

Slow ecosystem responses conditionally regulate annual carbon balance over 15 years in Californian oak-grass savanna



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ABSTRACT

Many ecophysiological and biogeochemical processes respond rapidly to changes in biotic and abiotic conditions, while ecosystem-level responses develop much more slowly (e.g., over months, seasons, years, or decades). To better understand the role of the slow responses in regulating interannual variability in NEE, we partitioned NEE into two major ecological terms—gross primary productivity (GPP) and ecosystem respiration (Reco). We tested a set of hypotheses on seasonal scales using the flux and environment data collected from 2000 to 2015 in an oak-grass savanna area in California where ecosystems experience a wet winter and spring and a five-month-long summer drought each year. In our results, the spring season (Apr.–Jun.) contributed more than 50% of annual GPP and Reco. An analysis of outliers showed that each season could introduce significant anomalies in annual carbon budgets. The magnitude of the contribution depends on biotic and abiotic seasonal circumstances across the year and the particular sequences. We found that: (1) extremely wet springs reduced GPP in the years of 2006, 2011 and 2012; (2) soil moisture left from those extremely wet springs enhanced summer GPP; (3) groundwater recharged during the spring of 2011 was associated with the snowpack depth accumulated during the winter between 2010 and 2011; (4) dry autumns (Oct.–Dec.) and winters (Jan.–Mar.) decreased Reco significantly; (5) grass litter produced in previous seasons might increase Reco, and the effect of litter legacy on Reco was more observable in the second year of two consecutive wet springs. These findings confirm that biotic and abiotic extremes and legacies can introduce variations to annual ecosystem carbon balance, other than those that might be explained by the fast responses.

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1. Introduction

Net ecosystem exchange of CO₂ (NEE) measures ecosystem carbon balance directly using the eddy-covariance methods. NEE varies greatly across years, and this interannual variability reflects ecosystem responses to changes in biotic and abiotic conditions. These include ecophysiological or biogeochemical responses that occur rapidly following changes in environmental factors (e.g., within a few seconds, minutes, hours, or days). Many other responses, however, may include multiple ecosystem-level processes and thus develop much more slowly (e.g., over months, seasons, years, or decades) (Woodward, 1987). Previous studies focus more on the rapid responses (Richardson et al., 2007). The

role of the slower responses in regulating interannual variability in NEE has not been addressed explicitly in the ecosystem CO₂ flux research community (Baldocchi, 2008).

Photosynthesis and respiration are two major ecosystem processes that determine the magnitude of NEE over particular timescales. Partitioning NEE into two terms—gross primary productivity (GPP) and ecosystem respiration (Reco)—allows us to improve our process-based understandings of interannual variability in NEE. Increases in the magnitude in NEE will occur when biophysical conditions conspire to cause GPP to outpace Reco or vice versa. Thus, many ecosystems (e.g., grasslands) can act as carbon sinks one year and then carbon sources another year as photosynthesis and respiration respond to variations in biotic and abiotic conditions independently and differentially (Falk et al., 2008; Flanagan et al., 2002; Hastings et al., 2005; Ma et al., 2007). Whether a “near-neutral” ecosystems may become a permanent carbon source in the near future is a major concern (Frank et al., 2015; Grant et al., 2012) since climate extremes or other disturbances may accelerate such shift (Coursolle et al., 2012).

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Better predictive ability requires a better understanding of which ecosystem process—photosynthesis or respiration—may be more sensitive to the changing climate, and how the two processes drive ecosystems to transit between carbon sinks and carbon sources.

Although photosynthesis and respiration processes are complicated, a common understanding at the ecosystem level is that GPP and Reco correlate positively, meaning that GPP and Reco usually increase or decrease together (Baldocchi et al., 2015; Baldocchi, 2008). Previous studies have reported that variations in GPP are more responsible for changes in NEE than those in Reco (Ciais et al., 2005; Coursole et al., 2012; Novick et al., 2015b; Schwalm et al., 2010). In situations in which changes in GPP are greater than those in Reco, ecosystems can take up more CO₂ under a longer growing season, and vice versa. However, changes in Reco can also decouple from changes in GPP (Luyssaert et al., 2007; Piao et al., 2008), particularly when climate extremes (e.g., warm temperatures and droughts) occur (Wolf et al., 2016). Such situations are rarely reported in literature.

The impacts of climate fluctuations on ecosystem processes become less predictable as climate extremes occur more frequently (Cook et al., 2014; Frank et al., 2015; Grant et al., 2012; IPCC, 2012; Reichstein et al., 2013; Rosenzweig and Hillel, 1998). For example, droughts occurring during winters or springs in a Mediterranean climate zone could reduce both GPP and Reco significantly (Costa-Silva et al., 2015; Griffin and Anchukaitis, 2014; Ma et al., 2007). In contrast, mild drought in tropical forests may result in increases in photosynthesis due to fewer cloudy days and warmer temperatures, but consecutive droughts can cause increased mortality and reduced carbon uptake of tropical rainforests (Rowland et al., 2015). In colder regions, a warm or earlier spring can accelerate snow melting leading to increased soil moisture in forests and an accompanying increase in photosynthesis and respiration (Arain et al., 2002; Goulden et al., 1998; Suni et al., 2003; Valentini et al., 2000). In semi-arid ecosystems, a warm spring may cause severe drought due to faster soil drying (Scott et al., 2004; Wolf et al., 2016). Thus, similar types of climate extremes may lead to opposite effects on ecosystem CO₂ fluxes in different ecosystem types across a variety of climate zones. To better understand how climate extremes affect annual ecosystem carbon balance, we need case studies that can be used to tease out how climate extremes in individual seasons or years can trigger different processes and ecosystem responses (Ma et al., 2007; Suni et al., 2003).

Biotic components in ecosystems (e.g., green vegetation, soil organic matter, and soil microbial communities) carry out ecosystem photosynthesis and respiration. As these biotic components interact with environmental factors (e.g., light, temperature, moisture, and nutrients) at fine time scales (e.g., seconds and minutes), some responses may be slower due to delays in the timing of various biogeochemical or biophysical processes. Over a longer period, such as a few days, the phases of the time series between CO₂ fluxes and environmental variables display lags or asymmetries, known as hysteresis or lagged effects (Richardson et al., 2007). Once such asymmetries accumulate over increasingly longer periods (e.g., months, seasons, or years), legacy or carry-out effects may begin to present (Frank et al., 2015; Ma et al., 2007; Smith et al., 2009). Legacy effects may cause unusual changes in NEE, but this phenomenon has not drawn much attention. Because legacies, either biotic or abiotic, require time to build up, legacy effects may not be detectable until months or years later (le Maire et al., 2010; Sala et al., 2012; van der Molen et al., 2011). Also, legacy effects are associated with multiple ecosystem components and can result from accumulations of ecophysiological and biogeochemical processes. For these reasons, understanding legacy effects depends on the availability of a long-term data set (Richardson et al., 2007).

We have measured ecosystem CO₂ fluxes and related biotic and abiotic variables in an oak-grass savanna in California for 15

years and are getting to the stage where we can tease out sources of long-term variability in ecosystem CO₂ fluxes. The study sites experience wet, mild winters and dry, hot summers—a typically Mediterranean-type climate. In the study area, summer drought is expected each year and can last five months (Bartolome, 1979; Xu and Baldocchi, 2004). In recent years, droughts during winter and spring have become more frequent, as the western United States has been experiencing intense, prolonged drought (Funk et al., 2014; Griffin and Anchukaitis, 2014; Wolf et al., 2016). How will such droughts influence annual carbon budgets? Will they cause a transition of the ecosystem from being a carbon sink to being a carbon source? Will the effects of winter droughts be similar to the consequences of spring or summer droughts on photosynthesis or respiration? What biotic and abiotic conditions might trigger slow ecosystem responses?

To answer these questions, we summarize here a few of physiological and ecological features between oak trees and annual grasses. For example, oak leaves emerge at the end of March and stay photosynthetically active during the summer. Oak photosynthesis and transpiration are reduced gradually by stomatal or non-stomatal limitations (Xu and Baldocchi, 2003) or by limits of water movement from roots to leaves (Novick et al., 2015a). In the late summer, oak trees are photosynthetically active in the early morning. Depending on the degree of drought, senescence processes of oak leaves may start as early as mid-summer during dry years. Besides such canopy responses to drought, oak trees may establish deeper roots to enable to groundwater access in spring and summer (Miller et al., 2010). By comparison, annual grasses germinate following the first rainfall (>10 mm) in the autumn and grow slowly during the winter, grow and develop rapidly in the spring, and then die-out as the onset of the dry summer. At the end of the growing season, the grassland accumulates dead biomass on the surface, which provide carbon substrates for decomposition during the following seasons (Ma et al., 2007). Given these similarities and differences, we hypothesize that: (1) oak trees would have higher photosynthesis during a summer following an extremely wet spring; (2) autumn or winter droughts would inhibit ecosystem respiration; (3) the particular sequences of dry and wet seasons or years in a time series is a factor in the developments of legacy effects (e.g., legacies of soil moisture or litter).

