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Standing litter as a driver of interannual CO₂ exchange variability in a freshwater marsh

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[1] The San Joaquin Freshwater Marsh (SJFM) is a seasonally flooded *Typha* wetland in Southern California that is characterized by high rates of Aboveground Net Primary Production (ANPP) and a large accumulation of standing leaf litter. The ANPP, Gross and Net Ecosystem CO₂ Exchange (GEE and NEE), and Enhanced Vegetation Index (EVI) at the SJFM fluctuate by ~40% from year to year, in ways that are not directly attributable to variation in weather or the maximum green Leaf Area Index (LAI_{max}). We tested the hypothesis that this variation is caused by a negative feedback between ANPP, the buildup of leaf litter, shading of green leaves by litter, a reduction in GEE and NEE, and a subsequent reduction in ANPP. Litter manipulations on replicated plots demonstrated that the presence of standing litter decreased plot-level NEE by 17 to 47% and surface EVI by 25 to 48%, even as green Leaf Area Index (LAI_{green}) was held constant. Plot level NEE and surface EVI remained tightly correlated, and largely decoupled from LAI_{green}, as standing litter was varied. This pattern paralleled that observed for the entire marsh, where NEE and EVI remained tightly correlated, and largely decoupled from LAI_{max}, from year to year. Correcting LAI_{green} and LAI_{max} for the amount of shading caused by standing litter improved the correlations between LAI and EVI and NEE, indicating that EVI and NEE are most sensitive to the amount of unshaded LAI. The accumulation of standing litter at the SJFM decouples the relationships between LAI and EVI and NEE, and appears to be important for controlling the interannual variability observed at the site.

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1. Introduction

[2] Rocha and Goulden [2008a] demonstrated large interannual carbon uptake variability under consistent environmental conditions at the San Joaquin Freshwater Marsh (SJFM) in Southern California. This variability resulted from changes in photosynthesis, and was difficult to attribute to interannual weather differences. Interannual photosynthetic variability was correlated with changes in surface greenness as measured by the Enhanced Vegetation Index (EVI), which were unrelated to differences in canopy green Leaf Area Index (LAI_{green}). These observations point to an unknown factor that changed the photosynthetic efficiency of the canopy (the rates of gross or net CO₂ exchange per LAI) and decoupled the expected relationships between LAI and EVI and carbon uptake.

[3] The SJFM is a highly productive freshwater marsh that is characterized by a large accumulation of standing

litter (Figure 1). The ability of litter accumulation to drive interannual carbon uptake variability at the SJFM is unknown, though previous studies have shown that litter can alter ecosystem function, and confound the relationship between green leaf area and remotely sensed vegetation indices. Litter accumulation can decrease productivity and limit the ability of an ecosystem to respond to environmental factors [Knapp and Seastedt, 1986; LeCain *et al.*, 2000; Wilsey *et al.*, 2002]. Differential responses of Aboveground Net Primary Production (ANPP) to weather in burned and unburned tallgrass prairie were attributed to the accumulation of litter and the resulting decrease in NPP in unburned stands [Knapp and Seastedt, 1986; Briggs and Knapp, 1995]. Litter addition suppressed cattail growth in a Chesapeake Bay freshwater marsh by changing the physical structure of the plant canopy [Jordan *et al.*, 1990]. Shading by standing litter caused oscillations and chaotic dynamics in perennial grass ANPP through a time delayed inhibitory effect on plant growth [Tilman and Wedin, 1991].

[4] Cattail marshes have high rates of ANPP and produce copious amounts of litter [Findlay *et al.*, 1990; Asaeda *et al.*, 2002]. The amount of litter at the SJFM is approximately double the average ANPP at the site [Rocha, 2008] (2200 gC m⁻² in 2004), and much higher than that observed for tallgrass prairie. Much of the litter at the SJFM remains upright [cf. Davis and van der Valk, 1977], and has the

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Figure 1. Photograph showing the accumulation of standing litter at the SJFM.

potential to shade subsequent year's leaves and reduce photosynthesis. Previous studies have suggested that standing litter affects photosynthesis in freshwater ecosystems. *Bonneville et al.* [2008] found that the correlation between canopy photosynthesis and aboveground green biomass in a freshwater marsh was improved by accounting for the amount of dead vegetation.

[5] The presence of standing litter also confounds the interpretation of remotely sensed vegetation indices. The Normalized Difference Vegetation Index (NDVI), a common predictor of green leaf area, poorly correlates with green leaf area in mixtures of litter and green vegetation [*Huete and Jackson*, 1987; *van Leeuwen and Huete*, 1996; *Wessman et al.*, 1997]. The effect of litter on NDVI depends on its abundance, brightness, and orientation. Large amounts of litter on top of green leaf area markedly decreased NDVI, whereas small amounts of litter on top of low green leaf area had little to no effect on NDVI [*van Leeuwen and Huete*, 1996]. It is clear that litter affects both the intercanopy light environment and canopy reflectance, which are both important factors related to canopy carbon fluxes [*Asner et al.*, 1998].

[6] We hypothesized that a negative feedback between ANPP, the buildup of leaf litter, shading of green leaves by litter, a reduction in Gross and Net Ecosystem CO_2 Exchange (GEE and NEE), and a subsequent reduction in ANPP influences the interannual Net Ecosystem Production (NEP) variability at the SJFM. We approached this issue by sequentially manipulating standing litter in replicated 2.25 m^2 plots, and measuring the effects on the intercanopy light environment, canopy reflectance, and NEE. We focused on three questions: (1) How does NEE and EVI change under constant $\text{LAI}_{\text{green}}$ and increased standing litter? (2) Are changes in NEE and EVI under constant $\text{LAI}_{\text{green}}$ and increased standing litter sufficient to account for the interannual GEE and NEE variation observed for the entire marsh? (3) Can changes in the amount of standing litter under constant $\text{LAI}_{\text{green}}$ reproduce the observed correlations between EVI, LAI and NEE observed in the long-term eddy covariance record (i.e., the tight correlation

between NEE and EVI that was largely decoupled from $\text{LAI}_{\text{green}}$)?

2. Methods

2.1. Field Site

[7] Detailed descriptions of the San Joaquin Freshwater Marsh and long-term interannual measurements of NEE, LAI, and EVI are presented by *Rocha and Goulden* [2008a]. The SJFM is dominated by cattail (*Typha spp.*), and water levels in the SJFM are managed for research and wildlife habitat. The marsh is typically flooded to a depth of $\sim 1 \text{ m}$ above the mineral soil in winter, after which water levels gradually decline through evapotranspiration and subsurface drainage. The lone exception to this pattern in the last 10 years occurred in 2004, when the marsh remained dry year-round because of concern about the West-Nile virus and a management decision to reduce mosquito habitat. Plant growth and photosynthesis were negligible in 2004 because the initiation of plant growth requires the presence of standing water [*Rocha*, 2008]. We therefore excluded 2004 from subsequent analyses because the goal of this study was to determine the affect of standing litter on carbon uptake.

