Inter-annual variability in carbon dioxide exchange of an oak/grass savanna and open grassland in California

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Abstract

To understand the dynamics of ecosystem carbon cycling, CO\textsubscript{2} fluxes were measured over and under an oak–grass savanna and over a proximate grassland in California. The measurements were made from 2000 to 2006 using the eddy covariance technique. Annual net carbon exchange (NEE) ranged from $-155$ to $-56$ gC m\textsuperscript{-2} year\textsuperscript{-1} and from $-88$ to $141$ gC m\textsuperscript{-2} year\textsuperscript{-1} at the savanna and nearby grassland, respectively. Inter-annual variability in NEE was significantly related to length of growing season for the savanna, grassland, and tree canopy. We partitioned the NEE into two separate terms—primary productivity (GPP) and respiration (ecosystem respiration, $R_{eco}$)—and found that the GPP and $R_{eco}$ of the savanna and grassland depended primarily on the amount of seasonal precipitation that occurred while grass and tree canopies were simultaneously active rather than depending on annual precipitation. We also found that NEE was greatly constrained by both $R_{eco}$ and GPP and $R_{eco}$ was significantly constrained by GPP. $R_{eco}$ increased by 79 gC m\textsuperscript{-2} year\textsuperscript{-1} with each 100 gC m\textsuperscript{-2} year\textsuperscript{-1} increase in GPP. In addition, measuring CO\textsubscript{2} exchange separately in the overstory and understory of the savanna over multiple years enabled us to partition $R_{eco}$ into heterotrophic and autotrophic respiration terms in a new and direct way. The sensitivity of $R_{eco}$ to GPP ($dR_{eco}/dGPP$) and the baseline of respiration terms both provide useful tools for understanding the dynamics of ecosystem CO\textsubscript{2} uptake under current conditions of climate and ecosystem succession stage.

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1. Introduction

The metabolism of ecosystems is complex and highly dynamic because ecosystems consist of coupled, non-linear processes that possess many positive and negative feedbacks, which in combination exhibit ‘emergent-scale’ properties (Levin, 2002). Continuous and year-long measurements of CO\textsubscript{2} between vegetation and the atmosphere are enabling scientists to discover emergent scale properties by quantifying how the metabolism of complex ecosystems respond to perturbations in biophysical variables on daily, seasonal, and annual time scales. For example, it is widely known that leaf photosynthesis saturates at high light levels (Farquhar et al., 1980; Monsi and Saeki, 2005). At the canopy scale, photosynthesis is either a linear or quasi-linear function of available light, depending upon leaf area index and canopy nutrition (Baldocchi and Amthor, 2001; Gilmanov et al., 2003). Furthermore,
canopy light use efficiency is enhanced when sunlight is diffuse rather than direct (Gu et al., 2002; Niyogi et al., 2004). Another emergent-scale process identified by continuous carbon flux measurements concerns the link between soil respiration and soil moisture, where pulses in respiration occur after isolated rain events (Huxman et al., 2004; Jarvis et al., 2007; Xu et al., 2004).

At present, complex features of ecosystem metabolism at longer, multi-year time scales are relatively unknown. Length of growing season is the emergent-scale factor that corresponds best to net ecosystem carbon exchange of deciduous forests (Baldocchi et al., 2001), but this result may not explain the inter-annual variability of CO₂ exchange for other types of ecosystems or climate spaces (Monson et al., 2005). To assess inter-annual variations of carbon fluxes and discover new emergent-scale processes, datasets gathered over longer durations (typically 5–10 years in duration) are needed (Baldocchi and Wilson, 2001; Ito et al., 2005).

Long-term flux measurement studies allow answers to emergent-scale questions in several ways. First, they increase the probability that an ecosystem will experience a range of climate conditions and extremes, such as droughts, excessive rainfall, periods of prolonged cloudiness, or heat spells within a region or season (Barr et al., 2007; Ciais et al., 2005; Diffenbaugh et al., 2005; Dunn et al., 2007; Houghton, 2000). Second, long-term data sets provide adequate information to examine the conditional statistics associated with seasonal, rather than annual, climate (Black et al., 2000; Gilmanov et al., 2006). Third, long-term flux studies provide investigators the opportunity to examine carry-over effects that may be introduced by either favorable or deleterious conditions during antecedent years (Barford et al., 2001). Finally, long-term studies provide investigators opportunities to observe a disturbance and the recovery from it or to span a natural sequence of ecological development coupling with fluctuations of climate (Amiro et al., 2006; Stoy et al., 2006a).

