

Mature semiarid chaparral ecosystems can be a significant sink for atmospheric carbon dioxide

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Abstract

Carbon flux in arid and semiarid area shrublands, especially in old-growth shrub ecosystems, has been rarely studied using eddy covariance techniques. In this study, eddy covariance measurements over a 100-year old-growth chamise-dominated chaparral shrub ecosystem were conducted for 7 years from 1996 to 2003. A carbon sink, from -96 to $-155 \text{ g C m}^{-2} \text{ yr}^{-1}$, was determined under normal weather conditions, while a weak sink of $-18 \text{ g C m}^{-2} \text{ yr}^{-1}$ and a strong source of $207 \text{ g C m}^{-2} \text{ yr}^{-1}$ were observed as a consequence of a severe drought. The annual sink strength of carbon in the 7-year measurement period was $-52 \text{ g C m}^{-2} \text{ yr}^{-1}$. The results from our study indicate that, in contrast to previous thought, the old-growth chaparral shrub ecosystem can be a significant sink of carbon under normal weather conditions and, therefore, be an important component of the global carbon budget.

Keywords: arid and semiarid area, carbon balance, chaparral ecosystem, eddy covariance, evapotranspiration (ET), net ecosystem exchange (NEE), old-growth, shrub, southern California

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Introduction

Human activity has increased global atmospheric CO_2 by about 30%, from 280 ppm to over 360 ppm, since the beginning of the Industrial Revolution (Amthor, 1995; Houghton *et al.*, 2001), and this increase will continue if action is not taken. The average annual anthropogenic CO_2 emissions of approximately 8 Gt C yr^{-1} (6.3 Gt C yr^{-1} from combustion of fossil fuels and 1.6 Gt C yr^{-1} from changes in land use) is greater than the sum of atmospheric accumulation (3.2 Gt C yr^{-1}), ocean uptake (1.7 Gt C yr^{-1}) and land-atmosphere flux (1.4 Gt C yr^{-1}). An additional sink of approximate $2\text{--}4 \text{ Gt C yr}^{-1}$ is required to balance the global carbon budget (Schimel *et al.*, 2001). Terrestrial ecosystems are thought to be the biggest reservoirs for this 'missing carbon' and could mitigate the rising levels of CO_2 in the atmosphere. Knowledge of the dynamics of carbon in terrestrial ecosystems is essential for understanding global carbon balance and for future management. In recent years, there has been a concerted effort to determine the magnitude, patterns and controls of terrestrial carbon flux using eddy covariance techniques (Valentini *et al.*, 1996; Baldocchi *et al.*, 2001; Yu *et al.*, 2005). To this end, regional

networks of eddy covariance towers have been established. These include Ameriflux and Fluxnet-Canada in North America, Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) in South America, CarboEuroFlux in Europe, OzFlux in Australasia, China Flux and Asia Flux in Asia, and AfriFlux in Africa (Fluxnet <http://daac.ornl.gov/FLUXNET/>). Because of the large uncertainty of terrestrial fluxes (Tans *et al.*, 1990), and the desire, by some, to emphasize large terrestrial carbon sinks, there has been a bias toward flux measurements in systems anticipated to represent large current or future CO_2 flux or carbon sequestration potential (Running *et al.*, 1999). This has resulted in a preponderance of forest and agricultural studies (53% and 21%, respectively, of all Fluxnet eddy towers), and a relative paucity of studies in nonforest and non-agricultural ecosystems (a total of 26% of all Fluxnet towers), especially those expected to be of low current and future net carbon uptake (Fluxnet <http://daac.ornl.gov/FLUXNET/>). As a result, many stressed ecosystems (Buchmann & Schulze, 1999; Running *et al.*, 1999; Reichstein *et al.*, 2002; Hastings *et al.*, 2005), as well as old-growth ecosystems (Jarvis, 1989; Melillo *et al.*, 1996; Carey *et al.*, 2001), have been little studied even though they may be significant in their contribution to current carbon balance and may be important in carbon sequestration or release in the future (Oechel *et al.*, 1993, 2000).

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Among ecosystems poorly understood and under-represented in the eddy covariance studies of CO₂ flux are arid and semiarid ecosystems, especially shrublands. Arid and semiarid woody shrublands make up approximately 35% of the global terrestrial surface area and 24% of the global soil organic carbon, and 16% of the global aboveground biomass (Atjay *et al.*, 1979; Shmida, 1985), yet represent only 6% of the currently installed eddy covariance towers in Ameriflux and 17% in Fluxnet (based on the eddy tower information on Fluxnet <http://daac.ornl.gov/FLUXNET/>). We lack sufficient data and understanding of arid and semiarid ecosystems to properly parameterize and validate models of current and future global terrestrial carbon balance. Shrublands are a major component of arid and semiarid ecosystems worldwide and little effort has been made to adequately understand them. Given their large area and potentially large carbon sink or source, woody shrubs deserve serious study.