Together with these questions and process-based understandings, we have three objectives in this study. First, we will examine fifteen-year-long trends in annual NEE. Second, we will quantify contributions of each season to annual GPP and Reco and their interannual variations. Third, we will examine unusual biotic and abiotic events within each season and test whether those events affect annual carbon budgets.

2. Methods

2.1. Study sites

Our study sites are located in an oak/grass savanna (Tonzi Ranch, 38.438N, 120.968W) and an open grassland (Vaira Ranch, 38.418N, 120.958W) ecosystem in the foothills of the Sierra Nevada in California, USA. The average elevation is 177 m at the savanna site and 129 m at the grassland site. The sites are about 2 km apart, and both experience a Mediterranean climate with wet, mild winters and dry, hot summers. Based on data between 1926 and 2000 from a climate station (Camp Pardee, California, 38.258N, 120.858W) located approximately 26 km from the study site, annual precipitation was 513 mm, with standard deviation 207 mm, and annual mean air temperature was 16.6°C, with standard deviation 0.8°C (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca1428>).

Deciduous blue oaks (*Quercus douglasii*) dominate the savanna site with 144 trees per hectare in a 200 × 200 m sampling plot. Their average height is about 14 m, and their mean basal area is 0.2 m². The savanna understory and open grassland were dominated by annual, cool-season C3 species, including *Brachypodium distachyon* L., *Hypochaeris glabra* L., *Trifolium dubium* Sibth., *Trifolium hirtum* All., *Dichelostemma volubile* A., and *Erodium botrys* Cav. The landscape structures of the savanna and open grassland site are distinct from one another. At the savanna site, oak trees cover about 40% of the landscape within a square kilometer of the flux tower; at the open grassland site only a few sparsely scattered oak trees are distributed within the footprint area of the flux tower (Kim et al., 2006).

The soil of the oak–grass savanna is an Auburn very rocky silt loam (Lithic haploxerepts). The soil is about 0.75 m deep, overlaying fractured rock. Additional details on the site have been reported in previous papers (Tang et al., 2003; Xu and Baldocchi, 2003; Xu and Baldocchi, 2004).

2.2. Data collection and processing

CO₂ fluxes, water vapor, and meteorological variables were measured continuously using eddy covariance (EC) systems at the savanna (October 2001–October 2015) and open grassland (October 2000–October 2015) sites. The savanna tower was 23.5 m in height, and the grassland tower was 2 m high. The flux system consisted of a 3D sonic anemometer (Model 1352, Gill Instruments Ltd., Lymington, England) and an open-path infrared gas analyzer (IRGA, Li 7500, Li-Cor Inc., Lincoln, NE, USA). Data were collected at 10 Hz by either a laptop or a datalogger (CR1000, Campbell Scientific, Inc., Logan, UT, USA). Photosynthetically active radiation (PAR) was measured with a quantum sensor (Kipp and Zonen PAR-Lite, Delft, Holland). Air temperature and relative humidity were measured with a shielded and aspirated sensor (HMP-45A, Vaisala, Helsinki, Finland). Soil temperature at depths of 0.02, 0.04, 0.08, 0.16 and 0.32 m were measured with lab-made type-T thermocouple sensors with three replications at each depth. Soil volumetric water content was measured with time-domain reflectometer probes (ML2x, Delta-T Devices, Burwell, Cambridge, UK) at depths of 0.05, 0.10, and 0.20 m at the grassland site and at depths of 0.05, 0.20, and 0.50 m at the savanna site; one to three probes were installed and their averages were used for representing soil moisture at each depth at each site. All channels from meteorological and soil sensors, except the rain gauge, were scanned every 5 s and 30 min means were stored with data-loggers (CR10X or CR23X, Campbell Scientific Inc., Logan, UT, USA). For more details of the experimental design and the sensor specification, refer to Xu and Baldocchi (2004) and Ma et al. (2007).

For long-term, continuous measurements, data gaps are unavoidable and are not randomly distributed. To calculate annual integrations, we filled data gaps with methods developed and validated by Ma et al. (2007) and subsequently improved. In short, a linear interpolation was used to fill short gaps (<2.5 h), and a mean diurnal variation approach was used to fill larger gaps. If a gap was longer than several weeks, smoothing methods were applied to improve previous estimates. Nighttime gaps were filled with temperature functions of nighttime NEE (Xu and Baldocchi, 2004). We employed filtered measurements in a series of linear regression models between nighttime NEE measured under high turbulence conditions (e.g., friction velocity > 0.2 m s⁻¹) and soil temperature at 4 cm depth. Each linear regression model was established within a 15-day moving window continuously over the course of each year. The canopy storage term of CO₂ was computed for the savanna site only. Daytime Reco was estimated with the assumption that the relationship between nighttime NEE and soil temperature holds during daytime (Xu and Baldocchi, 2004). GPP was evaluated by subtracting Reco from NEE on the half-hour scale. Based on the

typical oak phenology, annual budgets were integrated from 1 October of one year to 30 September of the next year to span the hydrological year, instead of the calendar year. In the rest of this paper, a year means a hydrological year as defined.

Uncertainties in annual budgets were estimated with the bootstrap technique based on the Monte Carlo approach (Hagen et al., 2006; Ma et al., 2007). A 95% confidence interval was determined using Efron's percentile method (Efron and Tibshirani, 1993). The range of uncertainties was approximately ±50 gC m⁻² year⁻¹ in annual NEE, and ±100 gC m⁻² year⁻¹ in annual GPP and Reco, depending on individual hydrological years.

Four stages of phenology were recorded, including (1) date of grass green-up, (2) date of oak leaf-out, (3) date of grass senescence, and (4) date of oak litter-fall. The onset and ending date of each phenological stage was defined as the time when 60–70% of plants showed the same phenology (Ma et al., 2007). Observations of oak phenology after 2009 were compared and corrected by continuous observations from upward-pointing digital cameras (Ryu et al., 2012). Lengths of growing season were defined for oak trees, annual grasses, and the savanna as a whole. In particular, the length of growing season of oak trees is the number of days between the date of oak leaf out in the spring and the date of litter fall in the autumn, and the length of growing season of the grassland is the number of days between the date of grass germination and the date of die-out of annual grasses. The length of growing season for the savanna was the number of days between the date of grass germination in the autumn and the date of oak litter fall in the following autumn.

We sampled grass litter by clipping 3 replicates of grass litter; each within a 20 × 20 cm² sampling square. Litter samples were cleaned in the lab and dried 48 h in an oven set at 65 °C. The dry weight was measured with a digital scale in the laboratory.

We downloaded data of snowpack depth at the Station of Carson Pass (38.69°, -120.00°, 2546 m above sea level) at http://cdec.water.ca.gov/cgi-progs/stationInfo?station_id=CXS, operated by Natural Resources Conservation Service of Department of Water Resources, California.

2.3. Terms in data analysis

We defined the following terms to quantify and compare seasonal and annual GPP and Reco.

The seasonal GPP or Reco was the integration of GPP or Reco within each climate season, including autumn (Oct.–Dec.), winter (Jan.–Mar.), spring (Apr.–Jun.), and summer (Jul.–Sep.).

The anomaly of annual GPP or Reco was the difference between the annual integration of each hydrological year and the 15-year mean, labeled as ΔGPP or ΔReco in the text.

The anomaly of seasonal GPP or Reco was the difference between the annual GPP or Reco for each season within each year and the 15-year mean of each season.

The contribution of each season to variations in annual GPP or Reco was the percentage of the seasonal GPP or Reco vs. the annual GPP or Reco within the same hydrological year.

The contribution of each season to the anomaly of annual GPP or Reco was the percentage of a seasonal anomaly in GPP or Reco vs. the annual anomalies of the same hydrological year, labeled as PSA (%).

We performed statistical analyses using a statistical software SAS (Version 9.4, SAS Institute Inc., Cary, NC, USA). For the analysis of linear regression, R² was the determination coefficient of linear regressions. The significance level was set to 0.05.