To date, only a few flux studies of duration 5 years or more have been published. The paucity of long-term data stems partly from the fact that the first cohort of FLUXNET field studies did not start until the early to mid-1990s (Baldocchi et al., 2001; Valentini et al., 2000; Wofsy et al., 1993). Examples of long-term (5 to 15 years in duration) CO₂ flux studies include reports from boreal forests (Barr et al., 2007; Dunn et al., 2007; Hollinger et al., 2004; Suni et al., 2003), temperate deciduous forests (Barford et al., 2001; Curtis et al., 2005; Goulden et al., 1996; Ito et al., 2005; Saigusa et al., 2005; Stoy et al., 2006b; Wilson and Baldocchi, 2001; Carrara et al., 2003), sub-tropical savanna (Beringer et al., 2007) and herbaceous or shrubland vegetation (Gilmanov et al., 2006; Haszpra et al., 2005). The picture evolving from these data is that different combinations of factors explain inter-annual variability of net ecosystem CO₂ exchange in different biomes and climate spaces. For example, inter-annual variability in net ecosystem CO₂ exchange at the aforementioned temperate deciduous forest site is attributed to a combination of factors including occurrence of a summer drought, extent of summer cloudiness and absence or presence of winter snow (Goulden et al., 1996). In contrast, the inter-annual variability of CO₂ exchange for a boreal conifer forest corresponds to variations in water table, air temperature, and summertime solar radiation (Dunn et al., 2007). Meanwhile, inter-annual variability of CO₂ exchange for a boreal deciduous aspen site is linked to inter-annual differences in leaf area index and summer drought (Barr et al., 2007). Apparently, a variety of factors drive inter-annual variability in CO₂ exchange, but a common message from existing studies is that the most important factors are present in the growing season, or the factors are closely related to the metabolism of plants.

No long-term studies of inter-annual variability in CO₂ exchange have emanated from savanna ecosystems in Mediterranean climates. Because savannas experience wide variation in inter-annual rainfall and temperature, the inter-annual variation of CO₂ exchange of Mediterranean-type savanna ecosystems is expected to have attributions different from that of sub-tropical, temperate and boreal ecosystems. In addition, Mediterranean-type ecosystems normally experience pronounced periods of drought each year. Consequently, the length of savanna growing seasons differs greatly from that of temperate and boreal forests, which have growing-season lengths driven primarily by temperature. One may thus expect inter-annual variations in carbon fluxes of Mediterranean-type ecosystems to display behavior that is even more complex and responds more dramatically to perturbations in water conditions.

We hypothesize that inter-annual differences in net ecosystem exchange (NEE) in the Mediterranean ecosystems studied here – as reflected in the processes of photosynthesis (GPP) and ecosystem respiration (R eco) – will depend more on seasonal climate (especially during the growing season) than on mean annual air temperature or precipitation. Besides seasonal climate, extreme weather events and previous biophysical conditions also contribute to inter-annual variability in NEE, but those are secondary factors because of their infrequency in multi-year time scales.

In this paper we report on a 5–6 year study of CO₂ exchange at a pair of study sites in California (an oak
savanna and annual C3 grassland). The objectives of this paper are to quantify inter-annual variations of NEE in CO₂ at the savanna and grassland sites and to explain the sources of the variation. In particular, we explore the effects of the length of growing season on inter-annual variability in NEE, examine how variations in GPP and \( R_{\text{eco}} \) relate to inter-annual variability in NEE (particularly through responses to temperature, water, and radiation conditions), and explore the relationship between \( R_{\text{eco}} \) and GPP at the yearly time-scale and at different ecosystem niche spaces.

2. Materials and methods

2.1. Study site

Our study sites are located in an oak/grass savanna (Tonzi Ranch, 38.43°N, 120.96°W) and an open grassland (Vaira Ranch, 38.41°N, 120.95°W) ecosystem in the foothills of the Sierra Nevada in California, USA. The elevation is 177 m at the savanna site and 129 m at the grassland site. The sites are about 2 km apart.

The study sites experience a Mediterranean climate with wet, mild winters and dry, hot summers (Fig. 1). Based on climate data from a climate station (Camp Pardee, California, 38.25°N, 120.85°W) located approximately 26 km from the study site, the multi-year average of annual precipitation was 562.1 mm, with standard deviation 193.3 mm, and annual mean air temperature was 16.5 °C, with standard deviation 0.7 °C (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?-cacamp+nca).

Deciduous blue oaks (Quercus douglasii) dominate the savanna site with 144 stem per hectare in a 200 m × 200 m sampling plot. Their average height is 9.41 ± 4.33 m, and their mean basal area is 0.074 ± 0.0869 m² (Chen et al., 2006). The savanna understory and open grassland were dominated by cool-season C3 annual species, including Brachypodium distachyon L., Hypochaeris glabra L., Trifolium hirtum All., Dichetostemma 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 kilometer of the flux tower; at the open grassland site only a few sparsely distributed oak trees are distributed within the footprint area of the flux tower (Kim et al., 2006). Vertically, the savanna consists of two vegetation layers – overstory trees and understory grasses – whereas the open grassland consists of one layer of grasses in a relatively open area.

The soil of the oak–grass savanna is an Auburn very rocky silt loam (Lithic haploxerepts). The soil profile is about 0.75 m deep and overlaid fractured rock. More detail on site has been reported in companion papers (Tang et al., 2003; Xu and Baldocchi, 2003; Xu and Baldocchi, 2004).

2.2. Data collection

CO₂ fluxes, water vapor, and meteorological variables were measured continuously using eddy covariance (EC) systems at the savanna (April, 2001–October, 2006) and open grassland (October, 2000–October, 2006) sites. At the savanna site, an eddy-covariance system was installed in the understory and above the overstory, in order to separate fluxes in the two components. The overstory tower was 23 m in height, and the understory tower was 2 m high. Details of the experimental design and the sensor specification have been presented in previous papers by Xu and Baldocchi (2004) and Baldocchi et al. (2004).

