

**The Dynamics of Energy, Water and Carbon Fluxes in a Blue Oak (*Quercus douglasii*)  
Savanna in California, USA**

Dennis Baldocchi, Qi Chen<sup>1</sup>, Xingyuan Chen, Siyan Ma, Gretchen Miller, Youngryel Ryu,  
Jingfeng Xiao<sup>2</sup>, Rebecca Wenk and John Battles

Department of Environmental Science, Policy and Management  
137 Mulford Hall  
University of California, Berkeley  
Berkeley, CA 94720

**“Ecosystem Function in Global Savannas: Measurement and Modeling at Landscape to  
Global Scales” – edited by Michael J. Hill and Niall P. Hanan and published by  
CRC/Taylor and Francis**

September 28, 2009

Corresponding author

[baldocchi@berkeley.edu](mailto:baldocchi@berkeley.edu)

<sup>1</sup>University of Hawaii

<sup>2</sup>Meteorology Department, Pennsylvania State University

*All his leaves  
Fall'n at length,  
Look, he stands,  
Trunk and bough  
Naked strength.*

The Oak, Alfred Lord Tennyson

## **Introduction**

Oak trees and their savanna woodlands have played many important roles in the history, development and ecology of California, and the American West (Pavlik et al. 1991; Tyler, Kuhn, and Davis 2006). Starting with the Spanish Mission period through today, cattle have grazed the oak savanna, producing beef for our dinner, leather for our shoes and tallow for our soap. In the mid 19<sup>th</sup> century, 49'ers mined the oak savanna for gold and used its wood for cooking, heating and building mine shafts. Today, the oak savanna provides many ecological services and benefits to the region. Oak savannas vegetate the watersheds of the many rivers stemming from the Sierra Nevada and Coastal mountain ranges. By doing so, they protect the soils of this hilly terrain, they provide habitat for wildlife and acorns that have sustained the Native American population and wildlife for millennia. From a hydrologic perspective, runoff from these watersheds provides water for a large fraction of California's multi-billion dollar agricultural economy and its population of 35 million, plus, inhabitants.

Despite, their intrinsic value, California's oak savannas are suffering in today's world. Regeneration failure (Tyler, Davis, and Mahall 2008), exotic diseases (e.g. sudden oak death syndrome) (Rizzo and Garbelotto 2003) and invasive species (Seabloom et al. 2006) are among the key ills that this biome faces. Land use change is another issue threatening oak savannas. Many oak savannas are being converted to vineyards or are being carved into ranchettes, thereby

fragmenting the landscape (Huntsinger, Buttolph, and Hopkinson 1997; Heaton and Merenlender 2000). In the future, California's oak savannas may experience a shift or reduction in their native range with global warming (Kueppers et al. 2005; Loarie et al. 2008).

One way to assess the health of an ecosystem is to study the dynamics of its 'breathing' (Baldocchi 2008). For instance, investigators can quantify how ecosystem metabolism responds to environmental perturbations by measuring carbon, water vapor and energy fluxes between an ecosystem and the atmosphere, quasi-continuously and over multiple years. Then they can use these fluxes measurements to validate and parameterize ecosystem carbon and water cycle models, which, in turn, can be used to predict and diagnose ecosystem behavior and integrate fluxes in time and space (Moorcroft 2006; Baldocchi and Wilson 2001).

In this chapter we present information on the energy, water and carbon fluxes of a Californian blue oak (*Quercus douglasii*) savanna. To acquire this information we use a multi-faceted approach that reflects a contemporary convergence of the fields of micrometeorology, ecosystem ecology and eco-hydrology. Energy, water vapor and carbon dioxide exchange data are derived from seven years of nearly-continuous eddy covariance measurements over a blue oak (*Quercus douglasii*) savanna near Ione, California (latitude: 38.43 N; Longitude: 120.96 W). The mass and energy flux data, shown here, are evaluated on daily, annual and multi-year time-scales. We interpret these fluxes with a suite of ancillary measurements, pertaining to climate, canopy structure, physiological function at the tree and leaf scales and the underlying soil processes. Finally, we upscale the carbon dioxide flux information across the blue oak biome with the aid of remote sensing. The overarching question asked and answered in this chapter is: how do factors associated with leaf, tree and canopy function and structure, climate and soil conspire to enable these woodlands to sustain themselves in the extreme and variable

## Mediterranean-type climate of California?

Information produced in this chapter add a new biophysical component to former ecological analyzes of California oak savanna (Griffin 1988; Barbour and Minnich 2000). Flux measurements from a savannas in the Mediterranean-type climate of California also provides information that is relevant towards understanding the function and structure of European oak savannas, known as dehesa and montado (Joffre, Rambal, and Damesin 2007; Pereira et al. 2007), because they share many similarities. Finally, these woodlands are situated at one end of the North American climate-niche gradient, so these measurements provide critical information for upscaling carbon fluxes across the continent using a combination of flux data, remote sensing and climate data (Xiao et al. 2008).

## Biogeography

Californian, oak savanna consists of evergreen and deciduous species. This biome is situated on the coastal and Sierra Nevada mountain foothills that circumscribe the outlying border of the Great Central Valley. Its spatial extent occupies over 45,000 km<sup>2</sup> of land area, an area that represents about 11% of the state of California (Tyler, Kuhn, and Davis 2006).

The climate space of *Quercus douglasii* includes regions where mean annual air temperature ranges between 14 and 16 °C and mean annual precipitation ranges between 400 and 800 mm per year (Griffin 1988; Major 1988). Colder temperatures and wetter conditions favor conifers (Stephenson 1998) and warmer temperatures and drier conditions favor annual grasslands and native perennial grasses (Major 1988; Heady 1988).

While mean climate conditions provide constraints on the biogeography of blue oak, oak savanna must endure inter-annual and intra-annual extremes in precipitation. Annual precipitation, based on a 50 year record at Camp Pardee (Latitude: 38.250°N; Longitude,

120.867°W.) ranges between 200 and 1200 mm per year and it experiences a standard deviation of 196 mm per year; typically, surplus rainfall occurs during late winter and early spring of *El Niño* years and deficit rainfall occurs during *La Niña* years. Moreover, the rainfall regime across the California oak savanna region is highly seasonal (Major 1988; Ma et al. 2007). In the late autumn and early winter (November through February), seasonal rainfall commences. This prompts the grasses to germinate and grow, while the deciduous oaks are leafless and dormant. In spring (March through May), the grasses and trees function simultaneously; the grasses experience exponential growth, then reproduce, and oak trees leaf-out and achieve full canopy. Between June and November the region is rainless, causing the grasses to die, while the trees assimilate carbon and transpire water.