Despite the vigorous growth of global carbon research, the role of old-growth stands in the carbon balance remains a controversy. Carbon exchanges between old stands and the atmosphere were predominantly assumed to be in a state of dynamic equilibrium (Odum, 1969; Salati & Vose, 1984) and an insignificant carbon sink (Jarvis, 1989; Melillo *et al.*, 1996). However, in recent years, observations (Malhi *et al.*, 1998; Carey *et al.*, 2001; Paw *et al.*, 2004), ecosystem models (Chambers *et al.*, 2001) and biomass inventories (Phillips *et al.*, 1998) have suggested that old-growth forests can be significant carbon sinks. The underestimate of carbon sequestration by old-growth terrestrial stands could be as high as 4.3–7.6% of the missing sink (Carey *et al.*, 2001). Therefore, old-growth stands may have been seriously underestimated in their capability of carbon uptake globally. This may be due, in part, to applying mono-specific, even age-growth models to natural stands, as well as to assuming that the ratio of respiring biomass to photosynthetic canopy increases as age increases (Carey *et al.*, 2001). As a result of concerns for the climatic effects of increasing atmospheric CO₂, the identification of the source sink relationships of natural ecosystems (including old and undisturbed ecosystems) has recently drawn considerable attention (Keeling *et al.*, 1996; Malhi *et al.*, 1998; Carey *et al.*, 2001). The paradigm regarding the insignificant carbon sequestration of old-growth forests has been reevaluated (Malhi *et al.*, 1998; Carey *et al.*, 2001; Knohl *et al.*, 2003; Paw *et al.*, 2004). However, the assessment of carbon uptake for the old-growth shrubland has remained largely unexplored.

In this study, we report on the net ecosystem exchange (NEE) of CO₂ for 7 years in a 100-year-old mature Mediterranean-type chamise (*Adenostoma fasci-*

culatum)-dominant chaparral ecosystem in southern California using eddy covariance techniques. This semi-arid Mediterranean type chaparral ecosystem occurs in the southwest United States and northern central Mexico. Our study site lies at a location only 20 km from the desert floor to the east and in the position of the climatic gradient between desert and semiarid (Scheid & Zedler, 1983). It was selected to provide insights into the carbon dynamics of mature arid and semiarid shrub ecosystems. Average historical fire frequency for this chaparral-type ecosystem is about 35 years (Zammit & Zedler, 1994). Stands older than 60 years have been considered 'decadent' (Hanes, 1971) as their physiological functions (Rundel & Parsons, 1980), biomass, leaf area, and cover may be decreased (Oechel & Reid, 1984; Reid, 1985) and tissue respiration increased (Oechel & Reid, 1984). Thus, chaparral with an age of 100 years was considered 'mature' or 'old-growth,' even 'over-mature' or 'senescent.'

Based on previous studies, we asked: (1) is this 100-year-old chaparral stand senescent at the level of ecosystem metabolism, specifically in carbon exchange with the atmosphere (i.e. little or no net CO₂ uptake)? (2) What is the status and strength of any sink or source? and (3) what is the relationship between NEE and interannual variability in rainfall, the major limiting factor in most arid and semiarid ecosystems? To answer these questions, we quantified the magnitude of NEE, addressed the seasonality and interannual variability of NEE for this semiarid open shrubland ecosystem and monitored climatic and other environmental parameters.

Materials and methods

Site description

This study was conducted at the Sky Oaks Field Station (33°23'N, 116°37'W), operated by San Diego State University and located in southern California, at about 1420 m elevation and 75 km east of Pacific Ocean. This region lies at the climatic gradient between desert and semiarid area and is characterized by a Mediterranean climate with cold, wet winters and hot, dry summers. Most precipitation falls between the months of November and April (Poole & Miller, 1975) with an average annual precipitation of 349 mm. Light snow occurs several days during the winter, and occasionally hot, dry Santa Ana winds blow from northeast over the desert in the late summer and fall. This stand was a chamise (*A. fasciculatum*)-dominated chaparral ecosystem, which is the typical chaparral type in California occupying most of the hills and lower mountain slopes (Hanes, 1971, 1977). In addition, Red Shank (*Adenostoma sparsifolium*) was a major component of this ecosystem.

Chamise is a drought tolerant sclerophyllous evergreen shrub with a belowground lignotuber. While chaparral typically burns on average about every 35 years, the last fire at this site was in 1901 (Zammit & Zedler, 1994). Soil types include Sheephead (Ultic Haploxeroll) and Tollhouse (Entic Haploxeroll), both of which are considered loamy, mixed, mesic and shallow. The terrain is rough broken land over substrates of granite or micaceous schist. Soil fertility is quite low (Greenwood, 1983).

Environmental measurements

The following micrometeorological variables were measured every 10 s and stored as 30 min means using a data logger (CR23X, Campbell Scientific Inc., Logan, UT, USA): wind vector (RM Young Wind Sentry, R. M. Young Company, Traverse, MI, USA) at 6 m above the ground, relative humidity (RH) and air temperature (HMP45C, Vaisala Inc., Helsinki, Finland) at both 5.8 and 2.5 m, incident solar radiation between 400 and 1100 nm (LI-2005 pyranometer, Li-COR Inc., Lincoln, NE, USA) and photosynthetically active radiation (PAR; LI-190SB, Li-COR Inc.) at 2.3 m, net radiation (Q*7.1, Radiation Energy Balance Systems (REBS) Inc., Seattle, WA, USA) at 2.5 m above ground, precipitation (TR525, Texas Electronics Inc., Dallas, TX, USA) at 2.3 m, soil temperature (type-T thermocouples, Omega Engineering, Stamford, CT, USA) at 2, 5, 10, 20, 30, and 40 cm depths, soil moisture (Hydra, Vitel Inc., Chantilly, VA, USA before August 30, 2002 and CS615, Campbell Scientific Inc. Logan, UT, USA after August 30, 2002) at 5, 10, 20, 30, and 40 cm depths, and atmospheric pressure (PTB101B, Vaisala Inc.), and four soil heat flux plates (HFT3, REBS Inc.) at 2 cm depth below the ground surface to measure ground heat flux.

