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Patterns and controls of long-term CO₂ flux measurements through fire and drought events from
three semi-arid chamise-dominated chaparral stands

By

ANDREA N. FENNER
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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DAVIS

and

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of

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Abstract

Chaparral ecosystems (*Adenostoma fasciculatum*) are the most extensive native plant community in California and are a biodiversity hotspot for native fauna and flora. Undisturbed chaparral ecosystems have been reported to be significant carbon sinks under normal weather conditions (Luo et al., 2007). With climate models predicting an increase in fire and drought frequency in semi-arid regions due to climate change, carbon storage by chaparral ecosystems is likely to be affected by these changes (Storey et al., 2020). While attention to carbon source-sink dynamics in chaparral ecosystems has gained more interest over the recent decade, understanding the controls and patterns of long-term CO₂ flux measurements through wildfire and drought events is still poorly understood. Here, I present long-term CO₂ flux measurements from three varying-aged chaparral ecosystems to better understand the temporal patterns and controls on CO₂ flux and the effects of stand age on carbon sequestration. Through this work, I found that under current climatic conditions, chaparral ecosystems can take up to a decade or more to sequester carbon following a fire and exposure to abnormal rainfall events as the investigated once burned ~20-year-old chaparral ecosystem (US-SO2) acted as a carbon source emitting up to 848 gCm⁻²yr⁻¹ for eight years post-fire. The stand reverted back to a carbon sink sequestering -69 to -343 gCm⁻²yr⁻¹ eleven years post-fire. Contrary to the claim that old-growth ecosystems are in a carbon-neutral state, I found that the investigated old-growth 178-year-old chaparral ecosystem (US-SO4) was a source of CO₂ to the atmosphere releasing up to 447 gCm⁻²yr⁻¹ (Odum, 1969; Salati and Vose, 1984; Tan et al., 2011). The meteorological controls of seasonal NEE in a twice burned ~20-year-old chaparral ecosystem (US-SO3) were soil temperature and relative humidity. Monthly NEE was driven by variations in soil temperature, net radiation, and relative humidity. US-SO3 released 45 gCm⁻²yr⁻¹ to

830 $\text{gCm}^{-2}\text{yr}^{-1}$ for nine of the fifteen-year study period and for five years sequestered $-14 \text{ gCm}^{-2}\text{yr}^{-1}$ to $-1003 \text{ gCm}^{-2}\text{yr}^{-1}$. Understanding the controls and patterns of long-term CO_2 flux in chaparral ecosystems through fire and drought is needed to assess the role of chaparral ecosystems in reducing atmospheric CO_2 .

Introduction

Semi-arid regions cover approximately 17.7% of the earth's land area and along with other dryland ecosystems can store up to 15% of the world's surface organic carbon (Lal, 2003). Semi-arid terrestrial ecosystems can strongly impact the global carbon cycle and have the potential to offset anthropogenic carbon dioxide (CO₂) emissions (Friedlingstein et al., 2020). One semi-arid ecosystem that has proven to be a sink of atmospheric CO₂ in the past and possibly in the future is chaparral. With chaparral being the most extensive biotic community in California covering over 13 million acres and 13% of total land area, it has been shown to be a significant carbon sink (Jacobsen & Pratt, 2018; Norton et al., 2006; Luo et al., 2007). Stand-level carbon sequestration has proven to be dependent on fire frequency, prolonged drought events, and stand age (Law et al., 2004; Amiro et al., 2003; Amiro, 2001; Wirth et al., 2002). In California, interannual rainfall variability is predicted to increase over the next several decades due to climate change (Hanan et al., 2017). Changes in interannual rainfall will likely influence the frequency of wildfires, drought, and how chaparral ecosystems respond to these extreme weather events (Hanan et al., 2017). Over the past several decades, California has seen an increase in wildfires due to warmer temperatures and low rainfall (Baltar et al., 2014). Abnormal fire and drought regimes have the potential to alter carbon source-sink dynamics in chaparral ecosystems (Luo et al., 2007). Frequent drought compounded by increased fire disturbance can result in reduced seedbank production, hydraulic failure of xylem tissue, branch dieback, or widespread mortality leading to a reduction in gross primary productivity (GPP) and carbon storage (Storey et al., 2020). Recently burned, young, and regrowing stands have been reported to be sources of CO₂ while mature stands are net sinks of CO₂ (Wirth et al., 2002; Law et al., 2004; Dore et al., 2008). To prevent potential overestimations of carbon sequestration in

chaparral ecosystems, multidecadal CO₂ flux measurements through fire and drought events are needed to understand carbon storage capabilities.

Carbon storage in chaparral ecosystems may also be affected by stand age. Many have argued that old-growth ecosystems are in a carbon-neutral state in which ecosystem respiration is balanced by gross primary productivity (Odum, 1969; Salati and Vose, 1984; Tan et al., 2011). This has been widely debated as old-growth chaparral and various old-growth forests have proven to be significant carbon sinks (Luo et al., 2007; Zhou et al., 2006; Tan et al., 2011; Zhang et al., 2006). With climate models predicting an increase in drought events during the twenty-first century, it remains unclear if old-growth chaparral ecosystems will remain significant carbon sinks, reach a state of equilibrium, or act as sources of CO₂ to the atmosphere (Storey et al., 2020). To gain a better understanding of the role old-growth chaparral ecosystems play in the global carbon budget, assessment of carbon uptake through drought events and over a time period that extends the average study time is needed.