Consequently, there is a tight anti-correlation between soil moisture and soil temperature and a positive correlation between soil temperature and intercepted solar radiation. Soil temperature ranges between 5 and 35 °C, while soil moisture ranges between 40 and 5% and mean midday visible sunlight ranges between 300 and 1500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The highest soil temperatures occur when the soil is driest and the sunshine is greatest.

## **Structure and Function**

### ***Canopy Architecture***

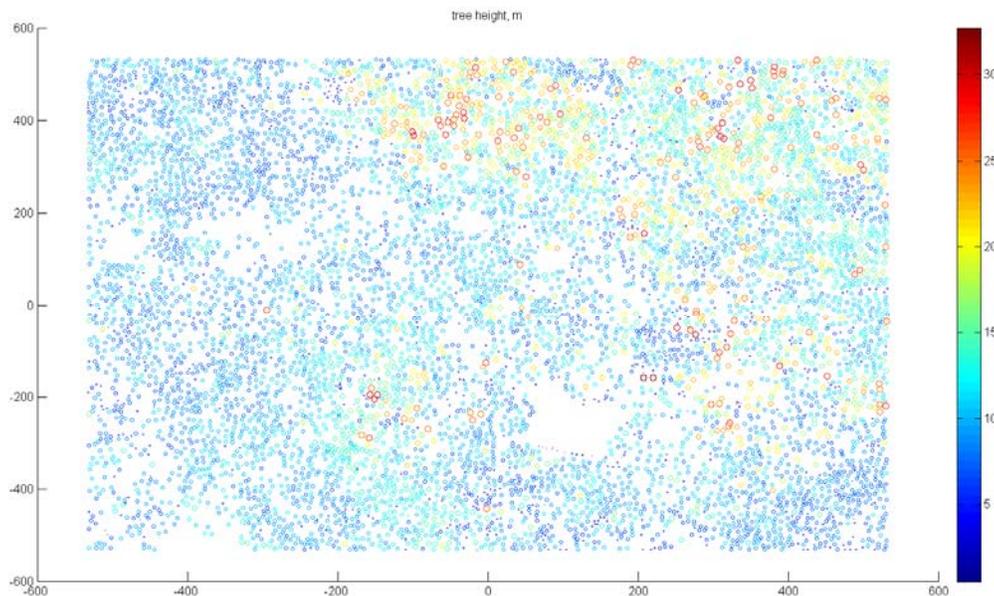
From structural and functional perspectives Mediterranean tree-grass savanna ecosystems are distinct from many other ecosystems. These systems are: 1) heterogeneous in space; 2) they consist of a mix of contrasting plant growth forms (herbaceous and woody; deciduous and evergreen, annual and perennial); 3) they possess physiological and architectural features to endure and tolerate extreme soil water deficits, which enable them to survive harsh

environmental conditions; 4) they often reside on undulating topography; and 5) they are grazed regularly and burn periodically.

We have quantified the structural features of the oak woodland with a variety of direct and remote sensing methods, including airborne LIDAR, IKONOS and AVIRIS images and ground based measurements of light transmission (Chen, Baldocchi et al. 2008; Chen et al. 2006). The openness and heterogeneity of the canopy is best visualized with a two-dimensional plot of tree location and crown diameter (Figure 1). On average, the trees are about 9.4 +/- 4.3 m tall, the oak and pine trees cover about 63% of the landscape and constitute a leaf area index of 0.7. Additional tree demographic and structural information is listed in Table 1.

**Table 1. Properties of individual trees and oak woodland stand for a seasonally grazed, blue oak woodland, near Ione, CA**

Metric	Mean	Std
Crown Area(m <sup>2</sup> )	39.23	41.2
Crown Radius(m)	3.18	1.54
Tree height(m)	9.41	4.33
Trunk height (m)	1.75	1.35
Crown height (m)	7.66	4.56
Basal area (m <sup>2</sup> )	0.0744	0.084
Stem volume (m <sup>3</sup> )	0.734	1.23
Stem biomass (kg)	440.43	739.6
Leaf area (m <sup>2</sup> )	38.32	64.36
LAI	0.706	0.408
Stems per hectare	144	
Fraction oaks (%)	50.1	
Fraction pine (%)	13.6	
Fraction ground (%)	36.3	



**Figure 1** A map of tree location, height and crown size of a blue oak savanna, near Ione, CA. The horizontal dimensions of the figure are 1000 m by 1000 m and the flux measurement tower is at the center. Canopy structure was quantified using an airborne LIDAR during the summer of 2009.

### *Leaf and Tree Physiology*

To understand how the leaves and plants modulate carbon and water fluxes, we made frequent measurements of leaf photosynthesis, stomatal conductance, pre-dawn water potential, and tree transpiration. Leaf gas exchange measurements, based on an environmentally-controlled cuvette system, were made over the course of a growing season to deduce information on photosynthetic capacity and stomatal conductance model parameters (Xu and Baldocchi 2003). These oak leaves achieve extremely high values of maximum carboxylation velocity,  $V_{cmax}$  ( $110-120 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) during the early period of their growing season, when moisture is ample (Xu and Baldocchi 2003);  $V_{cmax}$  is the key model parameter of the Farquhar-von Caemmerer-Berry photosynthesis model (Farquhar, Caemmerer, and Berry 1980). Then  $V_{cmax}$  and leaf nitrogen drop dramatically, and in concert, as soil moisture is depleted.

The maximum  $V_{cmax}$  values are comparable to values of well-watered and fertilized crops

and they exceed typical values for native oak trees in temperate biomes (Wilson, Baldocchi, and Hanson 2001; Wullschlegel 1993). Blue oak leaves must develop high-capacity, light harvesting and carbon assimilation systems during the short period when soil water is available in order to acquire enough carbon to offset respiratory costs for the rest of the year. To achieve high rates of photosynthesis they need the mechanics to do so. In other words, high levels of  $V_{cmax}$  require high levels of Rubisco, which require high levels of nitrogen, which requires the production of thick leaves (Xu and Baldocchi 2003; Reich, Walters, and Ellsworth 1997).

Summer drought in California is particularly severe, and is more extreme than the conditions that vegetation may face in other Mediterranean-climate regions. For example, we measured pre-dawn water potentials values as low as  $-6.0$  MPa (Xu and Baldocchi 2003), far below the conventional wilting point of  $-1.5$  MPa (Sperry 2000). In contrast, oaks growing on the coastal range of California experience less negative pre-dawn water potentials, down to  $-4.0$  MPa (Griffin 1973), and predawn water potentials measured on Mediterranean oaks tend to be on the order of  $-3.0$  MPa (Joffre, Rambal, and Damesin 2007).

