

# 7

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

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### CONTENTS

Introduction .....	135
Biogeography.....	137
Structure and Function.....	138
Canopy Architecture .....	138
Leaf and Tree Physiology.....	138
Canopy Scale: Energy and Water Fluxes .....	141
Canopy Scale: Carbon Fluxes .....	143
Discussion .....	146
Acknowledgments .....	149
References.....	149

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 et al., 2006). Starting with the Spanish Mission period till today, cattle have grazed the oak savanna, producing beef for our dinner, leather for our shoes, and tallow for our soap. In the mid-nineteenth century, 49ers 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. In doing so, they protect the soils of this hilly terrain and 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 multibillion dollar agricultural economy and its population of more than 35 million inhabitants.

Despite their intrinsic value, California's oak savannas are suffering in today's world. Regeneration failure (Tyler et al., 2008), exotic diseases (e.g., sudden oak death syndrome) (Rizzo and Garbelotto, 2003), and invasive species (Seabloom et al., 2006) are among the key problems that this biome faces. Land use change is another issue threatening oak savannas. Many oak savannas are being converted to vineyards or being carved into ranchettes, thereby fragmenting the landscape (Huntsinger et al., 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 an ecosystem's 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 flux 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 (Baldocchi and Wilson, 2001; Moorcroft, 2006).

In this chapter, we present information on energy, water, and carbon fluxes of a Californian blue oak (*Quercus douglasii*) savanna. To acquire this information, we use a multifaceted approach that reflects a contemporary convergence in 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, and 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 following overarching question is asked and answered in this chapter: How do factors associated with leaf, tree, 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?

The information produced in this chapter adds a new biophysical component to former ecological analyses of California oak savanna (Griffin, 1988; Barbour and Minnich, 2000). Flux measurements from savannas in the Mediterranean-type climate of California also provide information that is relevant for understanding the function and structure of European oak savannas, known as *dehesa* and *montado* (Joffre et al., 2007; Pereira et al., 2007), because they share many similarities. Finally, savanna 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).

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## Biogeography

The 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, which represents about 11% of the state of California (Tyler et al., 2006).

The climate space of *Quercus douglasii* includes regions where the mean annual air temperature ranges between 14 and 16°C, and the 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 (Heady, 1988; Major, 1988).

Although the mean climate conditions provide constraints on the biogeography of blue oak, the 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, whereas 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, whereas the trees assimilate carbon and transpire water.

Consequently, there is a tight anticorrelation 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, whereas 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 maximum.

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## Structure and Function

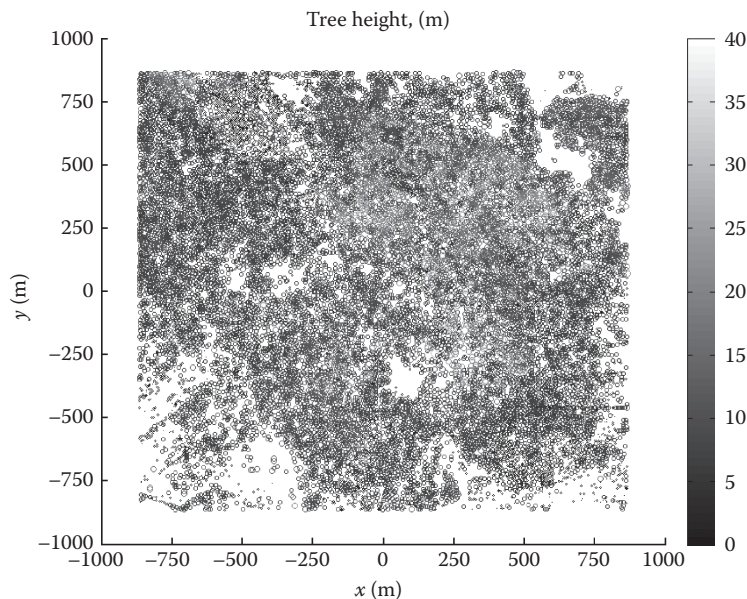
### Canopy Architecture

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, and 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 et al., 2006, 2008a). The openness and heterogeneity of the canopy is best visualized with a two-dimensional plot of tree location and crown diameter (Figure 7.1). On average, the trees are about  $9.4 \pm 4.3$  m tall; the oak and pine trees cover about 63% of the landscape and constitute an LAI of 0.7. Additional tree demographic and structural information is listed in Table 7.1.