With many chaparral ecosystems found on north and south-facing slopes, understanding how abiotic factors such as temperature, radiation, and water and nutrient availability change with slope-aspect and how that affects carbon storage on an annual, seasonal, and monthly scale is key. Chaparral residing on south-facing slopes are often exposed to higher solar insolation, increased evapotranspiration, and reduced soil moisture retention (Miller et al., 1983). In similar arid shrub ecosystems, precipitation is the controlling factor of annual CO₂ flux (Bell et al., 2012). Seasonal flux is controlled by photosynthetically active radiation (PAR) and soil temperature and soil moisture controls monthly NEE (Bell et al., 2012). Despite extensive research examining the climatic drivers of NEE on various temporal scales in a variety of ecosystems, little is known about the meteorological controls of NEE in south-facing chaparral

ecosystems subject to extreme weather events (Tamrakar et al., 2018; Gilmanov et al., 2004; Wang et al., 2008). Identifying the meteorological drivers of annual, seasonal, and monthly CO₂ flux in chaparral ecosystems residing on south-facing slopes exposed to multiple fire and drought events is needed to better understand carbon sequestration strength in these complex ecosystems.

In the following work, I sought to address these gaps in knowledge by examining long-term CO₂ flux in varying-aged chaparral ecosystems exposed to fire and drought. Research for all three chapters took place at Sky Oaks Field Station in Southern California. In the first chapter, multidecadal CO₂ flux data from a chamise-dominated chaparral ecosystem spanning a wildfire and multiple drought events was examined. Chapter two investigates the effects of stand age on CO₂ flux by comparing NEE from an old-growth 178-year old chaparral ecosystem and a mature 20-year old chaparral ecosystem. The third chapter identifies the meteorological drivers of annual, seasonal, and monthly CO₂ flux in a chaparral ecosystem residing on a south-facing slope following two fires and exposure to multiple drought events. Given its extensive geographic range and threat from human activity, understanding the source-sink dynamics of semi-arid chaparral ecosystems is key to understand their potential role in reducing atmospheric CO₂ and restoring balance to the global carbon budget.

Chapter 1

Long-term CO₂ flux measurements from a semi-arid chaparral ecosystem through a wildfire and drought events: Twenty years of eddy covariance data

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Abstract

Chaparral ecosystems (*Adenostoma fasciculatum*) are the most extensive plant community in California where undisturbed stands under normal weather conditions are carbon sinks (Luo et al., 2007). Despite chaparral and other Mediterranean-type ecosystems covering only 2.3% of the Earth's surface, these ecosystems are biodiversity hotspots and historically centers of cultural development and high population densities often subject to frequent and/or intense wildfires (Underwood et al., 2018 and Joffre and Rambal, 2001). As temperatures increase and precipitation decreases due to climate change wildfires and drought events are expected to become more frequent in chaparral ecosystems. A key step to determining the role chaparral play in the global carbon budget is to quantify CO₂ flux through wildfire and drought events. In this study, we used eddy covariance techniques to measure the net ecosystem exchange (NEE) of CO₂ during the hydrological years (beginning July 1st and ending June 30th of the following year) of 1997 to 2019 from a ~20-year-old chaparral stand (US-SO2; burned in 2003) in Southern California. From 1997 to 2002 the ecosystem was a carbon sink sequestering $-100 \pm 46 \text{ gCm}^{-2}\text{yr}^{-1}$. A carbon source of $207 \text{ gCm}^{-2}\text{yr}^{-1}$ was observed from 2002 to 2003 following a severe drought. In July of 2003 a wildfire caused the chaparral stand to switch from a carbon sink to a post fire source of CO₂ releasing $375 \pm 137 \text{ gCm}^{-2}\text{yr}^{-1}$ during the years of 2006

to 2013. A decade after the fire, the stand reverted back to a carbon sink sequestering -245 ± 87 $\text{gCm}^{-2}\text{yr}^{-1}$ from 2014 to 2020. Findings from this study show that wildfires coupled with long-term drought conditions can result in a loss of carbon for a decade after a fire. As fire and drought become more prevalent in chaparral ecosystems this sink of carbon could shift to a long-lasting carbon source.

Keywords: fire, carbon, CO₂ flux, chaparral, eddy covariance, NEE

Introduction

Terrestrial ecosystems strongly impact the global carbon cycle. Terrestrial uptake by photosynthesis is substantial (about 200-400 GtCy^{-1}) (Pan et al., 2013) creating the potential for large offsets to anthropogenic CO₂ emissions (Friedlingstein et al., 2020). However, gross primary productivity (GPP) is offset by ecosystem respiration, fire, deforestation and other land use change. Currently, terrestrial ecosystems are estimated to absorb approximately 30% of annual CO₂ emissions from human activity (Way et al., 2021). This number could be much larger or smaller depending on ecosystem management (including land use change, revegetation, and fire management) and climate change. Knowledge of the current patterns and controls on terrestrial ecosystem carbon budgets are crucial to help offset anthropogenic CO₂ emissions. One ecosystem with potential for net CO₂ storage in the past and possibly in the future is chaparral. Chaparral is the most extensive biotic community in California and has been reported to be a significant carbon sink mitigating rising atmospheric CO₂ levels (Luo et al., 2007). Stand-level carbon sequestration has proven to be dependent on fire frequency and stand age (Law et al., 2004; Amiro et al., 2003; Amiro, 2001; Wirth et al., 2002). Yet the impact of fires on carbon flux is often not considered in estimates of carbon sequestration by terrestrial ecosystems leading to

potential overestimations (Dore et al., 2008). Disturbance, stand age, and scale of disturbance are essential to accurately estimate carbon sequestration in terrestrial ecosystems.