Eddy covariance measurements

NEE was measured using the eddy covariance techniques (Baldocchi *et al.*, 1988). Eddy covariance measurements were made from March 17, 1997 to July 16, 2003 when the stand and equipment were consumed and measurements were interrupted by a natural fire thereafter. Fluctuations in vertical, streamwise and lateral wind speed, wind direction, and temperature were measured at 10 Hz using a three-dimensional sonic anemometer-thermometer (before October 25, 2001, Model SWS-211/3K, Applied Technologies Inc, Boulder, CO, USA, then switched to a Windmaster Pro, Gill Instruments Ltd., Lymington, Hampshire, UK). CO₂ and H₂O vapor fluctuations were measured using a fast response, 10 Hz, closed-path infra-red gas analyzer (IRGA) with a pressure transducer (LI-6262, Li-COR Inc.) on dates before October 25, 2001. After this date,

CO₂ and H₂O vapor fluctuations were measured using a 10 Hz open path analyzer (LI-7500, Li-COR Inc.). The sonic anemometer and open-path IRGA were 4.5 m above the ground surface and 2.5 m above the mean height of the vegetation. Calibration was carried out every 2–4 weeks using a gas standard for CO₂ and a dew point generator (LI-610, Li-COR Inc.) for water vapor.

Raw CO₂ and H₂O vapor fluctuations were recorded as mean voltages and converted to densities by multiplying by the requisite calibration constant (Vourlitis & Oechel, 1997). Mass (CO₂ and H₂O vapor), energy and momentum fluxes were computed following a coordinate rotation of the vertical and lateral wind vectors, and stored on a laptop computer as 30 min averages using a 400 s running mean and digital recursive filtering technique (McMillen, 1988). Carbon and water flux estimates were corrected for the simultaneous flux of heat and H₂O vapor for the measurements from the open-path IRGA and only H₂O vapor correction for the measurements from the closed-path IRGA (Webb *et al.*, 1980; Suyker & Verma, 1993).

Eddy covariance data reduction and gap filling

The percentage of eddy covariance data collected during the measurement period varied from 60% to 99% among 7 years. Data gaps were primary caused by power, computer, or sensor failures, instrument calibration, and data rejection following quality assessment during data postprocessing. The rejection criteria used to screen data in the postprocessing included: rain and snow events, incomplete 30 min data collections, out-of-range signals from either the sonic anemometer or IRGA, spikes with the standard deviation of CO₂, H₂O and/or temperature variance greater than 2 from the mean.

A critical friction velocity (u^*) threshold is often used to exclude eddy flux data and avoid the underestimation of carbon source strength under calm wind conditions (Goulden, 1996; Reichstein *et al.*, 2002). At our study site, the u^* threshold was determined to be 0.275 m s^{-1} (Fig. 1). At this point, increasing u^* yielded little increase in apparent CO₂ efflux. The night-time NEE data showed a linear increase with u^* when $u^* < 0.275 \text{ m s}^{-1}$, and an asymptotic NEE of approximately $0.042 \text{ (mg CO}_2 \text{ m}^{-2} \text{ s}^{-1})$ after $u^* \geq 0.275 \text{ m s}^{-1}$ (Fig. 1). Carbon flux in the range where $u^* < 0.275 \text{ m s}^{-1}$ were corrected based on the relationship between u^* and night-time carbon flux with $u^* \geq 0.275 \text{ m s}^{-1}$.

For half-hourly data, short gaps of 1/2 h during the daytime and 1/2 to 3 h during the night-time with relatively uniform conditions or rates of environmental change were filled by linear interpolation (Falge *et al.*, 2001). The mean diurnal variation with a 10-day window was used to fill larger gaps (Falge *et al.*,

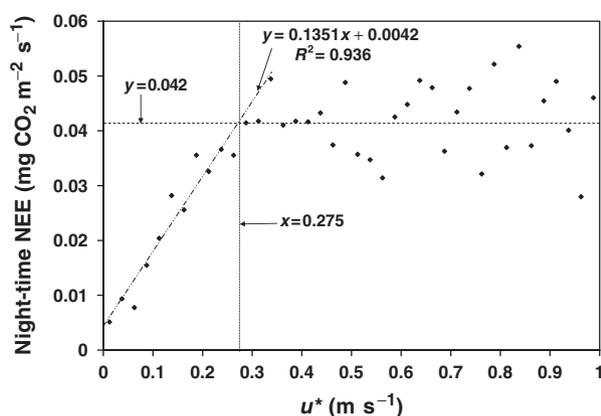


Fig. 1 Night-time net ecosystem exchange (NEE) as a function of friction velocity (u^*). Data measured during 1996 to 2003 were sorted by u^* with intervals of 0.025 m s^{-1} and the average values are presented. The threshold of u^* was determined to be 0.275 m s^{-1} . The night-time NEE data showed a linear increase with u^* when $u^* < 0.275 \text{ m s}^{-1}$, and an asymptotic NEE of approximately $0.042 \text{ (mg CO}_2 \text{ m}^{-2} \text{ s}^{-1})$ after $u^* \geq 0.275 \text{ m s}^{-1}$.