There are many issues regarding the effects of moderate and severe drought on photosynthesis (Cornic 2000). For example, do stomata adjust to soil water deficits while photosynthetic capacity remains unchanged? Or is there a down-regulation in photosynthetic capacity with soil moisture deficits? Some researchers argue that modest soil water deficits induce stomatal closure, which in turns reduces the internal  $CO_2$  concentration and subsequently down-regulates photosynthesis (Cornic 2000); this physiologically induced reduction in photosynthesis does not imply a change in photosynthetic capacity. An opposing line of evidence, derived from studies on Mediterranean oaks in Europe and California, suggests that oaks exposed to chronic soil water deficits down-regulate their photosynthetic capacity, decrease

their mesophyll conductance and dissipate excess photon flux energy via the xanthophyll cycle (Chaves et al. 2002; Flexas et al. 2007). Our data show that seasonal changes in  $V_{cmax}$  are negatively correlated with pre-dawn water potential, suggesting a down-regulation of photosynthetic capacity with drought. This drought-mediated reduction in  $V_{cmax}$  comes in concert with progressive stomatal closure. However, the drought induced reduction in photosynthesis is also associated with a progressive reduction in  $C_i/C_a$  (Xu and Baldocchi 2003), which is consistent with the conclusions of Cornic (Cornic 2000). Furthermore, we find that stomatal conductance is a constant fraction of the product between leaf photosynthesis, relative humidity and the reciprocal of  $CO_2$  concentration (Collatz et al. 1991) for both wet and dry soil moisture conditions.

While water is a precious commodity to blue oaks during the summer, there are some inefficiencies and leaks in the system. Sapflow occurs at night and the magnitude of nocturnal transpiration increases with vapor pressure deficit, indicating that stomatal closure is not complete at night (Fisher et al. 2007).

### **Canopy Scale: Energy and Water Fluxes**

Solar radiation is the main energy source to the ecosystem and the microclimate. On an annual basis the site receives about  $6.59 \pm 0.14 \text{ GJ m}^{-2} \text{ y}^{-1}$  of global solar radiation ( $R_g$ ) (Table 2). Year-to-year variation in  $R_g$  ranged between 6.46 and 6.70  $\text{MJ m}^{-2} \text{ y}^{-1}$ . This value is consistent with historical measurements at two climate stations in sunny northern California (Major 1988). This much solar energy has the potential to produce about  $3600 \text{ gC m}^{-2} \text{ y}^{-1}$  of photosynthesis, if the vegetation had a year-round growing season, ample soil moisture and a photosynthetic efficiency of 2% (Ruimy, Dedieu, and Saugier 1996).

Net radiation is defined as the sum of the gains and losses of incoming shortwave and

longwave radiation, and is a function of albedo and emissivity. On an annual basis,  $3.17 \pm 0.098 \text{ GJ m}^{-2}$  of net radiation is available to the woodland (Table 2). In comparison, the neighboring annual grassland net radiation budget ranged between 2.1 and  $2.3 \text{ GJ m}^{-2}$  during 2001 and 2002 (Ryu et al. 2008; Baldocchi, Xu, and Kiang 2004). About  $1 \text{ GJ m}^{-2}$  more energy is available to the oak savanna, compared to the neighboring grassland, because the savanna is optically darker and its cooler, transpiring leaves causes it to radiate less long-wave energy.

Net radiation is partitioned into sensible and latent heat flux and in heating the soil. On an annual basis sensible heat flux of the savanna woodland equals  $1.87 \pm 0.22 \text{ GJ m}^{-2}$ , almost double that of latent heat exchange ( $0.96 \pm 0.13 \text{ GJ m}^{-2}$ ). Soil heat flux is close to zero on an annual basis.

**Table 2 Annual sums of energy flux densities over an oak savanna in California.  $R_g$  is solar radiation,  $R_n$  is net radiation,  $\lambda E$  is latent heat flux,  $H$  is sensible heat flux, and  $G$  is soil heat flux.**

Variable	Location	Year						
		01_02	02_03	03_04	04_05	05_06	06_07	Avg
$R_g$ ( $\text{GJ m}^{-2}$ )	Above canopy	6.70	6.48	6.69	6.46	6.47	6.76	6.59
$R_n$ ( $\text{GJ m}^{-2}$ )	Above canopy	3.25	3.22	3.17	3.08	3.04	3.29	3.17
$\lambda E$ ( $\text{GJ m}^{-2}$ )	Above canopy	0.93	1.02	0.79	1.15	1.02	0.83	0.96
$H$ ( $\text{GJ m}^{-2}$ )	Above canopy	2.06	1.87	2.11	1.62	1.66	1.91	1.87
$G$ ( $\text{GJ m}^{-2}$ )	Below canopy	0.03	0.04	0.06	0.02	0.03	0.03	0.04

Across the sunny Mediterranean climate of California, potential evaporation typically exceeds annual precipitation (Hidalgo, Cayan, and Dettinger 2005). At our field site, annual potential evaporation was 1429 mm (Table 3). This sum vastly exceeds mean annual actual evaporation (390 mm per year) and rainfall (565 mm per year) and is about 400 mm greater than potential evaporation from an annual grassland (Ryu et al. 2008). On the other hand, these

eddy covariance measurements of actual evaporation compare well with a seventeen-year, water balance study performed in an oak woodland watershed, northeast of Sacramento, CA; actual evaporation was estimated to equal 368 +/- 69 mm per year (Lewis et al. 2000).

**Table 3 Annual sums of water balance components. Ppt is annual precipitation,  $E_p$  is potential evaporation,  $E_t$  is total evaporation,  $E_o$  is overstory evaporation,  $E_u$  is understory evaporation**

Variable	Year						
	01_02	02_03	03_04	04_05	05_06	06_07	Avg
$Ppt$ (mm yr <sup>-1</sup> )	493	509	465	628	884	411	565
$E_p$ (mm yr <sup>-1</sup> )	1412	1421	1427	1394	1411	1510	1429
$E_t$ (mm yr <sup>-1</sup> )	381	416	320	469	416	339	390
$E_o$ (mm yr <sup>-1</sup> )	243	254	197	276	222	189	230
$E_u$ (mm yr <sup>-1</sup> )	137	162	123	193	194	149	160
$E_u/E_t$	36%	39%	39%	41%	47%	44%	41%

Some eco-hydrological models compute seasonal trends in actual evaporation as a function of equilibrium evaporation ( $E_{eq}$ );  $E_{eq}$  is a function of available energy and these ‘potential’ evaporation rates are down-regulated in a linear fashion with respect to decreasing volumetric soil moisture (Rodriguez-Iturbe 2000; Chen, Rubin et al. 2008). We quantified the functional relationship between evaporation and volumetric soil moisture applying the Markov Chain Monte Carlo method to three years of evaporation data (Chen, Rubin et al. 2008). Under well-watered conditions, the ratio between actual and equilibrium evaporation ( $E_a/E_{eq}$ ) is about 0.65. This  $E_a/E_{eq}$  value is much lower than the typical values for wet, irrigated, extensive vegetation, 1.26, also known as the Priestley –Taylor coefficient (Priestley and Taylor 1972). The ratio,  $E_a/E_{eq}$ , declines when the root-weighted volumetric water content drops below 0.12 cm<sup>3</sup> cm<sup>-3</sup> and the ratio approaches zero as volumetric soil moisture approaches 0.06 cm<sup>3</sup> cm<sup>-3</sup>.