Table 1

Annual integrations of net ecosystem exchange of CO₂ (NEE), gross ecosystem productivity (GPP), and ecosystem respiration (Reco), in unit of gC m⁻² year⁻¹, for the savanna and annual grassland sites, respectively. Notice that each hydrological year (HY) is set from October to next September.

HY	Savanna			Grassland		
	NEE	Reco	GPP	NEE	Reco	GPP
2000–2001	–	–	–	–	–	–
2001–2002	–176	(±58)	867	(±97)	1044	(±128)
2002–2003	–175	(±62)	1015	(±114)	1190	(±142)
2003–2004	–119	(±68)	784	(±87)	903	(±109)
2004–2005	–110	(±61)	1317	(±145)	1426	(±170)
2005–2006	–26	(±63)	1067	(±119)	1093	(±131)
2006–2007	–61	(±65)	937	(±103)	998	(±124)
2007–2008	–64	(±57)	786	(±86)	850	(±98)
2008–2009	–94	(±60)	996	(±116)	1090	(±131)
2009–2010	–233	(±62)	914	(±103)	1146	(±140)
2010–2011	–96	(±61)	1045	(±114)	1141	(±127)
2011–2012	–114	(±47)	903	(±97)	1017	(±113)
2012–2013	–48	(±42)	909	(±85)	958	(±98)
2013–2014	–147	(±52)	790	(±74)	937	(±102)
2014–2015	–80	(±58)	910	(±98)	990	(±123)
Mean	–110		946		1056	
Standard Deviation	57		141		145	

3. Results

3.1. The 15-year variations in ecosystem CO₂ fluxes and seasonal contributions

Annual NEE, GPP, and Reco were estimated for each hydrological year (Table 1). Over the 15 years, the annual grassland shifted between a carbon sink and source, and it behaved as a carbon neutral on average (7 gC m⁻² year⁻²) with ±114 gC m⁻² year⁻¹ of standard deviation. The largest carbon source occurred in the hydrological year of 2011 with 262 gC m⁻² year⁻¹ (Fig. 1a). Over the study period the annual grassland shifted towards a likely carbon source, but the increasing trend was not statistically significant (F-test, $p=0.15$).

Unlike the grassland, the oak savanna persisted as a carbon sink with mean –110 gC m⁻² year⁻² and ±57 gC m⁻² year⁻¹ of standard deviation over the 15 years. Annual NEE was quite close to zero in 2006 and 2013. The largest carbon sink of the savanna site was –233 gC m⁻² year⁻¹, measured during the 2010 hydrological year. The savanna continued to function as a carbon sink during the extended 2013–2015 drought.

Overall, the length of growing season increased at both sites. Compared with the period 2001–2007, the length of growing season increased 33 days in the grassland and 12 days in the oak savanna during 2008–2015 (Fig. 1b).

On average, the spring season contributed 60–80% of annual GPP and 50–70% of annual Reco at the two sites (Fig. 2). During the summer, oak trees were still photosynthetically active and contributed 20–30% of annual GPP, while summer Reco was only 10% of the annual integration. The ranges between upper and lower percentiles shown in Fig. 2 also indicate that variations of seasonal Reco were larger than those of GPP. Reco were more variable during the autumn and winter than during the spring and summer.

3.2. Outliers in the relationship between GPP and Reco

Reco positively correlated with GPP. On average an increase of ~90 gC m⁻² year⁻¹ in annual Reco was associated with an increase of 100 gC m⁻² year⁻¹ in annual GPP for the savanna, and Reco increased by ~56 gC m⁻² year⁻¹ for a 100 gC m⁻² year⁻¹ increase in GPP for the grassland site.

Outliers presented in the relationship between annual anomalies in GPP and Reco (Fig. 3). At the savanna site, data points from the years 2002, 2006, 2010, and 2014 fell outside of the 95%

confidence interval; outliers were the years 2001, 2006, 2011, and 2014 at the grassland site. These outliers indicated decoupling of the relationship between GPP and Reco. We wondered what ecosystem processes and responses might explain this decoupling.

For example, the grassland in 2011 showed an increase in Reco (a positive annual anomaly, $\Delta\text{Reco} > 0$) but a decrease in GPP (a negative annual anomaly, $\Delta\text{GPP} < 0$) (Fig. 2b) when the ratio of ΔReco to ΔGPP equaled –2.4 (Table 2). In the same year, ΔGPP and ΔReco both increased and obtained a ratio of ΔReco to ΔGPP equal to 1.2 at the savanna (Table 2), within the confidence interval (Fig. 2a).

The ratio of ΔReco to ΔGPP provided an overall picture on an annual basis, but it could not be used to distinguish contributions of the seasons. We therefore quantified the percentage of seasonal anomaly that contributed to the annual anomaly (PSA, see details in Methods). We set up a normal range of PSA between –25% and 25% to reflect usual fluctuations in annual GPP and Reco. When PSA is outside of this range, it means that fluctuations in GPP or Reco may be unusually large (Fig. 4).

Using 2011 as an example again, the PSA values shown in Fig. 4 indicated which season might result in ΔReco greater than the value it would be if constrained by ΔGPP at the savanna. In the left-side panels of Fig. 4, the arrows point to the PSA values for either GPP or Reco. These values show that only the autumn Reco was out of the normal range, with PSA equal to approximately +50%, suggesting that the positive anomaly in annual Reco might be resulted from particular biotic and abiotic characteristics of the autumn.

The right-side panels of Fig. 4 for the same year (2011) indicate that the grassland GPP decreased 70% during the winter but remained within the normal range in other seasons. In contrast, the grassland Reco increased 60% during the autumn but stayed within the normal range in other seasons.

Comparing the PSA values across seasons of each year helped us to quantify which season added most significantly to annual anomalies and to check further which ecosystem processes—photosynthesis or respiration—had unusual responses during that season.

3.3. Processes involved in seasonal anomalies of GPP

Drought effects on GPP and Reco had been studied by Ma et al. (2007), who reported that spring droughts would hurt annual GPP and Reco the most. This conclusion was drawn from a 6-year-long dataset measured at the same sites used in the present study. Here we ask whether this relationship is present in a dataset more than

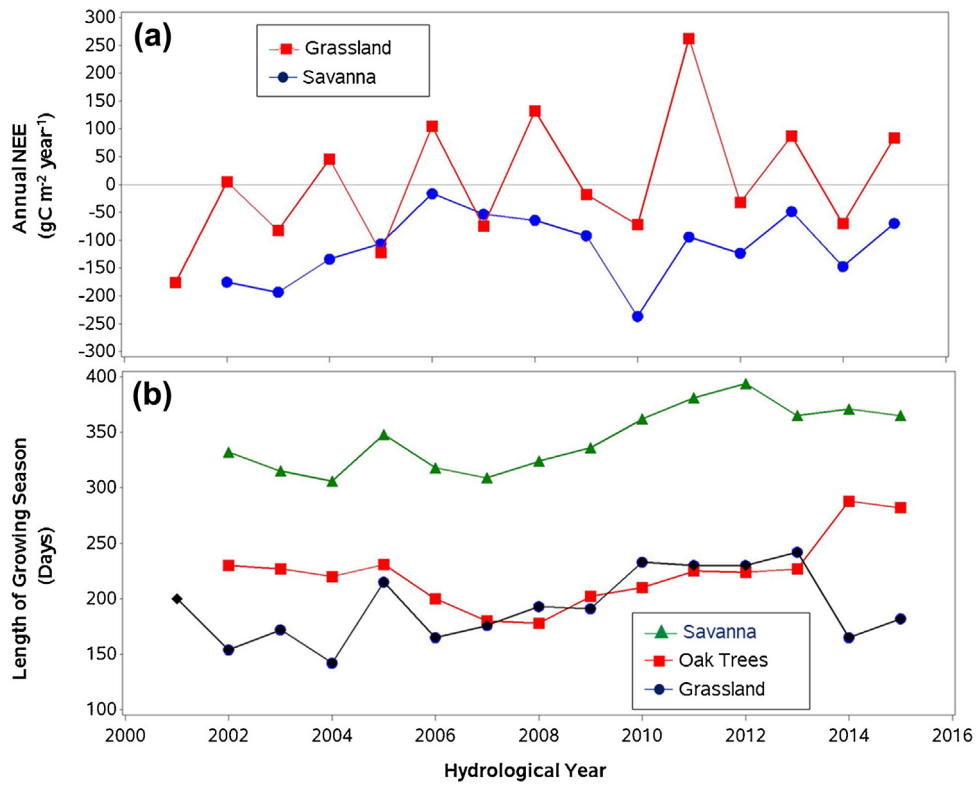


Fig. 1. The 15-year variations: (a) annual integration of net ecosystem exchange of CO₂ (NEE) at the savanna and grassland sites (Notes: uncertainties for each hydrological year are listed in Table 1; a negative value of NEE indicate a carbon sink, vice versa); (b) length of growing season for oak trees, annual grasses, and the savanna (Notes: detailed definitions are described in Methods).