2001). And the half-hourly data were integrated into daily data. The remaining gaps in daily NEE were filled using BIOMAP modeling (BIOMAP <http://www.fs.fed.us/pnw/corvallis/mdr/mapss/biomap.htm>) and water vapor evapotranspiration (ET) were filled by BiomeBGC modeling (Thornton *et al.*, 2002). For annual sums of NEE and ET, a large gap was not filled from August 5, 1998 to April 4, 1999, which was too large to estimate with confidence. However, NEE and ET during this period were estimated for long-term cumulative fluxes from precipitation.

Data in the measurement period were processed and analyzed based on the hydrological year, which started on July 1st and ended on June 30th of the following year. Each hydrological year was divided into three seasons: the dry season (July 1st to October 31st, generally hot temperatures and low water availability), the winter season (November 1st to February 28th, generally adequate water but low radiation and temperatures) and the growing season (March 1st to June 30th, generally favorable warm and moist conditions and plants were typically growing fastest).

Results

System performance

Energy balance closure was used to assess the performance of the eddy covariance system (McMillen, 1988; Vourlitis *et al.*, 2001). The 30 min values of sensible heat flux (H) plus latent heat flux (LE) were compared against the net radiation (R_n) minus ground heat flux (G) for each hydrological year (see Fig. 2 for an example

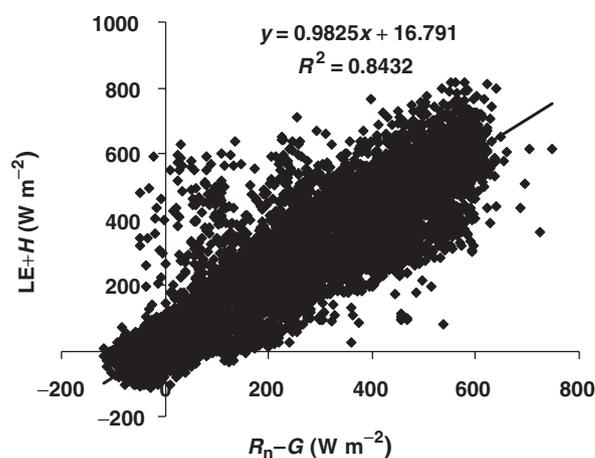


Fig. 2 Energy enclosure at 1999 to show an example of the relationship between $H + LE$ measured by eddy covariance and $R_n - G$ measured by meteorological sensors.

at 1999). The least-square regression curves were fitted to the graphs. The goodness of fit was quantified with an average r^2 of 0.84 ± 0.05 , average slope of regression was 0.93 ± 0.06 and the average intercept was $22 \pm 14 \text{ W m}^{-2}$ during measuring period. These results indicated that our eddy covariance system had generally good performance, but slightly underestimated $H + LE$ compared with $R_n - G$. This energy closure deficit might be explained by the difference among the sampling frequencies and measuring footprints of various sensors. In addition, the energy stored under plant canopy and in the soil layer between the soil surface and the soil heat flux plates was not considered.

Environmental conditions

Over the measurement period of 1996–2003, the overall annual mean of R_n , PAR, RH, air temperature and surface soil temperature at the depth of 0–30 cm were 127 W m^{-2} , $460 \mu\text{mol m}^{-2} \text{ s}^{-1}$, 43%, 14 and 15°C , respectively. The interannual patterns of the radiation, air temperature and RH were similar from year to year, while the magnitude and temporal distribution of precipitation at the study site varied significantly. The annual total precipitation during the measurement period ranged from 175.3 mm (2001–2002) to 804.7 mm (1997–1998) with a mean of 374.7 mm during the study period.

The environmental variables showed strong seasonality at the study site. According to the calculated overall seasonal means in 1996–2003, the winter season had lower radiation (R_n 60 W m^{-2} and PAR $260 \mu\text{mol m}^{-2} \text{ s}^{-1}$) than the dry season (152 W m^{-2} and $547 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and the growing season (160 W m^{-2}

Table 1 Seasonal and annual means of micrometeorological variables during the measurement period of 1996–2003

Season	Net radiation (W m^{-2})	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Air temperature ($^{\circ}\text{C}$)	RH (%)	Soil surface temperature at 2 cm depth ($^{\circ}\text{C}$)	Precipitation (mm)	Soil moisture between 0 and 30 cm (%)
Dry	152	547	21.0	31	22.5	64.4	9
Winter	60	260	8.3	48	6.2	209.5	13
Growing	160	550	13.1	48	15.6	100.7	17
Overall annual average	124	452	14.1	42	14.8	374.7*	13

The dry season started from July 1st and ended on October 31st, the winter season was from November 1st to February 28th in the following year, and the growing season was from March 1st to June 30th.

*Annual total precipitation.

PAR, photosynthetically active radiation; RH, relative humidity.

and $550 \mu\text{mol m}^{-2} \text{s}^{-1}$; Table 1). However, there was no significant radiation difference between the growing season and the dry season. Both air and soil temperature at the surface were highest in the dry season (21.0 and 22.5°C , respectively), with lower values during the growing season (13.1 and 15.6°C , respectively) and the winter season (8.3 and 6.2°C , respectively). RH was similar in the winter season and the growing season (48% and 48%), but lower in the dry season (31%). The winter season commonly had the greatest rainfall, followed by the growing season, while the dry season had the least, approximately 209, 100.7 and 64.4 mm, respectively, on average. Soil moisture was highest in the growing season (17% volumetric content) followed by the winter season (13%), and the dry season had lowest soil moisture (9%).