Over the past several decades there has been a significant increase in wildfire frequency in California due to an increase in temperature, drought, and flammable vegetation brought on by climate change (Baltar et al., 2014). Wildfires result in an initial release of stored carbon to the atmosphere and modifies conditions that can affect carbon flux for decades after a fire (O'Donnell et al., 2009 and O'Neill et al., 2002). Fire can also alter decomposition rates via changes in soil moisture, soil temperature, and microbial community composition (Fritze et al., 1994; Imeson et al., 1992; O'Donnell et al., 2009; O'Neill et al., 2002). Effects of fire on carbon flux varies depending on fire intensity and rate of recovery post fire. Previous studies show that recently burned, young, and regrowing stands act as carbon sources to the atmosphere while mature stands are a net sink of CO₂ (Wirth et al., 2002; Law et al., 2004; Dore et al., 2008). Conversion of a Siberian Scots pine ecosystem, a forested region of Oregon, and a ponderosa pine forest from carbon sinks to carbon sources following fire was due in part to a reduction in net ecosystem production, as decomposition of necromass produced by fire caused heterotrophic respiration to outpace net primary production (Dore et al., 2008; Wirth et al., 2002; Amiro, 2001).

Chaparral historically burns every 25 to 65 years and re-establish closed or nearly closed canopies within 10 years following fire (Luo et al., 2007 and Storey et al., 2021). However, climate change and land cover transformations have the ability to change fire regimes among chaparral ecosystems, with an increase in fire frequency being observed in many regions around the world (Storey et al., 2021). Insufficient time between fires (< 12 years) can decrease reestablishment of obligate-seeding chaparral species resulting in type conversion to invasive

and/or coastal sage species (Storey et al., 2021; Jacobsen et al., 2004; Zedler et al., 1983). Colonization of non-native species due to increased fire frequency can alter ecosystem processes and affect carbon sequestration in chaparral ecosystems. Abnormal drought regimes due to climate change can also diminish post-fire recovery in shallow- and deep-rooted chaparral species (Storey et al., 2020). Drought-related impacts can range from widespread mortality to branch dieback reducing carbon sink strength in chaparral ecosystems (Davis et al., 2002; Storey et al., 2020; Venturas et al., 2016). Given that chaparral is the most extensive vegetation type in California, there is utility in continuous CO₂ flux measurements from chaparral ecosystems that extends past the usual experimental measurement period of a few years to help assure that carbon sequestration levels are accurately represented. Therefore, we have continued the work presented by our colleagues Luo and others in 2007 that investigated CO₂ uptake by a 100-year old-growth chamise-dominated chaparral ecosystem from 1996 to 2003. Results from this study found that the 100-year old-growth chaparral stand was a carbon sink ranging from -96 to -155 gCm⁻²yr⁻¹ under normal weather conditions (annual precipitation levels within ± 100 mm of the 60-year mean of 349 mm) (Luo et al., 2007). Drought conditions diminished sink strength to -18 gCm⁻²yr⁻¹ eventually causing the stand to become a source of 207 gCm⁻²yr⁻¹ to the atmosphere (Luo et al., 2007). The objective of this study was to extend the measurement period of CO₂ flux for the same 100-year old-growth chaparral ecosystem previously examined by Luo and others. In July of 2003, the old-growth chaparral stand was exposed to a wildfire making the post fire age of the stand 20-years-old as of July 2023. Here we are one of the first to present multidecadal CO₂ flux data from a chamise-dominated chaparral ecosystem spanning a wildfire and multiple drought events. We hypothesized that the fire in 2003 would result in an initial release of CO₂ to the atmosphere up to one-year post fire. And, as the stand begins to recover,

gross primary productivity would outpace ecosystem respiration causing the stand to revert back to an annual carbon sink sequestering carbon consistently throughout the rest of the study period.

Materials and Methods

Site description

This study was conducted at Sky Oaks Field Station located in southern California at an elevation of approximately 1420 m and ~75 km east of the Pacific Ocean (Luo et al., 2007; Fig. 1.1). Carbon flux from the chaparral stand referred to in Ameriflux as US-SO2 (33° 22.433'N 116° 37.373'W, elevation: 1394m) was investigated. The chaparral stand was burned once in the last century and a half in July of 2003 by the Coyote Wildfire. At the time of the fire, based on stem rings, fire maps, and aerial photography, the stand was approximately 158 years old (Luo et al., 2007). The chaparral stand is a chamise (*Adenostoma fasciculatum*)-dominated chaparral ecosystem with Red Shank (*Adenostoma sparsifolium*) also being a major component (Luo et al., 2007). This region is characterized by a Mediterranean climate with hot, dry summers and cold, wet winters (Luo et al., 2007). Precipitation on average is 349 mm annually and falls between November and April in the form of rain and snow (Luo et al., 2007). Soil types include Tollhouse (Enthic Haploxeroll) and Sheephead (Ultic Haploxeroll) (Luo et al., 2007). The hydrological year is divided into three seasons: the dry season (July 1st to October 31st), winter season (November 1st to February 28th), and growing season (March 1st to June 30th) (Luo et al., 2007). The growing season is characterized by warm and moist conditions that promote plant growth (Luo et al., 2007). During the dry season water availability is low and temperatures are high (Luo et al., 2007). The winter season is characterized by low temperatures and radiation levels with adequate water availability (Luo et al., 2007).

