Commonalities of carbon dioxide exchange in semiarid regions with monsoon and Mediterranean climates

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Abstract

Comparing biosphere-atmosphere carbon exchange across monsoon (warm-season rainfall) and Mediterranean (cool-season rainfall) regimes can yield information about the interaction between energy and water limitation. Using data collected from eddy covariance towers over grass and shrub ecosystems in Arizona, USA and Almeria, Spain, we used net ecosystem carbon dioxide exchange (NEE), gross ecosystem production (GEP), and other meteorological variables to examine the effects of the different precipitation seasonality. Considerable crossover behavior occurred between the two rainfall regimes. As expected in these usually water-limited ecosystems, precipitation magnitude and timing were the dominant drivers of carbon exchange, but temperature and/or light also played an important role in regulating GEP and NEE at all sites. If significant rainfall occurred in the winter at the Arizona sites, their behavior was characteristically Mediterranean whereby the carbon flux responses were delayed till springtime. Likewise, the Spanish Mediterranean sites showed immediate pulse-like responses to rainfall events in non-winter periods. The observed site differences were likely due to differences in vegetation, soils, and climatology. Together, these results support a more unified conceptual model for which processes governing carbon cycling in semiarid ecosystems need not differ between warm-season and cool-season rainfall regimes.

Keywords: semiarid, carbon dioxide, Mediterranean, monsoon, net ecosystem exchange

Introduction

Arid and semiarid areas occupy around one third of the Earth's land surface (Schlesinger et al., 1990) and store about 15% of the world's surface organic carbon (Lal, 2004) and 20-30% of the total organic and inorganic carbon (Eswaran et al., 2000; Rasmussen, 2006). In these dryland regions, water is the major limiting element for ecosystem mass exchange and productivity (Noy-Meir, 1973) as well as an important factor in how energy from net radiation is partitioned at the land surface (Small and Kurc, 2003). As most of the world's ecosystems experience substantial water limitation for some part of the year (Jenerette et al., 2011), studies of aridland water and carbon exchange can give important and more broadly applicable insights into water-limited ecosystem functioning.

Semiarid landscapes worldwide are under increasing pressures to provide products and services to expanding human populations and economic activity. In these regions precipitation is often sporadic and seasonal. Among semiarid zones, temperate monsoon and Mediterranean climates represent important extremes of seasonal precipitation as monsoon systems have concentrated rainfall in the warm, summer season, while in Mediterranean areas much of the precipitation occurs in the cool season. These seasonal changes in atmospheric forcing via inputs of radiation, temperature, vapor pressure, and wind provide an opportunity to see how other constraints besides water limitation may play roles in governing ecosystem carbon exchange.

In semiarid monsoon, or warm-season, precipitation systems, rainfall arrives around the peak in atmospheric energy input. This brings about a strong competition for soil water between plants and direct evaporation to the atmosphere from bare soil, demanding a fast response by the

vegetation to quickly use, or lose, available water. The sporadic nature of rainfall, as well as the response of the ecosystem to it, gives rise to the Pulse paradigm (Huxman et al., 2004; Noy-Meir, 1973; Reynolds et al., 2004). This paradigm for ecosystem CO_2 cycling posits that small rainfall events provoke quick periods, or pulses, of heterotrophic respiratory efflux but do not evoke a photosynthetic response (Huxman et al., 2004). Larger precipitation events (> ~10 – 20 mm) are needed to sufficiently moisten the soil to greater depths (> ~5 - 10 cm) to provoke longer-term pulses of photosynthesis and autotrophic respiration due to plant growth. Total seasonal rainfall is strongly correlated with the number of larger storms (Emmerich, 2007; Huxman et al., 2004), and thus total photosynthesis is well correlated with seasonal rainfall totals in these regions (Anderson-Teixeira et al., 2011; Kurc and Small, 2007; Scott et al., 2010; Scott et al., 2009). Likewise, in above-average rainfall years these ecosystems tend to be sinks of carbon (Anderson-Teixeira et al., 2011; Emmerich, 2003; Leuning et al., 2005; Mielnick et al., 2005; Scott et al., 2010; Scott et al., 2009). Much less is known about constraints other than water in semiarid monsoon systems that may occur outside the main growing season, especially in mid-latitude regions where the seasonal shift in climate forcing is substantial.

In Mediterranean, or cool-season, precipitation climates, water arrives when the atmospheric energy inputs are reduced and thus, water availability and available energy are strongly asynchronous. When the energy is low, unlike the fast response to rain events for monsoonal systems, water tends to accumulate in the soil until there is enough energy to activate respiratory and photosynthetic responses. Photosynthesis and respiration fluxes peak in the spring or early summer depending on precipitation season length, soil moisture storage, temperature, and light. This biological activity then tapers off and cease as the dry season

progresses and soil moisture becomes more limiting. Thus, in Mediterranean systems there are strong correlations between total photosynthesis and winter and spring rainfall totals (Aires et al., 2008; Ma et al., 2007) or even total annual precipitation (Xu and Baldocchi, 2004). However, while there is a positive relationship between yearly precipitation and net ecosystem exchange of CO_2 (NEE) (Luo et al., 2007), the variability in NEE is more strongly correlated with the timing of the rainfall and winter temperatures that determine the growing season length (Ma et al., 2007; Serrano-Ortiz et al., 2009). For some Mediterranean ecosystems, interpreting net CO_2 exchanges during dry season conditions is further complicated by ventilation of CO_2 from carbonate-rich soil, which may or may not have a biological source (Rey et al., 2012; Sanchez-Cañete et al., 2011; Serrano-Ortiz et al., 2009; Serrano-Ortiz et al., 2010).

In this paper we compare and contrast responses of two semiarid monsoon and two Mediterranean ecosystems to examine how precipitation seasonality influences patterns of ecosystem photosynthesis and net CO_2 flux. By doing so, we highlight when these fluxes are limited by atmospheric conditions or surface water supply. Also, we ask if there were crossovers in behavior that may blur the lines between monsoonal and Mediterranean responses. For example, are there times when Mediterranean systems display rapid pulse-like responses, and conversely, are there times when monsoon-dominated systems are constrained by cooler winter-season temperatures? To address these questions, we test the following hypotheses: 1) monsoon ecosystems given sufficient wintertime precipitation, exhibit a "Mediterranean response" , whereby the response of photosynthesis and net CO_2 uptake are delayed till spring, and 2) Mediterranean systems exhibit "monsoon" or pulse-like responses of photosynthesis and NEE when significant precipitation (> ~ 10 mm) falls in the non-winter

season. Moreover, we ask whether seasonal precipitation has the same effect on ecosystem photosynthesis and hypothesize that: 3) monsoon ecosystem photosynthesis is more responsive to variations in precipitation than in Mediterranean systems due to the co-occurrence of precipitation and warmer temperatures conducive to plant activity.

Methods

Meteorological and flux data collected for this study were collected over a grassland and savanna in southern Arizona, USA and a grassland and shrubland in Almería, southern Spain. Table 1 summarizes basic climate and vegetation information about the sites. At all sites, the eddy covariance technique was used to measure land-atmosphere fluxes, and micrometeorological measurement details for each site are presented elsewhere (Rey et al., 2012; Scott et al., 2010; Scott et al., 2009; Serrano-Ortiz et al., 2009). In brief, the wind and sonic temperature were sampled at 10 Hz by 3D sonic anemometers (CSAT3, Campbell Scientific Inc., USA) and the water vapor and CO_2 densities were measured by open-path infrared gas analyzers (Li-7500, LiCor Inc., USA). Covariances were calculated every half-hour after removing spikes and using Reynolds block averaging. We calculated fluxes of heat, water and CO_2 using the covariances and applying a 2D coordinate rotation and accounting for density effects. Net ecosystem exchange of CO_2 (NEE) was computed by adding the 30 minute change in CO_2 storage term to the carbon dioxide flux. The storage term was estimated by using on the change in concentration measured by the IRGA at the top of the towers. At the two taller towers (MON1 and MON2) where profile measurements of CO_2 were available for part of the records, this simple method of only using the change in IRGA concentration was shown to produce negligible error (Scott et al., 2010; Scott et al., 2009).