2.2. Litter Manipulations

[8] The litter manipulation experiment was conducted during the month of peak NEE (July) in 2007. The marsh was flooded to a depth of 1 m in February 2007, and standing water disappeared by June. Cattail canopy development began in late February 2007 and had reached maturity by late June.

[9] We sequentially manipulated the amounts of standing litter ($\text{LAI}_{\text{litter}}$) and green leaf area ($\text{LAI}_{\text{green}}$) in four 2.25 m^2 experimental plots to determine the effects of standing litter on intercanopy Photosynthetic Active Radiation (PAR), NEE, and EVI. We conducted the manipulations $\sim 50 \text{ m}$ southeast of the eddy covariance tower, in an area that was out of the tower fetch so as not to interfere with the micrometeorological measurements. The manipulation plots were within $\sim 15 \text{ m}$ of each other, in an area that appeared homogenous and typical of the larger marsh. The manipulations and associated measurements were made between 11 A.M. and 2 P.M. local time on four clear days over a week. Scaffold was constructed adjacent to each plot, and rectangular PVC chamber frames within each plot, before beginning, to allow easy access while minimizing disturbance.

[10] Each plot was sequentially manipulated to four treatment levels. The first treatment level (Added Litter) involved adding Cattail litter from a nearby 1-m^2 plot. The second treatment level (Original Litter) involved removing this supplemental litter. The third treatment level (No Litter) involved removing all remaining litter. The fourth treatment level (No Litter & Reduced $\text{LAI}_{\text{green}}$) involved removing $\sim 35\%$ of the green leaf area. All material was removed from the plots by clipping litter or living plants at the soil surface.

[11] We used repeated measures ANOVA with a post hoc paired t-test to determine the statistical significance of our treatment effects at the 90% confidence level. Statistical analysis was done in Minitab (Minitab Inc., State College, PA, USA).

2.3. Biomass Harvests and Calculation of LAI

[12] We recorded green and standing litter leaf biomass for each plot treatment. Collected green and standing litter leaves were dried in an oven at 65°C for 1–2 days before recording the dry weight. Dry weights were used to calculate LAI_{litter} and LAI_{green} based on the observed specific leaf areas [Rocha and Goulden, 2008a].

2.4. Canopy Reflectance and Light Profiles

[13] Surface reflectance was measured at a spectral resolution of 1 nm from 325 to 1075 nm using a FieldSpec[®] Handheld UV/VNIR Spectroradiometer (Analytical Spectral Devices (ASD), Boulder, CO). Fifteen to twenty unobstructed (i.e., free from artificial shadows) spectral measurements were obtained for each treatment from a height of 1.5 m above the canopy using the 10° field of view optic. Reflectances were calibrated using a white reference panel (99% Spectralon[®], Labsphere Inc., North Sutton, NH) prior to the start of each set of spectral measurements. We also measured the spectra of green cattail leaves and standing litter to determine the influence of each member on canopy reflectance. Green cattail vegetation and litter was harvested from the marsh and immediately placed in front of a dark background for spectral reflectance measurements.

[14] Each spectral plot was visually inspected, and only high quality data were used in subsequent analyses. We emphasized EVI instead of the more commonly used Normalized Difference Vegetation Index (NDVI) because EVI is less sensitive to background reflectance than NDVI [Huete *et al.*, 2002] and because past work has shown that EVI is often tightly correlated with whole canopy CO₂ uptake. EVI was calculated from reflectance at 680 nm (ρ_{680}), 800 nm (ρ_{800}), and 510 nm (ρ_{510}):

$$\text{EVI} = \frac{2 * (\rho_{800} - \rho_{680})}{\rho_{800} + 6 * \rho_{680} - 7.5 * \rho_{510} + 1} \quad (1)$$

Canopy PAR profiles were measured in each treatment at 0.5 m height intervals starting at the soil surface. Ten measurements were taken at each height with a 1-m integrating light bar (Sunscan probe type SS1, Delta-T Devices, Cambridge, UK). PAR at each height (PAR_{intercanopy}) was averaged and converted to fraction of above canopy PAR (PAR_{intercanopy}/PAR_{above canopy}). Constrained linear regressions (y-intercept set to zero) between log transformed PAR_{intercanopy}/PAR_{above canopy} and height were used to quantify canopy light attenuation for each treatment [Pierce and Running, 1988].

2.5. Tent Gas Exchange

[15] Net Ecosystem CO₂ Exchange was measured using large clear rectangular chambers following Arnone and Obrist [2003]. Rectangular PVC chamber frames were constructed around each plot and left in place for the duration of the experiment. The chamber enclosed a rectangular volume of 5.63 m³ and was slightly taller than the canopy. We used a close-fitting removable cover constructed from translucent plastic sheeting (Tufflite material, Covalence Plastics, Minneapolis, MN) to enclose the chamber during measurements. The plastic sheet attenuated 17% of total light and enhanced the diffuse fraction by 25%.

Temperature increased 1-to-2°C min⁻¹ during the gas exchange measurements. The chamber enclosed three fans along with an open path Infrared Gas Analyzer (IRGA) (LI-7500) and a LI-6400 cuvette (both from LiCor, Lincoln, NE). The LI-7500, LI-6400 cuvette, and two table fans were mounted on a tripod and placed within the vegetation. The third fan was a low-pressure blower (static pressure: 152 ft⁻³ min⁻¹) attached to a duct that facilitated mixing from the top of the chamber to the bottom.

[16] The LI-7500 and LI-6400 autologged CO₂ concentration and air temperature at 1 Hz after the plastic covering was placed over the frame. A laptop computer connected to the LI-7500 monitored the CO₂ and H₂O trace in the chamber for 1.5 to 3 min. Air temperature from the LI-6400 thermocouple was used to correct the LI-7500 CO₂ and water observations to mixing ratio using the ideal gas law. The water- and temperature-corrected CO₂ trace over time was then used to determine the NEE following Jasoni *et al.* [2005]. We made sure that initial CO₂ concentrations for each trace were within 10 ppm of each other (~380 ppm) and used the first 100 s of data to calculate NEE. We report NEE according to the meteorological sign convention, where negative NEE indicates carbon uptake and positive NEE indicates carbon loss. Differences in NEE between treatments reflect changes in net photosynthesis, and not respiration, because litter respiration rates are low when litter is dry [Kuehn *et al.*, 2004].

2.6. Landsat Data

[17] We obtained midsummer (end of June–mid-August) Landsat images (Landsat 5 or 7) that included the SJFM (Path: 40 or 41, Row: 37) for each year from 1999 to 2007 [see also Rocha and Goulden, 2008a]. Landsat images were cross-calibrated against a LEDAPS surface reflectance image (http://ledaps.nascom.nasa.gov/ledaps/ledaps_NorthAmerica.html) and surface reflectance was used to calculate the midsummer Enhanced Vegetation Index (EVI). The Landsat record was used to determine differences in midsummer surface reflectance between years, as well as the spectral properties of green cattail vegetation and standing dead litter. Surface reflectance for the SJFM was taken from a 90 by 90 m area immediately upwind of the eddy covariance tower. The spectrum for green vegetation was acquired from pixels containing the largest EVI values for the entire period. The spectrum for standing dead litter was acquired from a year when the marsh was not flooded (2004) and the growth of green vegetation was negligible [Rocha, 2008]. Landsat data were taken after the hydroperiod, and surface water did not affect the vegetation indices.

