Landsat EVI anomalies (b) in 2008 following the 2007 drought in the Control (closed circles) and Experimental (open circles) Ponds. Daily GEEs were normalized by the seasonal minimum daily GEE (i.e., maximum gross carbon uptake) in each pond and later smoothed using a 10-day moving average. EVI anomalies were calculated by removing the seasonal mean EVI for each pond, and error bars in Figure 9b represent standard errors.

morning when temperatures were at a minimum. The morning respiration peak may have arisen from increased litter moisture from morning dew that frequently forms at the site (personal observation). Water is often an important controller of vegetation activity in Mediterranean systems [Ma et al., 2007; Pereira et al., 2007], and it is likely that plant phenology and ecosystem respiration is limited more by water availability than temperature.

4.2. Long-Term Effects of Drought

[28] Long-term effects of drought were expressed through the biological controls on carbon uptake at the marsh. The effect of drought carried over into subsequent years by reducing LAI_{max} and canopy photosynthesis, and by shifting the seasonal cycles of NEE, GEE, and EVI (Figures 3, 7, 8, and 9). Carbohydrate reserves formed during the previous year play an important role in controlling plant growth in this system [Rocha and Goulden, 2009]. The lack of photosynthesis during drought likely reduced the carbohydrate reserves that are needed to support rapid leaf area development during spring, which delayed the start of the growing season and peak carbon uptake, and decreased LAI_{max} and peak carbon uptake. The delay in carbon uptake is likely due to slow vegetation recovery following drought and indicates that perturbations can influence leaf phenology in subsequent years. This finding differs from traditional phenological models that rely solely on abiotic controls to initiate leaf area development [White et al., 1997; Chuine, 2000]. Biotic control on leaf phenology has received little attention, despite observations of altered leaf phenology following fire [Peckham et al., 2008] or intense herbivory [Carroll and Quiring, 2003]. Biotic controls on leaf phenology are important in this system and may explain the difficulty in predicting the start of the growing season at the SJFM [Rocha and Goulden, 2008].

[29] Legacies from the 2007 drought resulted in large differences in the long term carbon balance of the two marshes. Both ponds were sources of carbon to the atmosphere over the 6-year period (Figure 3 and Table 1), though the Experimental Pond was a larger source of carbon to the atmosphere by the end of the experiment. The Experimental Pond stored ~181 g m⁻² more carbon than the Control Pond prior to the 2007 drought. The 2007 drought switched the carbon sink strength between the two ponds by creating a persistent yearlong loss of carbon, and decreasing subsequent carbon sequestration through reductions in LAI_{max}. The loss of carbon during 2007 was equivalent to 2 years of the maximum annual carbon sequestration (-323 gC m⁻² y⁻¹) [Rocha and Goulden, 2008] observed over the historical record, while the combined effects of the 2007 drought and subsequent reductions in annual NEE after drought was equivalent to 4 years of the maximum annual carbon sequestration. The amount of carbon lost during and after drought indicates that droughts can have substantial and long lasting impacts on wetland carbon balance.

5. Conclusions

[30] This study indicates that freshwater marshes are particularly sensitive to drought, and stresses the importance of both biotic and abiotic controls in determining ecosystem carbon balance over a variety of temporal scales. Climate

projections indicate more arid conditions over the next century [IPCC, 2007; Hayhoe et al., 2004], increasing the likelihood of wetland degradation through water diversions and a lowering water table. If the SJFM is representative of other freshwater marshes, then future climatic and socio-economic changes will likely result in a decrease in the carbon sequestration potential of these systems. Future management should take into account both the short- and long-term impacts of drought to minimize carbon loss from these systems.

[31] **Acknowledgments.** We thank Bill Bretz, Peter Bowler and the Irvine Ranch Water District (IRWD) for managing and supporting the San Joaquin Marsh Reserve, and Greg Winston, Steve Quan, and Scot Parker for their assistance in the field. We also would like to thank Gaius Shaver, Dennis Baldocchi, and two anonymous reviewers for comments on earlier drafts of this manuscript.