The flux data were filtered for spikes, instrument malfunctions, and poor quality. Rejection criteria used to screen data were: rain events, out-of-range signals, and spikes with the standard deviation of [CO_2], [H2O] and/or sonic temperature. The amount of missing 30-minute NEE data for the entire period of data was 8.8%, 11.3%, 25.3%, and 37.4% at MON1, MON2, MED1, and MED2, respectively, with more frequent gaps during periods of precipitation and cold temperatures. Also, we applied published friction velocity (u_*) thresholds (0.15 m s^{-1} - MON1 and MON2, 0.10 m s^{-1} - MED1, 0.20 m s^{-1} – MED2) to omit NEE fluxes when there was not sufficient turbulence to make representative flux measurements (Malhi et al., 1998). Applying the u* threshold eliminated 7.0/21.8%, 13.4/43.2%, 3.4/20.2%, and 11.5/32.7% (day/night) of the remaining NEE data at MON1, MON2, MED1, and MED2, respectively.

There are several techniques commonly used to gap-fill and partition EC-derived NEE. Each technique introduces its own significant systematic error, yet despite this the overall temporal patterns of the partitioned fluxes (gross ecosystem production, GEP, and ecosystem respiration, R) and their magnitudes relative to each other remain robust regardless of technique (Lasslop et al., 2010). Accordingly, we focus herein on these temporal patterns at each site and their relative magnitudes between the sites rather than absolute magnitudes in our analysis below.

We partitioned NEE into R and GEP by first determining 30-minute R by fitting an exponential function to air temperature and nighttime NEE data over a moving ~ 5-day window (Reichstein et al., 2005), where the window position and size were adjusted to ensure that data from pre-rain (dry) periods were not grouped together with data following storms. This model was then used to fill missing nighttime NEE data and model daytime respiration. Missing daytime values

of NEE were filled by fitting a 2nd order polynomial to the response of NEE to PAR for morning and afternoon periods, separately, over a 5-day moving window. If the window contained less than 60 values of NEE (roughly one half of the data potentially available in five days) the window was incrementally increased one day at a time until this condition was met. Finally, GEP was determined by GEP = R – NEE. We used the standard sign convention for NEE with NEE> 0 indicating a net loss of CO_2 to the atmosphere (source) and NEE < 0 indicating CO_2 uptake by the ecosystem (sink). R and GEP are always positive. After computing daily sums of these quantities there were cases where daily GEP was negative. This indicated an underestimation of daily R so on these occasions GEP was zeroed with the magnitude of that negative quantity added back into R. In the case of MED1 and MED2 where there is evidence of CO_2 ventilation from rock and soil cavities (Rey et al., 2012; Sanchez-Cañete et al., 2011; Serrano-Ortiz et al., 2009), this daily partitioning process captures the effects of this process on the daily magnitude of R, but not its sub-daily temporal dynamics. However, it is because of this process that we did not compare R between sites below. Linear regression was used to determine the strength of the relationship between GEP and precipitation during spring (1-January – 31-May) and summer (15-June – 31 October) at the monsoon sites, and 1-September – 1-August at the Mediterranean sites. These periods were chosen based on overall patterns of GEP shown at these sites (see next section). Specific pair-wise slope comparisons were made using Tukey's Honestly Significant Difference (HSD) test, if F-test criteria testing for slope differences described in Zar (Zar, 1974) were met. Standard errors to calculate HSD were made using the pooled sum of squares, with HSD scores needing to exceed 5.35 to be significant at $p < 0.01$.

As a measure of atmospheric evaporative demand, we computed the reference crop evaporation rate, ET_o (Shuttleworth, 1993). Reference crop evaporation is an estimate of the evaporation, which would occur from a short, well-watered grass with a fixed-height of 0.12 m, an albedo of 0.23 and a surface resistance of 69 s m^{-1}.

As detailed site vegetation measurements to quantify phenological changes were not routinely sampled at the sites, we used National Aeronautics and Space Administration's (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI, (Huete et al., 2002)), which was available as a composite 16-day, 250 m product (MOD13Q1; ORNL DAAC, 2011) as a measure of vegetation greenness and phenological activity over the course of this study at each site. EVI was averaged over the 9 pixels (a 0.75 x 0.75 km square) around and centered on the tower.

Results

Meteorological and phenological conditions

The seasonal cycle of air temperature at all of these northern latitude sites was similar, but the higher latitude/elevation MED2 was clearly cooler (Fig. 1). The rest of the sites were all cool in winter, while the monsoon sites were considerably warmer in the summer, especially in May and June prior to onset of the summer monsoon. The seasonality of precipitation was clearly opposite with monsoon sites peaking in summer and Mediterranean sites in winter (Fig. 1). Precipitation variability was high, and annual totals ranged between 230 – 404 mm at MON1, 162 -335 mm at MON2, 262 – 378 mm at MED1 and 182 – 1143 mm at MED2. MED2 was the only site that had occasional periods of precipitation falling as snow in the winter months. But

these were storm specific, and the snow typically melted within a few days after the storm. The monsoon sites had a higher atmospheric evaporative demand, as quantified by ET_o (Fig. 1), primarily due to higher solar radiation and vapor pressure deficit. The ratio P/ET_o was always less than unity at the monsoon sites indicating that these sites were always water-limited at the monthly timescale, while $P/ET_o > 1$ for the months of November through February at the Mediterranean sites. Vegetation greenness, as quantified by EVI (Fig. 1), differed considerably among the sites, especially at the Mediterranean ones. At MON1, EVI was higher than, but had a very similar annual cycle to, MON2. At MED1, EVI increased monotonically over the fall months, peaked in February/March, then decreased to minimum levels in the summer. At MED2, EVI increased slightly in fall, bottomed out again from December through February, ramped up to a peak EVI in May, and then declined to low values in August and September.

NEE and GEP

The seasonal patterns of NEE at the monsoon sites were very similar (Fig. 2) with little winter activity, occasional springtime net uptake (NEE < 0), and inactive dry fore-summers. The periods of spring net uptake at MON2 tended to begin and end earlier than at MON1, likely because the mesquite trees at MON1 are less freeze tolerant and green-up later than perennial grasses. The start of the monsoon around July result in periods of net efflux followed by peaks in uptake in August and September that taper off in the drier and cooler fall months.

The patterns of NEE at the Mediterranean sites reveal short and highly variable periods of low net uptake in winters and peak springtime uptake (Fig. 2). At MED1, periods of net uptake began in mid-October and sometimes continued on through spring, a pattern which occurred

rarely at MED2. The spring net uptake peaks were larger and occurred later at the wetter and colder MED2, where spring temperatures lagged behind MED1 by around two months. The dry and hot summer months were characterized by net releases of CO_2.

Disaggregating NEE into its component fluxes, allows us to see the role that plants, as quantified by GEP, contributed to the patterns of net $C0_2$ flux at these sites. At the monsoon sites, there were both occasional spring and regular summer/fall growing seasons (Fig. 3), while periods of net uptake (Fig. 2) were more limited and almost always lagged behind the onset of significant vegetation growth (photosynthesis) especially in summer. At the Mediterranean sites, photosynthesis usually began in fall and extended into spring or even early summer, but GEP was lower and more discontinuous across the fall and winter at the higher and colder MED2 site. In spring, the peak in mean GEP at MED1 was slightly broader and occurred earlier than at MED2. These ensemble patterns of GEP were quite similar to the phenological patterns (Fig. 1-EVI)

To demonstrate the role of water availability and temperature on vegetation growth and carbon uptake at these sites, we selected two example years representing dry and wet conditions from each site. Based on the patterns of flux activity shown at the sites (Fig. 2 and 3), we display two calendar years for monsoon sites and two year length records beginning on the 1st of September for the Mediterranean sites. The latter is analogous to the concept of a "hydrological year" commonly used in Mediterranean and snowmelt-dominated systems.