3. Results

3.1. Effect of Litter Manipulations on LAI and Canopy Properties

[18] Average LAI_{green} in the Original Litter treatment was 2.3 m² m⁻², and LAI_{litter} was 3.0 m² m⁻². The LAI_{green} in the experimental plots in July 2007 was comparable to, or slightly less than, that observed in the larger long-term interannual survey in September 2007 (2.6 m² m⁻²), confirming that the manipulation plots were typical of the larger marsh. The LAI_{litter} in the experimental plots was similar to,

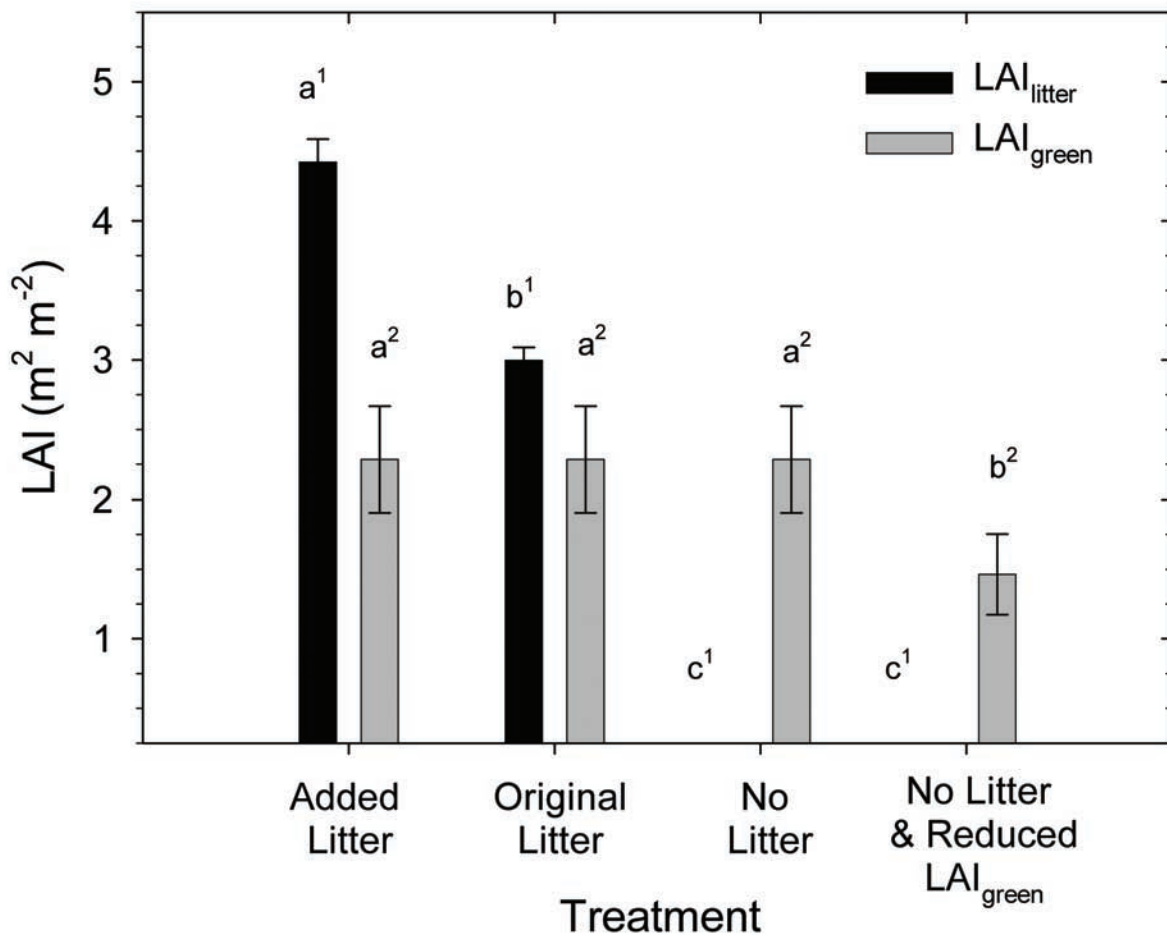


Figure 2. Average green (gray bars; LAI_{green}) and standing litter (dark bars: LAI_{litter}) leaf area index for each treatment. Error bars represent standard errors. Different letters indicate significant differences at the 90% confidence level, while superscript numbers indicate comparisons of (1) LAI_{litter} and (2) LAI_{green} among treatments.

or slightly less, than the LAI_{green} observed in the long term survey during the previous year ($4.4 \text{ m}^2 \text{ m}^{-2}$), implying that the litter remains standing for roughly one year after leaf senescence.

[19] We added on average 47% more standing litter in the Added Litter treatments and reduced green leaf area by 35% in the No Litter & Reduced LAI_{green} treatments (Figure 2). LAI_{green} remained constant in the Added, Original, and No Litter treatments, while LAI_{litter} ranged from $3.0 \text{ m}^2 \text{ m}^{-2}$ to zero (ANOVA $p < 0.01$). LAI_{green} was reduced from 2.3 to $1.5 \text{ m}^2 \text{ m}^{-2}$ in the No Litter & Reduced LAI_{green} treatment ($p < 0.01$).

[20] The removal of green leaf area and litter increased the amount of light reaching the soil surface (Figure 3). PAR decreased exponentially from the top to the bottom of the canopy following Beer's law [Jones, 1992]. Soil surface PAR was lowest in the Added Litter treatment and highest in the No Litter & Reduced LAI_{green} treatment. The attenuation of PAR, as measured by the slope of log transformed $\text{PAR}_{\text{intercanopy}}/\text{PAR}_{\text{above canopy}}$ and height, was 62% larger in the Added Litter treatment than in the No Litter & Reduced

LAI_{green} treatment. Removal of all standing litter decreased the attenuation of PAR by 45%.

[21] The addition of litter and reduction of leaf area markedly changed the spectral reflectance of the canopy (Figure 4). The surface spectral reflectance of each treatment resulted from the mixture of living green vegetation and standing litter (Figure 4, inset plot). Green vegetation exhibited absorption in the visible and strong reflectance in the NIR. This increase in reflectance in the NIR for green vegetation is known as the "red edge" [Horler *et al.*, 1983]. Litter reflectance lacked a red edge, and was brighter in the visible and darker in the NIR than green vegetation. The red edge was most pronounced in the No Litter treatment. The red edge also responded to changes in green leaf area and was 11% reduced in the No Litter & Reduced LAI_{green} compared to the No Litter treatment.