Net ecosystem exchange of carbon and water vapor

The overall averaged seasonal NEE in 1996–2003 was calculated to be a large sink of $-103.9 \text{ g C m}^{-2} \text{ season}^{-1}$ during the growing season (Table 2), which was associated with a high leaf area index (LAI), mild temperature and sufficient water supply. The average NEE of the dry season and the winter season were 27.3 and $26.3 \text{ g C m}^{-2} \text{ season}^{-1}$, respectively. Both seasons were weak sources, which resulted from NEE being limited by low radiation and temperature in the winter season and by low water availability in dry season (Krause, 1975). The highest seasonal ET occurred during the growing season with $192.8 \text{ mm season}^{-1}$ (Table 2). In that period, ET was almost double the amount of precipitation ($100.7 \text{ mm season}^{-1}$). The large ET in this season was related to greater soil water availability, warm temperatures, high radiation and vigorous plant transpiration. During the dry season, ET

Table 2 Average seasonal net ecosystem exchange (NEE), evapotranspiration (ET) and precipitation in the measurement period of 1996–2003

Season	NEE (g C m^{-2})	ET (mm)	Precipitation (mm)
Dry	27.3	107.5	64.4
Winter	26.3	80.4	209.5
Growing	-103.9	192.8	100.7

Negative values of NEE denoted for ecosystem carbon sink from atmosphere, and positive values of NEE denoted for ecosystem carbon source to atmosphere.

($107.5 \text{ mm season}^{-1}$) was higher than the seasonal precipitation ($64.4 \text{ mm season}^{-1}$). This suggested that chaparral plants in this mature stand were able to access the water reserves stored at depth of weathered bedrock to supply their water needs when the incoming precipitation did not meet their demands (Sternberg *et al.*, 1996). ET and precipitation were calculated to be 80.4 and $209.5 \text{ mm season}^{-1}$, respectively, in the winter season, in which ET was lower than precipitation due to limited radiation levels and temperatures.

Annual total NEE varied greatly from year to year. Listed according to the sink strength from strong to weak, then to source, the hydrological year of 2000–2001 presented a strongest carbon sink of -155 g C m^{-2} (Fig. 3), followed by a carbon sink of -100 g C m^{-2} in 1999–2000, and a carbon sink in 1997–1998 was -96 g C m^{-2} . The annual carbon budget for the period of 2001–2002 was close to being in balance with a weak carbon sink of -18 g C m^{-2} . In contrast, the period of 2002–2003 showed a strong carbon source of 207 g C m^{-2} . Data gaps limited the ability to estimate annual NEE and ET in the hydrological years of 1996–1997 and 1998–1999.

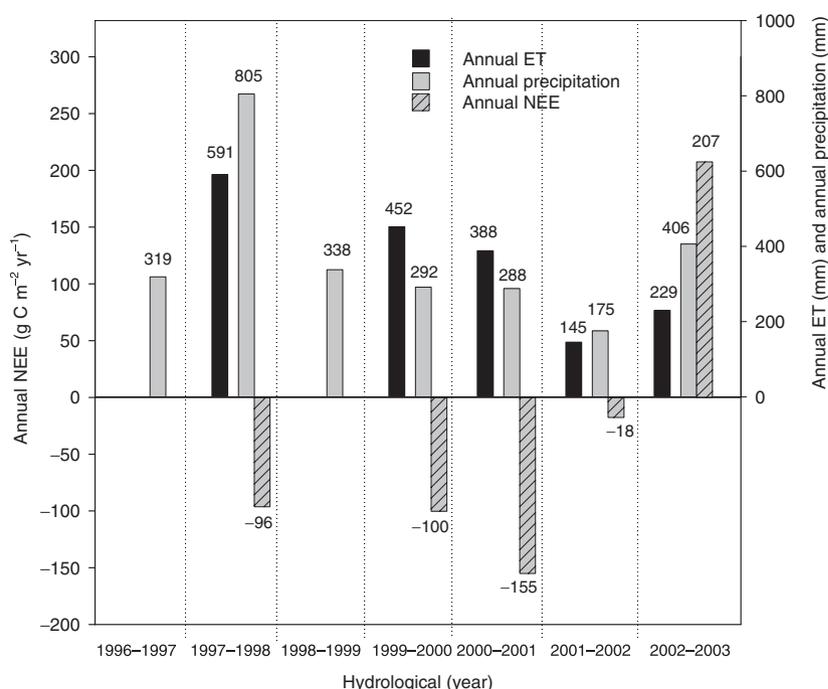


Fig. 3 Total annual net ecosystem exchange (NEE), evapotranspiration (ET) and precipitation over the measurement period of 1996–2003. Data availability limited the calculation of NEE and ET in 1996–1997 and 1998–1999.

The 60-year average annual precipitation was 349 mm at our study site (from 1949 to 2002), which was extrapolated from the nearby weather station at Palomar Mountain Observatory using MTCLIM method (Kimball *et al.*, 1997; Thornton & Running, 1999). This value is close to the annual mean precipitation of 374.7 mm during the measurement period of 1996–2003. If the normal range was defined as precipitation variation within ± 100 mm from the 60-year mean (349 mm), then the hydrological year of 1997–1998 (805 mm) can be considered a wet year, 1996–1997 (319 mm), 1998–1999 (338 mm), 1999–2000 (292 mm), 2000–2001 (288 mm) and 2002–2003 (406 mm) can be considered normal years, and 2001–2002 (175 mm) should be considered a severe drought year (Fig. 3).