### Leaf and Tree Physiology

To understand how 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,  $V_{\text{cmax}}$  (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);  $V_{\text{cmax}}$  is the key model parameter of the Farquhar–von Caemmerer–Berry photosynthesis model (Farquhar et al., 1980). Then  $V_{\text{cmax}}$  and leaf nitrogen drop dramatically, and in concert, as soil moisture is depleted.



**FIGURE 7.1**  
(See color insert following page xxx.) 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 × 1000 m, and the flux measurement tower is at the center. Canopy structure was quantified using an airborne LIDAR during the summer of 2009.

**TABLE 7.1**  
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)	0.41	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	

The maximum  $V_{\text{cmax}}$  values are comparable to values of well-watered and fertilized crops, and they exceed typical values for native oak trees in temperate biomes (Wullschlegel, 1993; Wilson et al., 2001). Blue oak leaves must develop high-capacity, light harvesting, and carbon assimilation systems during the short period when soil water is available to acquire enough carbon to offset respiratory costs for the rest of the year. They need the mechanics to achieve high rates of photosynthesis. In other words, high levels of  $V_{\text{cmax}}$  require high levels of Rubisco, which requires high levels of nitrogen, which, in turn, requires the production of thick leaves (Reich et al., 1997; Xu and Baldocchi, 2003).

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 potential 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 pre-dawn water potentials measured on Mediterranean oaks tend to be in the order of  $-3.0$  MPa (Joffre et al., 2007).

There are many issues regarding the effects of moderate and severe drought on photosynthesis (Cornic, 2000). For example, does stomata adjust to soil water deficits although 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 turn, reduces the internal  $\text{CO}_2$  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  $V_{\text{cmax}}$  are negatively correlated with pre-dawn water potential, suggesting a down-regulation of photosynthetic capacity with drought. This drought-mediated reduction in  $V_{\text{cmax}}$  comes in concert with progressive stomatal closure. However, the drought-induced reduction in photosynthesis is also associated with a progressive reduction in the ratio between internal and atmospheric  $\text{CO}_2$  (Xu and Baldocchi, 2003), which is consistent with the conclusions of Cornic (2000). Further, we find that stomatal conductance is a constant fraction of the product between leaf photosynthesis, relative humidity, and the reciprocal of  $\text{CO}_2$  concentration (Collatz et al., 1991) for both wet and dry soil moisture conditions.

Although water is a precious commodity to blue oaks during the summer, there are some inefficiencies and leaks in the system. Saphflow 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  $6.59 \pm 0.14 \text{ GJ m}^{-2} \text{ year}^{-1}$  of global solar radiation ( $R_g$ ) (Table 7.2). Year-to-year variation in  $R_g$  ranged between 6.46 and 6.70  $\text{MJ m}^{-2} \text{ year}^{-1}$ . This value is consistent with historical measurements at two climate stations in sunny northern California (Major, 1988). This amount of solar energy has the potential to produce about 3600  $\text{gC m}^{-2} \text{ year}^{-1}$  of photosynthesis, if the vegetation had a year-round growing season, ample soil moisture, and a photosynthetic efficiency of 2% (Ruimy et al., 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 7.2). In comparison, the neighboring annual grassland net radiation budget ranged between 2.1 and 2.3  $\text{GJ m}^{-2}$  during 2001 and 2002 (Baldocchi et al., 2004; Ryu et al., 2008). About 1  $\text{GJ m}^{-2}$  more energy is available to the oak savanna, compared with the neighboring grassland, as the savanna is optically darker and the cooler transpiring leaves cause it to radiate less longwave 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.

Across the sunny Mediterranean climate of California, potential evaporation typically exceeds annual precipitation (Hidalgo et al., 2005). At our field

Q2

TABLE 7.2  
Annual Sums of Energy Flux Densities Over an Oak Savanna in California

Variable	Location	Year						Avg
		01_02	02_03	03_04	04_05	05_06	06_07	
$R_g$ ( $\text{GJ m}^{-2}$ )	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

Note:  $R_g$  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.