3.2. Effect of Litter on EVI and NEE

[22] The EVI and -NEE measured in the Original Litter experimental plots was comparable to, or slightly greater than that observed in the long term survey during 2007. EVI was 0.28 in the experimental plots and 0.23 in the long term survey; -NEE was $11 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in the experimental

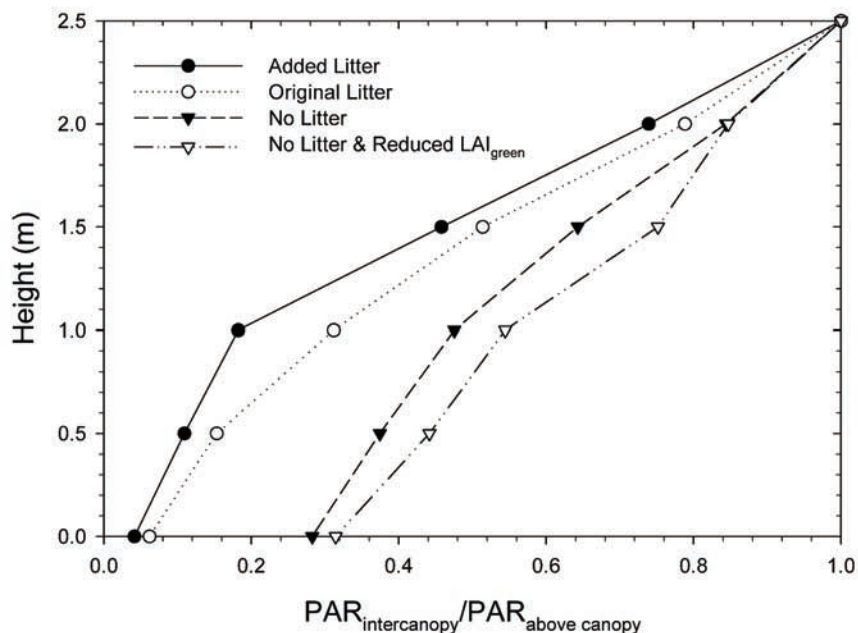


Figure 3. Average light profiles for the different treatments. Added Litter plots are represented by solid circles, Original Litter plots are represented by open circles, No Litter plots are represented by closed triangles, and No Litter & Reduced LAI_{green} plots are represented by open triangles.

plots and $8.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the long term survey. EVI differed significantly between experimental treatments (ANOVA $p < 0.001$) (Figure 5a). EVI was largest in the No Litter treatment and lowest in the Added Litter treatment. EVI differences between the No Litter and No Litter & Reduced LAI_{green} treatments indicated that EVI was sensitive to changes in green leaf area. However, EVI also differed between treatments with the same LAI_{green} (i.e.,

Added, Original, & No Litter treatments) (Figure 2), establishing that the presence of standing litter decouples the relationship between EVI and LAI_{green}.

[23] -NEE differed significantly between experimental treatments (ANOVA $p = 0.005$) (Figure 5b). -NEE was largest in the No Litter treatment and lowest in the Added Litter treatment. The Original Litter treatment had the second highest rates of -NEE. -NEE in the No Litter &

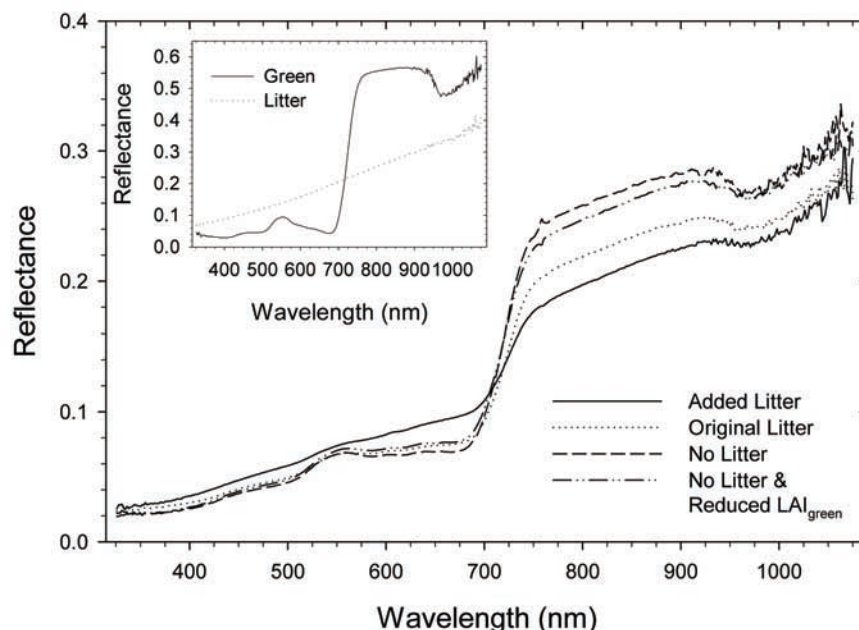


Figure 4. Average spectra obtained from the different litter manipulation treatments and spectral reflectance for green Cattail vegetation and Cattail litter (inset plot).

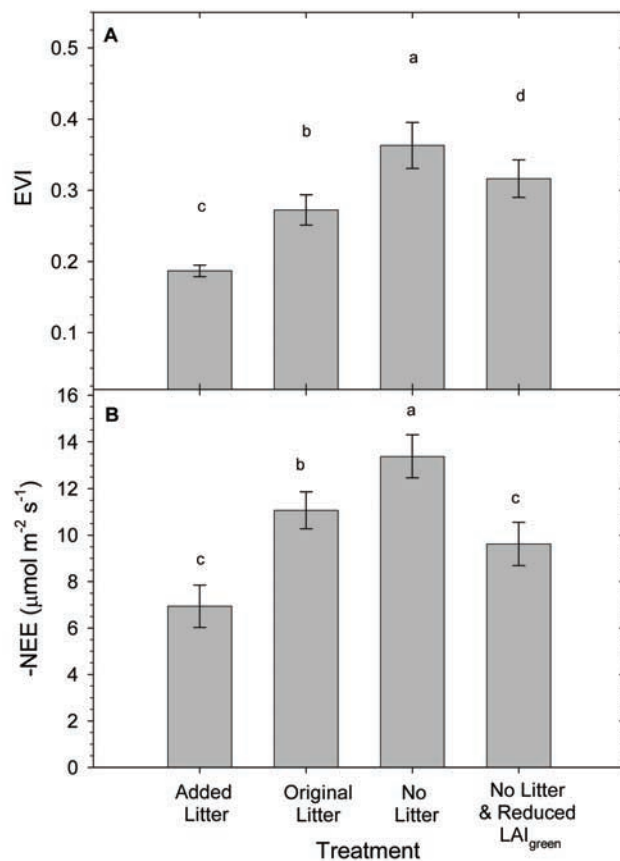


Figure 5. Average (a) enhanced vegetation index (EVI) and (b) Net Ecosystem Exchange of CO₂ (-NEE) for each treatment. Error bars represent standard errors, and different letters indicate significant differences at the 90% confidence level.

Reduced LAI_{green} treatment fell between the Original and Added Litter treatments. Differences in -NEE between the No Litter and Original Litter treatment were statistically significant ($p = 0.02$), whereas differences in -NEE between the Added and No Litter & Reduced LAI_{green} treatment were not ($p = 0.20$). -NEE in the Original Litter treatment was higher than -NEE in the Added Litter ($p = 0.08$) and the No Litter & Reduced LAI_{green} treatment ($p = 0.07$). The response of -NEE to each treatment was consistent across-plots and establishes that the presence and the amount of standing litter affects carbon uptake.