The overstory tower collected fluxes from trees and grasses, including tree canopy photosynthesis (\( A_{c} \)), tree canopy respiration (\( R_{\text{above_tree}} \)), tree root respiration (\( R_{\text{root_tree}} \)), grass photosynthesis (\( A_{c_{\text{grass}}} \)), grass respiration (\( R_{\text{above_glass}} \)), grass root respiration (\( R_{\text{root_grass}} \)), and heterotrophic respiration (\( R_{\text{hetero}} \)). The understory tower collected data on \( A_{c_{\text{grass}}} \), \( R_{\text{above_glass}} \), \( R_{\text{root_grass}} \), and \( R_{\text{hetero}} \). Table 1 presents algebraic functions used to represent CO₂ fluxes of savanna woodland, understory grassland, tree canopy, and open grassland.

We recorded four stages of phenology for the grasses and trees, 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

![Fig. 1. Monthly precipitation (PPT) and mean air temperature (\( T_{a} \)) according to historical climate data from 1948 to 2005 at Camp Pardee, California. Error bars are standard deviations.](image-url)
Table 1
Algebraic functions for presenting CO₂ fluxes of four ecosystem niche spaces: savanna, understory grassland, tree canopy, and open grassland. CO₂ fluxes are gross primary productivity (GPP), ecosystem respiration (R̄), net ecosystem exchange of CO₂ (NEE), tree gross photosynthesis (A), and tree canopy net photosynthesis (Aₜ). In subscript, “over” is for savanna; “under” for understory grassland; “grassland” for open grassland. Other symbols in subscript have been described in texts.

<table>
<thead>
<tr>
<th>Ecosystem niche space</th>
<th>Photosynthesis term</th>
<th>Respiration term</th>
<th>Net exchange</th>
</tr>
</thead>
<tbody>
<tr>
<td>Savanna</td>
<td>GPP̄ₜ = Aₜ + Aₜ_grass</td>
<td>R̄̄ₜ = Rₜ_above + Rₜ_above_grass + Rₜ_root + Rₜ_hetero_savanna</td>
<td>NEEₜ = −(GPP̄ₜ − R̄̄ₜ)</td>
</tr>
<tr>
<td>Understory grassland</td>
<td>GPPₜ_under = Aₜ_under</td>
<td>R̄ₜ_below + Rₜ_hetero_grass</td>
<td>NEEₜ_under = −(GPPₜ_under − R̄ₜ_below)</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>Aₜ = GPP̄ₜ − GPPₜ_under</td>
<td>R̄ₜ_above + R̄ₜ_below − R̄ₜ_eco</td>
<td>Aₜ = Aₜ − Rₜ_above_tree = −(NEEₜ − NEEₜ_under)</td>
</tr>
<tr>
<td>Open grassland</td>
<td>GPP̄ₜ_grassland = Aₜ_grass</td>
<td>R̄ₜ_below + Rₜ_root_grass + Rₜ_hetero_grass</td>
<td>NEEₜ_grassland = −(GPP̄ₜ_grassland − R̄ₜ_grassland)</td>
</tr>
</tbody>
</table>

2.3. Data processing

For long-term and continuous measurements, data gaps are unavoidable and are not randomly distributed. The average rate of yearly data coverage in flux studies is approximately 65% (Falge et al., 2001). For this study, instrument or power failure caused 26–35% of the data to be missing on an annual basis over the 5–6 year study period. Measurements taken under conditions of low turbulent mixing (friction velocity < 0.1 m s⁻¹) or heavy rainfall (half-hour precipitation > 10 mm), or in other unpredictable situations resulted in another 15–17% of missing data.

Gap-filling methods have been developed and compared by a number of groups (Falge et al., 2001; Hui et al., 2004; Iwata et al., 2005; Reichstein et al., 2005; Ruppert et al., 2006; Stauch and Jarvis, 2006). Although there is no universal method, it is necessary to apply a consistent gap-filling method to make comparisons between years or across sites and to prevent biases (Wilson and Baldocchi, 2001; Stoy et al., 2006b). For this study, we use linear interpolation to fill short gaps (<3 h) and mean diurnal trend to fill larger gaps. Nighttime gaps were filled with the temperature functions of nighttime NEE during the wet season. Because the temperature function failed during the dry summer (Xu and Baldocchi, 2004), we employed filtered measurements and developed a series of linear regression models between nighttime NEE measured under high turbulence conditions and soil temperature at 4 cm depth. Each linear regression model was established within a moving window over the course of each year. We also compared our gap-filled dataset with one produced using the neural network method of Papale and Valentini (2003) and found that the two datasets agreed well.

We calculated NEE with corrections to the canopy storage term of CO₂ and partitioned NEE into GPP and R̄. The canopy storage term of CO₂ was computed based on the temporal CO₂ concentration changes derived from open path IRGAs of the overstory and understory EC system (Yang et al., 1999). Daytime R̄ was estimated with the assumption that the relationship between nighttime NEE and soil temperature holds during daytime (Xu and Baldocchi, 2004) although a potential error is introduced when making this assumption (Atkin et al., 1998; Liu et al., 2006; Loreto et al., 2001; Sharp et al., 1984). On the half-hour scale, GPP was evaluated by subtracting R̄ from NEE. Annual NEE, R̄, and GPP were integrated from 23 October (Day 296) of 1 year to 22 October (Day 295) of the next year to span the hydrological year instead of the calendar year.