A growing number of Mediterranean savanna studies are indicating the importance of deep water sources to sustain oak trees during the long, hot dry summer (Joffre, Rambal, and Damesin 2007; Baldocchi, Xu, and Kiang 2004). To address the hypothesis that ‘oaks tap deeper

sources of water' we draw on other data—the change in the soil moisture after the rains ceased and the grass died. Between day 150 and 309, our soil moisture budget detected a loss of 48 mm of water from the upper 0.60 m layer of the soil profile. In contrast our eddy covariance measurements of evaporation indicate that 114 mm of water evaporated from the landscape during this period and of this total, 20 mm of water was lost from the dry grass layer in the understory. Based on this water budget, we concluded that 66 mm of water, or 57% of the total, came from other sources. We originally surmised that a significant fraction of moisture probably came from below the fractured shale layer, supporting the measurements of Lewis and Burgy (1964). More recently, we established 3 wells at the site and have monitored their changes in water table. These new measurements support the hypothesis that the oak trees are tapping deep sources of water during the summer. Diurnal fluctuations in the depth to the groundwater table are observed during the oak active season and disappear when senescence of the oaks is complete. The depth to the water table increases during the daylight hours, when the trees are transpiring, and decreases during the nighttime, indicating recharge of the aquifer. For data from seven days in July 2007, we found that groundwater uptake ( $ET_g$ ) was between 0.25 and 0.45 mm d<sup>-1</sup> using a method developed by Vincke and Thiry (2008). In contrast, the eddy covariance system measured total daily evapotranspiration at rates between 0.50 and 0.84 mm d<sup>-1</sup>, indicating that approximately 55% of transpired water came from deep sources. Similar patterns have been noted in other dryland or riparian ecosystems (Loheide, Butler, and Gorelick 2005).

### **Canopy-Scale Carbon Fluxes**

Blue oak woodlands in California are small, net carbon sinks on an annual basis (-92 +/- 48 gC m<sup>-2</sup> y<sup>-1</sup>) over six years; for perspective, the mean net carbon exchange, derived from 500

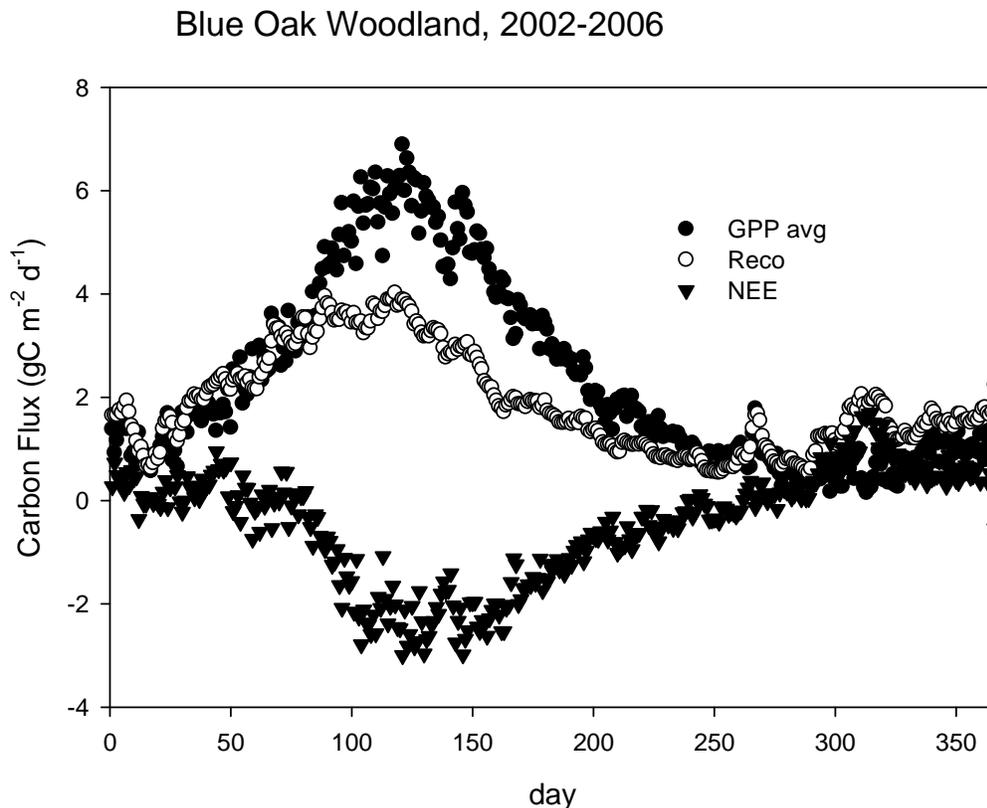
plus site-years of measurements across the FLUXNET network, is  $-183 \text{ gC m}^{-2} \text{ yr}^{-1}$  (Baldocchi 2008).

This relatively small net carbon flux is the residual between two relatively large and offsetting carbon fluxes. On average, gross primary productivity produces a carbon sink of  $1031 \text{ g C m}^{-2} \text{ yr}^{-1}$  and ecosystem respiration produces a carbon source of  $939 \text{ gC m}^{-2} \text{ yr}^{-1}$  (Ma et al. 2007) (Table 4). Consequently, inter-annual variability in net carbon exchange is explained by a tight relationship with spring-time cumulative rainfall which strongly modulates cumulative photosynthesis and respiration.