At the monsoon sites in 2006, there was a severe drought prior to the monsoon and an above-average monsoon rain totals, and 2010 had above-average cool season rainfall and an average

monsoon (Fig. 4 and 5). In 2006, there was little GEP and NEE before monsoon onset. Significant photosynthesis began about a week after the larger rains at the end of July. At the monsoon onset, there was a large respiratory efflux (NEE > 0) and the period of net uptake did not occur until after GEP was greater than ~2.5 (MON1) and 2.0 gC m^{-2} d^{-1} (MON2). Likewise, it ended at a similar level of GEP, which peaked and declined shortly after the bulk of the monsoon rainfall had ended. In 2010 there was a similar pattern of response during the monsoon, but this El Niño year's wet cool season brought about sustained periods of photosynthesis and net uptake in spring. The response of the vegetation in the spring was different than in the monsoon as it lagged much farther behind the rainfall. Also, net uptake did not lag far beyond the onset of photosynthesis to the same degree as it had in the monsoon seasons. The spring onset of photosynthesis, defined GEP>0 for five consecutive days, did not begin until the temperature exceeded 7.0 °C, quantified by the 10-day average daily temperature prior to onset (T_{10}). Across all years, T_{10} averaged 12.2°C at MON1 and 7.3°C at MON2 . While the seasonal patterns of GEP and NEE for these years at the monsoon sites were broadly similar, NEE was usually higher at MON1, indicating less net $C0_2$ uptake overall (Scott et al., 2009). Also, although there was considerably more cool-season precipitation at MON1 in 2010, the spring GEP and net uptake response were smaller.

At MED1, GEP responded immediately to the onset of fall rains, and the larger amount of early rainfall in 2007-2008 gave rise to a longer and more vigorous winter of photosynthesis (Fig. 6). While '08-'09 precipitation totals eventually caught up and then exceeded '07-'08 totals, this was not until temperatures had declined. Photosynthesis continued to decline from December 2008 until February 2009 despite the additional water, and more substantial photosynthesis

occurred in the spring of 2009 only after average temperatures had warmed (mean T_{10} = 10.6 °C). With little precipitation in the spring of 2008, photosynthesis ceased in early April (Fig. 6). However a large 40 mm pulse in May brought about significant vegetation growth for another month. Periods of uptake were brief at this site and did not generally occur until GEP exceeded ~1.5 gC m^{-2} d^{-1}.

At MED2, precipitation totals were low in 2004-2005 and very high in 2009-2010 (Fig. 7). In autumn, photosynthesis began shortly after the arrival of rainfall in both years. Precipitation was high enough in 2009 to generate a period of considerable GEP and net uptake, which were quickly truncated by winter storms that brought large amounts of precipitation and cooler temperatures near the end of December (Fig. 7). In the spring of both years, longer periods of photosynthesis began in March –April, associated with an average T_{10} = 5.6 °C. Here, periods of significant uptake generally did not lag behind periods of vegetation growth and were associated with a lower GEP threshold of ~ 0.5 gC m^{-2} d^{-1}.

Precipitation and Photosynthesis

Seasonal GEP was closely tied to precipitation at all sites (Fig. 8; all regressions significant at $p<0.05$), with significant GEP:P slope differences both within and between sites ($F_{5,25}$=26.5; $p<0.05$). Pairwise Tukey's HSD testing shows this was due to MON1's springtime photosynthetic sensitivity to precipitation being significantly lower than in summer at this site and at MED1 (Fig. 8). The sensitivity for MON1-summer, MON2-both seasons, and MED1 did not significantly differ, while it was lower than all others at MED2 (Fig. 8).

Discussion

We examined land-atmosphere carbon exchange from semiarid monsoon and Mediterranean sites in order to examine how precipitation seasonality influences seasonal patterns of CO_2 fluxes. The variability of annual precipitation, especially relative to the mean, in dryland regions is well known (Goodrich et al., 2008; Lázaro et al., 2001), and the importance of this variability to ecosystem-level gas exchange is manifested because of prevailing water-limited status of plants and microbes in these systems (Jenerette et al., 2011). While, as expected, the variability in precipitation drove the large interannual variation in NEE and GEP at every site (Fig. 1, 2, 3), there were commonalities in the flux responses across the dominant rainfall regimes that depended on the precipitation seasonality.

We hypothesized that our monsoon sites would exhibit a characteristic Mediterranean response given sufficient cool-season precipitation. This was supported by the presence of significant GEP and net $C0_2$ uptake in the spring (Fig. 2 and 3) that was not an immediate response to recent precipitation and rather a response to warming temperatures (and/or light) and precipitation that had accumulated in the soil much earlier (Fig. 4 and 5). Previous studies have analyzed seasonal and annual variability of $C0_2$ fluxes at the individual semiarid monsoon sites used in this study (Scott et al., 2010; Scott et al., 2009) and elsewhere (Eamus et al., 2001; Hastings et al., 2005; Kurc and Small, 2007; Leuning et al., 2005; Perez-Ruiz et al., 2010). In concurrence with smaller datasets (Scott et al., 2010; Scott et al., 2009), the annual cycles of GEP and NEE at MON1 and MON2 indicate a dominant annual growing season and period of net uptake governed by the timing and the strength of the North American Monsoon and a separate, but occasional, growing season in spring given sufficient cool-season rainfall (Fig. 2 and 3). This mix of slow and delayed versus fast and immediate responses support Reynolds et

al. (2004), who suggested that the simple rainfall-pulse-then-biological-pulse-response is too limited and should be modified to include the concept of pulses of soil moisture recharge which are differentially utilized depending on plant functional types and site conditions (soil type, meteorology). Also similar to the Mediterranean responses, the decrease in temperatures and/or light in winter led to suppressed fluxes despite the occurrence of precipitation. This behavior has been observed at other mid-latitude monsoon sites (Anderson-Teixeira et al., 2011; Kurc and Small, 2007), but not at warmer, low latitude locations with higher winter temperatures (Hastings et al., 2005).

While the general patterns of fluxes at the monsoon sites were quite similar, there were some important differences. Springtime GEP was higher and NEE was lower in 2010 at MON2 even with less antecedent P (Fig. 4 and 5), and this spring photosynthetic response at MON1 was weaker throughout all the years of this study (Fig. 8). We speculate that this was due to the denser herbaceous vegetation and higher water holding capacity of the clay-rich soils at MON2. Also while during the main monsoon growing season GEP at MON1 is usually greater and more sensitive to precipitation relative to MON2 (Fig. 3, 8), there tends to be less net $C0_2$ uptake (Fig. 2) that may be due to greater standing biomass stemming from differences in vegetation composition (woody vs. herbaceous) that lead to higher respiration costs at MON1 (Scott et al., 2010; Scott et al., 2009).

We also hypothesized that the Mediterranean sites would exhibit a characteristic monsoon response, with immediate pulses of carbon flux activity (Huxman et al., 2004), when significant precipitation falls in the non-winter season. This was supported by the rapid onset of fluxes

responding to the return of rainfall in autumn (Fig. 6 and 7) or even late spring rain events (May, 2008, Fig. 6). Similarly, the large variability and seasonal timing in NEE shown at MED1 and MED2 in this study (Fig.2) are supported by previous studies (Rey et al., 2012; Serrano-Ortiz et al., 2009). The length of the growing season is dominated by the amount and timing of precipitation (Aires et al., 2008; Rey et al., 2012; Serrano-Ortiz et al., 2009; Xu and Baldocchi, 2004) and governs the interannual NEE variability (Ma et al., 2007). However, due to differences in altitude and thus, differences in temperature, plant growth at the lower elevation MED1 is more vigorous (Fig. 1-EVI and 3) during the fall and winter and can act as a carbon sink during this period (Fig. 3), while growth was more limited in fall and especially winter at MED2, where there was a distinct cessation of photosynthesis likely due to the colder temperatures and occasional snowfall (Serrano-Ortiz et al., 2007). Thus, carbon accumulated (NEE < 0) more often at the end of spring and continued till late summer at MED2 (Fig. 2). Seasonal precipitation amounts also control the length of the dry period in summer. During the dry period, the ecosystems acted as net sources, emitting the CO_2 probably due to a combination of processes (respiration, photo-degradation, and ventilation from rock and soil cavities).