To assign statistical uncertainties to the annual sum of NEE, R̄, and GPP, we applied the bootstrap technique with the Monte Carlo approach (Efron and Tibshirani, 1993), a computer-based technique for making statistical inferences. The technique has been used in assigning statistical uncertainties in modeling GPP (Hagen et al., 2006). The range of estimation is determined using a one-sampling percentile method and a 95% confidence interval. We found that the uncertainty resulting from daily integration of NEE varied from year to year and was approximately ±50 gC m⁻² year⁻¹ for all sites—the savanna, open grassland, and tree canopy (Table 2).

We performed all statistical calculations with the standard statistical software SAS (Version 9.1, SAS Institute Inc., Cary, NC, USA). For linear regression analysis, we determined the probability of significance, P, using F-test or t-test, at the significant level of 0.05 or 0.1. R² was the determination coefficient of linear regressions.
Table 2: Annual net ecosystem exchange of CO₂ (NEE, gC m⁻² year⁻¹) and uncertainties (in round brackets) over oak/grass savanna, open grassland, and understory grassland. For tree canopy, the values are annual net photosynthesis ($A_n$, gC m⁻² year⁻¹).

<table>
<thead>
<tr>
<th>Hydrological year</th>
<th>NEE Savanna (gC m⁻² year⁻¹)</th>
<th>NEE Open Grassland (gC m⁻² year⁻¹)</th>
<th>NEE Understory Grassland (gC m⁻² year⁻¹)</th>
<th>NEE Tree Canopy (gC m⁻² year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000–2001</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2001–2002</td>
<td>–144 (±50)</td>
<td>61 (±53)</td>
<td>237 (±31)</td>
<td>–381 (±55)</td>
</tr>
<tr>
<td>2002–2003</td>
<td>–116 (±50)</td>
<td>–6 (±51)</td>
<td>294 (±22)</td>
<td>–409 (±54)</td>
</tr>
<tr>
<td>Mean</td>
<td>–98 (±51)</td>
<td>38 (±52)</td>
<td>269 (±28)</td>
<td>–367 (±55)</td>
</tr>
<tr>
<td>STD</td>
<td>51</td>
<td>118</td>
<td>47</td>
<td>68</td>
</tr>
</tbody>
</table>

a Hydrological year starts on 23 October (Day 296) and ends on 22 October (Day 295) of the next year. 
b STD refers to standard deviation.

3. Results

3.1. Inter-annual variability in NEE

Annual NEE of the two contrasting Mediterranean-type ecosystems fluctuated from year to year (Table 2). Annual NEE ranged from −144 to −35 gC m⁻² year⁻¹ and from −88 to 189 gC m⁻² year⁻¹ at the savanna and open grassland sites, respectively. On average, the savanna was a carbon sink and the grassland was a carbon source over the yearly time scale. However, the grassland became a carbon sink in 2005, when the region received relatively high spring precipitation.

By partitioning carbon fluxes above and below the savanna, we found that the tree canopy was the major carbon sink with an average uptake of −367 gC m⁻² year⁻¹, and its understory grassland and soil combined was a consistent carbon source, with average efflux of 269 gC m⁻² year⁻¹, which can be attributed to the root respiration of trees and grasses and the heterotrophic respiration of soil microbes (Table 1).

Inter-annual variability in NEE, measured by standard deviation (STD), was around 51 gC m⁻² year⁻¹ for the savanna and 118 gC m⁻² year⁻¹ for the open grassland (Table 2). The tree canopy experienced slightly higher inter-annual variability in NEE than did the savanna as a whole, while the understory grassland had less inter-annual variation in NEE.

3.2. Length of growing season

The length of savanna growing season varied from year to year (Table 3). Grasses experienced an average growing season of 175 days, with a 27-day standard deviation, whereas trees experienced a longer average growing season of 221 days, with a 12-day standard deviation. Defining the days between grass green-up and oak litter-fall, we found that the savanna growing season was 331 days on average, with a 22-day inter-annual deviation. This nearly month-long inter-annual variability in savanna growing season far exceeds long-term trends in growing season phenology, which are on the order of a day per decade (Menzel et al., 2006).

Annual NEE showed a relationship with growing season length at the savanna and grassland, but the level of significance of this relationship was different for the ecosystem niches. For the savanna, annual NEE was a non-linear function of its growing season length ($P = 0.1526, R^2 = 0.548$) (Fig. 2a). In contrast, a linear function described the relationship between grassland NEE and its growing season length ($P = 0.0353, R^2 = 0.54$) (Fig. 2b). Similarly to the grassland, the tree canopy showed a significantly linear relationship between NEE and its growing season length ($P = 0.0134, R^2 = 0.90$) (Fig. 2c).