**Table 4 Annual net ecosystem exchange of  $\text{CO}_2$  ( $NEE$ ,  $\text{gC m}^{-2} \text{ yr}^{-1}$ ), gross primary productivity ( $GPP$ ) and ecosystem respiration ( $R_{eco}$ ) and uncertainties (in round brackets) (Ma et al. 2007). Hydrological year starts on 23 October (Day 296) and ends on 22 October (Day 295) of the next year.**

Hydrological Year	$NEE$ ( $\text{gC m}^{-2} \text{ yr}^{-1}$ )		$GPP$ ( $\text{gC m}^{-2} \text{ yr}^{-1}$ )		$R_{eco}$ ( $\text{gC m}^{-2} \text{ yr}^{-1}$ )	
<b>2001 - 2002</b>	-144	( $\pm 50$ )	888	( $\pm 75$ )	744	( $\pm 48$ )
<b>2002 - 2003</b>	-116	( $\pm 50$ )	1091	( $\pm 65$ )	975	( $\pm 49$ )
<b>2003 - 2004</b>	-52	( $\pm 62$ )	899	( $\pm 56$ )	847	( $\pm 41$ )
<b>2004 - 2005</b>	-143	( $\pm 47$ )	1360	( $\pm 66$ )	1217	( $\pm 56$ )
<b>2005 - 2006</b>	-35	( $\pm 44$ )	1113	( $\pm 53$ )	1078	( $\pm 52$ )
<b>2006-2007</b>	-78	( $\pm 56$ )	904	( $\pm 65$ )	773	( $\pm 44$ )
<b>2007-2008</b>	-79	( $\pm 48$ )	797	( $\pm 46$ )	718	( $\pm 42$ )
<b>Mean<math>\pm</math>STD</b>	-92	$\pm 43$	1007	$\pm 193$	907	$\pm 189$

Net ( $NEE$ ) and gross ( $GPP$ ) carbon uptake and ecosystem respiration ( $R_{eco}$ ) experience pronounced seasonal variation (Figure 2). Peak carbon fluxes occur during the spring, shortly after leaf expansion when soil moisture is ample;  $GPP$ ,  $R_{eco}$  and  $NEE$  peak at rates near 6, 4 and  $-3 \text{ gC m}^{-2} \text{ d}^{-1}$ , respectively. Over a year, this ecosystem operates, technically, as an evergreen ecosystem. The grass is green and photosynthesizing during the winter dormant period and the trees are photosynthesizing during the dry summer period when the grass is dead.

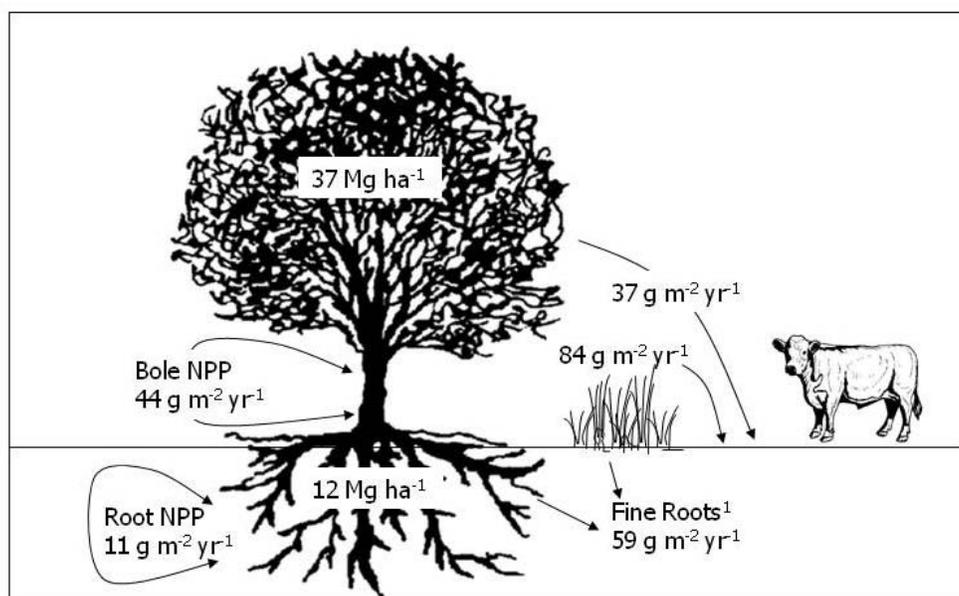


**Figure 2** Seasonal variation in gross primary productivity, ecosystem respiration and net ecosystem exchange. These data are presented for daily integrals averaged over the period between 2001 through 2006.

Episodic rain events during the summer period can cause huge pulses in soil respiration (Baldocchi, Tang, and Xu 2006; Xu and Baldocchi 2004). Two mechanisms are possible for producing enhanced respiration rates after summer rainfall events. One is a physical displacement of soil air and CO<sub>2</sub> by the downward moving front of water in the soil. But this effect is short-lived and the volume of air in the soil profile is relatively small. The other effect is attributed to a rapid activation of heterotrophic respiration (Baldocchi, Tang, and Xu 2006; Xu, Baldocchi, and Tang 2004). The size of these respiration pulses diminish with successive rain events as the size of the labile carbon pool diminishes.

We recently produced an independent carbon budget of the stand by measuring litterfall, fine root production and stem and root growth (Figure 3). The stand maintains 37 Mg C ha<sup>-1</sup> in

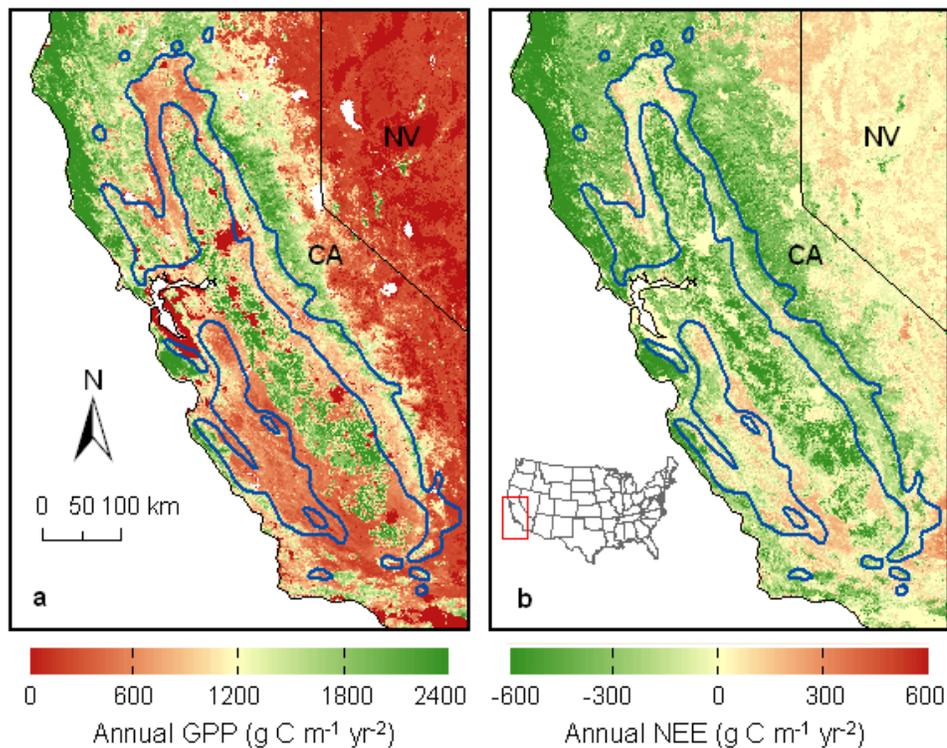
above ground biomass and 12 MgC ha<sup>-1</sup> in below ground biomass. Net primary productivity of the oak woodland is defined as the sum of the differences in carbon gains and losses. Above ground net primary productivity of the oak woodland equals 235 gC m<sup>-2</sup> y<sup>-1</sup>. This sum is comprised of bole increment growth (44 gC m<sup>-2</sup> y<sup>-1</sup>) plus litterfall (37 gC m<sup>-2</sup> y<sup>-1</sup>) and fine root production (59 gC m<sup>-2</sup> y<sup>-1</sup>) and grass (84 gC m<sup>-2</sup> y<sup>-1</sup>) and root net primary production (59 gC m<sup>-2</sup> y<sup>-1</sup>). Overall, this biometric carbon budget compares well with an independent estimate of *NPP* (283 gC m<sup>-2</sup> y<sup>-1</sup>), derived from our eddy covariance measurements (Ma et al. 2007).