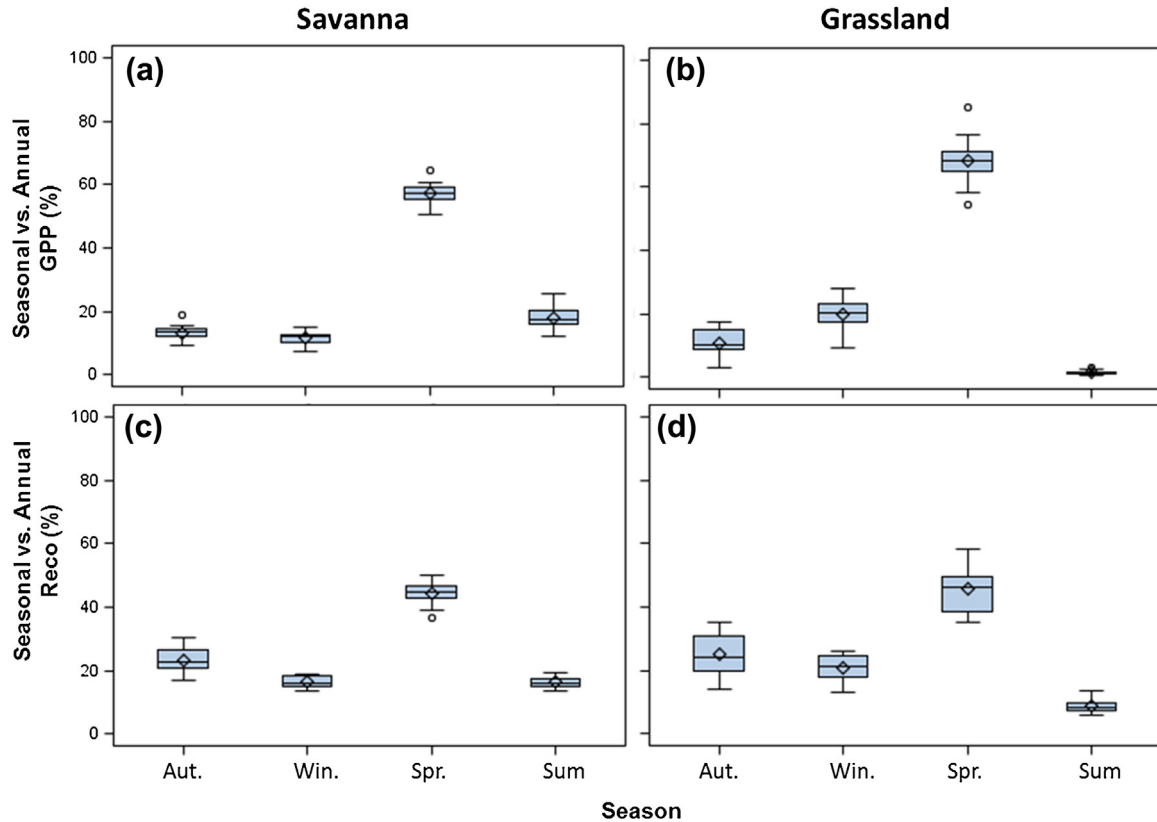


Fig. 2. Proportions of seasonal integration to annual integration of gross ecosystem productivity (GPP) or ecosystem respiration (Reco) at the savanna site (a,c) and at the annual grassland site (b, d), respectively. Each boxplot presents mean (in diamond), median, 25% and 75% percentiles, and outliers (in circle), describing the distributions of GPP or Reco for each season (n = 15 years).

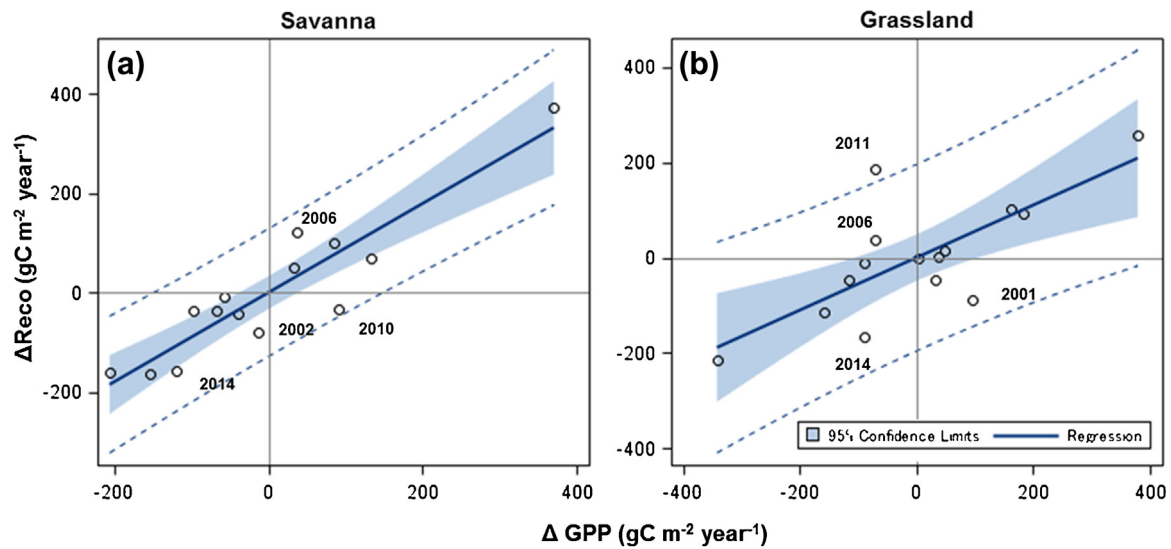


Fig. 3. The inter-relationship between the annual anomalies of ecosystem respiration (ΔReco) and of gross ecosystem productivity (ΔGPP) at the savanna site (a) and the annual grassland site (b), respectively. The horizontal and vertical reference lines are the zero anomalies (i.e. if the 15-year mean of GPP or Reco occurs). These reference lines separate the 2D domain into four quadrants: I, II, III, and IV (counterclockwise). The solid lines and shadowed areas are regression lines and upper and lower limits with 95% confidence interval; the dashed lines are prediction limits for individual predicted values.

twice as long (i.e., 15 years). High statistical significance still held for most of the years ($R^2 > 0.9$) when three outliers (i.e., 2006, 2011, and 2012) were omitted (Fig. 5).

We noticed that the spring precipitation of the three outlier years exceeded the 15-year average by more than 200 mm (Fig. 5). In these extremely wet springs, light levels were lower, and temperatures were colder, probably due to more cloudy or raining days (Fig. 6a, F-test, $p < 0.0001$, $R^2 = 0.78$). Such a light-temperature-rain condition reduced the savanna GPP most significantly (-50%) in the spring of 2012. Interestingly, the effects of lower light and temperature conditions on GPP were not that significantly in the spring of 2006 (-25%) and 2011 ($+25\%$) even though PAR and temperature in the spring of 2011 were lower than other two years (Fig. 5a). It indicates that effects of other conditions might cancel out the effects of light-temperature on photosynthesis.

During the early spring, the timing of oak leaf-out was significantly delayed by colder temperatures (Fig. 6b). Oak leaves emerged about 18, 10, and 6 days later than the 15-year average (Day 82) in the spring of 2006, 2011, and 2012, respectively.

Lower light levels and colder temperature did not influence GPP significantly at the grassland since the PSA values in the spring of 2006, 2011, and 2012 were within the normal range (Fig. 4).

During the wetter springs, accumulated sums of photosynthesis and evapotranspiration were lower (Fig. 7a, F-test, $p = 0.006$, $R^2 = 0.51$). Consequently, soil moisture was conserved and become available to oak trees during the subsequent seasons, resulting in higher oak photosynthesis during the summer months (Fig. 7b, F-test, $p = 0.056$, $R^2 = 0.29$).