The largest ET (591 mm) was recorded in 1997–1998, which coincided with the period of heaviest rain (805 mm) resulting from El Niño effects in the region (Fig. 3). The lowest ET (145 mm) occurred in 2001–2002, which also coincided with the lowest precipitation recorded (175 mm). This very low ET may have been the result of low soil water availability, plant stomatal closure, leaf and branch shedding and/or plant death from the severe drought (Dallman, 1998). The water budget between incoming rain and outgoing water vapor in 2001–2002 were similar with ET only 30 mm lower than the precipitation. The annual ET in 1997–1998 and 2002–2003 was 591 and 229 mm, respectively, which

were much lower than precipitation for the same periods, 804 and 406 mm, respectively (Fig. 3). This might be a consequence of water loss as drainage or runoff in intensive rain events. In contrast to this, the annual ET in 1999–2000 and 2000–2001 (451 and 388 mm, respectively) exceeded the corresponding precipitation (291 and 288 mm, respectively; Fig. 3), which indicates that chamise has deep tap roots that can reach water at considerable depths to supply their biological demands (Krause, 1975; Poole & Miller, 1975; Jones & Graham, 1993). This survival strategy reflects the long-term adaptation of chaparral shrubs to the tough environmental conditions with low water availability.

To estimate NEE and ET during the full 7-year period, including the large gap, we plotted averaged daily NEE/ET against annual precipitation for each available season in each hydrological year. The least-square regression lines were fitted to find a regression equation for the dry, winter and growing season, respectively. Then the remaining gaps of cumulative NEE and ET were filled using these equations accordingly. This allowed us to generate cumulative estimates of NEE ($-361.3 \text{ g C m}^{-2}$) and ET (2839 mm) in the full 7-year period from 1996 to 2003 (Fig. 4). The observed precipitation in the same period was 2623 mm, which was 216 mm less than estimated ET. These calculations indicate that this ecosystem sequestered carbon at an approximate rate of $-52 \text{ g C m}^{-2} \text{ yr}^{-1}$ and a ET rate of

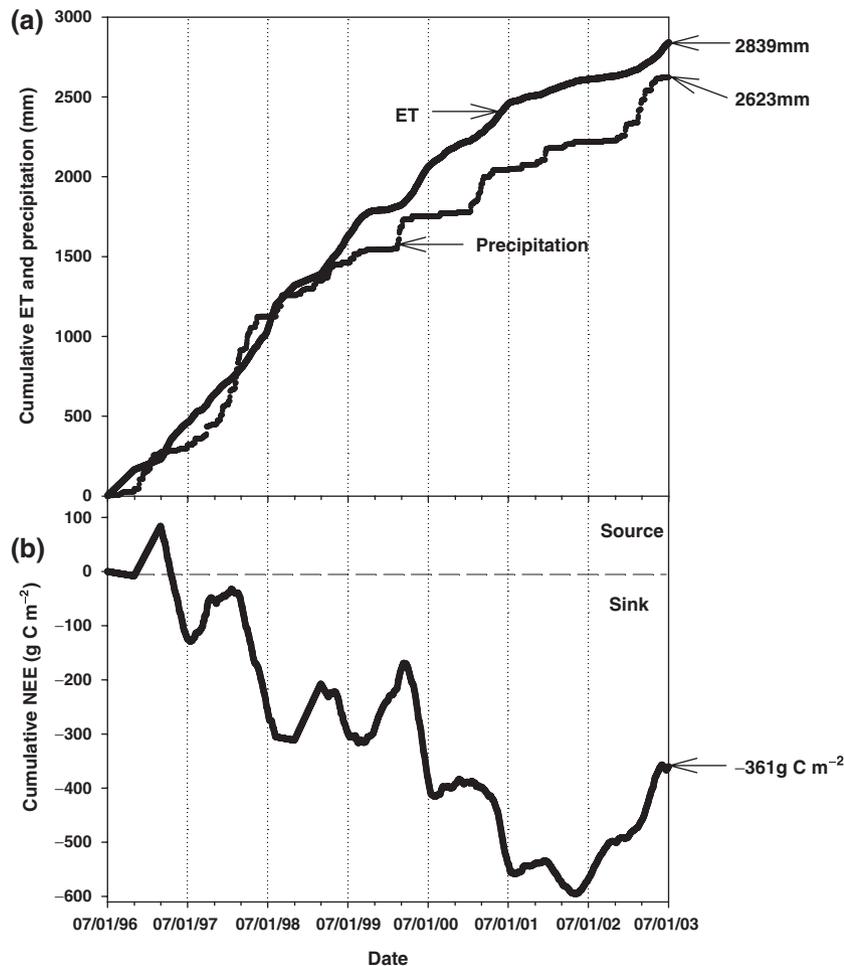


Fig. 4 (a) Cumulative evapotranspiration (ET) and precipitation and (b) cumulative net ecosystem exchange (NEE) during the 7-year measurement period of 1996–2003. The large gaps in 1996–1997 and 1998–1999 were filled according to the regression relationship between daily NEE/ET and annual precipitation.

406 mm yr⁻¹ on average over the measurement period. Precipitation was about 30 mm yr⁻¹ less than the estimated ET. The extra water supply for ET likely came from ground water draining from up slope during the rainy season and reserved at depth in the soil.