3.3. Reconciling the Relationships Between LAI_{green}, EVI, and NEE

[24] We observed poor correlations between LAI_{green} and -NEE (Figure 6a, inset plot; $p = 0.60$) and LAI_{green} and EVI (Figure 6b, inset plot; $p = 0.72$) for our experimental manipulations and hypothesized that shading by standing litter was confounding these relationships. We tested this hypothesis by estimating the amounts of unshaded LAI_{green}, which we calculated by multiplying LAI_{green} by the fraction of green to total leaf area ($f_G = \text{LAI}_{\text{green}} / (\text{LAI}_{\text{green}} + \text{LAI}_{\text{litter}})$) for each treatment and plot. Correcting green leaf area for the amount of standing litter markedly improved the

correlations between leaf area and EVI and -NEE. Unshaded green leaf area ($f_G * \text{LAI}_{\text{green}}$) was positively related to -NEE (Figure 6a; $r = 0.57$; $p = 0.02$) and EVI (Figure 6b, $r = 0.60$; $p = 0.01$).

3.4. Comparing Tower and Litter-Experiment Observations

[25] Observations from the litter experiment matched the long-term patterns observed for the marsh as a whole (Figure 7 [Rocha and Goulden, 2008a]). Interannual variability in green leaf area (i.e., LAI_{max}) was not significantly correlated with either carbon uptake (Figure 7a; $p = 0.15$) or midsummer EVI (Figure 7c; $p = 0.22$), while carbon uptake and midsummer EVI were tightly correlated (Figure 7e; $r = 0.78$; $p = 0.02$). The litter manipulations showed that the presence or absence of standing litter can decouple the relationship between green leaf area (LAI_{green}) and both carbon uptake (Figure 7b; $p = 0.60$) and EVI (Figure 7d; $p = 0.73$), while maintaining a tight correlation between carbon uptake and EVI (Figure 7f; $r = 0.84$; $p < 0.001$).

[26] Differences in midsummer Landsat surface reflectance spectra in each year resulted from the mixture of living green vegetation and standing litter (Figure 8) as observed in the reflectance spectra of the litter experimental treatments (Figure 4). Landsat spectra for green vegetation and litter in the visible and NIR display the characteristic features observed in Figure 4 (inset plot), with strong

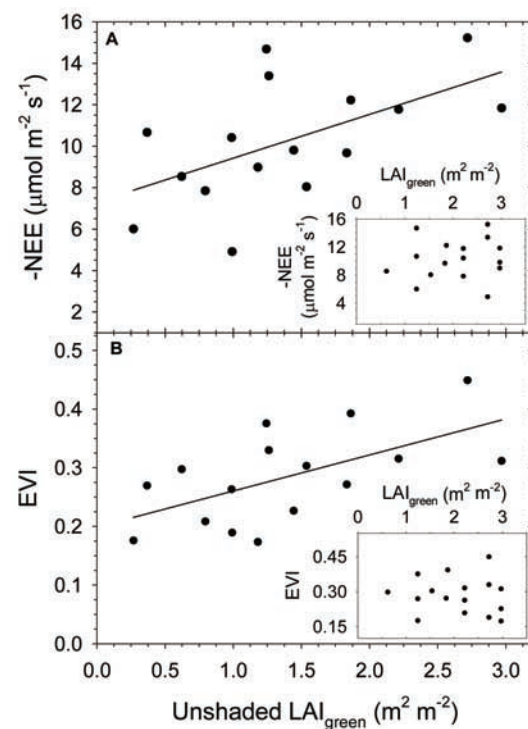


Figure 6. Relationships between measured (a) NEE and unshaded green leaf area (LAI_{green}) and (b) EVI and unshaded green leaf area; measured LAI_{green} and NEE (Figure 6a, inset plot) and measured LAI_{green} and EVI (Figure 6b, inset plot). Lines indicate regressions that are significant at the 95% confidence level.