**TABLE 7.3**  
Annual Sums of Water Balance Components

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

Note: *Ppt* is annual precipitation, *E<sub>p</sub>* is potential evaporation, *E<sub>t</sub>* is total evaporation, *E<sub>o</sub>* is overstory evaporation, and *E<sub>u</sub>* is understory evaporation.

site, annual potential evaporation was 1429 mm (Table 7.3). 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 17-year water balance study performed in an oak woodland watershed, northeast of Sacramento, California; actual evaporation was estimated to equal  $368 \pm 69$  mm per year (Lewis et al., 2000).

Some eco-hydrological models compute seasonal trends in actual evaporation as a function of equilibrium evaporation (*E<sub>eq</sub>*); *E<sub>Equation</sub>* is a function of available energy and these potential evaporation rates are down-regulated in a linear fashion with regard to decreasing volumetric soil moisture (Rodriguez-Iturbe, 2000; Chen et al., 2008b). We quantified the functional relationship between evaporation and volumetric soil moisture applying the Markov Chain Monte Carlo method to 3 years of evaporation data (Chen et al., 2008b). Under well-watered conditions, the ratio between actual and equilibrium evaporation (*E<sub>a</sub>/E<sub>eq</sub>*) is about 0.65. This *E<sub>a</sub>/E<sub>Equation</sub>* value is much lower than the typical values for wet, irrigated, and extensive vegetation, 1.26, also known as the Priestley–Taylor coefficient (Priestley and Taylor, 1972). The ratio, *E<sub>a</sub>/E<sub>eq</sub>*, 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 (Baldocchi et al., 2004; Joffre et al., 2007). 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 three wells at the site and have monitored their changes in a water table. These new measurements support the hypothesis that 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. We found that groundwater uptake ( $ET_g$ ) of data for seven days in July 2007 was between 0.25 and 0.45 mm d<sup>-1</sup> on using a method developed by Vincke and Thiry (2008). In contrast, the eddy covariance system measured total daily ET 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 observed in other dryland or riparian ecosystems (Loheide et al., 2005).

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## Canopy Scale Carbon Fluxes

The Blue oak woodlands in California are small, net carbon sinks on an annual basis ( $-92 \pm 48$  gC m<sup>-2</sup> year<sup>-1</sup>); for perspective, the mean net carbon exchange over six years, derived from more than 500 site years of measurements across the FLUXNET network, is  $-183$  gC m<sup>-2</sup> year<sup>-1</sup> (Baldocchi, 2008).

This relatively small net carbon flux is the residual between two relatively large and offsetting carbon fluxes. On average, gross primary productivity creates a carbon sink of 1031 gC m<sup>-2</sup> year<sup>-1</sup>, and ecosystem respiration produces a carbon source of 939 gC m<sup>-2</sup> year<sup>-1</sup> (Ma et al., 2007) (Table 7.4). 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.

Net ( $NEE$ ) and gross ( $GPP$ ) carbon uptake and ecosystem respiration ( $R_{eco}$ ) experience pronounced seasonal variation (Figure 7.2). 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  $-3$  gC m<sup>-2</sup> d<sup>-1</sup>, respectively. Over a year, this ecosystem operates, technically, as an evergreen ecosystem. The grass is green and photosynthesizing during the dormant winter period; and the trees are photosynthesizing during the dry summer period when the grass is dead.