For these water-limited ecosystems, photosynthesis was strongly coupled to precipitation (Fig. 8). We hypothesized that the monsoon sites would be more responsive given the higher typical growing season temperatures. This was partially supported in that response of GEP to precipitation was significantly lower than the rest of the sites at MED2, but the sensitivity at MED1 was not distinct from both MON1 (summer only) and MON2 (both seasons), suggesting a similar ecosystem rain use efficiency (GEP/P). This is quite surprising given the differences in the plant composition, structure, and soils between the sites (Table 1). However, it was also

clear that, even at one site (MON1, Fig. 8), rain use efficiency can clearly vary between the spring and summer periods. While more investigation is needed, we suggest that the diminished sensitivity at MON1 (spring) and MED2 may be due to similar reasons concerning how cool-season precipitation is translated into springtime plant available soil moisture via site-specific soil properties. Temperatures and/or light appear to limit plant activity during winter at MON1 and MED2 (Fig. 3, 4, 7), precipitation that falls during this time may quickly infiltrate past the root zone in the very sandy soils (MON1) or drained (groundwater recharge) by the karst terrain (MED2) before the plants can utilize this water in the subsequent growing season (Cantón et al., 2010).

Finally, while precipitation was the dominant control, the depression in energy input in the winter at these mid-latitude sites also played a governing seasonal role (Fig. 4-7). Starting dates of springtime photosynthesis had antecedent temperatures (T_{10}) that declined from ~12°C at the warmest MON1 site to the ~6°C at coolest MED2 site, suggesting some thermal adaptation of ecosystem photosynthesis (Baldocchi et al., 2001; Yuan et al., 2011). Temperature also likely played an important role in determining when periods of photosynthesis transitioned into periods of net uptake. At the monsoon sites, this transition was reached when GEP increased above ~ 1 gC m^{-2} d^{-1} in the spring and ~ 2 - 2.5 gC m^{-2} d^{-1} in the summer (Fig. 4 and 5). Periods of net uptake occurred when GEP was above ~ 0.5 gC m^{-2} d^{-1} in the spring at MED2 and ~ 1 – 1.5 gC m^{-2} d^{-1} in the fall at MED1 (Fig. 6 and 7). The magnitude of these GEP thresholds increase with temperature at the sites probably due to the strong positive relationship between temperature and respiration, which must be exceeded by GEP to have net uptake.

Conclusions

In this comparison of semiarid sites dominated by differences in winter and summer precipitation, many commonalities in the response of CO_2 fluxes to atmospheric forcing were observed. Precipitation magnitude and timing were the dominant drivers of carbon exchange, but temperature also played an important role in regulating gross and net ecosystem carbon uptake at all sites. Also, the fluxes rapidly responded to precipitation events in a pulsed manner (even at the Mediterranean sites) but mainly in the warm season when temperatures were not limiting. In the coolest parts of the winter season, photosynthesis and uptake were not responsive to precipitation. Rather, precipitation accumulated in the soil and fueled springtime growth after it had warmed. Cumulative photosynthesis was strongly related to precipitation within and across sites. The site-specific differences like the magnitude and timing of the periods of photosynthesis and net $C0_2$ uptake are likely related to the differences in site composition (e.g., MON2 - grass and MON1 - mixed grass and tree), soils (e.g., low versus high soil water holding capacity) and atmospheric forcing (e.g., temperature differences between MED2 and the other sites). Together, these results support a more unified conceptual model of carbon cycling in semiarid ecosystems, such that the description of the ecosystem processes that contribute to carbon exchanges need not differ between warm-season and cool-season rainfall regimes. Using the modified Pulse Paradigm of Reynolds et al. (2004), pulses of soil moisture recharge are acted upon by biology (plants and microbes) to generate pulses on carbon flux responses, whose timing and magnitude depends on environmental triggers like temperature and light.

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Table 1. Physical description of the study sites.

Site Abbreviations and Names	MON1 Santa Rita Mesquite Savanna	MON2 Kendall Grassland	MED1 Balsablanca	MED2 El Llano de los Juanes
Location	Santa Rita Exp. Range Arizona, USA	Walnut Gulch Exp. Watershed Arizona, USA	Cabo de Gata Almería, Spain	Sierra de Gádor Almería, Spain
Data Period	Jan,2004 – Dec,2010	May,2004 – Dec,2010	Jun,2006 – Dec,2010	May,2004 – Dec,2010
Elevation (m)	1120	1530	195	1600
Mean Air Temperature (period of study, ºC)	19.2	17.5	17.3	11.9
Annual precipitation (period of study, mm)	324	262	319	632
Ecosystem description and dominant species	Sonoran Desert upland, dry savanna with deciduous C_3 mesquite trees *(Prosopis velutina)* and an understory of various perennial C_4 bunchgrasses (*Eragrostis lehmanniana*), annual C_4 grasses (*Bouteloua aristidoides*), and interspersed	Chihuauhuan Desert upland, semidesert perennial C_4 grassland (*Bouteloua spp.* until 2006 and *Eragrostis lehmanniana* after) interspersed with small shrubs and herbaceous annuals	Mediterranean steppe, 7 km from the coast, perennial C_3 tussock grass (*Stipa tenacissima*) interspersed with other perennial species	Mediterranean shrubland plateau, 25 km from the coast, perennial C_3 grasses (*Festuca scariosa*) and shrubs (*Genista pumila, Hormathophilla spinosa*)

	with various subshrubs and succulents			
Average canopy height (m)	2.5 (trees), 0.5 (grasses)	0.5	0.75	0.5
Peak Leaf Area Index and peak month	~1 (August)	~1 (August)	~1 (January)	~1 (May)
Vegetation coverage (%)	50 (total) with 35% tree cover	40	60	50
Soil depth and type	1-2 m, deep, loamy sands	1 – 2 m, deep, very gravelly, sandy to fine loams	0 – 0.3 m, thin sandy loams underlain by marine carbonate sediments	0-1.5 m, silt loams underlain by limestone bedrock

Figure Captions

Figure 1. Mean monthly air temperature, precipitation, reference crop evaporation (ET_o), and MODIS Enhanced Vegetation Index (EVI) during the period of study. Error bars represent +/- 1 standard deviation from the mean, which are not shown for precipitation as they dwarf the magnitude of the means.

Figure 2. Daily net ecosystem exchange of CO_2 (NEE) for all sites. Individual years are shown along with the ensemble daily mean (thick solid line).

Figure 3. Daily gross ecosystem production (GEP) for all sites. Individual years are shown along with the ensemble daily mean (thick solid line).