GPP in the summer of 2011 was the highest of the three years with extremely wet springs (shown by the bigger arrow in Fig. 7b), suggesting that oak trees might have accessed water resources other than soil moisture remaining from the wet spring. Groundwater depth measured from 2009 to 2015 showed that the shallowest record occurred during the spring of 2011. During the same period, a big jump occurred in the time series of groundwater depth. We further checked the interannual variations in the snowpack depth in the nearby mountains and found a several-month lag between the peak of groundwater recharge and the peak of snowpack

Table 2

Ratios of the difference from the 15-year mean of ecosystem respiration (ΔReco) versus that of gross ecosystem productivity (ΔGPP) for each hydrological year (HY) at the savanna site and the annual grassland site.

Site	Quadrant (directions of ΔGPP and ΔReco)								
	I (+,+)		II (-,+)		III (-,-)		IV (+,-)		
	HY	$\Delta\text{Reco}/\Delta\text{GPP}$	HY	$\Delta\text{Reco}/\Delta\text{GPP}$	HY	$\Delta\text{Reco}/\Delta\text{GPP}$	HY	$\Delta\text{Reco}/\Delta\text{GPP}$	
Savanna	2003	0.5*			2002	4.7*	2010	-0.4*	
	2005	1.0			2004	1.0			
	2006	3.7*			2007	0.2*			
	2009	1.6			2008	0.8			
	2011	1.2			2012	1.0			
					2013	0.4*			
					2014	1.3*			
					2015	0.5			
	Grassland	2003	0.5	2006	-0.5*	2002	0.2	2001	-1.0*
		2005	0.7	2011	-2.4*	2004	0.7	2007	-1.8*
2009		0.3			2008	0.6			
2010		0.6			2013	0.4			
2012		0.1			2014	1.7*			
					2015	0.1			

Notes: "+" and "-" mean the positive and negative ΔGPP or ΔReco , respectively; "*" indicates the hydrological years that significantly diverges from the regression line shown in Fig. 3.

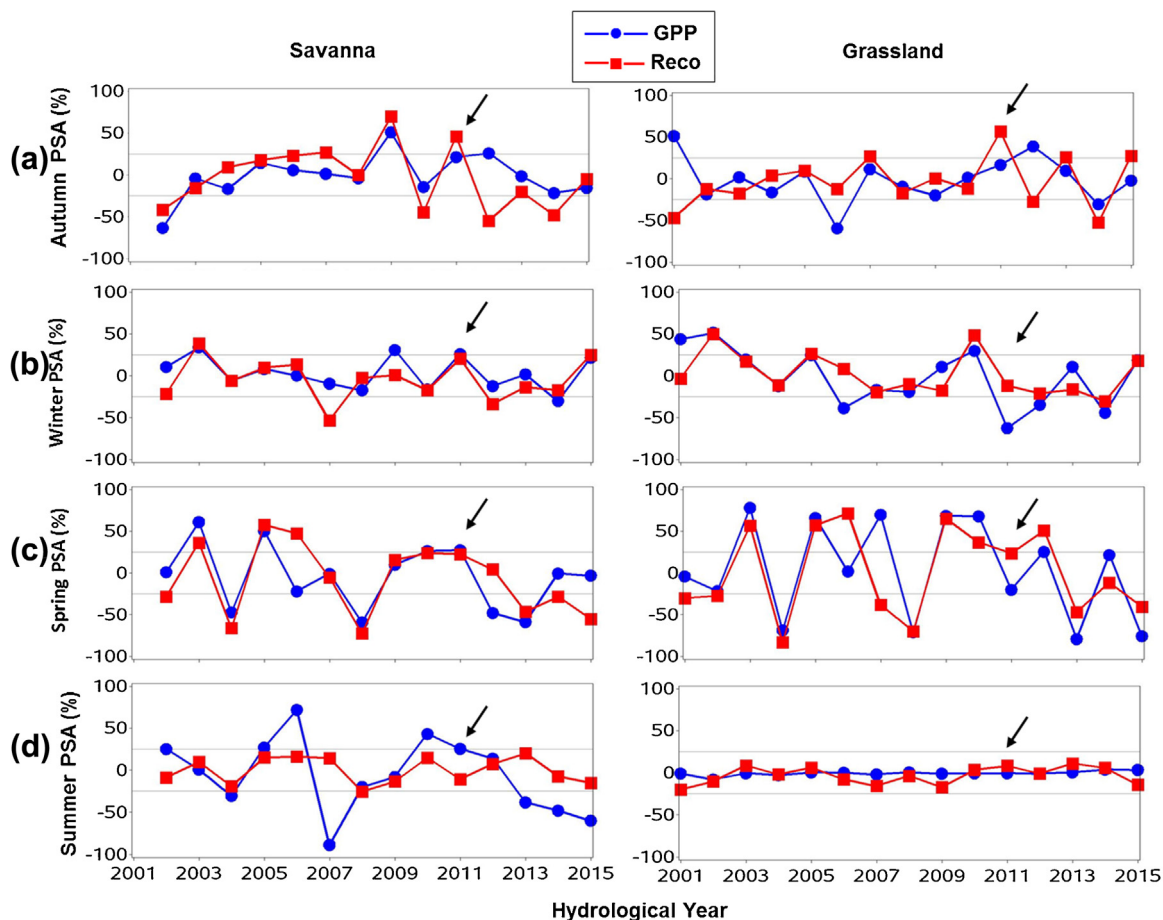


Fig. 4. Percentages of seasonal anomalies (PSA, %) relevant to annual anomalies of gross ecosystem productivity (GPP) or ecosystem respiration (Reco) for each season: (a) autumn (Oct.–Dec. of previous year), (b) winter (Jan.–Mar.), (c) spring (Apr.–Jun.), and (d) summer (Jul.–Sep.) at the savanna (the four panels on the left column) and grassland (the 4 panels of the right column) sites, respectively. Values within the horizontal lines between –25% and 25% are considered to be regular variations in GPP or Reco. Arrows point to the example year (i.e. 2011) described in the text.

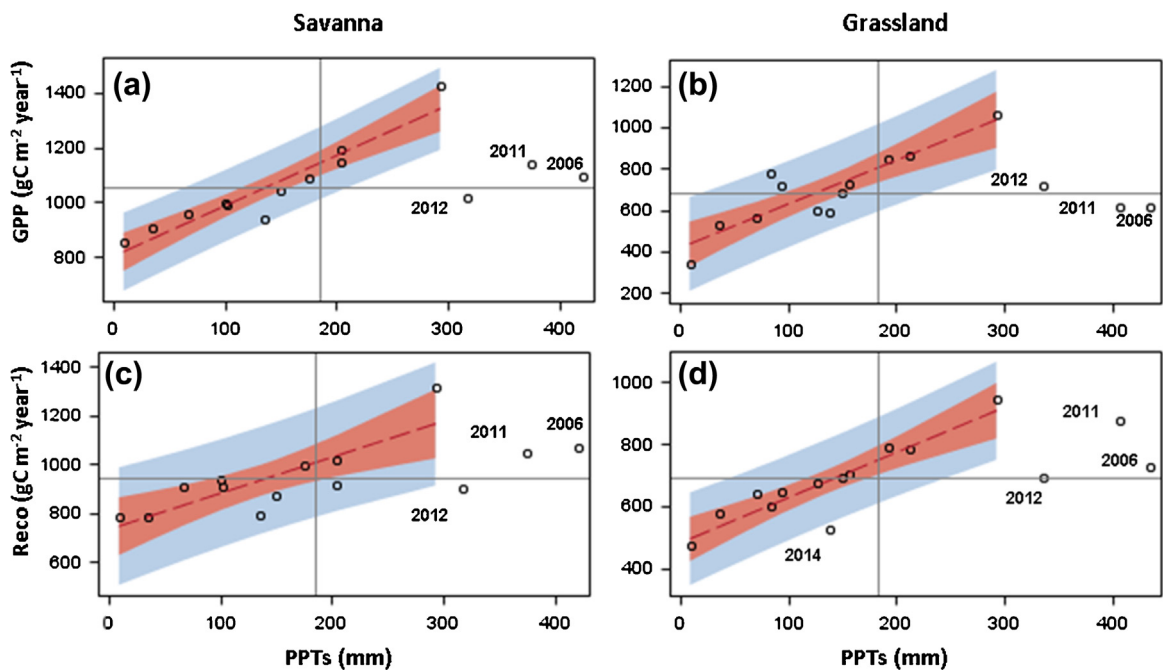


Fig. 5. The relationships between gross ecosystem productivity (GPP) and spring precipitation (PPTs), and between ecosystem respiration (Reco) and PPTs at the savanna site (a and c) and at the annual grassland site (b and d), respectively. The cross lines show the 15-year averages of GPP, Reco, and spring precipitation for each site. The dashed lines are regression lines; the darker shaded areas are upper and lower limits with 95% confidence interval; the lighter shaded areas are prediction limits for individual predicted values. Notice that the three points labelled “2006”, “2011”, and “2012” are excluded from the linear regression analysis.