TABLE 7.4

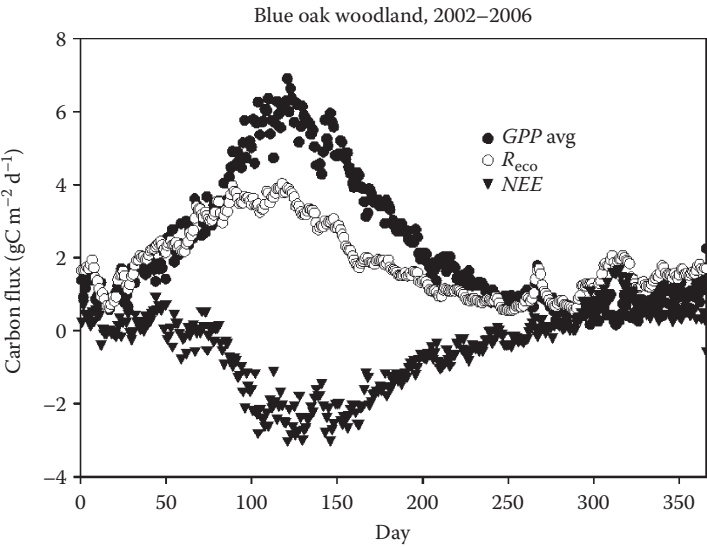
Annual Net Ecosystem Exchange of CO<sub>2</sub> (*NEE*, gC m<sup>-2</sup> year<sup>-1</sup>), Gross Primary Productivity (*GPP*), and Ecosystem Respiration (*R<sub>eco</sub>*) and Uncertainties (in parentheses)

Hydrological Year	<i>NEE</i> (gC m <sup>-2</sup> year <sup>-1</sup> )		<i>GPP</i> (gC m <sup>-2</sup> year <sup>-1</sup> )		<i>R<sub>eco</sub></i> (gC m <sup>-2</sup> year <sup>-1</sup> )	
2001–2002	–144	(±50)	888	(±75)	744	(±48)
2002–2003	–116	(±50)	1091	(±65)	975	(±49)
2003–2004	–52	(±62)	899	(±56)	847	(±41)
2004–2005	–143	(±47)	1360	(±66)	1217	(±56)
2005–2006	–35	(±44)	1113	(±53)	1078	(±52)
2006–2007	–78	(±56)	904	(±65)	773	(±44)
2007–2008	–79	(±48)	797	(±46)	718	(±42)
Mean ± STD	–92	±43	1007	±193	907	±189

Source: Data from Ma, S., D. D. Baldocchi, L. Xu, and T. Hehn, 2007. *Agricultural and Forest Meteorology* 147, 151–171.

Note: Hydrological year starts on October 23 (day 296) and ends on October 22 (day 295) of the next year.

Episodic rain events during the summer period can cause huge pulses in soil respiration (Xu and Baldocchi, 2004; Baldocchi et al., 2006). 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

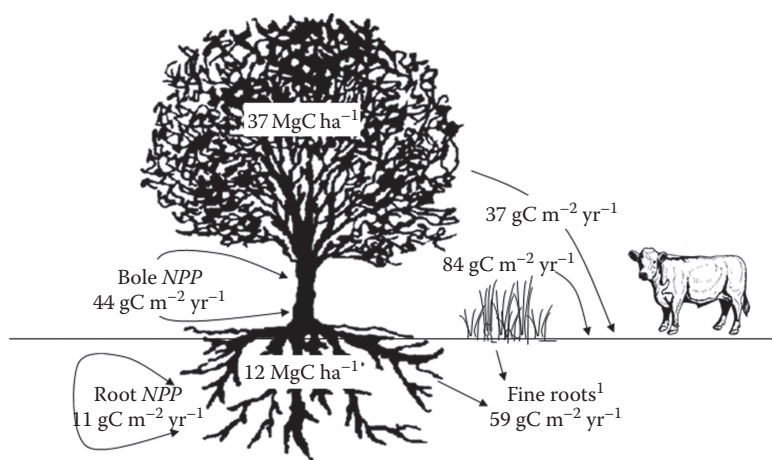


**Q4** **FIGURE 7.2** Seasonal variation in gross primary productivity, ecosystem respiration, and net ecosystem exchange. These data are presented for daily integrals averaged over the period between 2002 and 2006.

downward moving front of water in the soil. However, 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 (Xu et al., 2004; Baldocchi et al., 2006). The size of these respiration pulses diminish with successive rain events as the size of the labile carbon pool diminishes.