**Figure 3** Summary of carbon budget for oak woodland near Ione, CA for the 2007-2008 hydrological growing season. Boxes represent pools (MgC ha<sup>-1</sup>); arrows represent fluxes (gC m<sup>-2</sup> year<sup>-1</sup>).

Using a combination of flux data from the entire AmeriFlux network, environmental drivers from MODIS sensor on the TERRA satellite, and regression tree analysis (Xiao et al. 2008), we produced maps of *GPP* (Figure 4a) and *NEE* (Figure 4b) for the blue oak woodland domain of California. The area-averaged fluxes of *GPP* and *NEE* were 932 and -150 gC m<sup>-2</sup> y<sup>-1</sup>, respectively. When summed up on an area-basis, the net and gross carbon fluxes equaled -

8.6 and 53.8 TgC y<sup>-1</sup>, respectively.

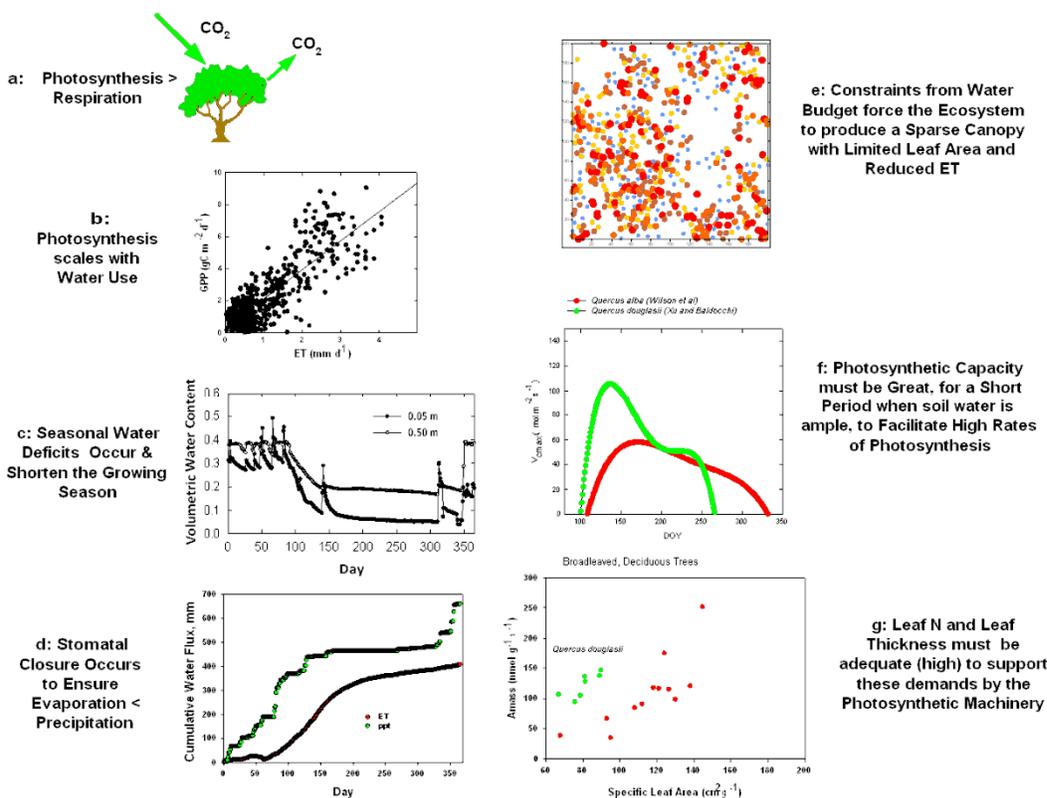


**Figure 4** Spatial map of net ecosystem carbon exchange for the blue oak biome. Fig. 4a is for annual gross primary productivity (GPP); Fig. 4b. is for net annual ecosystem carbon exchange (NEE). These data are extracted from the map of Xiao et al. (2008) and are derived using data from the MODIS sensor and the AmeriFlux network.

## Discussion

To survive and thrive, the oak trees in the California savanna must coordinate how much water they use to gain enough carbon to offset respiratory needs and evaporative demand. This task is achieved by a series of multiple constraints (Figure 5). First, stand-level photosynthesis must exceed ecosystem respiration. But the act of photosynthesis comes with an additional cost, water loss via transpiration and evaporation. From a biophysical standpoint, the ecosystem cannot evaporate more water than is available (through precipitation minus runoff and infiltration). To balance its water supply and use, individual plants and assemblages of plants can exploit a variety of plausible mechanisms. On short, time scales (hours to season),

physiological adjustments, such as down-regulation by stomata closure (Cornic 2000) or by changes in hydraulic conductance (Sperry 2000) can be invoked to reduce transpiration. But this drought-induced stomatal closure inhibits photosynthesis. So the plant must develop leaves with a high photosynthetic capacity in order to assimilate enough carbon during the short hydrological growing season. This task is accomplished by producing leaves with high nitrogen content (Xu and Baldocchi 2003; Ma et al. 2007). On longer timescales (years to millennia) morphological and ecological adaptations or modifications can lead to reduced transpiration. For instance, a plant can: 1) develop smaller leaves that convect heat more efficiently (Taylor 1975; Baldocchi and Xu 2007); 2) produce more reflective leaves that reduce its solar heat load (Gates 1980); 3) adopt drought-deciduous behavior so it can drop leaves when soil moisture deficits are severe (Jolly and Running 2004); or 4) produce deep roots that tap otherwise unreachable sources of water (Lewis and Burgy 1964). At the landscape scale, the leaf area index that the canopy establishes must scale with the amount of water that is available and nutrient content of the leaves (Baldocchi and Meyers 1998; Eamus and Prior 2001). With 500 mm of rainfall, an oak canopy in California cannot form a closed canopy and must have a low leaf area index. This limitation in leaf area limits light capture and potential photosynthesis.