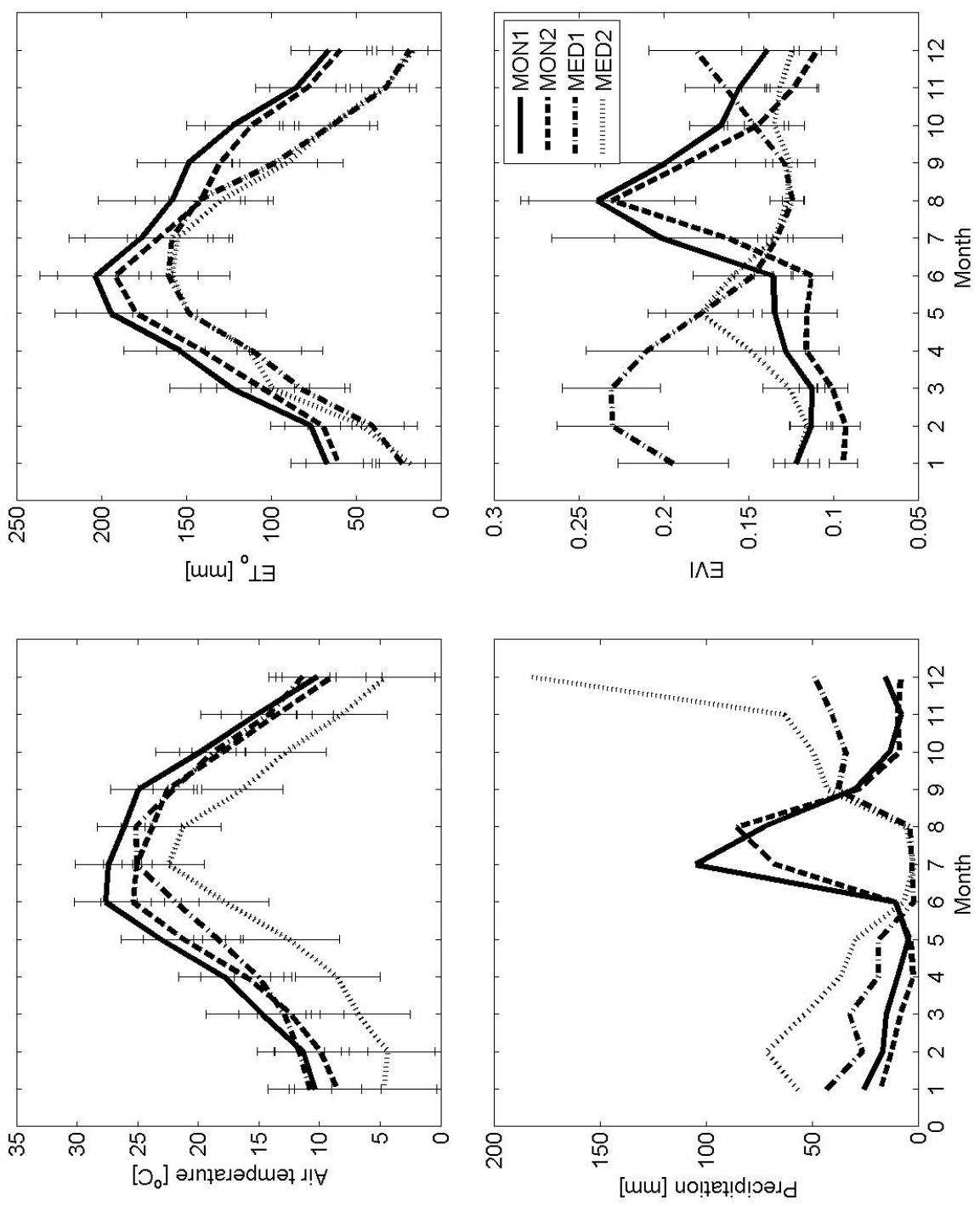
Figure 4. Two example calendar years of cumulative precipitation (P), daily average air temperature (T_a), gross ecosystem production (GEP) and net ecosystem exchange (NEE) at MON1.

Figure 5. Two example calendar years of cumulative precipitation (P), daily average air temperature (T_a), gross ecosystem production (GEP) and net ecosystem exchange (NEE) at MON2.

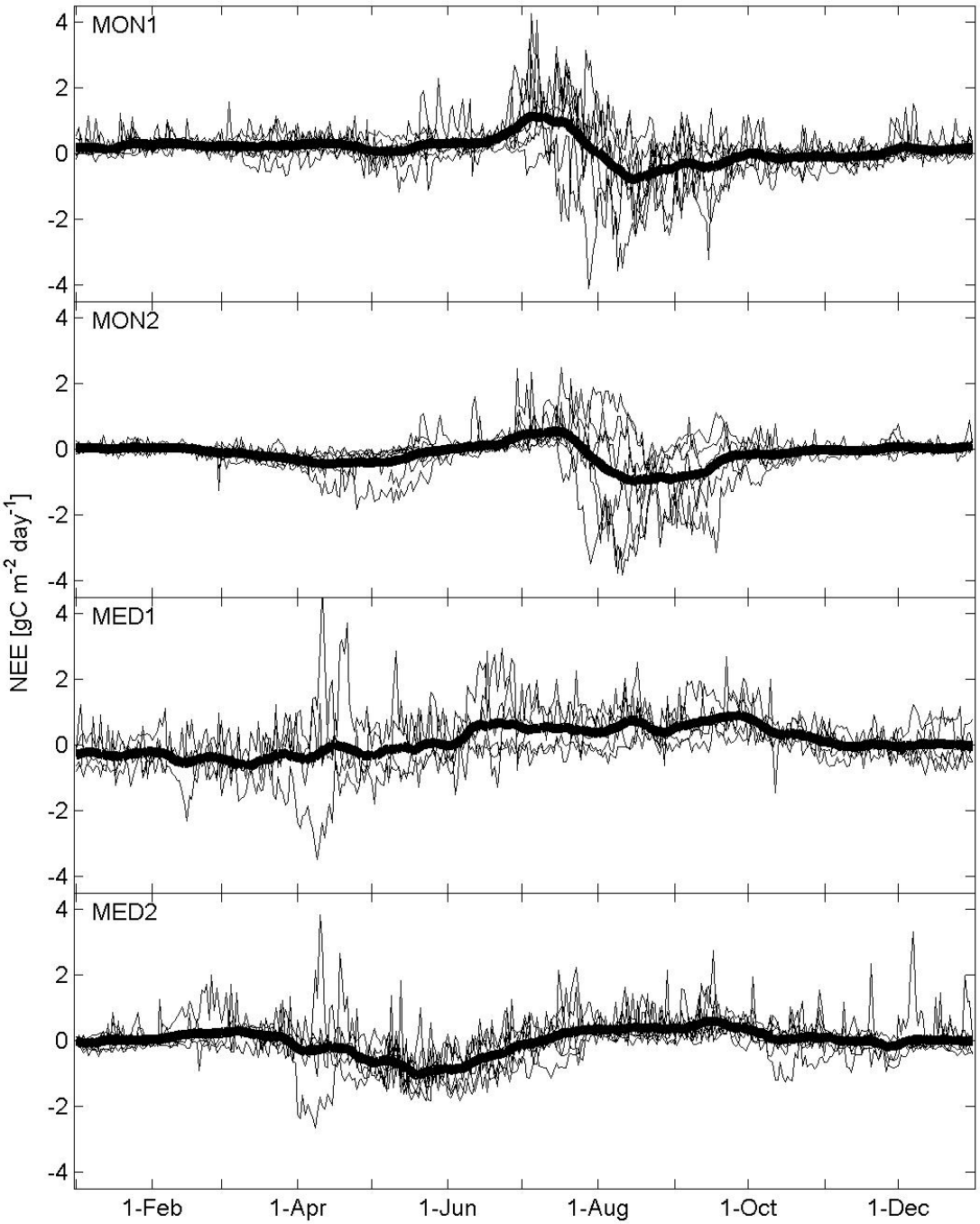
Figure 6. Two example hydrological years (September – August) of cumulative precipitation (P), daily average air temperature (T_a), gross ecosystem production (GEP) and net ecosystem exchange (NEE) at MED1.