Interestingly, annual NEE of the tree canopy was clustered among years, except for the year 2006, when the trees experienced an extremely short growing season. This extremely short tree growing season resulted from retardation of the date of leaf-out. The date of leaf emergence (10 April, Day 100) in 2006 was ~17 days later than the average date of leaf emergence (24 March, Day 83). To explain this result, we examined the 5-day moving average of soil temperature and found that the oak trees experienced a cool period with soil temperature less than 12 °C immediately before the leaves emerged (Fig. 3). A similar chilly period also occurred in the spring of 2002, when it resulted in ~8 days of delay of leaf-out. Apparently, temperature during specific spring time
The duration of grass growing season was linked to the timing of rains in the early fall or late spring (Xu and Baldocchi, 2004). During the fall of 2004–2005, rains commenced approximately 2 weeks earlier in the fall than they had in the fall of 2003–2004. This caused the grassland to green-up 25 days earlier than in the fall of 2004–2005. At the end of grass growing season, the spring rains stopped on 2 March (Day 62) of 2004 and 16 June (Day 167) of 2005. As a result, the grass growing season of 2003–2004 was 71 days shorter than that of 2004–2005, and carbon uptake was reduced significantly. In the extreme wet year (2004–2005), sufficient autumn rainfall allowed grasses to grow 2 months longer than they had in 2003–2004. In contrast, 2005–2006 also had a wet spring, but the grass-growing season was 49 days shorter than that of 2004–2005. We noticed in the field that the grass community did not develop well because the ground surface was covered with an extraordinary amount of litter produced in 2004–2005. The litter had not decomposed as completely as usual, so it hampered the emergence of grass.

3.3. Processes behind annual NEE—photosynthesis and respiration

To understand the mechanisms behind the relationship between annual NEE and growing season length, we examined how NEE, GPP, and R_{eco} are related to one another and how they responded to changes in temperature, precipitation, and radiation over the course of year. The seasonal patterns of NEE, GPP, and R_{eco} at the savanna and grassland are illustrated by smoothing daily-integration over the study years (Fig. 4). We distinguished stages of carbon uptake using zero NEE as a criterion. In Stage I_{a} (Fig. 4), the savanna and open grassland released CO_{2} to the atmosphere. During this period, grass had germinated on both sites, but the rates of grass photosynthesis and respiration were low and almost balanced each other, resulting in a small positive NEE. The grassland started to take up carbon about 1 month earlier than the savanna, whereas the savanna started to take up CO_{2} when the tree started to photosynthesize at the end of Stage I_{b}. During Stage II, trees and grasses functioned simultaneously. Grasses reached the maximum photosynthesis rate at the end of April, and tree carbon assimilation increased rapidly at the same time. Grasses died out around the end of May, resulting in the grassland NEE crossing the zero line. With the cessation of springtime rains, the spring-summer drawdown of the soil water reservoir began and imposed physiological limits on tree photosynthesis (Xu and Baldocchi, 2003). During the summer, tree canopy photosynthesis rates decreased gradually in response to the deficit of soil moisture. Savanna R_{eco} decreased even more dramatically. Thus, summer drought greatly suppressed tree respiration while tree photosynthesis was low but still functioning (Fig. 4).

Annual GPP and R_{eco} were significantly related to precipitation during the second stage (Fig. 5) but were not related to annual precipitation or precipitation during any other season. At the savanna, the best-fit lines were significant \( P = 0.0108, \ R^{2} = 0.86 \) for GPP vs. PPT; \( P = 0.0399, \ R^{2} = 0.64 \) for R_{eco} vs. PPT). At the grassland, the best-fit lines were significant \( P = 0.0327, \ R^{2} = 0.83 \) for GPP vs. PPT; \( P = 0.0404, \ R^{2} = 0.89 \) for R_{eco} vs. PPT). Therefore, the ecosystem increased carbon assimilation and respiration simultaneously during years of greater precipitation.

In contrast, greater GPP did not necessarily produce greater net carbon uptake, especially for the savanna (Fig. 6). For example, the absolute value of NEE in the 2001–2002 hydrological year was the second greatest in the five hydrological years, but GPP and R_{eco} were the second lowest in the 5 years (Fig. 6a). The amount of
carbon uptake in 2001–2002 was very close to that in 2004–2005, which had the wet spring and the highest GPP. Because trees played an essential role in carbon uptake in the savanna, we examined how the tree canopy responded to changes in temperature and incoming PAR (Fig. 7). Interestingly, tree net photosynthesis was the highest while incoming PAR was the lowest in the 5 years (Fig. 7a). Meanwhile, tree canopy respiration was the lowest when air temperature was the lowest (Fig. 7b). During the critical period of 2001–2002, there were not many rain events. In addition to less rainfall, temperature in 2001–2002 was not as high as in previous years, which may have contributed to the lower respiration rate.
as usual (for example in 2003–2004). A possible weather condition combining less rain with lower temperature is cloudiness. Thus, cloudiness may have enhanced tree photosynthesis due to the availability of diffused light (Gu et al., 2002; Niyogi et al., 2004).

More importantly, tree canopy respiration was restricted by lower temperatures in 2001–2002. By comparison, the 2005–2006 hydrological year had the same GPP as the 2001–2002 year, but the absolute value of NEE of 2005–2006 was extremely low.
In contrast, the 2003–2004 year had much lower $R_{eco}$ although the 2 years showed similar temperature levels. Lack of spring precipitation significantly decreased $R_{eco}$ in 2003–2004 (Fig. 5c). These results show that annual NEE was regulated by the two terms $R_{eco}$ and GPP.

