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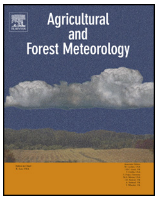

Slow ecosystem responses conditionally regulate annual carbon balance over 15 years in Californian oak-grass savanna

Siyan Ma[a,*], Dennis Baldocchi[a], Sebastian Wolf[a,b], Joseph Verfaillie[a]

[a] Ecosystem Science Division, Department of Environmental Science, Policy and Management, University of California at Berkeley, Berkeley, CA 94720, USA
[b] Department of Environmental Systems Science, ETH Zurich, 8092 Zurich, Switzerland

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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 CO_2 (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 CO_2 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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[*] Corresponding author at: Department of Environmental Sciences, Policy, and Management, University of California at Berkeley, 130 Mulford Hall # 3114, Berkeley, CA 94720, USA.

E-mail address: syma@berkeley.edu (S. Ma).

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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; Coursolle 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 CO_2 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-e-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 CO_2 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 CO_2 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 CO_2 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 CO_2 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).