References

- Arnone, J. A., et al. (2008), Prolonged suppression of ecosystem carbon dioxide uptake after an anomalously warm year, *Nature*, 455, 383–386, doi:10.1038/nature07296.
- Baldocchi, D. D. (2003), Assessing ecosystem carbon balance: Problems and prospects of the eddy covariance technique, *Global Change Biol.*, 9, 479–492, doi:10.1046/j.1365-2486.2003.00629.x.
- Biesboer, D. D. (1984), Seasonal variation in nitrogen fixation, associated microbial populations, and carbohydrates in roots and rhizomes of *Typha latifolia* (Typhaceae), *Can. J. Bot.*, 62, 1965–1967, doi:10.1139/b84-267.
- Carroll, A. L., and D. T. Quiring (2003), Herbivory modifies conifer phenology: Induced amelioration by a specialist folivore, *Oecologia*, 136, 88–95, doi:10.1007/s00442-003-1240-5.
- Chander, G., B. L. Markham, and J. A. Barsi (2007), Revised Landsat-5 Thematic mapper radiometric calibration, *IEEE Geosci. Remote Sens. Lett.*, 4, 490–494, doi:10.1109/LGRS.2007.898285.
- Chuine, I. (2000), A unified model for budburst of trees, *J. Theor. Biol.*, 207, 337–347, doi:10.1006/jtbi.2000.2178.
- Davidson, E. A., I. A. Janssens, and Y. Luo (2006), On the variability of respiration in terrestrial ecosystems: Moving beyond Q₁₀, *Global Change Biol.*, 12, 154–164, doi:10.1111/j.1365-2486.2005.01065.x.
- Englund, G., and S. D. Cooper (2003), Scale effects and extrapolation in ecological experiments, *Adv. Ecol. Res.*, 33, 161–213, doi:10.1016/S0065-2504(03)33011-9.
- Goulden, M. L., B. C. Daube, S.-M. Fan, D. J. Sutton, A. Bazzaz, J. W. Munger, and S. C. Wofsy (1997), Physiological responses of a Black Spruce forest to weather, *J. Geophys. Res.*, 102, 28,987–28,996, doi:10.1029/97JD01111.
- Goulden, M. L., M. C. Litvak, and S. D. Miller (2007), Factors controlling marsh evapotranspiration, *Aquat. Bot.*, 86, 97–106, doi:10.1016/j.aquabot.2006.09.005.
- Hall, F. G., D. E. Strelbel, J. E. Nickeson, and S. J. Goetz (1991), Radiometric rectification-toward a common radiometric response among multi-date, multisensor images, *Remote Sens. Environ.*, 35, 11–27, doi:10.1016/0034-4257(91)90062-B.
- Hayhoe, K., et al. (2004), Emissions pathways, climate change, and impacts on California, *Proc. Natl. Acad. Sci. U. S. A.*, 101, 12,422–12,427, doi:10.1073/pnas.0404500101.
- Hollinger, D. Y., et al. (2004), Spatial and temporal variability in forest-atmosphere CO₂ exchange, *Global Change Biol.*, 10, 1689–1706, doi:10.1111/j.1365-2486.2004.00847.x.
- Hsieh, C.-I., G. Katul, and T. Chi (2000), An approximate analytical model for footprint estimation of scalar fluxes in thermally stratified atmospheric flows, *Adv. Water Resour.*, 23, 765–772, doi:10.1016/S0309-1708(99)00042-1.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira (2002), Overview of the radiometric and biophysical performance of the MODIS vegetation indices, *Remote Sens. Environ.*, 83, 195–213.
- Hui, D., Y. Luo, and G. Katul (2003), Partitioning interannual variability in net ecosystem exchange between climatic variability and functional change, *Tree Physiol.*, 23, 433–442.
- Hurlbert, S. (1984), Pseudoreplication and the design of ecological field experiments, *Ecol. Monogr.*, 54, 187–211, doi:10.2307/1942661.
- IPCC (2007), *Climate Change: The Physical Science Basis. Contribution of working group I to the fourth assessment report of the Intergovern-*