Indeed, annual $R_{eco}$ was positively related to annual GPP (Table 4, Fig. 8). The regression line passed the significance test, with $P = 0.0081$, $R^2 = 0.93$ and $P = 0.0168$, $R^2 = 0.80$ for the savanna and grassland, respectively. For the tree canopy, the regression line was also significant ($P = 0.0201$, $R^2 = 0.87$). Since the regressions were likely parallel, we pooled all pairs of $R_{eco}$ and GPP together and established a dummy variable regression function ($P < 0.0001$, $R^2 = 0.95$). The common slope of $R_{eco}$ vs. GPP was 0.79 (t-test, $P < 0.001$) with a standard error of 0.098. The intercept was 124, 343, −219, and 230 gC m$^{-2}$ year$^{-1}$ for the savanna, the understory grassland, the tree canopy, and the grassland, respectively. Except for the intercept of the savanna, all were significantly different from zero. The meanings of the slope and intercepts are discussed in the next section.

### Table 4

Annual gross primary productivity (GPP, gC m$^{-2}$ year$^{-1}$) and ecosystem respiration ($R_{eco}$, gC m$^{-2}$ year$^{-1}$) over oak/grass savanna, open grassland, and understory grassland. For tree canopy, the values are annual tree gross photosynthesis ($A_c$, gC m$^{-2}$ year$^{-1}$) and tree canopy respiration ($R_{above}$, gC m$^{-2}$ year$^{-1}$).

<table>
<thead>
<tr>
<th>Hydrological year$^a$</th>
<th>Savanna</th>
<th>Open grassland</th>
<th>Understory Grassland</th>
<th>Tree Canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GPP</td>
<td>$R_{eco}$</td>
<td>GPP</td>
<td>$R_{eco}$</td>
</tr>
<tr>
<td>2000–2001</td>
<td>–</td>
<td>–</td>
<td>967</td>
<td>884</td>
</tr>
<tr>
<td>2001–2002</td>
<td>888</td>
<td>744</td>
<td>844</td>
<td>904</td>
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<td>2002–2003</td>
<td>1091</td>
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<td>993</td>
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<td>2003–2004</td>
<td>899</td>
<td>847</td>
<td>626</td>
<td>780</td>
</tr>
<tr>
<td>2004–2005</td>
<td>1360</td>
<td>1217</td>
<td>1313</td>
<td>1225</td>
</tr>
<tr>
<td>2005–2006</td>
<td>1113</td>
<td>1078</td>
<td>813</td>
<td>1002</td>
</tr>
<tr>
<td>Mean</td>
<td>1070</td>
<td>972</td>
<td>926</td>
<td>964</td>
</tr>
<tr>
<td>STD$^b$</td>
<td>193</td>
<td>186</td>
<td>230</td>
<td>151</td>
</tr>
</tbody>
</table>

$^a$ Hydrological year starts on 23 October (Day 296) and ends on 22 October (Day 295) of the next year.

$^b$ STD refers to standard deviation.
in some years. Such alternations between carbon sink and carbon source have been reported for a Canadian cool temperate grassland (Flanagan et al., 2002) and for European grassland (Gilmanov et al., 2007). Although some grasslands are carbon sinks (Hanan et al., 1998; Kato et al., 2006; Zhao et al., 2006) and some are consistent carbon source (Suyker et al., 2003), alternations between carbon sink and carbon source are not rare, especially when a ecosystem encounters extreme climatic events or disturbances (e.g. fire, logging) (Amiro et al., 2006; Barr et al., 2007; Carrara et al., 2003; Ciais et al., 2005; Diffenbaugh et al., 2005; Gilmanov et al., 2007; Houghton, 2000; Hutley et al., 2005).

Inter-annual variability in NEE varies with ecosystem type. In evergreen conifer forests, standard deviation between sampling years is as low as 7 gC m\(^{-2}\) year\(^{-1}\) (Hollinger et al., 2004). As an example of temperate deciduous forests, Harvard Forest has an inter-annual standard deviation of 38 gC m\(^{-2}\) year\(^{-1}\) during 1991–2000 (Barford et al., 2001), which is within the range of inter-annual variability in NEE in temperate deciduous forests (between 23 gC m\(^{-2}\) year\(^{-1}\) (Schmid et al., 2003) and 227 gC m\(^{-2}\) year\(^{-1}\) (Saigusa et al., 2005). In an Australian cool temperate Eucalyptus forest, inter-annual variability in NEE is up to 352 gC m\(^{-2}\) year\(^{-1}\) (Leuning et al., 2005), while it is ~40 gC m\(^{-2}\) year\(^{-1}\) in an Australian semi-arid savanna (Hutley et al., 2005). In an Oklahoma’s tallgrass prairie, the standard deviation is ~116 gC m\(^{-2}\) year\(^{-1}\) (Suyker et al., 2003). According to these data from the literature, inter-annual variability in NEE at our study site approximates the global average inter-annual variability in NEE across different ecosystem types. It is important to recognize that inter-annual variability in NEE may be significant when compared with magnitude of annual NEE, especially for the ecosystems with near-zero NEE.