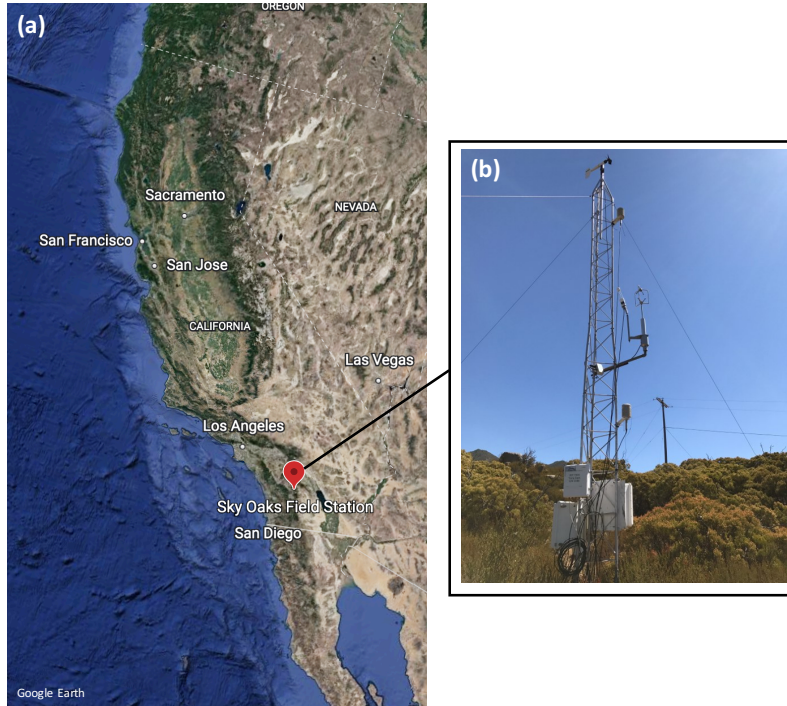


Fig. 1.1 Map of the location of the study site, Sky Oaks Field Station (a) and eddy covariance tower (b) US-SO2 (burned once in 2003). Eddy covariance tower is labeled by its AmeriFlux designation.

Eddy covariance measurements

Net ecosystem exchange (NEE) was measured using the eddy covariance techniques presented by Swinbank (1951) and Desjardins (1972). Eddy covariance (EC) measurements began in March of 1997 for US-SO2 with an interruption in July of 2003 when a wildfire consumed much of the above ground chaparral stand and corresponding EC tower (Luo et al., 2007). Eddy covariance measurements resumed in late 2005. Eddy covariance measurements during the hydrological years of 1997 to 2019 were selected and analyzed for this study. Using a 10 Hz open-path infra-red gas analyzer, CO₂ fluxes were measured and half-hourly means were calculated as the covariance between the vertical wind speed and CO₂ mixing ratio using the post-processing software EddyPro (Bell et al., 2012). Fluctuations in temperature, wind

direction, and wind speed were measured at 10 Hz using a three-dimensional sonic anemometer-thermometer (Windmaster Pro, Gill Instruments; Luo et al., 2007). The listed micrometeorological variables were collected every 10 seconds and reported as 30-minute means using a data logger (CR23X, Campbell Scientific Inc.): soil moisture and temperature at depths of 2, 5, 10, 20, 30, and 40 cm, relative humidity, wind vector, net radiation, incident solar radiation, air temperature, photosynthetically active radiation, precipitation, atmospheric pressure, and ground heat flux (Luo et al., 2007).

Statistical Analyses

A multiple linear regression (R, version 4.0.3) was used to determine the relationship between total annual NEE and average annual soil moisture, soil temperature, photosynthetically active radiation (PAR), relative humidity, air temperature, vapor-pressure deficit (VPD), NDVI, NDMI, net radiation, and total annual precipitation over the measurement period of 1997 to 2020. To identify the significant environmental variables, the multiple regression model used a stepwise linear regression. Spearman's rank and Shapiro-Wilk's tests were utilized to determine the amount of association between variables and to ensure the assumption of normality was met. Transformation of the data was not needed as the data was normally distributed.

Eddy covariance gap-filling and post-processing

On average about 70% to 99% of the eddy covariance data per year was collected over the 20-year study period. Failure to collect 100% of the eddy covariance data was due to instrument calibration, quality assessment of data, and computer, power, or sensor failures. Following a quality control check (QA/QC) and storage correction of data, post-processing by the REdDyProc package in R was conducted. Post-processing consisted of filtering periods with

low turbulent mixing via u^* filtering, gap-filling missing data, and partitioning NEE into ecosystem respiration (R_{eco}) and GPP (Wutzler et al., 2018). NEE was partitioned according to the method of Reichstein et al. (2005) which estimates a respiration–temperature relationship from nighttime data (Wutzler et al., 2018). Ecosystem respiration is estimated from the temporarily varying R_{eco} -temperature relationship and GPP is calculated as the difference between ecosystem respiration and NEE (Wutzler et al., 2018). Inability to gap-fill some missing flux data with the REddyProc package resulted in filling these data gaps by the Random Forest method, which utilized the missForest package in R (version 3.4.3).

NDVI and NDMI

To assess post-fire recovery processes and vegetation water content, the Normalized Difference Vegetation Index (NDVI) and the Normalized Difference Moisture Index (NDMI) were calculated annually over the study period of 1997 to 2020. Landsat 4-5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI) images with a spatial resolution of 30 m were obtained from USGS Earth Explorer to compare post-fire remote sensing data. NDVI was calculated from reflectance measured in the near-infrared (IR) and red (R) bands corresponding to bands 3 and 4 of the TM sensor and bands 4 and 5 of the OLI sensor. The index produces values ranging between -1 to 1 with values below 0.1 indicating areas of bare land, sand, water, snow or rocky areas (Toro Guerrero et al., 2016). Values from 0.2-0.3 correspond to shrubs or grassland and values between 0.6-0.8 represent forested or agricultural areas (Toro Guerrero et al., 2016).

$$NDVI = (IR - R) / (IR + R)$$

The NDMI is an index used to determine vegetation water content and is calculated from reflectance measured in the near-infrared (IR) and short-wave infrared (SWIR) spectral bands corresponding to bands 4 and 5 of the TM sensor and bands 5 and 6 of the OLI sensor. NDMI values range from -1 to 1 with negative values indicating areas of high water stress and values greater than 0.4 representing areas of little to no water stress.

$$\text{NDMI} = (\text{IR} - \text{SWIR}) / (\text{IR} + \text{SWIR})$$

The zonal statistics of the NDMI and NDVI values for the investigated chaparral stand were calculated by averaging the index values within the EC tower footprint (400 m radius) for each satellite image using the ArcGIS zonal statistics tool (Toro Guerrero et al., 2016).