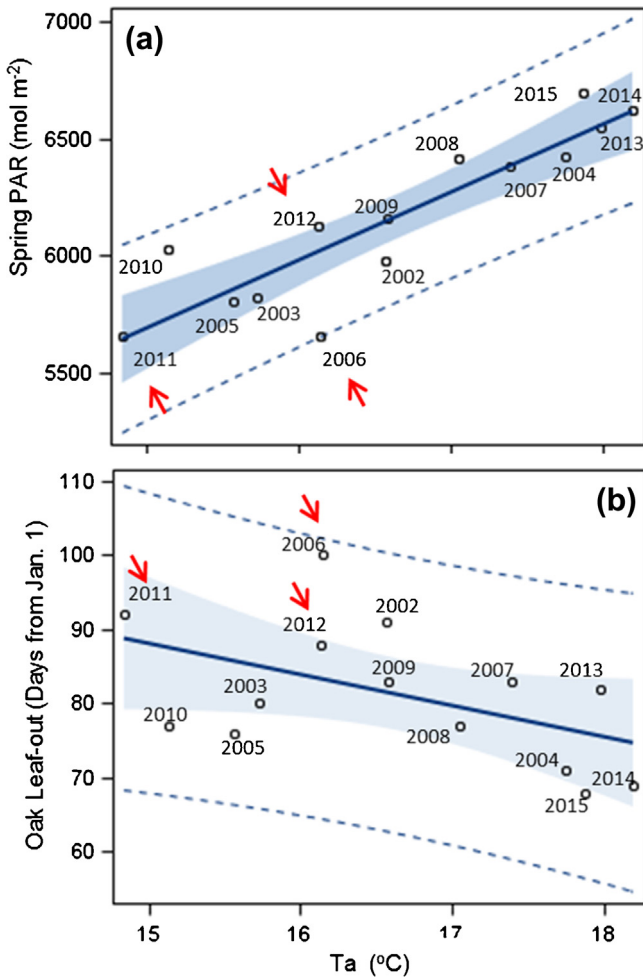


Fig. 6. During the spring seasons at the savanna site: (a) the relationship between photosynthetically active radiation (PAR) and air temperature (Ta); (b) the relationship between the date of oak leaf-out and air temperature. The solid and dashed lines and shadowed areas present similar meanings to those used in Fig. 5. Arrows point to the years with extremely wet springs that have been shown in Fig. 5.

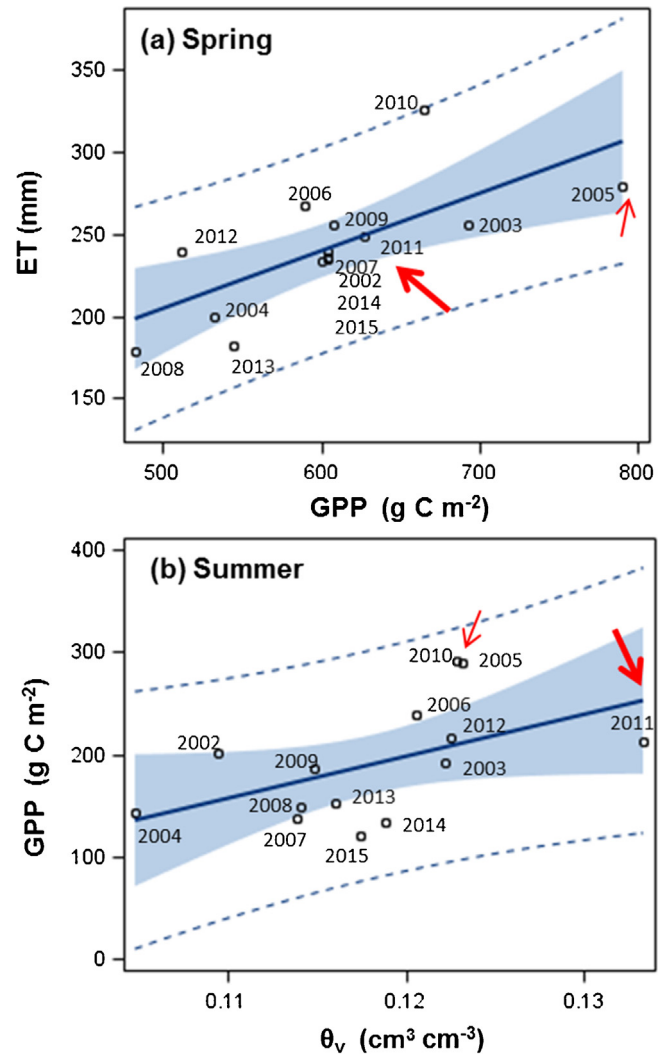


Fig. 7. At the savanna site: (a) the relationship between evapotranspiration (ET) and gross ecosystem productivity (GPP) during the spring (Apr.–Jun.); (b) the relationship between GPP and soil moisture averaged within the depth between 0 and 50 cm (θ_v) during the summer (Jul.–Sep.). The solid and dashed lines and shadowed areas present similar meanings to those used in Fig. 5. Arrows point to the example years with a regular or extremely wet spring (i.e., 2005 vs. 2011) to compare differences in spring ET and effects of moisture legacies on summer GPP.

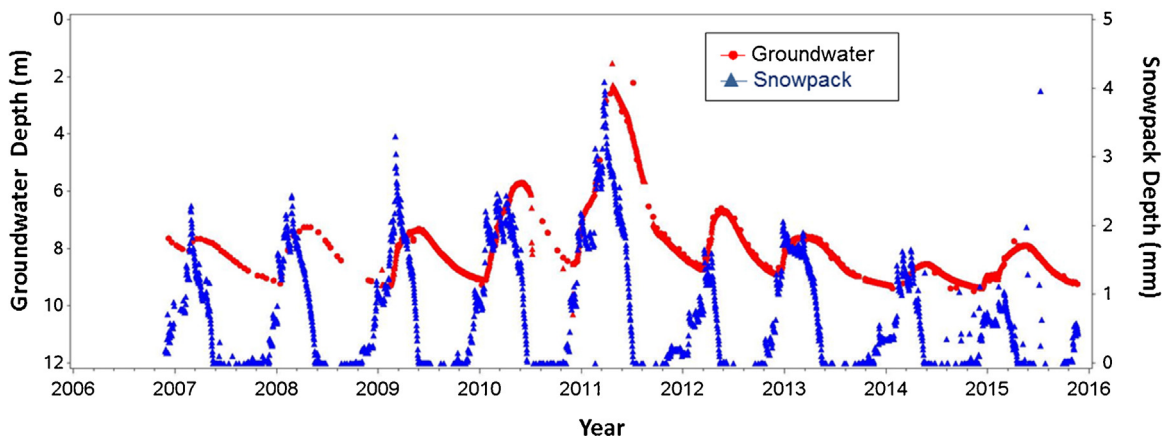


Fig. 8. Comparisons between on-site groundwater depth and changes in snowpack depth in the nearby mountains (details in Methods).

melting, apparently suggesting that significant groundwater recharge during the spring was associated with the depth of snow-pack accumulated during the preceding winter (Fig. 8).

3.4. Processes involved in seasonal anomalies of Reco

Respiration increases with increases in temperature and moisture. This general understanding was not always followed up at our study sites. We applied contour maps to address the influences of soil temperature and moisture on Reco together (Fig. 9). Variations in Reco were presented with contour levels from low Reco values (low values or blue area of Fig. 9) to high Reco value (higher values or red area of Fig. 9).

Responses of Reco to soil temperature and moisture varied from season to season. In general, Reco increased with increases in temperature and moisture during the autumn and winter (Fig. 9a and b), while during the spring and summer Reco decreased with increases in soil temperature but still increased with increases in soil moisture (Fig. 9c and d).

For this reason, wetter autumns (e.g., 2009 and 2011) increased Reco, while drier winters (e.g., 2010, 2012, and 2014) decreased Reco. In wetter but colder springs, Reco did not necessarily drop. For example, the spring of 2006 decreased GPP by 25% but increased Reco by 45%. Similar situations reoccurred in the spring of the years of 2011 and 2012 (Fig. 4a and c).