- mental Panel on Climate Change, edited by S. Solomon et al., Cambridge Univ. Press, Cambridge, U. K.
- Li, S., S. R. Pezeshki, and S. Goodwin (2004), Effects of soil moisture regimes on photosynthesis and growth in cattail (*Typha latifolia*), *Acta Oecol.*, *25*, 17–22, doi:10.1016/j.actao.2003.10.004.
- Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce (1970), Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed ecosystem, *Ecol. Monogr.*, *40*, 23–47, doi:10.2307/1942440.
- Ma, S., D. D. Baldocchi, L. Xu, and T. Hehn (2007), Interannual variability in carbon exchange of an oak/grass savanna and an annual grassland in California, *Agric. For. Meteorol.*, *147*, 157–171, doi:10.1016/j.agrformet.2007.07.008.
- Oksanen, L. (2001), Logic of experiments in ecology: Is pseudoreplication a pseudoissue?, *Oikos*, *94*, 27–38, doi:10.1034/j.1600-0706.2001.11311.x.
- Peckham, S. D., D. E. Ahl, S. P. Serbin, and S. T. Gower (2008), Fire-induced changes in green-up and leaf maturity of the Canadian boreal forest, *Remote Sens. Environ.*, *112*, 3594–3603, doi:10.1016/j.rse.2008.04.016.
- Pereira, J. S., et al. (2007), Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems—the effect of drought, *Biogeosciences*, *4*, 791–802, doi:10.5194/bg-4-791-2007.
- Richardson, A. D., et al. (2006), A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes, *Agric. For. Meteorol.*, *136*, 1–18, doi:10.1016/j.agrformet.2006.01.007.
- Richardson, A. D., A. Y. Hollinger, J. D. Aber, S. V. Ollinger, and B. H. Braswell (2007), Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange, *Global Change Biol.*, *13*, 788–803.
- Rocha, A. V., and M. L. Goulden (2008), Large interannual CO₂ and energy exchange variability in a freshwater marsh under consistent environmental conditions, *J. Geophys. Res.*, *113*, G04019, doi:10.1029/2008JG000712.
- Rocha, A. V., and M. L. Goulden (2009), Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a *Typha* marsh, *Agric. For. Meteorol.*, *149*, 159–168, doi:10.1016/j.agrformet.2008.07.010.
- Rocha, A. V., and G. R. Shaver (2009), Advantages of a two band EVI calculated from solar and photosynthetically active radiation fluxes, *Agric. For. Meteorol.*, *149*, 1560–1563, doi:10.1016/j.agrformet.2009.03.016.
- Rocha, A. V., D. L. Potts, and M. L. Goulden (2008), Standing litter as a driver of interannual CO₂ exchange variability in a freshwater marsh, *J. Geophys. Res.*, *113*, G04020, doi:10.1029/2008JG000713.
- Ruimy, A., P. G. Jarvis, D. D. Baldocchi, and B. Saugier (1995), CO₂ fluxes over plant canopies a literature review, *Adv. Ecol. Res.*, *26*, 1–68, doi:10.1016/S0065-2504(08)60063-X.
- Schindler, D. W., A. J. Armstrong, S. K. Holmgren, and G. J. Brunskill (1971), Eutrophication of lake 227 experimental lakes area northwestern Ontario by addition of phosphate and nitrate, *J. Fish. Res. Board Can.*, *28*, 1763–1782.
- Schulze, E. D. (1986), Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil, *Annu. Rev. Plant Physiol.*, *37*, 247–274, doi:10.1146/annurev.pp.37.060186.001335.
- Schwalm, C. R., et al. (2010), Assimilation exceeds respiration sensitivity to drought: A Fluxnet synthesis, *Global Change Biol.*, *16*, 657–670, doi:10.1111/j.1365-2486.2009.01991.x.
- Schwinning, S., O. E. Sala, M. E. Loik, and J. R. Ehleringer (2004), Thresholds, memory, and seasonality: Understanding pulse dynamics in arid/semi-arid ecosystems, *Oecologia*, *141*, 191–193, doi:10.1007/s00442-004-1683-3.
- Sherry, R. A., E. Weng, J. A. Arnone, D. W. Johnson, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo (2008), Lagged effects of experimental warming and doubled precipitation on annual and seasonal above-ground biomass production in a tallgrass prairie, *Global Change Biol.*, *14*, 2923–2936, doi:10.1111/j.1365-2486.2008.01703.x.
- Sierra, C. A., H. W. Loescher, M. E. Harmon, A. D. Richardson, D. Y. Hollinger, and S. S. Perakis (2009), Interannual variation of carbon fluxes from three contrasting evergreen forests: The role of forest dynamics and climate, *Ecology*, *90*, 2711–2723, doi:10.1890/08-0073.1.
- Stoy, P. C., et al. (2009), Biosphere-atmosphere exchange of CO₂ in relation to climate: A cross-biome analysis across multiple time scales, *Biogeosci. Discuss.*, *6*, 4095–4141, doi:10.5194/bgd-6-4095-2009.
- Thomas, D. K., B. E. Law, J. Irvine, J. G. Martin, J. C. Pettijohn, and K. J. Davis (2009), Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semi-arid mature ponderosa pine forest in Central Oregon, *J. Geophys. Res.*, *114*, G04006, doi:10.1029/2009JG001010.
- White, M. A., P. E. Thornton, and S. W. Running (1997), A continental phenology model for monitoring vegetation responses to interannual climatic variability, *Global Biogeochem. Cycles*, *11*, 217–234, doi:10.1029/97GB00330.
- Yuan, W., et al. (2009), Latitudinal patterns of magnitude and interannual variability in net ecosystem exchange regulated by biological and environmental variables, *Global Change Biol.*, *15*, 2905–2920, doi:10.1111/j.1365-2486.2009.01870.x.

M. L. Goulden, Department of Earth System Science, University of California, Irvine, CA 92697, USA.

A. V. Rocha, Marine Biological Laboratory Ecosystems Center, 7 MBL St., Woods Hole, MA 02543, USA. (arochoa@mbl.edu)