Results

Net ecosystem exchange of US-SO₂ burned in 2003

The chaparral stand (US-SO₂) within the footprint of the EC tower US-SO₂ was engulfed by a wildfire in July of 2003. Following the fire the stand acted as a source of carbon for eight years releasing 395 gCm⁻²yr⁻¹ in 2006-2007, 355 gCm⁻²yr⁻¹ in 2007-2008, 325 gCm⁻²yr⁻¹ in 2008-2009, 848 gCm⁻²yr⁻¹ in 2009-2010, 415 gCm⁻²yr⁻¹ in 2010-2011, 240 gCm⁻²yr⁻¹ in 2011-2012, 397 gCm⁻²yr⁻¹ in 2012-2013, and 202 gCm⁻²yr⁻¹ in 2013-2014 (Fig. 1.2; Table 1.1). The chaparral stand was a sink of CO₂ during the remaining six years of the study period sequestering -69 gCm⁻²yr⁻¹ in 2014-2015, -315 gCm⁻²yr⁻¹ in 2015-2016, -294 gCm⁻²yr⁻¹ in 2016-2017, -343 gCm⁻²yr⁻¹ in 2017-2018, -196 gCm⁻²yr⁻¹ in 2018-2019, and -144 gCm⁻²yr⁻¹ in 2019-2020 (Fig. 1.2; Table 1.1). As NDMI became less negative, an indication of reduced water

stress, sink strength increased during the hydrological year of 2014 and continued on average through the hydrological year of 2019 (Fig. 1.2).

Table 1.1 Total annual NEE and precipitation over the measurement period of 1997 to 2020 from US-SO2.

Year	NEE	Precipitation
	(g C m ⁻² yr ⁻¹)	(mm yr ⁻¹)
1997-1998	-96	805
1998-1999	-132	477
1999-2000	-100	292
2000-2001	-155	288
2001-2002	-18	175
2002-2003	207	406
2003-2004	ND	ND
2004-2005	ND	ND
2005-2006	ND	ND
2006-2007	395	196
2007-2008	355	387
2008-2009	325	304
2009-2010	848	530
2010-2011	415	418
2011-2012	240	170
2012-2013	397	204
2013-2014	202	259
2014-2015	-69	222
2015-2016	-315	281
2016-2017	-294	531
2017-2018	-343	125
2018-2019	-196	459
2019-2020	-144	342

Negative values of NEE indicated ecosystem carbon sink of CO₂ from the atmosphere. Positive values of NEE indicated ecosystem carbon source of CO₂ to the atmosphere. Limited data availability due to fire prevented the calculation of NEE and precipitation in 2003-2004, 2004-2005, and 2005-2006 (ND). Date of most recent fire was July of 2003.

Table 1.2 Annual averages of meteorological variables collected over the study period of 2006 to 2020 from US-SO2.

Year	PAR	Net Radiation	Relative Humidity	Air Temperature	Soil Temperature	VPD	Soil Moisture
	($\mu\text{mol m}^{-2}$)	(W m^{-2})	(%)	($^{\circ}\text{C}$)	($^{\circ}\text{C}$)	(kPa)	($\text{m}^3 \text{m}^{-3}$)
2006-2007	493	104	39	15	20	0.64	16
2007-2008	501	120	41	15	20	0.64	22
2008-2009	466	92	44	15	19	0.70	20
2009-2010	457	92	45	14	18	0.65	23
2010-2011	393	82	48	15	14	0.70	26
2011-2012	436	89	41	15	17	0.63	25
2012-2013	465	121	43	15	18	0.69	17
2013-2014	415	153	29	19	22	0.60	12
2014-2015	547	107	35	15	17	0.54	13
2015-2016	469	87	42	15	18	0.65	16
2016-2017	467	118	41	15	18	0.61	24
2017-2018	490	92	37	16	19	0.60	18
2018-2019	447	83	46	14	17	0.68	22
2019-2020	454	265	41	14	17	0.62	24