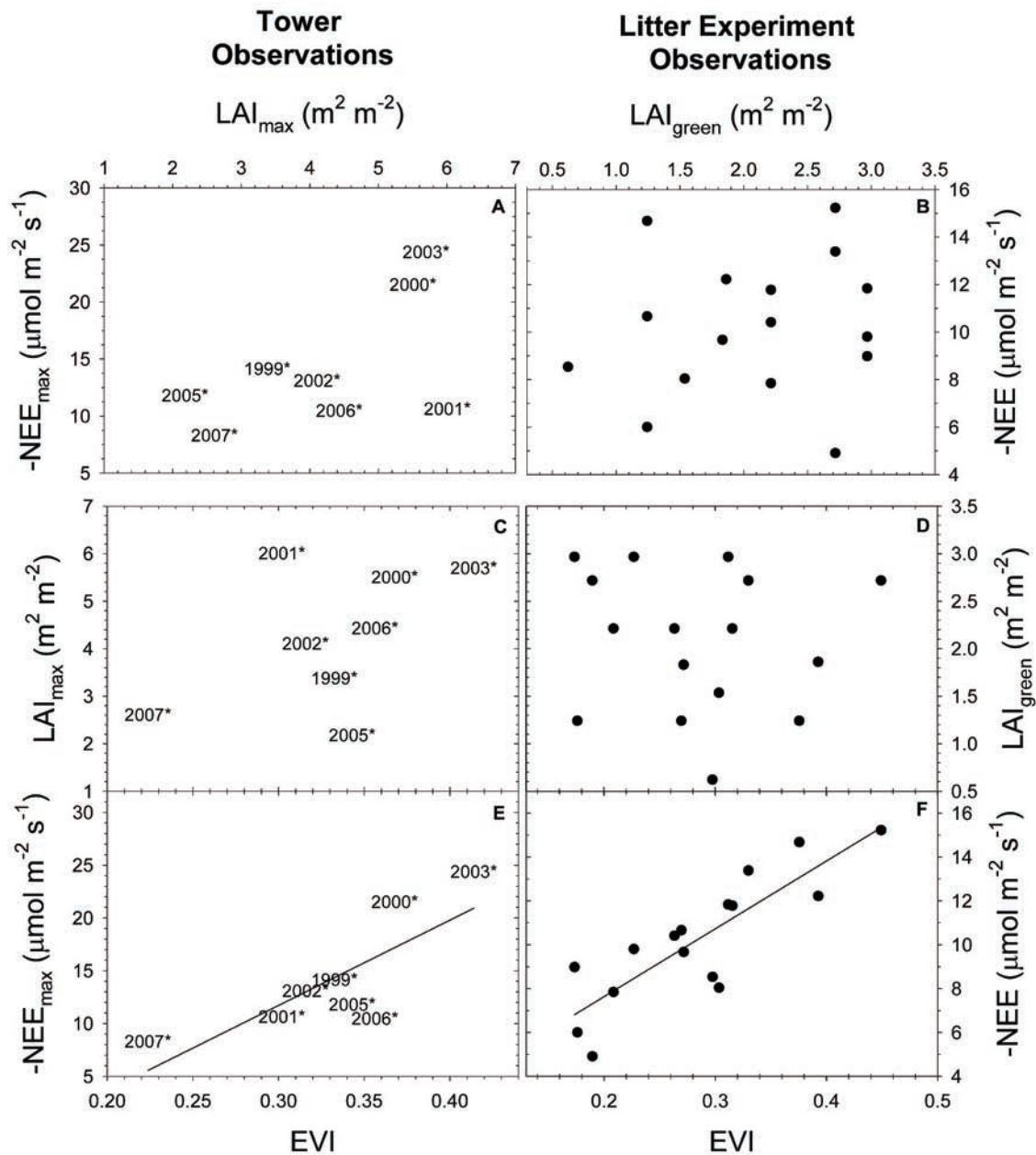


Figure 7. Comparisons between correlations of (a and b) green leaf area index and carbon uptake, (c and d) EVI and green leaf area index, and (e and f) EVI and carbon uptake for the (right) standing litter experimental manipulations and (left) tower-based observations from 1999 to 2007. Lines represent correlations that are significant at the 95% confidence level.

absorption in the visible and increased reflectance in the NIR for green vegetation (Figure 8a). Standing litter was more reflective in the ShortWave InfraRed (SWIR) (1200–2500 nm) than green vegetation. Higher reflectance in the SWIR and visible (i.e., 2001 and 2002) was observed following years with high LAI_{max} (i.e., 2000 and 2001), suggesting the presence of a large amount of litter near the top of the canopy (Figure 8b and Figure 8b inset plot).

[27] Relationships between leaf area, EVI and carbon uptake for the long-term observations improved once the

amount of shaded LAI_{max} was estimated (Figure 9). The amount of standing litter for a given year was estimated as the previous year's LAI_{max} and unshaded LAI_{max} was calculated following the approach used for the experimental plots (e.g., Figure 6). Unshaded LAI_{max} was unrelated to $-NEE_{max}$ ($p = 0.13$; $r = 0.63$), but the relationship between unshaded LAI_{max} and NEE_{max} explained more of the interannual variability in NEE_{max} than LAI_{max} alone (Figure 7a). Unshaded LAI_{max} was positively related to EVI ($p = 0.03$; $r = 0.79$) and unshaded LAI_{max} explained

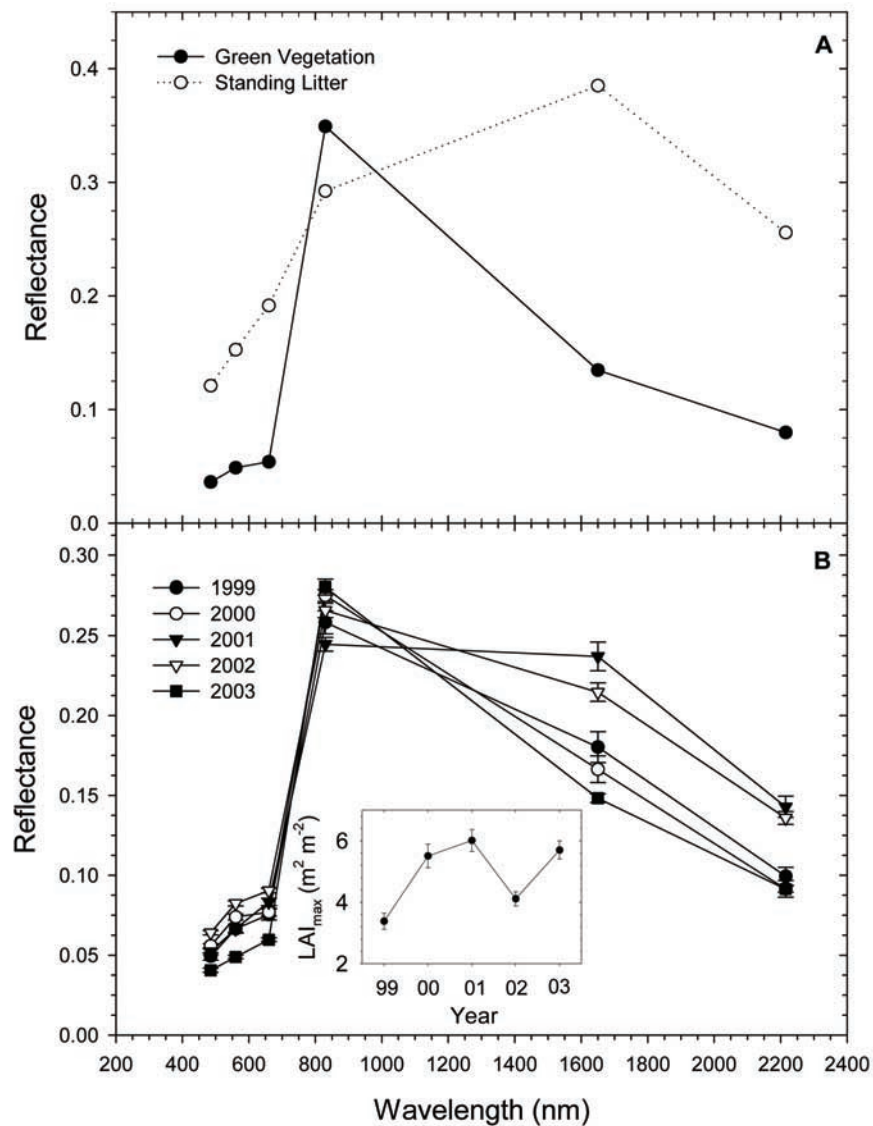


Figure 8. Surface reflectance spectra at the SJFM obtained from Landsat. (a) Landsat surface reflectance of green vegetation (closed circle) and standing litter (open circle) at the SJFM. (b) Interannual Landsat surface reflectance differences in the fetch of the eddy covariance tower, and differences in LAI_{max} at the SJFM from 1999 to 2003 (Figure 8b, inset plot). Error bars represent standard errors.

more of the interannual EVI variability than LAI_{max} alone (Figure 7c).

4. Discussion

4.1. Could Variation in Standing Litter Explain the Interannual Variability at the SJFM?

[28] The removal of litter from the manipulation plots increased light levels in the lower meter of the canopy by 70% (Figure 3) and rates of -NEE by 48% (Figure 5). The presence of litter unquestionably influenced NEE, though it remains uncertain whether this impact was quantitatively sufficient to account for the SJFM's interannual variability. The interannual relationship between LAI_{max} and tower-based NEE for the entire marsh showed a positive relation-

ship; years with increased CO₂ uptake coincided with years with higher LAIs (Figure 7a; 2000 and 2003). But there was also considerable scatter; years with similar maximum green leaf LAIs had NEEs that differed by as much as 38% (Figure 7a; 2000 and 2003 versus 2001). This scatter may be due, at least in part, to changes in the amount of standing litter, with the upper envelope of years (1999, 2000, 2003, 2005) reflecting periods when litter had a minor effect on -NEE and the lower envelope (2001, 2007) indicating periods when litter reduced -NEE considerably (see also Figure 7b).