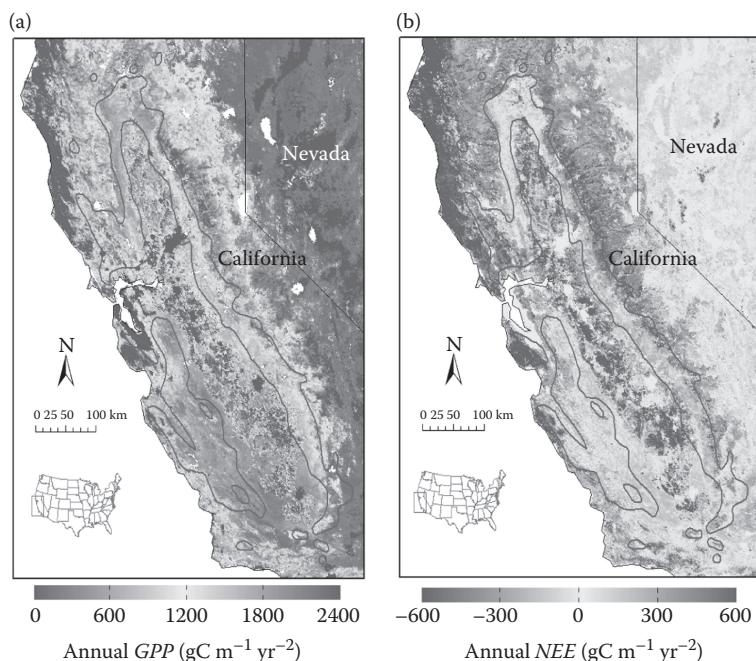
We recently produced an independent carbon budget of the stand by measuring litterfall, fine root production, and stem and root growth (Figure 7.3). The stand maintains 37 Mg C ha<sup>-1</sup> in above ground biomass and 12 Mg C ha<sup>-1</sup> in below ground biomass. Net primary productivity of the 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> year<sup>-1</sup>. This sum is comprised of bole increment growth (44 gC m<sup>-2</sup> year<sup>-1</sup>), litterfall (37 gC m<sup>-2</sup> year<sup>-1</sup>), fine root production (59 gC m<sup>-2</sup> year<sup>-1</sup>), grass (84 gC m<sup>-2</sup> year<sup>-1</sup>), and root net primary production (59 gC m<sup>-2</sup> year<sup>-1</sup>). Overall, this biometric carbon budget compares well with an independent estimate of *NPP* (283 gC m<sup>-2</sup> year<sup>-1</sup>), derived from our eddy covariance measurements (Ma et al., 2007).

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 7.4a) and *NEE* (Figure 7.4b) 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> year<sup>-1</sup>, respectively. When summed up on an area-basis, the net and gross carbon fluxes equaled -8.6 and 53.8 TgC year<sup>-1</sup>, respectively.



**Q5** FIGURE 7.3

Summary of carbon budget for oak woodland near Lone, CA, for the 2007–2008 hydrological growing season. Boxes represent pools (MgC ha<sup>-1</sup>); arrows represent fluxes (gCm<sup>-2</sup> year<sup>-1</sup>).