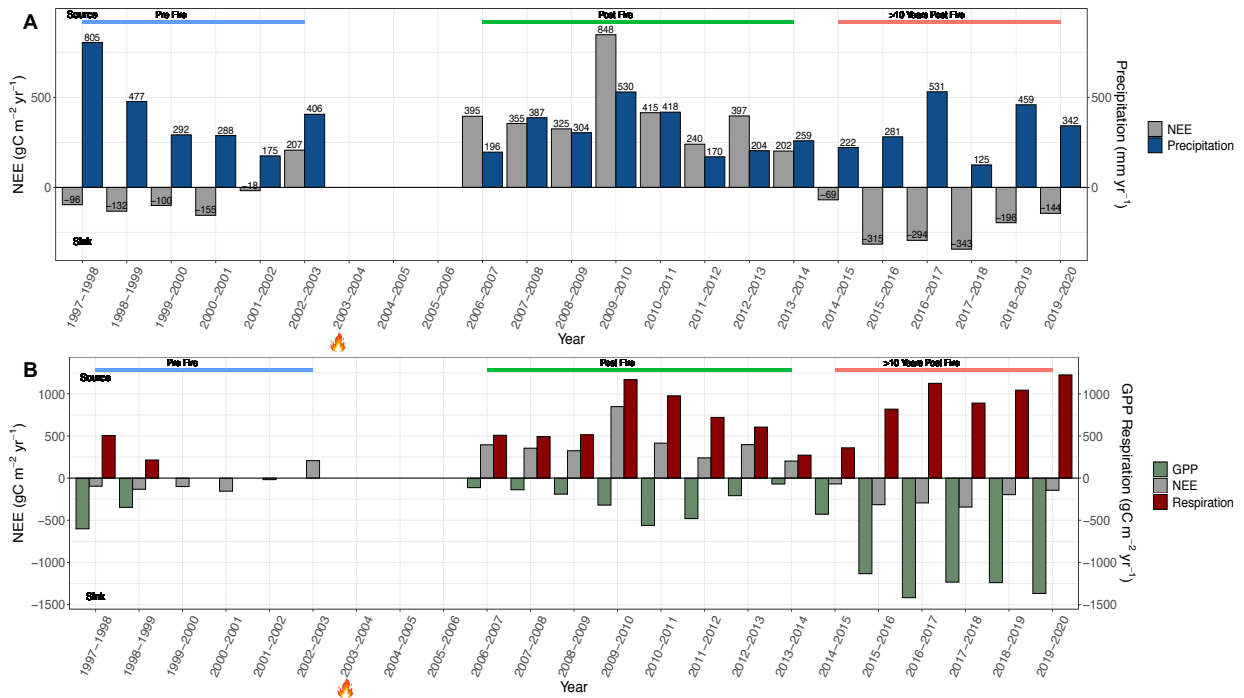


Fig. 1.2 (A) Total annual net ecosystem exchange (NEE) and precipitation and (B) total annual NEE, gross primary productivity (GPP), and ecosystem respiration over the measurement period

of 1997 to 2020 collected from US-SO₂. Limited data availability due to fire prevented the calculation of NEE and precipitation in 2003-2004, 2004-2005, and 2005-2006. NEE was unable to be partitioned into GPP and ecosystem respiration for the hydrological years of 1999 to 2002. Date of most recent fire was July of 2003.

Environmental Factors Controlling NEE

The stepwise regression model indicated that NDMI (p-value = 0.010, $r^2 = 0.20$) had a significant effect on annual NEE ($r^2 = 0.60$) (Table 1.3). Precipitation, soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, and NDVI had no effect on annual NEE ($r^2 = 0.60$) (Table 1.3). Pre-fire (1997-2003) annual NEE was positively correlated with air temperature, VPD, net radiation, and PAR (Fig. 1.3). Annual NEE was negatively correlated with precipitation, soil temperature, relative humidity, NDVI, and NDMI from 1997-2003 (Fig. 1.3). Post-fire (2006-2014) an increase in precipitation, soil moisture, relative humidity, PAR, VPD, and NDVI resulted in an increase in NEE (Fig. 1.3). An increase in soil temperature, air temperature, net radiation, and NDMI caused a decrease in annual NEE from 2006-2014 (Fig. 1.3). During the hydrological years of 2014 to 2019 NEE was positively correlated with precipitation, net radiation, PAR, NDVI and NDMI (Fig. 1.3). Annual NEE was negatively correlated with soil moisture, soil temperature, air temperature, relative humidity, and VPD from 2014-2020 (Fig. 1.3).

Table 1.3 Multiple regression and stepwise regression of total annual NEE and average annual soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, NDVI, NDMI, and total annual precipitation.

Multiple Regression				Stepwise Regression			
Environmental Parameters	r ²	Coefficient	P-value	Environmental Parameters	r ²	Coefficient	P-value
Precipitation	0.466	3.21	0.257	Precipitation	0.600	3.21	0.142
Soil Temperature		-8.53e ⁰¹	0.584	Soil Temperature		-8.52e ⁰¹	0.466
Soil Moisture		9.43e ⁻⁰²	0.998	--		--	
Air Temperature		-9.73e ⁰²	0.193	Air Temperature		-9.73e ⁰²	0.106
PAR		-1.03e ⁰¹	0.184	PAR		-1.03e ⁰¹	0.097
Net Radiation		-4.44	0.287	Net Radiation		-4.44	0.144
VPD		1.99e ⁰⁴	0.335	VPD		1.99e ⁰⁴	0.179
Relative Humidity		-5.29e ⁰²	0.222	Relative Humidity		-5.29e ⁰²	0.099
NDVI		1.16e ⁰⁴	0.142	NDVI		1.16e ⁰⁴	0.075
NDMI		-4.54e ⁰³	0.029	NDMI		-4.53e ⁰³	0.010