Discussion

Carbon sink in old-growth chaparral ecosystems

The annual NEE observed in this 100-year-old mature chaparral shrub ecosystem was -96, -100 and 155 g C m⁻² yr⁻¹ in 1997–1998, 1999–2000 and 2000–2001, respectively, under normal or humid weather conditions. These results are consistent with findings from many old-growth forest sites in the Fluxnet program (Malhi *et al.*, 1998; Carey *et al.*, 2001; Knohl *et al.*, 2003; Paw *et al.*, 2004) suggesting that old-growth stands of various types can be significant sinks of carbon. The observation of a carbon

sink in this study is in opposition to Hanes' statement that chaparral stands, especially chamise-chaparral, older than 60 years are decadent with the respect to carbon sequestration (Hanes, 1971). Why this and other 'old-growth' stands are a sink of carbon is a source of continuing speculation. It has been suggested that the possible causes for the old-growth stands to actively sequester carbon since the late 20th century (Phillips *et al.*, 2002) include increase of CO₂ fertilization of plant growth from the fast rise of atmospheric CO₂ (West *et al.*, 1993; Oechel *et al.*, 1994; Grace *et al.*, 1995), and nutrient fertilization from nitrogen deposition (Rasse, 2002). Alternatively, so-called 'old-growth' chaparral shrub ecosystems may not senesce, and may maintain a productive ratio of gross primary production (GPP) to plant and soil respiration.

Global changes, extreme events and disturbances can markedly influence NEE, and even change the sign of fluxes. Tundra changed from a long term net carbon sink to a source as a result of global warming

and drying of the soil (Oechel *et al.*, 1993). Fire changed a tallgrass prairie from net carbon sink to net carbon source (Suyker & Verma, 2001), and severe water stress reversed a rangeland from an average sink of $-120 \text{ g C m}^{-2} \text{ yr}^{-1}$ to a net carbon source of $155 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Meyers, 2001). When this mature chaparral site experienced a severe drought in year 2001–2002 with precipitation of 175.3 mm (60-year mean was 349 mm), ecosystem exchange of carbon shifted from a strong net sink of $-155 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the previous year to a weak sink of $-18 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2001–2002. This was due to the weakened physiological functions and self pruning of leaves and branches, which resulted in reduced active photosynthetic area. The negative effects of severe drought on carbon sequestration extended into the following year. When the rainy season brought adequate rainfall (406 mm) in the subsequent winter and spring, a large carbon loss ($207 \text{ g C m}^{-2} \text{ yr}^{-1}$) was observed from the ecosystem in 2002–2003. This large loss could be explained in several ways. Firstly, soil decomposition and microbial activity accelerated due to increased water availability coupled with improved accessibility to organic substrates from previously undecomposed organic matter and new litters following leaf and branch shedding. Secondly, over the short term, high concentrations of CO_2 likely accumulated in the soil pores during drought. During rain events, rain water may have filled soil pores displacing CO_2 from soil (Huxman *et al.*, 2004). Thus, the microbial respiration and the physical efflux from the soil appeared to have outweighed the photosynthetic assimilation rates given reduced plant vitality and leaf area resulting in a large net carbon loss from the ecosystem in 2002–2003.

However, as an ecosystem that is adapted to hot and dry weather conditions, chaparral ecosystems have the ability to recover rapidly from the severe drought effects if the length of drought is not excessive. The time period for this chaparral ecosystem to recover from a drought can be as short as 1 year. This recovery was indicated in an adjacent area of the same mature chaparral stand that did not burn in 2003, and showed a moderate carbon sink of $-77 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2004–2005 with an adequate rain fall of 511 mm.

Comparison with other studies

The number of eddy covariance measurement in old-growth stands is increasing and provides us better insights about carbon exchange in old-growth ecosystems. While some results support the conventional ecological assumption that old-growth stands are in dynamic equilibrium (DeBell & Franklin, 1987; Franklin, 2000; Saleska *et al.*, 2003), many old-growth forest

studies present moderate to strong carbon sequestration. The old-growth forest of mixed whitebark pine (*Pinus albicaulis*, Engelmann) and a subalpine species (*Abies lasiocarpa*, Nuttall) in the Rocky Mountains showed a significant carbon sink (Carey *et al.*, 2001). A 500-year-old old-growth mixed forest of Douglas-fir and western hemlock in southwestern Washington exhibited a significant net annual carbon uptake of -150 to $-190 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Field & Kaduk, 2004; Paw *et al.*, 2004). Three boreal forests of old aspen, old black spruce and old jack pine were observed to have carbon uptake values of -122 , -35 and $-78 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively (Griffis *et al.*, 2003). Inventory studies indicated that the biomass of an undisturbed old-growth tropical forest increased in recent years (Phillips *et al.*, 2002). The carbon sink in this old-growth tropical forest was confirmed by eddy covariance measurements and other methods, which was estimated to be somewhere between a moderate sink of $-40 \text{ g C m}^{-2} \text{ yr}^{-1}$ and a strong sink of $-590 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Malhi *et al.*, 1998; Tian *et al.*, 2000; Chambers *et al.*, 2001). The old-growth chaparral in this study sequestered carbon between -96 and $-155 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the measurement period under normal weather conditions, which was comparable with many published results from the old-growth forests worldwide. These findings demonstrate that old-growth stands of various types can be significant with respect to carbon sequestration, and the paradigm that old-growth ecosystems are in carbon equilibrium is not necessary true.