[29] The plot experiments were conducted in 2007, during a period when both LAI and -NEE were lower than in most previous years. 2007 falls near the lower envelope of years, with an -NEE that was ~30% below that observed in

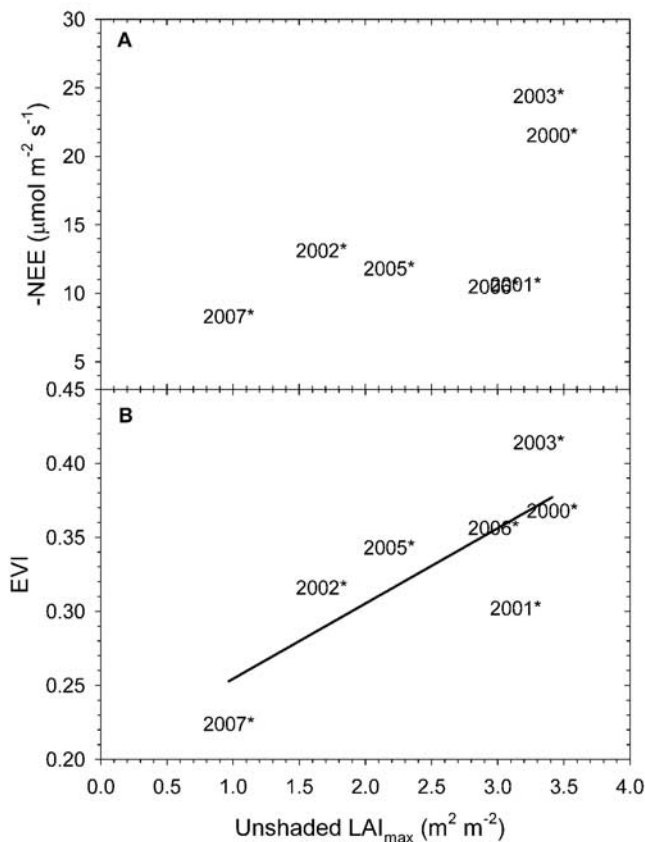


Figure 9. Relationships between (a) $-NEE_{max}$ and unshaded leaf area (Unshaded LAI_{max}) and (b) EVI and unshaded LAI_{max} for the SJFM from 2000 to 2007. Lines indicate regressions that are significant at the 95% confidence level.

2005 (Figure 7a). The observations in 2005 were made during a period when the marsh had very little standing dead litter. The marsh remained completely dry in 2004, as a result of a management decision, and ANPP during that year was negligible, resulting in a nearly complete depletion of standing litter for 2005 (personal observation). The LAI_{max} was similar between 2005 and 2007, implying that the accumulation of standing litter by 2007 was sufficient to reduce $-NEE$ by $\sim 30\%$. The removal of litter from the 2007 canopy increased NEE by 17% (Figure 5), which corresponds to a rate comparable to that observed for the whole marsh in 2005 (Figure 7). Additions of supplemental litter in the experimental manipulations further decreased $-NEE$ (Figure 5), indicating that the impact of litter does not saturate, and that reductions of $\sim 50\%$ during years with large amounts of litter are possible. We conclude that standing litter can have a sufficiently large effect on NEE to account for the observed interannual variability.

4.2. Does the Evidence Point to Standing Litter as a Main Driver of Interannual Variability at the SJFM?

[30] We have shown that the interannual NEP variability at the SJFM is the largest reported for any terrestrial ecosystem [Rocha and Goulden, 2008a], and have hypoth-

esized that these fluctuations are caused by a negative feedback between ANPP, the buildup of leaf litter, shading of green leaves by litter, a reduction in $-GEE$ and $-NEE$, and a subsequent reduction in ANPP. The critical remaining issue is whether variation in standing litter is, in fact, a main driver of interannual variability at the SJFM. Unfortunately, we lack the ideal data set to address this question (direct measurements of the interannual variability of standing litter), and the evidence at this point becomes circumstantial. However, four lines of evidence point to standing litter as a strong driver of interannual variability.

[31] First, Rocha and Goulden [2008a] were unable to relate the marsh's variability changes in the physical environment or LAI_{green} .

[32] Second, the experimental litter manipulations established that the middle steps of our hypothesized causal chain (i.e., a large accumulation of litter shades green leaves and reduces GEE and NEE) are physically plausible. Moreover, the remaining steps in the chain (i.e., high ANPP leads to the accumulation of litter, which influences subsequent GEE and ANPP) are widely accepted [Tilman and Wedin, 1991; Knapp and Seastedt, 1986; LeCain et al., 2000; Wilsey et al., 2002], leading to the conclusion that the overall mechanism is possible.

[33] Third, midsummer Landsat surface reflectances show a large increase in SWIR reflectance in 2001 and 2002 (Figure 8b). The observation during 2001 is especially noteworthy because it occurred during a year with a high LAI_{max} (Figure 8b, inset). Standing litter is more reflective in the SWIR than green vegetation because of the absence of leaf water in plant litter [Woolley, 1971]. The high SWIR reflectance in 2001 despite a high LAI_{max} can be best explained by the presence of a large amount of standing litter that increased the overall reflectance in the SWIR and red, and decreased the reflectance in the NIR (Figure 8) and the EVI (Figure 7). These observations also exclude the possibility of nutrient availability as a major driver of interannual variability because reflectance in the SWIR is insensitive to changes in leaf nutrient content at the canopy scale [Yoder and Pettigrew-Crosby, 1995; Xue et al., 2004]. The apparent increased abundance of standing litter in 2001 and 2002 may be a legacy of the ANPP during previous years. Years with above average leaf production (2000 and 2001) were followed by years with increased SWIR reflectance and presumably increased amounts of standing litter (2001 and 2002); years with below average leaf production (1999 and 2002) were followed by years with decreased SWIR reflectance and presumably decreased amounts of standing litter (2000 and 2003).

[34] Fourth, we found that the NEE and EVI remained tightly correlated, and largely decoupled from LAI_{green} , from year to year (Figure 7). This pattern is unusual and distinctive, since it is generally assumed that the correlation between CO_2 exchange and vegetation indices such as EVI is mediated by LAI_{green} , and that the correlations between LAI_{max} and either EVI or carbon uptake would be expected to be at least as strong as the correlation between EVI and carbon uptake. We were able to mimic the pattern in the tower observations by manipulating the amount of litter (Figure 7). Moreover, we found that at both the plot (Figure 6) and whole marsh levels (Figure 9), correcting green leaf area for the amount of shading caused by

standing litter improved the relationships between green leaf area, EVI and carbon uptake.

[35] We believe these four lines of evidence implicate standing litter as a strong driver of interannual variability at the SJFM. The first argument excludes the more conventional explanations for interannual variability; the second argument establishes that variation in standing litter could cause interannual variability of the magnitude observed; the third line of evidence indicates that standing litter varied between years; the fourth argument shows that an unusual and difficult to explain pattern in the long term interannual record can be well explained by variation in standing litter.