Our data also show that the longer the growing season is, the greater the magnitude of carbon uptake (Goulden et al., 1996; Baldocchi and Wilson, 2001). In the savanna, each additional day of tree-growing season increased the carbon uptake of ecosystem by 2.0 gC m\(^{-2}\), while in the open grassland carbon uptake increased by 4.0 gC m\(^{-2}\) with a single-day increase in grass-growing season. These rates are lower than the 5.9 gC m\(^{-2}\) day\(^{-1}\) increase in temperate deciduous forests (Baldocchi and Wilson, 2001) and the 6.9 gC m\(^{-2}\) increase in a boreal aspen forest with 1-day increase within full leaf duration (Barr et al., 2004).

A variety of biophysical factors drive length of growing season, and these factors differ from year to year (Cleland et al., 2006; Menzel et al., 2006). In this study, we found that the cool springs of 2002 and 2006, the biological legacy effects of 2005 on 2006, and the lack of spring precipitation in 2003–2004 affected length of growing season and the NEE of the savanna. Among these factors, however, spring-time precipitation is the predominant factor driving inter-annual differences in NEE; it does so by directly driving photosynthesis and ecosystem respiration, as shown in this study. Other factors, such as extreme weather events and previous biophysical conditions, are secondary because they occur with low frequency over multi-year scales. Distinguishing primary and secondary factors would be useful for a modeling approach that attempts...
to capture the likelihood of inter-annual variability in CO₂ fluxes.

Our finding that year-to-year variations in spring precipitation explain inter-annual variability in \( R_{\text{eco}} \) and GPP corroborates previously published findings. In 1970s, California grassland studies have found that and GPP corroborates previously published findings. In 1970s, California grassland studies have found that the 2- or 3-month precipitation during the growing season significantly controlled on inter-annual variations of grass yield in central California (Duncan and Woodmansee, 1975; Pitt and Heady, 1978). Xu and Baldocchi (2004) found that the timing of rain events was more critical in the same open grassland as the one studied here. The timing of rainfall in previous fall and spring seasons determines length of wet season, which Baldocchi (2004) found that the timing of rain events during a critical period may be more practicable than the timing of precipitation if daily precipitation data are unavailable.

There are arguments about whether photosynthesis or respiration contributes more to inter-annual variability of net ecosystem exchange of carbon. Fig. 8 refines the analysis of Valentini et al. (2000), who found that NEE fluctuated with changes in \( R_{\text{eco}} \) while GPP was constant. We confirm that \( R_{\text{eco}} \) is sensitive to temperature in years with sufficient water conditions, e.g., 2005–2006. However, during the dry year (2003–2004), water deficiency constrained both GPP and \( R_{\text{eco}} \). In the latter condition, both GPP and \( R_{\text{eco}} \) are important determinants of annual NEE (Suni et al., 2003). Similarly, declines in GPP and \( R_{\text{eco}} \) occurred simultaneously with the heat wave and drought of 2003 in Europe (Reichstein et al., 2006).

Based on observations in 2005–2006, one might expect a scenario in which higher temperatures and more spring precipitation would cause annual carbon uptake to decrease dramatically in California’s savanna areas; respiration would increase with the higher temperatures if soil water conditions are sufficient. However, higher temperature probably couples with less rainfall and lower temperature probably couples with increased cloudiness. High temperatures may enhance decomposition only when water conditions are adequate—a condition favorable to photosynthesis. Consequently, more photosynthetic products will benefit soil microbes in the rhizospheric zone (Atkin et al., 2005; Cramer et al., 2001). Future combinations of temperature and precipitation could disrupt complementarities among species and profoundly influence ecosystem carbon cycling on regional scales (Hayhoe et al., 2004; Kueppers et al., 2005).

Since terrestrial ecosystems function cumulatively as an effective sink of atmospheric CO₂, the average of the ratio \( R_{\text{eco}}/\text{GPP} \) should be less than one across multiple ecosystem types (Law et al., 2002). The linear regression analysis of \( R_{\text{eco}} \) vs. GPP over multiple years shows that the slope of \( R_{\text{eco}} \) vs. GPP (\( dR_{\text{eco}}/\text{dGPP} \)) will become more meaningful, \( dR_{\text{eco}}/\text{dGPP} \) is not equivalent to the ratio of \( R_{\text{eco}}/\text{GPP} \) if heterotrophic respiration is significantly non-zero. In this study, \( dR_{\text{eco}}/\text{dGPP} = 0.79 \), with statistical significance, means that \( R_{\text{eco}} \) will increase 0.79 gC m⁻² year⁻¹ with one unit of increase in GPP at the grassland even though \( R_{\text{eco}}/\text{GPP} \) varies inter-annually (Barr et al., 2007; Zhao et al., 2006). A conservative value of \( dR_{\text{eco}}/\text{dGPP} \) could be useful in future ecosystem carbon marketing because it reflects the capacity and/or variability in carbon balance for one type of ecosystem under current species compositions, climate fluctuations, and management practices.