**Figure 5** An eco-hydrological explanation for the structure and function of a blue oak savanna and its sustenance. For the oak savanna to survive in their highly seasonal wet/dry, cool/hot climate they must comply with several linked constraints. First, annual photosynthesis must exceed ecosystem respiration (a); the oaks have a difficulty in achieving high rates of photosynthesis during the growing season because the lack of summer rains causes volumetric soil moisture to drop below 5% and induces physiological stress; furthermore, the act of photosynthesis comes with a cost—evaporation (c); consequently, annual evaporation must be constrained such that it does not exceed annual precipitation, or the trees invest in deep roots that tap ground water(d); the landscape can reduce its total evaporation by establishing a partial canopy (e); and it can assimilate enough carbon if it adjusts and maximizes its photosynthetic capacity during the short spring wet period (f); high rates of photosynthesis are not free and come with producing thick leaves, rich in nitrogen and Rubisco.

Based on the data presented so far, we draw the conclusion that the blue oak savanna of California exerts both positive and negative effects on the climate system. On the pro side, oak savannas are modest sinks for carbon, taking up about  $100 \text{ gC m}^{-2} \text{ year}^{-1}$ , so they have the potential to mitigate anthropogenic carbon emissions. On the con side, they are optically darker than surrounding open grasslands. By absorbing more energy and by being aerodynamically rougher, compared to nearby grasslands, they evaporate more water (about 100 mm) and they

inject more sensible heat into the atmosphere ( $0.5 \text{ GJ m}^{-2} \text{ y}^{-1}$ ). Consequently, their air temperature is about 0.84 C degrees warmer than the surrounding grasslands (Baldocchi, Xu, and Kiang 2004). In California, water yield is a critical ecosystem service, so the negative effects of extra water use by the oak woodlands may outweigh their positive effect on the carbon budget. However, we should not discount the roles of oak woodlands for grazing, wildlife habitat, biodiversity, recreation and aesthetic value.

### **Acknowledgement**

This research was supported in part by the Office of Science (BER), U.S. Department of Energy, Grant No. DE-FG02-03ER63638 and through the Western Regional Center of the National Institute for Global Environmental Change under Cooperative Agreement No. DE-FC02-03ER63613. Other sources of support included the Kearney Soil Science Foundation, the National Science Foundation and the Californian Agricultural Experiment Station. We also express thanks to Ted Hehn, our long term lab technician, and Mr. Russell Tonzi for access to his ranch.

### **References**

- Baldocchi, D. 2008. TURNER REVIEW No. 15. 'Breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany* 56 (1):1-26.
- Baldocchi, D. D., and K.B. Wilson. 2001. Modeling CO<sub>2</sub> and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. *Ecological Modeling* 142:155-184.
- Baldocchi, D.D., J Tang, and L Xu. 2006. How Switches and Lags in Biophysical Regulators Affect Spatio-Temporal Variation of Soil Respiration in an Oak-Grass Savanna. *Journal Geophysical Research, Biogeosciences* 111:G02008, doi:10.1029/2005JG000063.
- Baldocchi, Dennis D., and Tilden Meyers. 1998. On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and trace gas fluxes over vegetation: a perspective. *Agricultural and Forest Meteorology* 90 (1-2):1-25.

- Baldocchi, Dennis D., and Liukang Xu. 2007. What limits evaporation from Mediterranean oak woodlands - The supply of moisture in the soil, physiological control by plants or the demand by the atmosphere? *Advances in Water Resources* 30 (10):2113-2122.
- Baldocchi, Dennis D., Liukang Xu, and Nancy Kiang. 2004. How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland. *Agricultural and Forest Meteorology* 123 (1-2):13-39.
- Barbour, MG, and B Minnich. 2000. California upland forests and woodlands. In *North American Terrestrial Vegetation, 2nd Editions*, edited by M. Barbour and W. Billings. Cambridge UK: Cambridge Univ Press.
- Chaves, M. M., J. S. Pereira, J. Maroco, M. L. Rodrigues, C. P. P. Ricardo, M. L. Osorio, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field. Photosynthesis and growth. *Annals of Botany* 89:907-916.
- Chen, Q., D. Baldocchi, P. Gong, and M. Kelly. 2006. Isolating individual trees in a savanna woodland using small footprint lidar data. *Photogrammetric Engineering and Remote Sensing* 72 (8):923-932.
- Chen, Qi, Dennis Baldocchi, Peng Gong, and Todd Dawson. 2008. Modeling radiation and photosynthesis of a heterogeneous savanna woodland landscape with a hierarchy of model complexities. *Agricultural and Forest Meteorology* 148 (6-7):1005-1020.
- Chen, X. Y., Y. Rubin, S. Y. Ma, and D. Baldocchi. 2008. Observations and stochastic modeling of soil moisture control on evapotranspiration in a Californian oak savanna. *Water Resources Research* 44 (8).
- Collatz, G. James, J. Timothy Ball, Cyril Grivet, and Joseph A. Berry. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* 54 (2-4):107-136.
- Cornic, Gabriel. 2000. Drought stress inhibits photosynthesis by decreasing stomatal aperture - not by affecting ATP synthesis. *Trends in Plant Science* 5 (5):187-188.
- Eamus, D., and L. Prior. 2001. Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Advances in Ecological Research, Vol 32* 32:113-197.
- Farquhar, G. D., S. V. Caemmerer, and J. A. Berry. 1980. A Biochemical-Model of Photosynthetic Co<sub>2</sub> Assimilation in Leaves of C-3 Species. *Planta* 149 (1):78-90.
- Fisher, J. B., D. D. Baldocchi, L. Misson, T. E. Dawson, and A. H. Goldstein. 2007. What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. *Tree Physiology* 27 (4):597-610.
- Flexas, Jaume, M. Ribas-Carbo, A. Diaz-Espejo, J. Galmes, and H. Medrano. 2007. Mesophyll conductance to CO<sub>2</sub>: current knowledge and future prospects. *Plant, Cell & Environment* (0).
- Gates, D. M. 1980. *Biophysical Ecology*. Mineola, NY: Dover.
- Griffin, J.R. 1973. Xylem sap tension in three woodland oaks of central California. *Ecology* 54:152-159.
- . 1988. Oak woodland. In *Terrestrial Vegetation of California*, edited by M. G. Barbour and J. Major: California Native Plant Society.
- Heady, H.F. 1988. Valley grassland. In *Terrestrial Vegetation of California*, edited by M. G. Barbour and J. Major: California Native Plant Society.
- Heaton, E., and A.M. Merenlender. 2000. Modeling vineyard expansion, potential habitat