[36] We emphasize that this attribution is not exclusive, and that other factors, such as interannual shifts in the physical environment or interannual shifts in plant carbohydrate reserves [Rocha and Goulden, 2008b], may also contribute to the observed interannual variability. Nonetheless, we conclude that there is strong evidence to support the role of standing litter as a factor that influences interannual variability at the SJFM.

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References

- Amone, J. A., and D. Obrist (2003), A large daylight geodesic dome for quantification of whole-ecosystem CO₂ and water vapour fluxes in arid shrublands, *J. Arid Environ.*, *55*, 629–643, doi:10.1016/S0140-1963(02)00291-4.
- Asaeda, T., L. H. Nam, P. Hietz, N. Tanaka, and S. Karunaratne (2002), Seasonal fluctuations in live and dead biomass of *Phragmites australis* as described by a growth and decomposition model: Implications of duration of aerobic conditions for litter mineralization and sedimentation, *Aquat. Bot.*, *73*, 223–239, doi:10.1016/S0304-3770(02)00027-X.
- Asner, G. P., C. A. Bateson, J. L. Privette, N. El Saleous, and C. A. Wessman (1998), Estimating vegetation structural effects on carbon uptake using satellite data fusion and inverse modeling, *J. Geophys. Res.*, *103*, 28,839–28,853, doi:10.1029/98JD02459.
- Bonneville, M.-C., I. B. Strachan, E. R. Humphreys, and N. T. Roulet (2008), Net ecosystem CO₂ exchange in a temperate cattail marsh in relation to biophysical properties, *Agric. For. Meteorol.*, *148*, 69–81, doi:10.1016/j.agrformet.2007.09.004.
- Briggs, J. M., and A. K. Knapp (1995), Interannual variability in primary production in tallgrass prairie: Climate, soil moisture, topographic position, and fire as determinants of aboveground biomass, *Am. J. Bot.*, *82*, 1024–1030, doi:10.2307/2446232.
- Davis, C. B., and A. G. van der Valk (1977), The decomposition of standing and fallen litter of *Typha glauca* and *Scirpus fluviatilis*, *Can. J. Bot.*, *56*, 662–675, doi:10.1139/b78-073.
- Findlay, S., K. Howe, and H. K. Austin (1990), Comparison of detritus dynamics in two tidal freshwater wetlands, *Ecology*, *71*, 288–295, doi:10.2307/1940268.
- Horler, D. H. H., M. Dockray, and J. Barber (1983), The red edge of plant leaf reflectance, *Int. J. Remote Sens.*, *4*, 273–288, doi:10.1080/01431168308948546.
- Huete, A. R., and R. D. Jackson (1987), The suitability of spectral indices for evaluating vegetation characteristics on arid rangelands, *Remote Sens. Environ.*, *23*, 213–232, doi:10.1016/0034-4257(87)90038-1.
- Huete, A., H. Q. Liu, K. Batchily, and W. van Leeuwen (2002), A comparison of vegetation indices over a global set of TM images for EOS-MODIS, *Remote Sens. Environ.*, *59*, 440–451, doi:10.1016/S0034-4257(96)00112-5.
- Jasoni, R. L., S. D. Smith, and J. A. Arnone III (2005), Net ecosystem CO₂ exchange in Mojave Desert shrubland during the eighth year of exposure to elevated CO₂, *Global Change Biol.*, *11*, 749–756, doi:10.1111/j.1365-2486.2005.00948.x.
- Jones, H. G. (1992), *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*, 2nd ed., 428 pp., Cambridge Univ. Press, New York.
- Jordan, T. E., D. F. Whigham, and D. L. Correll (1990), Effects of nutrient and litter manipulations on the narrow-leaved cattail, *Typha angustifolia* L., *Aquat. Bot.*, *36*, 179–191, doi:10.1016/0304-3770(90)90081-U.
- Knapp, A. K., and T. R. Seastedt (1986), Detritus accumulation limits productivity of tallgrass prairie, *BioScience*, *36*, 662–668, doi:10.2307/1310387.
- Kuehn, K. A., D. Steiner, and M. O. Gessner (2004), Diel mineralization patterns of standing-dead plant litter: Implication for CO₂ flux from wetlands, *Ecology*, *85*, 2504–2518, doi:10.1890/03-4082.
- LeCain, D. R., J. A. Morgan, G. E. Schuman, J. D. Reeder, and R. H. Hart (2000), Carbon exchange rates in grazed and ungrazed pastures of Wyoming, *J. Range Manage.*, *53*, 199–206, doi:10.2307/4003283.
- Pierce, L. L., and S. W. Running (1988), Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer, *Ecology*, *69*, 1762–1767, doi:10.2307/1941154.
- Rocha, A. V. (2008), The importance of intrinsic controls in driving interannual NEP variability, Ph.D. dissertation, Dep. of Earth Syst. Sci., Univ. of Calif., Irvine.
- Rocha, A. V., and M. L. Goulden (2008a), Large interannual CO₂ and energy exchange variability in a freshwater marsh under consistent environmental conditions, *J. Geophys. Res.*, doi:10.1029/2008JG000712, in press.
- Rocha, A. V., and M. L. Goulden (2008b), Why is marsh productivity so high? New insights from eddy covariance and biomass measurements in a *Typha* marsh, *Agric. For. Meteorol.*, *113*, G04019, doi:10.1016/j.agrformet.2008.07.010.
- Tilman, D., and D. Wedin (1991), Oscillations and chaos in the dynamics of a perennial grass, *Nature*, *353*, 653–655, doi:10.1038/353653a0.
- van Leeuwen, W. J. D., and A. Huete (1996), Effects of standing litter on the biophysical interpretation of plant canopies with spectral indices, *Remote Sens. Environ.*, *55*, 123–138, doi:10.1016/0034-4257(95)00198-0.
- Wessman, C. A., C. A. Bateson, and T. L. Benning (1997), Detecting fire and grazing patterns in tallgrass prairie using spectral mixture analysis, *Ecol. Appl.*, *7*, 493–511, doi:10.1890/1051-0761(1997)007[0493:DFAGPI]2.0.CO;2.
- Wilsey, B. J., G. Parent, N. T. Roulet, T. R. Moore, and C. Potvin (2002), Tropical pasture carbon cycling: Relationships between C source/sink strength, above-ground biomass and grazing, *Ecol. Lett.*, *5*, 367–376, doi:10.1046/j.1461-0248.2002.00322.x.
- Woolley, J. T. (1971), Reflectance and transmittance of light by leaves, *Plant Physiol.*, *47*, 656–662.
- Xue, L., W. Cao, W. Luo, T. Dai, and Y. Zhu (2004), Monitoring leaf nitrogen status in rice with canopy spectral reflectance, *Agron. J.*, *96*, 135–142.
- Yoder, B. J., and R. E. Pettigrew-Crosby (1995), Predicting nitrogen and chlorophyll content and concentrations from reflectance spectra (400–2500 nm) at leaf and canopy scales, *Remote Sens. Environ.*, *53*, 199–211, doi:10.1016/0034-4257(95)00135-N.

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