Theoretically, autotrophic respiration (\( R_{\text{auto}} \)) reduces to zero when GPP = 0. Therefore, the regression intercepts would be equal to a “background” of annual \( R_{\text{hetero}} \) if vegetation were absent (e.g. off-season or removal). In this study we find the “background” level of \( R_{\text{hetero}} \) to be 124 gC m⁻² year⁻¹ and 299 gC m⁻² year⁻¹ for the savanna and the annual grassland, respectively.

The \( R_{\text{eco}} \) of the understory grassland includes \( R_{\text{hetero}} \), \( R_{\text{root_grass}} \), and \( R_{\text{root_tree}} \) (Table 1). Thus, when understory GPP = 0, for example during the off-season or after grasses are harvested, \( R_{\text{root_grass}} \) = 0. The “background” respiration of the understory is then equal to the sum of respiration by the soil microbes and tree roots (\( R_{\text{eco,under}} = R_{\text{hetero}} + R_{\text{root_tree}} \)). “Background” \( R_{\text{root_tree}} \) becomes the difference between the understory intercept and the savanna intercept; that difference is equivalent to the absolute value of the intercept of tree \( R_{\text{above}} \) vs. that of \( R_{\text{auto}} \) (Fig. 8).

An assumption in ecology is that a certain proportion of photosynthesis contributes to autotrophic respiration, including aboveground respiration (\( R_{\text{above}} \)) and root respiration (\( R_{\text{root}} \)) (Gifford, 1994). That is,

\[
R_{\text{above}} + R_{\text{root}} = c\text{GPP}; \quad (1)
\]

Furthermore, we define ecosystem respiration as:

\[
R_{\text{eco}} = R_{\text{above}} + R_{\text{root}} + R_{\text{hetero}}; \quad (2)
\]

Substituting Eq. (1) into Eq. (2) and rearranging:

\[
R_{\text{hetero}} = R_{\text{eco}} - c\text{GPP}; \quad (3)
\]

Based on our inter-annual regression for the savanna, the understory grassland, and the tree canopy, we also
know that:

\[ R_{\text{eco, over}} = 0.79 \text{GPP}_{\text{over}} + 124; \]  
\[ R_{\text{above, tree}} = 0.79A_c - 219; \]  

Thus,

\[ R_{\text{hetero, savanna}} = (0.79 - c)\text{GPP}_{\text{over}} + 124; \]  

At this point, \( c \leq 0.79. \)

Now, we know that

\[ R_{\text{root, tree}} = R_{\text{eco, over}} - R_{\text{above, tree}} - R_{\text{hetero, savanna}}; \]  

Substituting Eqs. (4)–(6) into Eq. (7) and rearranging:

\[ R_{\text{root, tree}} = (0.79 - c)\text{GPP}_{\text{over}} + 0.79\text{GPP}_{\text{under}} + 219; \]  

Based on the definition of soil respiration \( (R_{\text{soil}}) \),

\[ R_{\text{soil}} = R_{\text{eco, under}} = 0.79\text{GPP}_{\text{under}} + 343; \]  

Therefore, measuring CO\(_2\) exchange in the overstory and understory of the savanna over multiple years enables us to partition \( R_{\text{eco}} \) into heterotrophic and autotrophic respiration terms in a new, direct way although these analysis does not consider complexity of eco-physiological processes on short-term time scales, such as pulses in soil respiration after isolated rain evens within a continuous dry period (Xu et al., 2004) and different timing in diurnal or seasonal patterns of photosynthesis and respiration (Tang et al., 2005; Baldocchi et al., 2006). Over multi-year scales, all respiration terms are related to photosynthesis. Consequently, the inter-annual variation of these respiration terms is constrained by the inter-annual variability in photosynthesis. Thus, off-season warming events may not increase ecosystem respiration as dramatically as had been expected previously because GPP is nil.

5. Conclusions

This study provides evidence that annual carbon fluxes of a savanna and grassland ecosystem are conditional upon a combination of seasonal climate conditions and on inter-relationships between ecosystem respiration and gross primary productivity. These conditions fluctuate widely from year to year and can cause the grassland to switch from being a carbon sink to being a carbon source.

For each year of the study, NEE was determined in a complex fashion by both GPP and \( R_{\text{eco}} \), while \( R_{\text{eco}} \) was significantly constrained by GPP. GPP and \( R_{\text{eco}} \) of the savanna and grassland were shown to depend on the amount of seasonal precipitation, when grasses and trees were active simultaneously, instead of annual precipitation. Besides the primary climate driver (spring precipitation), we found three secondary factors of inter-annual NEE variation: temperature before oak leaf-out, cloudiness, and effects of biological legacy such as extraordinary previous-season growths.

We also used data from this inter-annual study to provide a novel, direct method of partitioning components of ecosystem respiration by measuring CO\(_2\) exchange in the overstory and understory over multiple years. The two parameters studied—the sensitivity of \( R_{\text{eco}} \) to GPP \( (dR_{\text{eco}}/d\text{GPP}) \) and the baseline of respiration terms—both provide useful tools for understanding the dynamics of ecosystem CO\(_2\) uptake in current stages of ecosystem composition and current climate conditions. These tools are also useful for detecting ecosystem succession and the effects of disturbances or anthropogenic management on ecosystem carbon metabolism in changing climates.

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