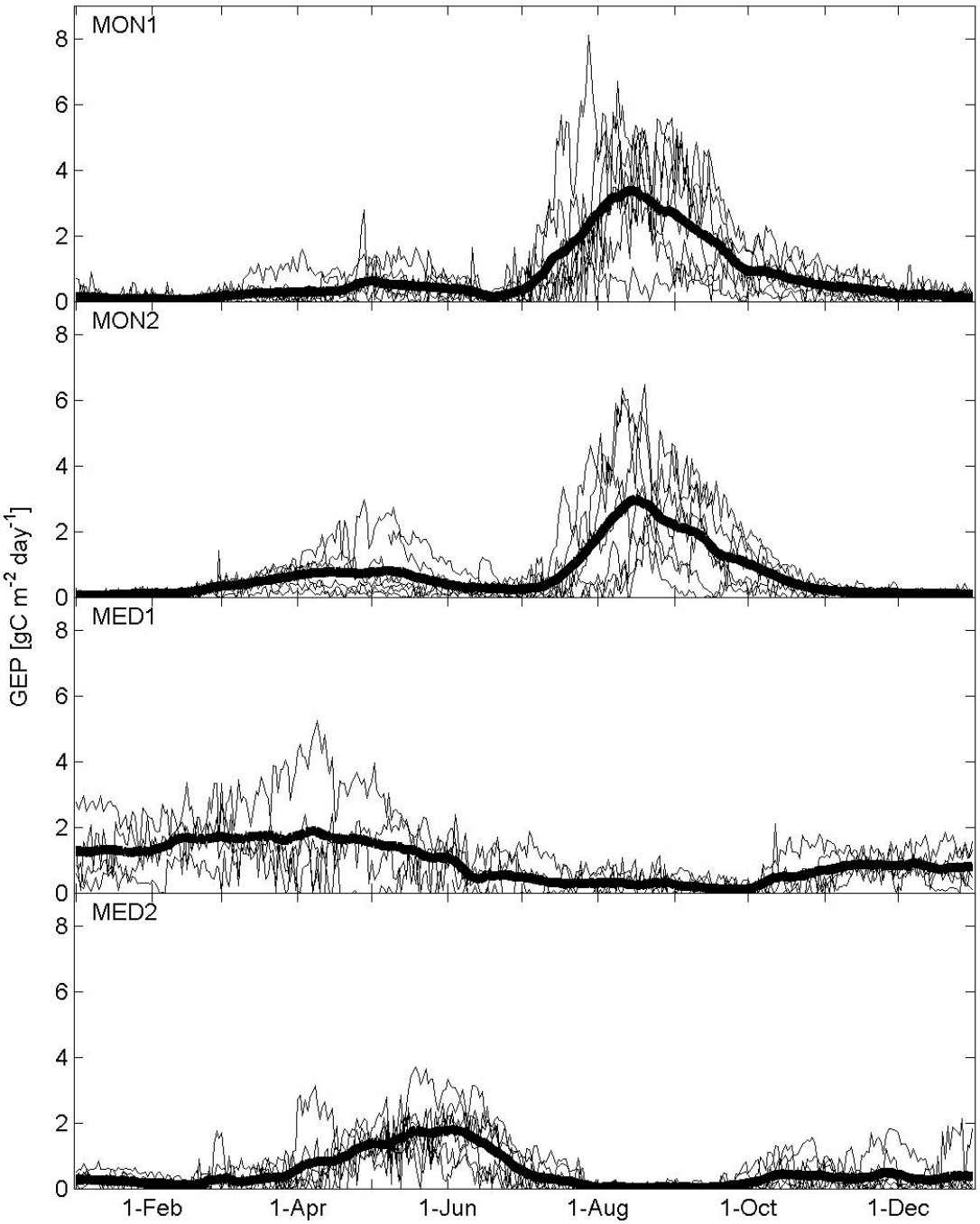
Figure 7. Two example hydrological years (September – August) of cumulative precipitation (P), daily average air temperature (T_a), gross ecosystem production (GEP) and net ecosystem exchange (NEE) at MED2.

Figure 8. Total precipitation (P) and photosynthesis (GEP). For the monsoon sites, spring (1-January – 31-May) and summer (15-June – 31 October) totals are separated due to the seasonally distinct growing seasons. For the Mediterranean sites, only 1-September – 1-August totals are shown. All least squares regressions are significant at $\alpha = 0.05$; regressions lacking a common superscript letter have slopes differing significantly at $p < 0.05$ (Tukey HSD).

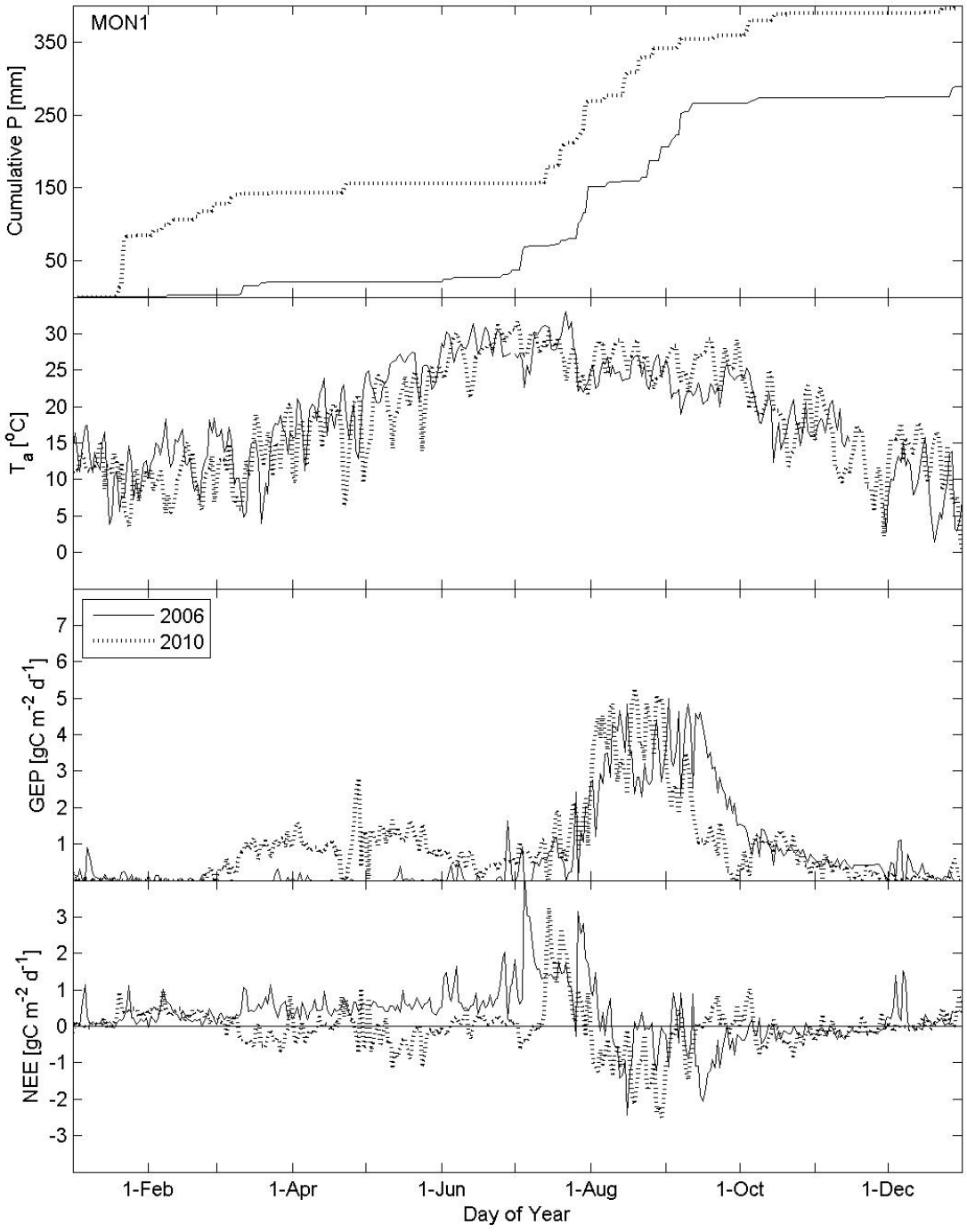

MON1
MON2
MED1
MED2
EVI
ET$_o$ [mm]
Air temperature [°C]
Precipitation [mm]
Month
Month