To accurately quantify landscape level carbon fluxes, various forms of disturbance should be considered. But current eddy covariance studies in shrub ecosystems are highly limited, thus constraining the comparison of our results to other shrub ecosystems. However, by comparison with those arid and semiarid ecosystems for which we do have data, a climax mature desert shrub site exhibited a net carbon sink of -39 and $-52 \text{ g C m}^{-2} \text{ yr}^{-1}$ over 2 years (Hastings *et al.*, 2005). Carbon sink was about $-12 \text{ g C m}^{-2} \text{ yr}^{-1}$ for a broad-leaved semiarid savanna in Southern Africa (Veenendaal *et al.*, 2004). The annual NEE observed over Mediterranean annual grassland in California was a sink of $-132 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2000–2001 season and a source of $29 \text{ g C m}^{-2} \text{ yr}^{-1}$ in 2001–2002 season (Xu & Baldocchi, 2004). Carbon gain over a *Picea abies* conifer forest ecosystem was $-450 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Valentini *et al.*, 2000) in Italy. Therefore, NEE of this mature chaparral shrub ecosystem ranging from -96 to $-155 \text{ g C m}^{-2} \text{ yr}^{-1}$ fell between the desert ecosystem, the grassland, and forests in the arid and semiarid area.

The sink strength of this mature chaparral was even comparable with ecosystems in other biomes. This chaparral ecosystem gained more carbon than nonforest

ecosystems, such as tundra ($40 \text{ g C m}^{-2} \text{ yr}^{-1}$, Oechel *et al.*, 2000), tall-grass prairie ($0 \text{ g C m}^{-2} \text{ yr}^{-1}$, Suyker & Verma, 2001), grazed grassland ($41 \text{ g C m}^{-2} \text{ yr}^{-1}$, Meyers, 2001), and even more than some evergreen forests, such as *Pinus sylvestris* (-5 to $90 \text{ g C m}^{-2} \text{ yr}^{-1}$, Lindroth *et al.*, 1998) and cypress (-37 to $-84 \text{ g C m}^{-2} \text{ yr}^{-1}$, Clark *et al.*, 1999). Although shrublands are commonly believed to sequester less carbon than that of forests, the chaparral stand studied sequestered carbon at a rate comparable with many other forest ecosystems, such as a beech ecosystem in Denmark (-124 to $-169 \text{ g C m}^{-2} \text{ yr}^{-1}$, Pilegaard *et al.*, 2001), an aspen ecosystem in Canada (-80 to $-290 \text{ g C m}^{-2} \text{ yr}^{-1}$, Black *et al.*, 1996), a broadleaf deciduous forest in Japan (-70 to $-150 \text{ g C m}^{-2} \text{ yr}^{-1}$, Yamamoto *et al.*, 1999) and even some tropical forests in the Amazon ($-102 \text{ g C m}^{-2} \text{ yr}^{-1}$, Malhi *et al.*, 1998). Contrasted to the well-accepted view that the old-growth stands are unimportant with respect to carbon uptake (Odum, 1969; Jarvis, 1989; Melillo *et al.*, 1996), the significant sequestration in this mature shrub ecosystem demonstrated that semiarid ecosystems can be as important as many more mesic ecosystems of the world. Many ecosystems with high GPP may also have high ecosystem respiration, and therefore, be not as productive with respect to carbon sequestration as at first expected.

Semiarid shrubs should be considered significant ecosystems in the global carbon budget. Despite the variation in weather and disturbance over the measurement period, the average carbon uptake still reached $-52 \text{ g C m}^{-2} \text{ yr}^{-1}$. As a result of anthropogenic CO_2 emission of 6.3 Gt C yr^{-1} , there is a net terrestrial uptake of carbon approximately 2 Gt C yr^{-1} (SRLUCF, 2000, for 1989–1998; Schimel *et al.*, 2001). This is actually only about $-16 \text{ g C m}^{-2} \text{ yr}^{-1}$ in net carbon uptake for the entire terrestrial surface. Therefore, to understand current terrestrial carbon budgets, the accuracy in measuring NEE worldwide must be better than $-16 \text{ g C m}^{-2} \text{ yr}^{-1}$ and very few vegetated ecosystems can, therefore, be ignored. Similarly, total uptake of all the anthropogenic CO_2 of 6.3 Gt C yr^{-1} (Schimel *et al.*, 2001) into terrestrial surface would require fluxes, on average, of only less than $-50 \text{ g C m}^{-2} \text{ yr}^{-1}$. The shrub ecosystem we studied with an average carbon sink of $-52 \text{ g C m}^{-2} \text{ yr}^{-1}$ took up an amount of carbon larger than the terrestrial average needed worldwide to offset all anthropogenic release (on an annual basis) even though it is considered, by many, to be a 'low productivity ecosystem.' In general, other terrestrial ecosystems show a greater annual net uptake of CO_2 . This implies that we are missing sufficient measurements across a sufficient range of biomes, ecosystems, land use categories and situations. Controls and management impacts on carbon flux in arid, semi-

arid regions, in shrub ecosystems and in old-growth ecosystems are all important as part of a complete plan for carbon management. Given its large land area (Atjay *et al.*, 1979) and its large potential to expand its area under heavy impacts from human activities and climate change (Goodale & Davidson, 2002; Jackson *et al.*, 2002), the arid and semiarid regions, including the shrub ecosystem phases, deserve more attentions from scientists and researchers. The existing old-growth shrubs, an important carbon pool of flux in arid and semiarid regions, should be evaluated as part of any management plan for optimal carbon fixation and maintenance of biodiversity and sustainability.

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