A significant amount of annual grass biomass became litter, covering the ground surface at the end of the growing season. Based on the litter samples between the years of 2009 and 2015, the average rate of litter reduction was approximately 50 g of dry weight per month (Fig. 10; F-test, $p < 0.0001$, $R^2 = 0.58$). During the dry year 2015, the rate of litter degradation was lower, approximately around $30 \text{ g m}^{-2} \text{ month}^{-1}$, since dry autumns and winter inhibited Reco (Fig. 10a and b). The amount of grass litter determined the initial size of the fast carbon pool for decomposition during subsequent seasons. Grass litter could also block light for newly germinated grasses, but such effects were not shown in our current dataset.

3.5. The sequence of the seasons and years

We wondered whether the conditions of previous season affected subsequent seasons. The patterns of anomalies in spring precipitations over the 15 years showed that 2006, 2011, and 2012 had unique characteristics (Fig. 11). These three years all had wet springs, and the springs of the previous years were also wet, thus exhibiting positive anomalies in precipitation.

These three cases showed that a wet spring with high GPP often followed another wet spring but with lower GPP. The autumn Reco anomaly contributed +50% of an annual anomaly in 2011, partially due to a significant amount of litter that provided organic material for decomposition. Such conditions—two consecutive years had wet springs—only occurred twice (i.e., 1982–1983 and 1995–1996) over the period between 1926 and 2000, which was 3% of the occurring frequency (Table 3).

In contrast, the situation of a dry spring year followed by a subsequent year also with a dry spring was not found during the historical period from 1927 to 2000. Such extreme continuous spring droughts, or even longer, had occurred several times over the past 15 years (2001–2002, 2007–2009, and 2013–2015), as shown in Fig. 11. Thus, we did observe more climate extremes at our study sites over the past 15 years.

4. Discussion

Over the past 15 years, the annual grassland in our study site shifted between being a carbon sink and being a carbon source. The

Table 3

Frequency (%) of water conditions (i.e., dry, normal, or wet) combined between current and previous springs during the historical period from 1927 to 2000 measured at the weather station Camp Pardee, California. A normal water condition refers to the anomaly of total precipitation during the spring months (Apr.–Jun.) greater than -50 mm but less than 50 mm ; a dry spring refers to a negative anomaly $\leq -50 \text{ mm}$; a wet spring refers to a positive anomaly $\geq 50 \text{ mm}$.

Current Spring	Previous Spring			Total (%)
	dry	normal	wet	
Dry	0	8.1	2.7	10.8
Normal	12.2	55.4	8.1	75.7
Wet	0	10.8	2.7	13.5
Total (%)	12.2	74.3	13.5	100

trend towards becoming a permanent carbon source was not statistically significant in our data, though it had been predicted by the “ecosys” model (Grant et al., 2012). Our savanna study site by contrast functions continuously as a carbon sink. Thus, the presence of oak trees stabilizes annual ecosystems carbon balance. However, droughts put oak trees at risk. During an extended dry summer, more leaves become senescent periodically, occurring as early as mid-summer. Meanwhile, drought can inhibit the formation of new leaf buds before the following spring. With more frequent occurrences of continuous droughts during wet seasons, the mortality of branches or whole trees may rise (Ma et al., 2011, 2007). Thus, we conclude that recent Californian droughts jeopardize the savanna, much as they have hurt forests and water resources on a broader scale (Griffin and Anchukaitis, 2014).

The annual grassland became a carbon source during certain years because of increases in Reco, particularly increases in heterotrophic respiration when warm temperatures coincided with wet autumns and winters. Under such conditions, a larger amount of dead biomass has the potential to decompose and be respired, causing annual carbon uptake to drop from the previous year when climate forcings are equal. On the contrary, dry autumns and winters decrease Reco significantly due to heterotrophic respiration being limited by droughts. A significant amount of litter remaining from previous growing seasons can enhance heterotrophic respiration because litter legacies add more organic material to the surface carbon pool for decomposition. This observation suggests that variations in Reco could decouple those in GPP due to an increase in organic materials from previous seasons (Luyssaert et al., 2007; Piao et al., 2008), leading to enhanced heterotrophic respiration during less active growing seasons or off-seasons (Piao et al., 2008). Nevertheless, a dry spring is the factor most responsible for severe decreases in GPP and Reco in this region (Ma et al., 2007).

At our study sites, the growing seasons of oak trees and annual grasses are longer over the past 15 year, yet a longer growing season may not result in more CO_2 uptake. In such years, the ratio of annual anomalies in Reco (ΔReco) versus those in GPP (ΔGPP) was greater than 1, indicating the conditions under which $\Delta \text{Reco} > \Delta \text{GPP}$. During the study period, dry autumns could delay grass germination, but extended spring rains may delay grass maturity. Warmer springs push the timing of oak leaf out earlier, while oak trees keep some green leaves as long as possible in dry autumns, even though the majority of litter-fall may start in the middle of summer (Ma et al., 2007). Overall, these changes in the phenology of trees and grasses resulted in increases in length of growing season, but enhanced heterotrophic respiration may decouple the responses of photosynthesis and respiration to changes in biotic and abiotic conditions.

Previous studies provide evidence that ecophysiological processes are “fast” and directly responsible for interannual variability in ecosystem CO_2 fluxes (Froelich et al., 2015; Richardson et al., 2007; van Gorsel et al., 2013). This 15-year study highlights that some of the ecosystem processes require an extended period of

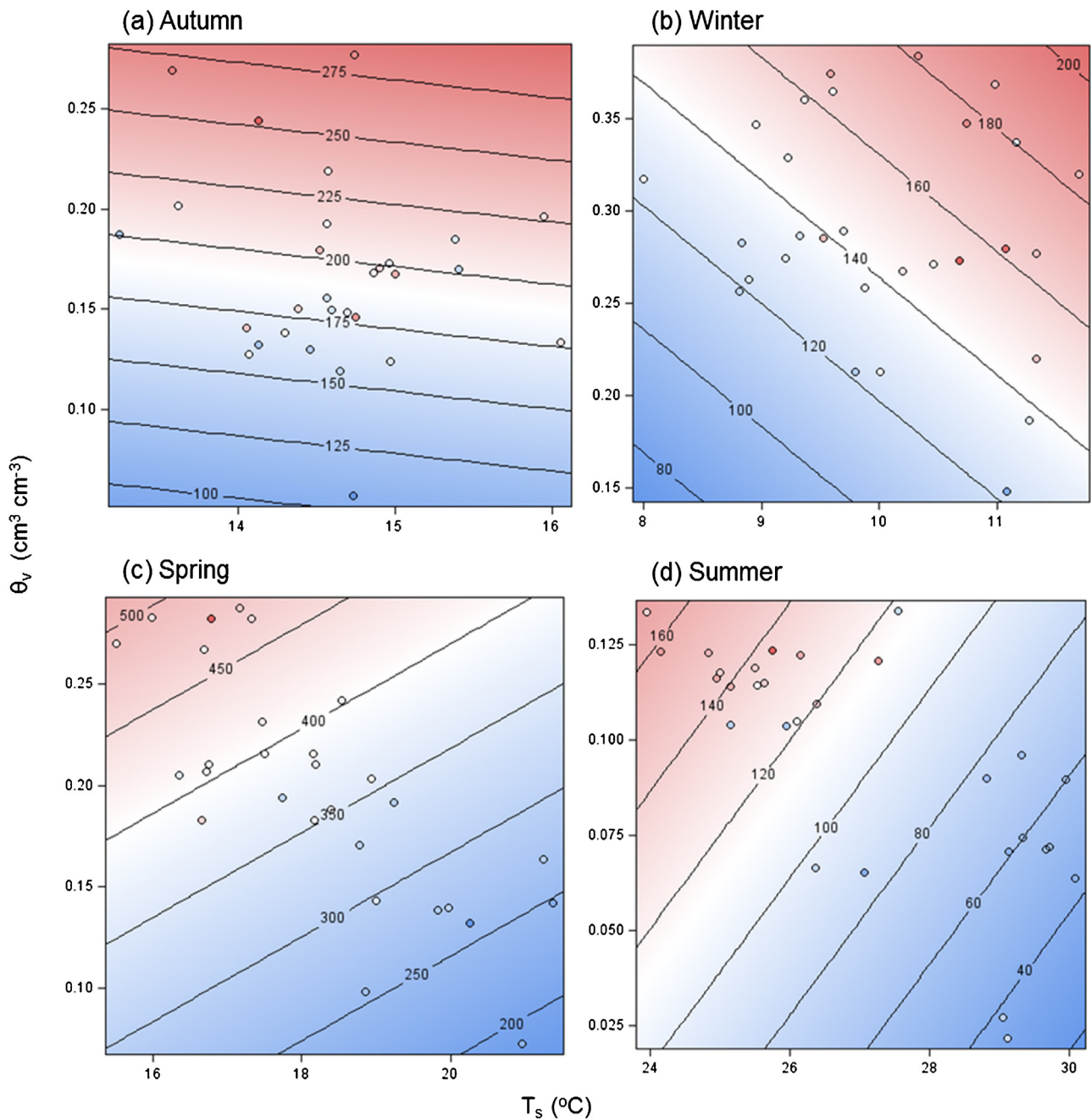


Fig. 9. Contour maps of ecosystem respiration (Reco , $\text{gC m}^{-2} \text{ season}^{-1}$), coinciding with variations in soil temperature at 4 cm depth (T_s) and moisture within the depth of 0–20 cm (θ_v) during each season at the grassland and savanna sites. Four seasons are defined as the autumn (Oct.–Dec.), winter (Jan.–Mar.), spring (Apr.–Jun.), and summer (Jul.–Sep.). (For interpretation of the references to color in the text, the reader is referred to the web version of this article.)