555

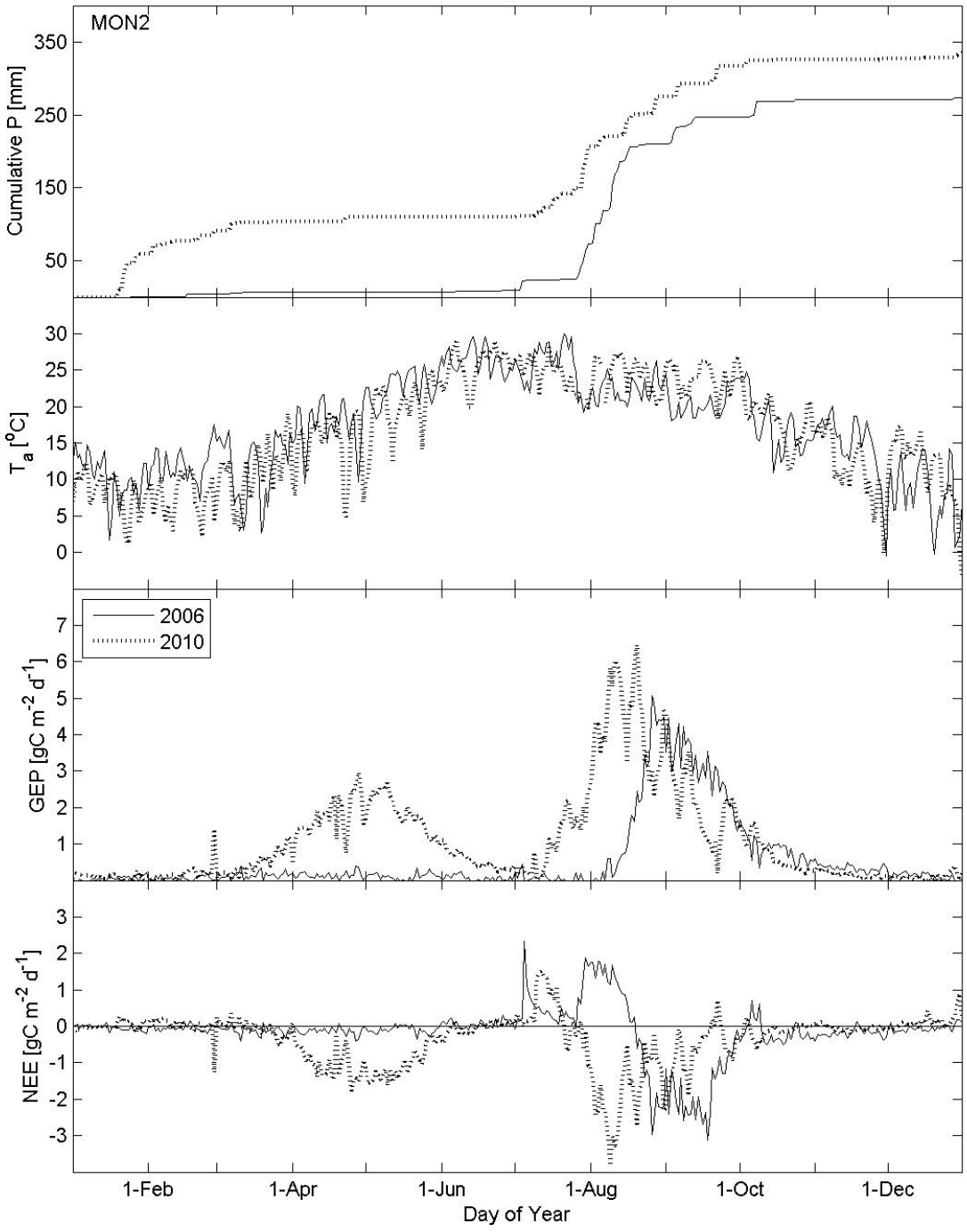

MON1
MON2
MED1
MED2
NEE [gC m-2 day-1]
4
2
0
-2
-4
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec


MON1
MON2
MED1
MED2
GEP [gC m-2 day-1]
0
2
4
6
8
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec

559
560

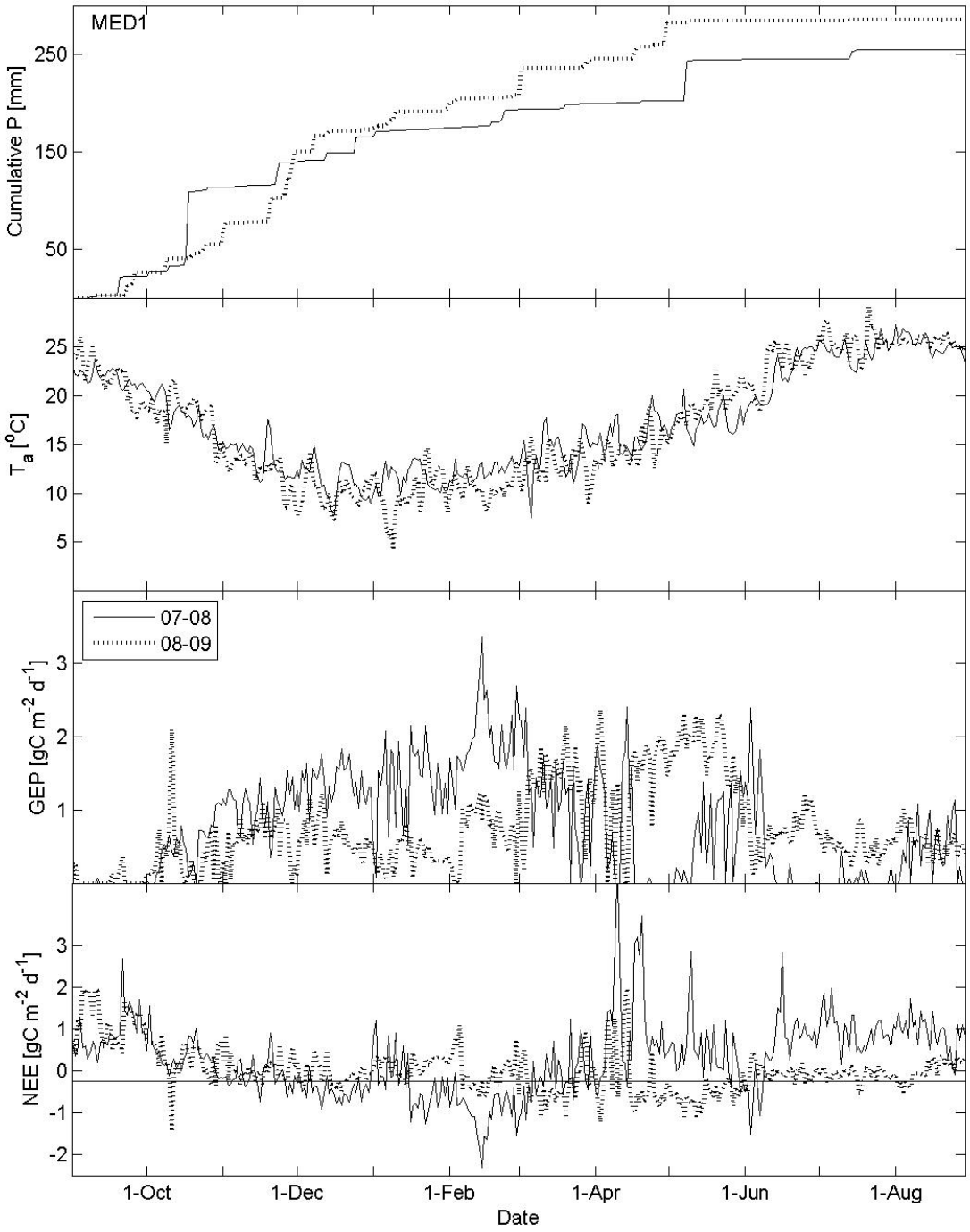

MON1
Cumulative P [mm]
350
250
150
50
T_a [°C]
30
25
20
15
10
5
0
2006
2010
GEP [gC m^{-2} d^{-1}]
7
6
5
4
3
2
1
NEE [gC m^{-2} d^{-1}]
3
2
1
0
-1
-2
-3
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
Day of Year