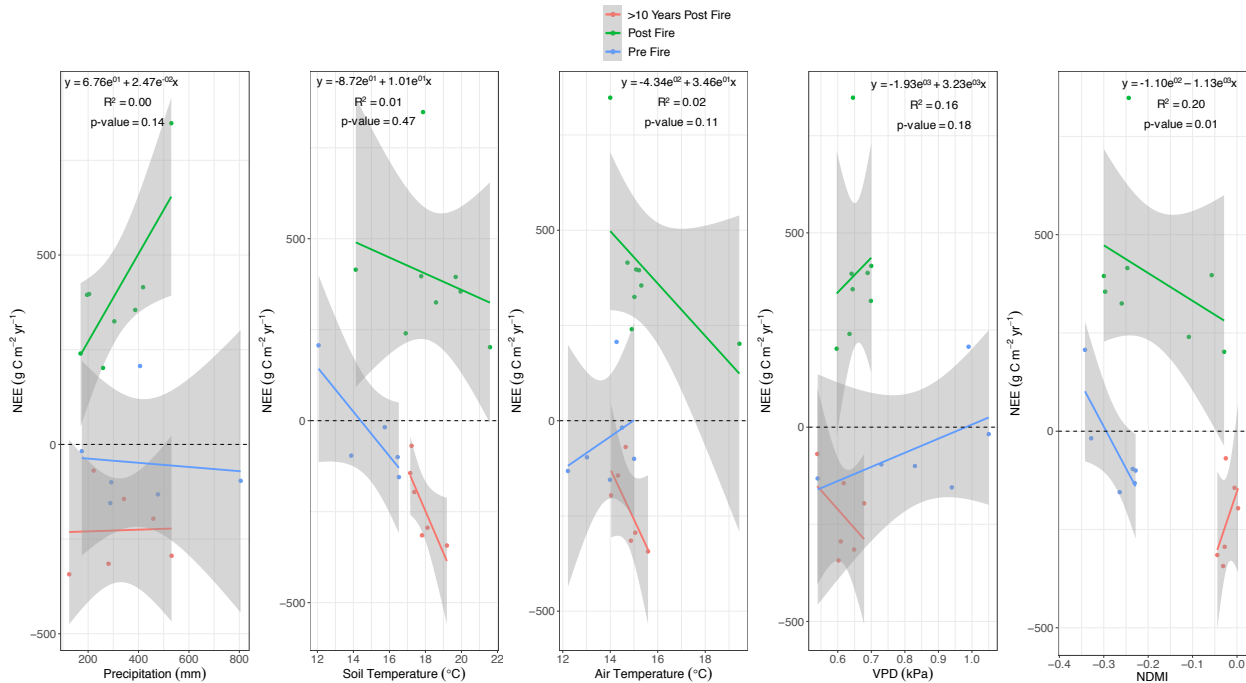


Fig. 1.3 Relationship of total annual net ecosystem exchange (NEE) with average annual soil temperature, air temperature, vapor pressure deficit (VPD), NDMI, and total annual precipitation

during the measurement period of 1997 to 2020 from US-SO2. Date of most recent fire was in July of 2003. Pre Fire (1997 – July 2003), Post Fire (2006 – 2014), >10 Years Post Fire (2014 – 2020). Ecosystem carbon sink from atmosphere denoted by negative NEE values and ecosystem carbon source to atmosphere denoted by positive NEE values.

Discussion

Luo and others found that during the hydrological years of 1997-1998, 1999-2000, and 2000-2001 the then 100-year-old investigated chaparral stand acted as a carbon sink ranging from $-96 \text{ gCm}^{-2}\text{yr}^{-1}$ to $-155 \text{ gCm}^{-2}\text{yr}^{-1}$ (Luo et al., 2007). Severe drought from 2001 to 2002 caused the old-growth chaparral stand to shift from a strong sink to a weak sink of $-18 \text{ gCm}^{-2}\text{yr}^{-1}$ due to a reduction in active photosynthetic area as a result of self-pruning of leaves and weakened physiological functions (Luo et al., 2007). The negative effects of drought continued into the following hydrological year in which $207 \text{ gCm}^{-2}\text{yr}^{-1}$ was released as a sudden increase in rainfall (406 mm) led to accelerated decomposition rates and the release of CO_2 from soil pores accumulated during the drought event (Luo et al., 2007). For this current study, we sought to build upon Luo's work and create a nearly continuous data set to observe CO_2 flux as the chaparral stand underwent a wildfire in July of 2003 and frequent drought events. Over the 20-year study period we found that the chaparral stand (US-SO2) acted as a carbon source during the hydrological years of 2006 to 2013 (Fig. 1.2). The stand reverted back to a carbon sink from 2014 to 2020 (Fig. 1.2).

Post-fire release of CO_2 by US-SO2 can be a result of multiple factors. Wildfires reduce CO_2 sink strength as a result of increased respiration and reduced primary productivity (Grau-Andres et al., 2019). Changes in soil temperature, soil moisture, and microbial community

composition following a fire can alter decomposition rates leading to the release of CO₂ to the atmosphere affecting carbon exchange for decades post fire (Fritze et al., 1994; Imeson et al., 1992; O'Donnell et al., 2009; O'Neill et al., 2002). We found that for nearly a decade after a wildfire in July of 2003, ecosystem respiration outpaced gross primary productivity (GPP) leading to a release of CO₂ by the chaparral stand from 2006 to 2014 (Fig. 1.2). This extended period of released CO₂ by the chaparral stand post fire may be attributed to multiple factors the first being the presence of biomass following the wildfire. Since the wildfire in 2003 was not a stand-replacing fire, large stores of belowground biomass and partially burned aboveground biomass were present at the site potentially attributing to increased decomposition rates during this extended period of released CO₂ (Stark, 1977 and Bissett and Parkinson, 1980). Another source for the prolonged release of CO₂ from 2006 to 2014 were the multiple years of below normal precipitation (Fig. 1.2). Low rainfall may have reduced microbial activity slowing the breakdown of soil organic matter and dead biomass and prolonging the rate of carbon removal by the stand (Qu et al., 2023 and Deng et al., 2021). In addition, reduced leaf area due to fire-induced mortality of vegetation coupled with below normal rainfall suppressed GPP causing ecosystem respiration to outpace GPP from 2006 to 2014 (Yu et al., 2022). Another indication that respiration and GPP were moisture driven is a surge in precipitation during the hydrological of 2009 resulted in a significantly large respiratory release indicating a rise in soil microbial activity and decomposition rates (Orchard and Cook, 1983; Fig. 1.2 & Fig. 1.3). During the Post Fire period (2006-2014), we found that precipitation had a significant effect on NEE (p-value = 0.034) validating that changes in NEE were moisture driven during the recovery period. Orchard and Cook in 1983 also reported seeing a positive correlation between water potential and soil microbial activity in which wetting of soil caused a large increase in respiration. An increase in

ecosystem respiration and a reduction in CO₂ uptake have also been observed in recently burned grassland, Black Spruce, and peatland ecosystems (Chen et al., 2019; Grau-Andres et al., 2019; O'Donnell et al., 2009). Overall, we found the breakdown of biomass, increased decomposition rates during surges of precipitation, decreased microbial activity during drought events, and reduced leaf area post-fire are factors that may have contributed to the release of CO₂ by the chaparral stand for nearly a decade following the Coyote Wildfire (Grau-Andres et al., 2019; Fig. 1.2).