- fragmentation. *California Agriculture* 54:12-20.
- Hidalgo, HG, DR Cayan, and MD Dettinger. 2005. Sources of variability of evapotranspiration in California. *Journal of Hydrometeorology* 6:3-19.
- Huntsinger, L., L. Buttolph, and P. Hopkinson. 1997. Ownership and management changes on California hardwood rangelands: 1985 to 1992. *Journal of Range Management* 50 (4):423-430.
- Joffre, R., S. Rambal, and C. Damesin. 2007. Functional Attributes in Mediterranean-type Ecosystems. In *Functional Plant Ecology*, edited by F. I. Pugnaire.
- Jolly, William M., and Steven W. Running. 2004. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari. *Global Change Biology* 10 (3):303-308.
- Kueppers, Lara M., Mark A. Snyder, Lisa C. Sloan, Erika S. Zavaleta, and Brian Fulfroost. 2005. Modeled regional climate change and California endemic oak ranges. *PNAS* 102 (45):16281-16286.
- Lewis, D., M. J. Singer, R. A. Dahlgren, and K. W. Tate. 2000. Hydrology in a California oak woodland watershed: a 17-year study. *Journal of Hydrology* 240 (1-2):106-117.
- Lewis, DC, and RH Burgy. 1964. Relationship between oak tree roots + groundwater in fractured rock as determined by tritium tracing. *Journal of Geophysical Research* 69:2579.
- Loarie, Scott R., B.E. Carter, K. Hayhoe, S. McMahon, R. Moe, C.A. Knight, and D. D. Ackerly. 2008. Climate change and the future of California's endemic flora. *PLOS one* 3:e2502.
- Loheide, S. P., J. J. Butler, and S. M. Gorelick. 2005. Estimation of groundwater consumption by phreatophytes using diurnal water table fluctuations: A saturated-unsaturated flow assessment. *Water Resources Research* 41 (7).
- Ma, S, D.D. Baldocchi, L. Xu, and T. Hehn. 2007. Inter-annual Variability in Carbon Dioxide Exchange of an Oak/Grass Savanna and Open grassland in California. *Agricultural and Forest Meteorology* 147:151-171.
- Major, J. 1988. California climate in relation to vegetation. In *Terrestrial Vegetation of California*, edited by M. Barbour and J. Major. Sacramento, CA: Native Plant Society of California.
- Moorcroft, Paul R. 2006. How close are we to a predictive science of the biosphere? *Trends in Ecology & Evolution* *Twenty years of TREE - part 2* 21 (7):400-407.
- Pavlik, B.M., P.C. Muick, S.G. Johnson, and M. Popper. 1991. *Oaks of California*. Los Olivos, CA: Cachuma Press.
- Pereira, J. S., J. Mateus, L. Aires, G. Pita, C. Pio, J. David, V. Andrade, J. Banza, T. S. David, T.A. Paco, and A. Rodrigues. 2007. Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems-the effect of drought. *Biogeosciences* 4:791-802.
- Priestley, C.H.B, and R.J. Taylor. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review* 100:81-92.
- Reich, Peter B., Michael B. Walters, and David S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. *PNAS* 94 (25):13730-13734.
- Rizzo, D. M., and M. Garbelotto. 2003. Sudden oak death: endangering California and Oregon forest ecosystems. *Frontiers in Ecology and the Environment* 1 (4):197-204.
- Rodriguez-Iturbe, I. 2000. Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research* 36 (1):3-9.
- Ruimy, A., G. Dedieu, and B. Saugier. 1996. TURC: A diagnostic model of continental gross primary productivity and net primary productivity. *Global Biogeochemical Cycles* 10

- (2):269-285.
- Ryu, Y., D.D. Baldocchi, S. Ma, and T. Hehn. 2008. Interannual variability of evapotranspiration and energy exchange over an annual grassland in California. *J. Geophys. Res.* 113: D09104, doi:10.1029/2007JD009263.
- Seabloom, E. W., J. W. Williams, D. Slayback, D. M. Stoms, J. H. Viers, and A. P. Dobson. 2006. Human impacts, plant invasion, and imperiled, plant species in California. *Ecological Applications* 16 (4):1338-1350.
- Sperry, John S. 2000. Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology* 104 (1):13-23.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25:855-870.
- Taylor, S.E. 1975. Optimal leaf form. In *Perspectives of Biophysical Ecology*, edited by D. M. Gates and R. B. Schmerl. New York: Springer-Verlag.
- Tyler, C. M., F. W. Davis, and B. E. Mahall. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. *Forest Ecology and Management* 255 (7):3063-3074.
- Tyler, C. M., B. Kuhn, and F. W. Davis. 2006. Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology* 81 (2):127-152.
- Vincke, Caroline, and Yves Thiry. 2008. Water table is a relevant source for water uptake by a Scots pine (*Pinus sylvestris* L.) stand: Evidences from continuous evapotranspiration and water table monitoring. *Agricultural and Forest Meteorology* 148 (10):1419-1432.
- Wilson, K. B., D. D. Baldocchi, and P. J. Hanson. 2001. Leaf age affects the seasonal pattern of photosynthetic capacity and net ecosystem exchange of carbon in a deciduous forest. *Plant, Cell and Environment* 24:571-583.
- Wullschleger, S.D. 1993. Biochemical limitations to carbon assimilation in C3 plants—a retrospective analysis of the A/Ci curves from 109 species. *Journal of Experimental Botany* 44:907-920.
- Xiao, Jingfeng, Qianlai Z, D.D. Baldocchi, B.E. Law, A.D. Richardson, J. Chen, R. Oren, G. Starr, A. Noormets, S. Ma, S.B. Verma, S. Wharton, S.C. Wofsy, P.V. Bolstad, S.P. Burns, D.R. Cook, P.S. Curtis, B.G. Drake, M. Falk, M.L. Fischer, D.R. Foster, L. Gu, J.L. Hadley, D.Y. Hollinger, G.G. Katul, M. Litvak, T.A. Martin, R. Matamala, S. G. McNulty, T.P. Meyers, R.K. Monson, J. W. Munger, W.C. Oechel, K. Tha Paw U, H. P. Schmid, R. L. Scott, G. Sun, A.E. Suyker, and M.S. Torn. 2008. Estimation of net ecosystem carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data. *Agricultural and Forest Meteorology* 148 (11):1827-1847.
- Xu, L., and D.D. Baldocchi. 2003. Seasonal trend of photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under prolonged summer drought and high temperature. *Tree Physiology* 23:865-877.
- Xu, L., D.D. Baldocchi, and Jianwu Tang. 2004. How Soil Moisture, Rain Pulses and Growth Alter the Response of Ecosystem Respiration to Temperature. *Global Biogeochemical Cycles* 18:DOI 10.1029/2004GB002281.
- Xu, Liukang, and Dennis D. Baldocchi. 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology* 123 (1-2):79-96.