561

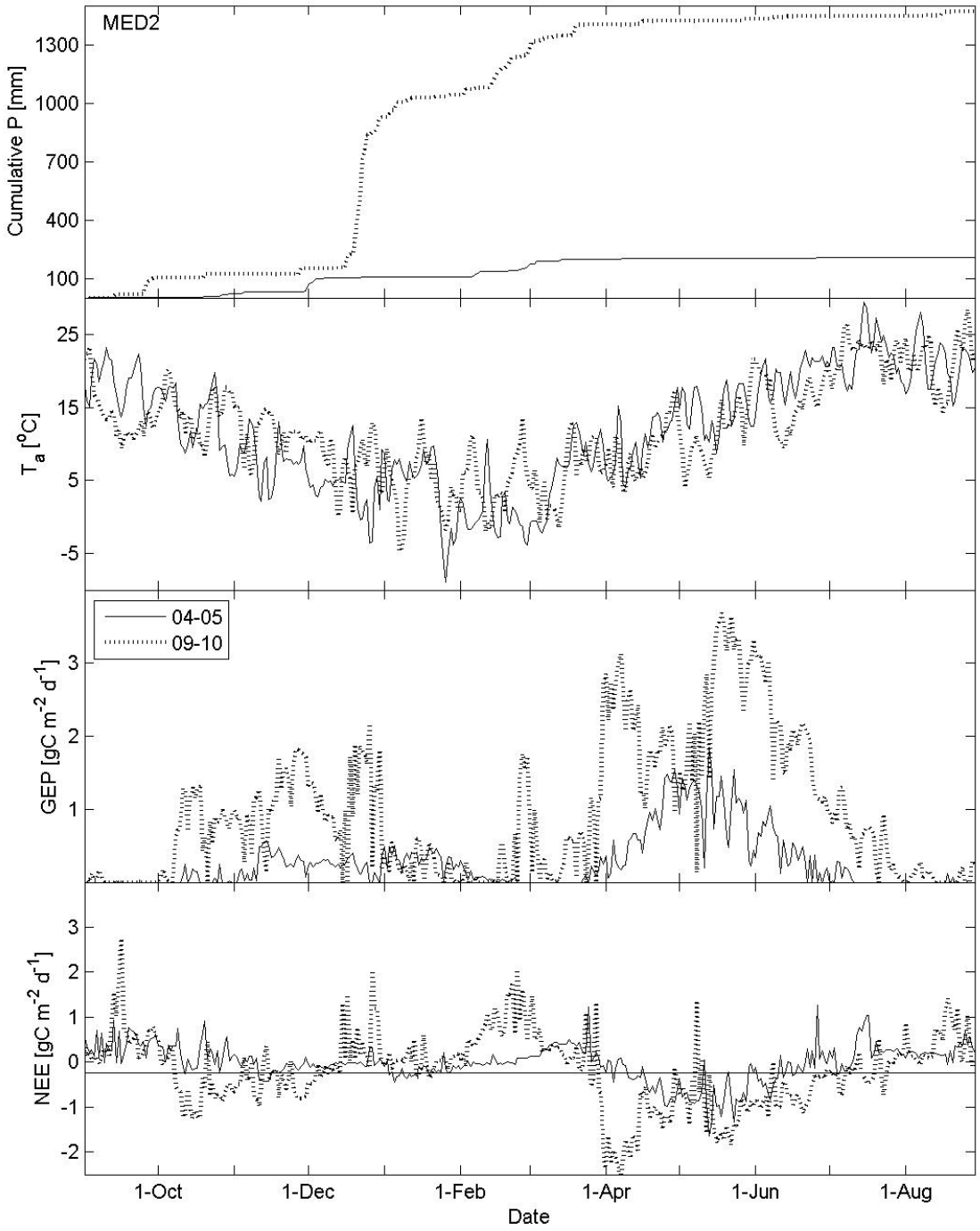

MON2
Cumulative P [mm]
350
250
150
50
T_a [°C]
30
25
20
15
10
5
0
2006
2010
GEP [gC m^{-2} d^{-1}]
7
6
5
4
3
2
1
NEE [gC m^{-2} d^{-1}]
3
2
1
0
-1
-2
-3
1-Feb
1-Apr
1-Jun
1-Aug
1-Oct
1-Dec
Day of Year

562

563

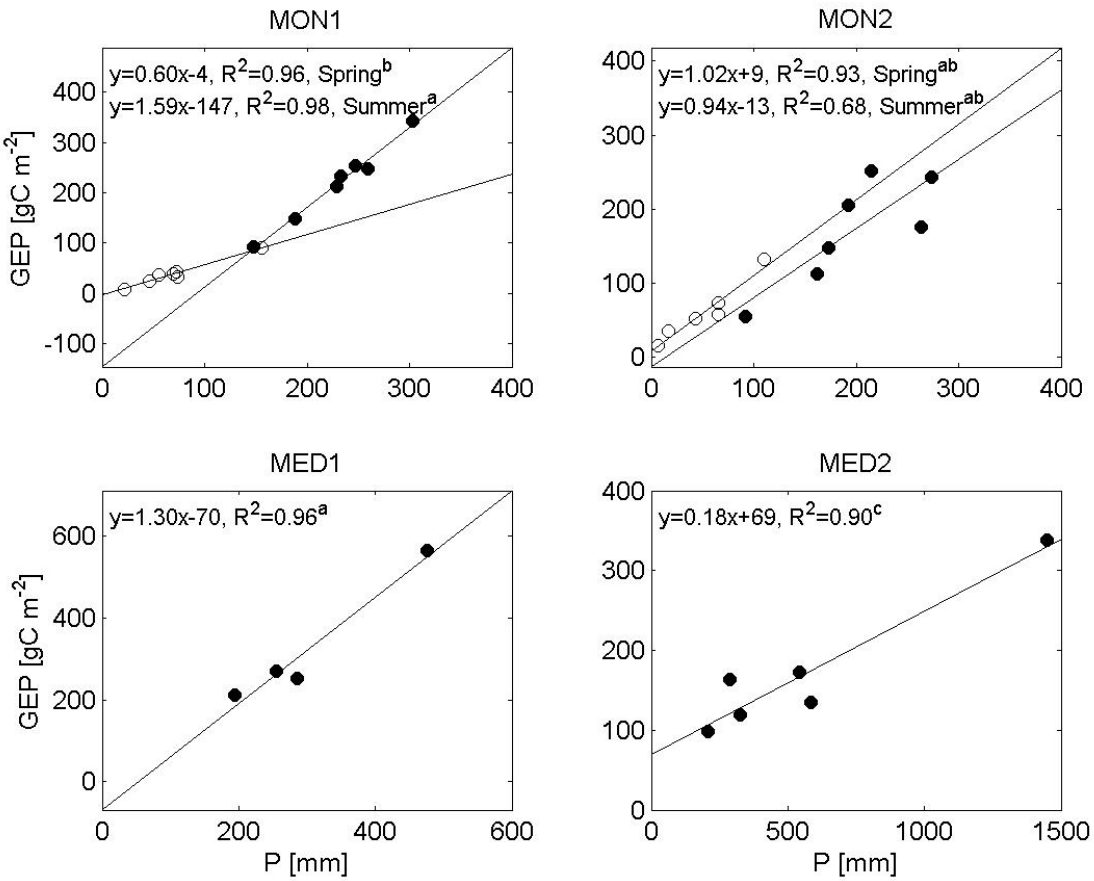

MED1
Cumulative P [mm]
250
150
50
T_a [^{o}C]
25
20
15
10
5
07-08
08-09
GEP [gC m^{-2} d^{-1}]
3
2
1
NEE [gC m^{-2} d^{-1}]
3
2
1
0
-1
-2
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
Date

564


MED2
Cumulative P [mm]
1300
1000
700
400
100
T_a [°C]
25
15
5
-5
04-05
09-10
GEP [gC m^{-2} d^{-1}]
3
2
1
NEE [gC m^{-2} d^{-1}]
3
2
1
0
-1
-2
1-Oct
1-Dec
1-Feb
1-Apr
1-Jun
1-Aug
Date

565

566


MON1
y=0.60x-4, R2=0.96, Springb
y=1.59x-147, R2=0.98, Summera
GEP [gC m-2]
MON2
y=1.02x+9, R2=0.93, Springab
y=0.94x-13, R2=0.68, Summerab
MED1
y=1.30x-70, R2=0.96a
GEP [gC m-2]
P [mm]
MED2
y=0.18x+69, R2=0.90c
P [mm]

567

568

***Highlights**

> We compare carbon dioxide fluxes at semiarid Mediterranean and monsoon sites.

> Fluxes at all sites showed periods of water and temperature/energy limitation for ecosystem photosynthesis and net carbon flux.

> Precipitation magnitude and timing were the dominant drivers of ecosystem net carbon uptake and photosynthesis.

> Low winter temperatures and/or light also regulated carbon exchange

> Total photosynthesis was strongly linked to seasonal precipitation amounts at all sites, with some site and season level differences likely due to how rainfall is converted to available plant soil water.