development (e.g., months, seasons, or years). Such slow processes and responses are hard to be observed because of their low frequency of occurrence, even across a decadal timescale. An unusual increase in local groundwater level may be responsible for the positive anomaly of annual GPP in 2011. This event occurred only once during the measuring period from 2009 to 2015. Its occurrence demonstrates the connection between the functioning of this savanna ecosystem in the foothills of the Sierra Nevada Mountain and the condition of the snowpack in the mountains. Warmer springs may also affect the hydrological cycling on the watershed-scale by rapid snowmelt at higher elevations and runoff in the early growing season. Although we confirm that such hydrological connections affect ecosystem photosynthesis and respiration, understanding slow ecosystem responses and how they affect the

annual budgets of ecosystem CO_2 fluxes in different ecosystems needs more studies.

This study provides evidence of the effects of water and litter legacies on interannual variability in ecosystem CO_2 , but we did not explore many other processes. Some researchers have studied nutrient legacies, age effects, harvests, or different types of disturbances (Coursolle et al., 2012; Peichl et al., 2010; Saigusa et al., 2008). For example, the availability of nutrients (e.g., nitrogen) is an important aspect of legacy effects (Jongen et al., 2013; van der Molen et al., 2011). At the savanna and grassland sites, photodegradation during the dry summer and late rain-induced respiration pulses may be associated with denitrification (Ma et al., 2012). As a result, fast-available nitrogen benefits the growth of grasses in the autumn, but it may cause less nutrient availability in the spring for

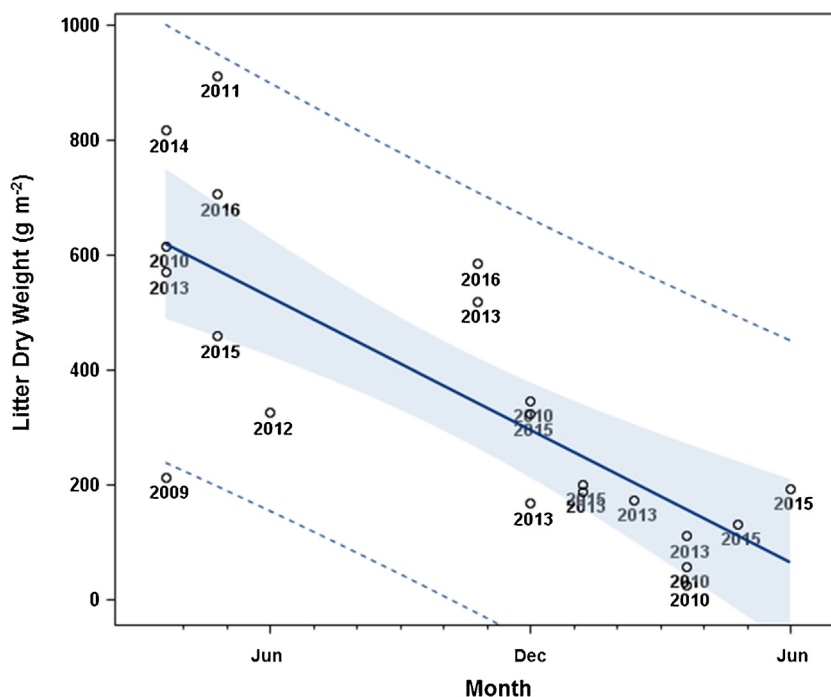


Fig. 10. Aboveground grass litters accumulated by the end of the growing season decayed throughout the following summers, autumns, and winters. The labels indicate the year when grass litter was sampled. The solid and dashed lines and shadowed areas represent similar meanings to those used in Fig. 5.

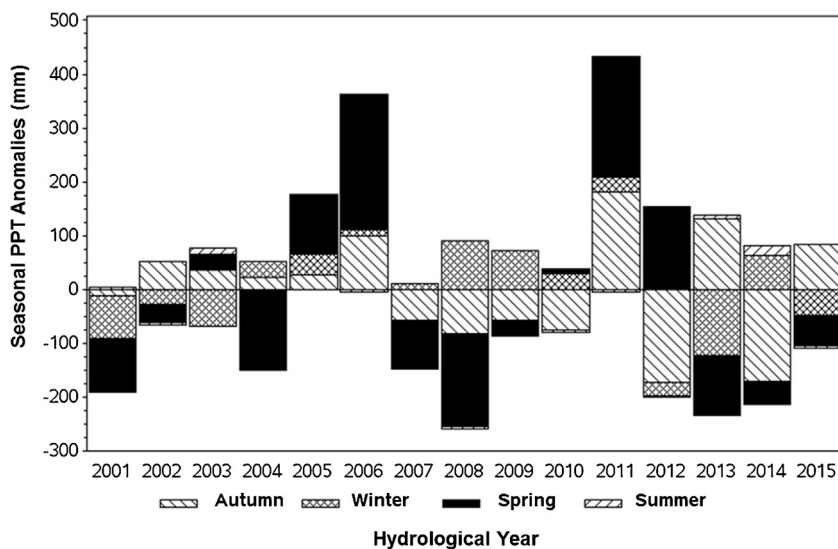


Fig. 11. Seasonal anomalies of precipitation (PPT) within each hydrological year from 2001 to 2015. The four seasons are defined as autumn (Oct.–Dec.), winter (Jan.–Mar.), spring (Apr.–Jun.), and summer (Jul.–Sep.). The zero line means zero anomalies (i.e. that PPT of the season matches its 15-year mean).

oak growth (Taylor et al., 1982), as seen in the spring of 2012. Future studies are needed to test how the order or sequence of seasons and years in the time series may influence the nutrient availability.

We also notice that the sequence of seasons and years is one of the determinants of slow ecosystem responses. In this study we observed that the pattern of two consecutive wet springs occurred three times over the past 15 years, while the same pattern happened only twice over the prior 74 years, a very low frequency of 3%. It suggests that extremely dry or wet situations are occurring at the study sites, in agreement with global climate projections (Cook et al., 2014; IPCC, 2012; Rosenzweig and Hillel, 1998). Thus, the savanna and annual grassland have been experiencing more extremes in precipitation and temperature in the past 15 years than previously. Increased occurrences of droughts and warm

temperatures in different seasons are harmful to ecosystem photosynthesis and respiration, likely pushing ecosystems towards becoming carbon sources. The potential for legacy effects, either biotic or abiotic, may differ across ecosystem types and climate zones. It will be interesting to extend such comparisons into different biomes.

5. Conclusions

This study focuses on seasonal events triggering some slow ecosystems responses in regulating interannual variability in ecosystem carbon balance. In the study area, the spring season is the most active growing season, and changes in this season contribute the largest uncertainties in annual budgets. Dry springs decrease

ecosystem photosynthesis and respiration, not surprisingly, but wet springs may either increase or decrease carbon fluxes.

Legacy effects, either due to unused spring soil moisture or accumulated litter, may amplify variations in the annual budget. Litter in wet autumn and winter seasons is responsible for an apparent divergence between GPP and Reco. These findings indicate that the presences of slow responses depends on many biotic and abiotic conditions, even including low-frequency hydrological events (e.g., the connection between on-site groundwater depth and snowpack depth in the mountain) and the sequence of dry or wet conditions over consecutive seasons and years. Without particular timings and sequences of these conditions, slow responses may not be detectable.

Over a decadal timescale, the responses of ecosystem photosynthesis and respiration to biotic and abiotic conditions are accumulative. Their impacts on interannual variability in GPP and Reco, and eventually on NEE, are observable on seasonal scales. Besides variations in GPP, variations in Reco can also cause ecosystems to shift from being carbon sink to being carbon source.

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