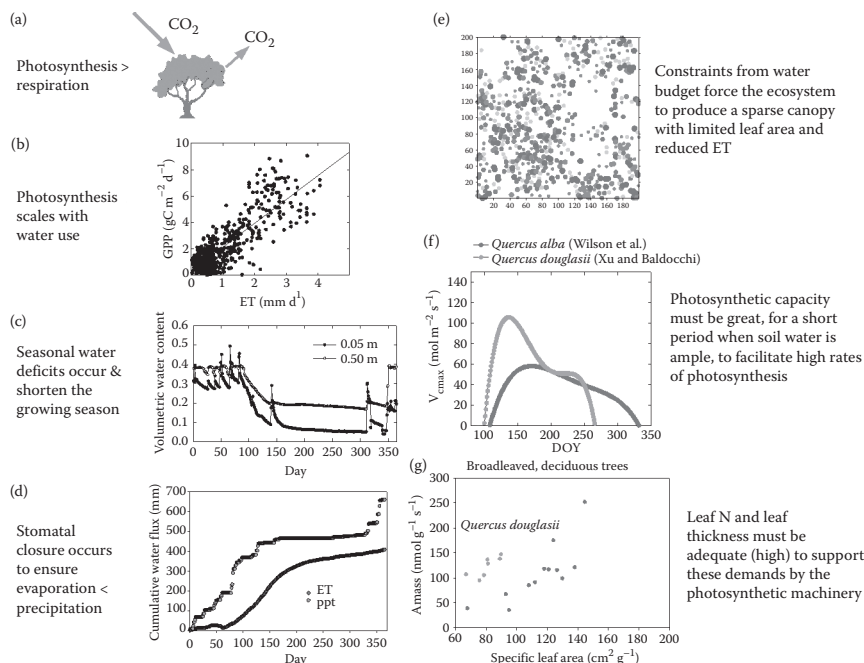


**FIGURE 7.4**

(See color insert following page xxx.) Spatial map of net ecosystem carbon exchange for the blue oak biome: (a) is for annual gross primary productivity (GPP); and (b) is for net annual ecosystem carbon exchange (NEE). (Adapted from Xiao, J. et al. 2008. *Agricultural and Forest Meteorology* 148, 1827–1847; and derived using data are from the MODIS sensor and the AmeriFlux network.)

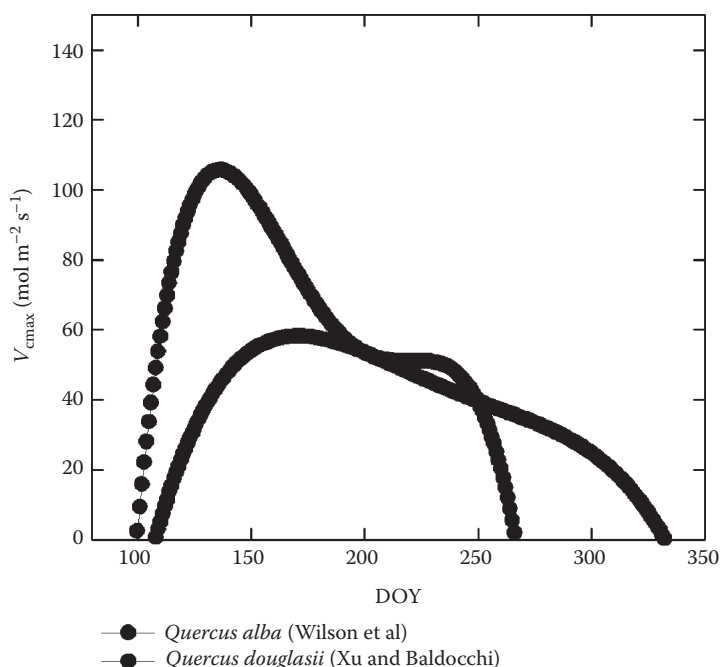
## Discussion

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 7.5). First, stand-level photosynthesis must exceed ecosystem respiration. However, 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 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. However, this drought-induced stomatal closure inhibits

**FIGURE 7.5**

(See color insert following page xxx.) An eco-hydrological explanation for the structure and function of a blue oak savanna and its sustenance. For the oak savannas to survive in highly seasonal wet/dry, cool/hot climate, they must comply with several linked constraints. (a) First, annual photosynthesis must exceed ecosystem respiration; (b) the oaks experience 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; (c) further, the act of photosynthesis comes with a cost—evaporation; (d) 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; (e) the landscape can reduce its total evaporation by establishing a partial canopy; (f) it can assimilate enough carbon if it adjusts and maximizes its photosynthetic capacity during the short spring wet period; and (g) high rates of photosynthesis are not free and come with producing thick leaves, rich in nitrogen and Rubisco.

photosynthesis. Thus, 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,



**Q6** FIGURE 7.6

2004); or (4) produce deep roots that tap otherwise unreachable sources of water (Lewis and Burgy, 1964). At the landscape scale, the LAI 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). An oak canopy in California with 500 mm of rainfall cannot form a closed canopy and must have a low LAI. This limitation in leaf area limits light capture and potential photosynthesis.

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 positive 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 negative side, they are optically darker than surrounding open grasslands. By absorbing more energy and by being aerodynamically rougher, compared with nearby grasslands, they evaporate more water (about 100 mm), and they inject more sensible heat into the atmosphere ( $0.5 \text{ GJ m}^{-2} \text{ year}^{-1}$ ). Consequently, their air temperature is about  $0.84 \text{ }^{\circ}\text{C}$  degrees warmer than the surrounding grasslands (Baldocchi et al., 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.

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