During the last six years of the study period the chaparral stand acted as a carbon sink. During the hydrological years of 2014 to 2019 we observed a significant increase in GPP with total annual GPP reaching $-1418 \text{ gCm}^{-2}\text{yr}^{-1}$ in 2016 when precipitation reached 531 mm yr^{-1} (Fig. 1.2). An increase in GPP indicated that water demands were being met promoting growth and sequestration of carbon (Fig. 1.2). We suggest the increase in sink strength was also attributed to the stand's ability to tap into water reserves deep within the soil profile to meet its biological demands during periods of drought (Luo et al., 2007). Lateral transport of soil organic carbon into nearby alluvial deposits, lakes, and ponds coupled with exportation of carbon from a nearby slope may have also contributed to increased carbon sequestration from 2014 to 2020 (Martinez-Mena et al., 2019).

Conclusions

Wildfires and prolonged drought events can play a significant role on annual carbon sequestration in chaparral ecosystems. As the frequency of extreme weather events increase due to climate change, understanding how carbon flux in chaparral ecosystems changes through wildfires and drought conditions is important for the accurate estimation of carbon sequestration

in chaparral. To our knowledge, our study is one of the first to provide two decades of carbon flux for a semi-arid chaparral ecosystem spanning a wildfire and multiple drought events. This research has revealed that chaparral ecosystems have the potential to be a source of CO₂ up to a decade following a wildfire when below and aboveground biomass persist post-fire and rainfall levels are higher or lower than normal. Given their extensive geographic range and threat from human activity, semi-arid chaparral ecosystems should be considered in management plans to ensure chaparral plays its potential role in restoring balance to the global carbon budget.

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Author Contributions Statement

Conceptualization: A.N.F and W.C.O.; Data Curation: A.N.F. and K.L.L.; Formal Analysis: A.N.F. and D.Z.; Funding Acquisition: D.Z. and W.C.O.; Investigation: A.N.F.; Methodology: A.N.F. and W.C.O.; Resources: A.N.F, K.L.L., D.Z., and W.C.O.; Software: A.N.F. and K.L.L.; Supervision: D.Z. and W.C.O.; Validation: A.N.F., D.Z., and W.C.O.; Visualization: A.N.F., K.L.L., D.Z., and W.C.O.; Writing - Original Draft Preparation: A.N.F.;

Writing – Review & Editing: A.N.F., K.L.L., D.Z., W.C.O., and committee; Submitted manuscript to journal for publication: A.N.F.

References

- Amiro, B. D. (2001). Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. *Global Change Biology*, 7, 253–268.
- Amiro, B. D., MacPherson, J. I., Desjardins, R. L., Chen, J. M., & Liu, J. (2003). Post-fire carbon dioxide fluxes in the western Canadian boreal forest: Evidence from towers, aircraft and remote sensing. *Agricultural and Forest Meteorology*, 115, 91–107.
- Baldocchi, D. D., Hicks, B. B., & Meyers, T. P. (1988). Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, 69, 1331–1340.
- Baltar, M., Keeley, J. E., & Schoenberg, F. P. (2014). County-level analysis of the impact of temperature and population increases on California wildfire data. *Environmetrics*, 25, 397–405.
- Bell, T. W., Menzer, O., Troyo-Diequez, E., & Oechel, W.C. (2012). Carbon dioxide exchange over multiple temporal scales in an arid shrub ecosystem near La Paz, Baja California Sur, Mexico. *Global Change Biology*, 18, 2570–2582.
- Bissett, J., & Parkinson, D. (1980). Long-term effects of fire on the composition and activity of the soil microflora of a subalpine, coniferous forest. *Canadian Journal of Botany*, 58(15), 1704–1721.
- Chen, J., Zhang, Y., Luo, Y., Zhou, X., Jiang, Y., Zhao, J., Chen, Y., Wang, C., Guo, L., & Cao, J. (2019). Contrasting responses after fires of the source components of soil respiration and ecosystem respiration. *European Journal of Soil Science*, 70(3), 616–629.

- Davis, S. D., Ewers, F. W., Sperry, J. S., Portwood, K. A., Crocker, M. C., & Adams, G. C. (2002). Shoot dieback during prolonged drought in *Ceanothus* (Rhamnaceae) Chaparral of California: A possible case of hydraulic failure. *American Journal of Botany*, 89(5), 820–828.
- Deng, L., Peng, C., Kim, D., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shangguan, Z., & Kuzyakov, Y. (2021). Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. *Earth-Science Reviews*, 214, 103501.
- Desjardins, R.L. (1972). A study of carbon-dioxide and sensible heat fluxes using the eddy correlation technique. PhD dissertation, Cornell University.
- Dore, S., Kolb, T. E., Montes-Helu, M., Sullivan, B. W., Winslow, W. D., Hart, S. C., Kaye, J. P., Koch, G. W., & Hungate, B. A. (2008). Long-term impact of a stand-replacing fire on ecosystem CO₂ exchange of a ponderosa pine forest. *Global Change Biology*, 14, 1801–1820.
- Friedlingstein, P., O’Sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., Le Quéré, C., Luijkx, I. T., Olsen, A., Peters, G. P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Alkama, R., . . . & Zheng, B. (2020). Global carbon budget 2020. *Earth System Science Data*, 12(4), 3269–3340.
- Fritze, H., Smolander, A., Levula, T., Kitunen, V., & Malkonen, E. (1994). Wood-ash fertilization and fire treatments in a Scots pine forest stand: Effects on the organic layer, microbial biomass, and microbial activity. *Biology and Fertility of Soils*, 17, 57–63.
- Grau-Andres, R., Gray, A., Davies, M. G., Scott, M. E., & Waldron, S. (2019). Burning increases post-fire carbon emissions in a heathland and a raised bog, but experimental manipulation of fire severity has no effect. *Journal of Environmental Management*, 233, 321–328.

- Imeson, A. C., Verstraten, J. M., van Mulligen, E. J., & Sevink, J. (1992). The effects of fire and water repellency on infiltration and runoff under Mediterranean type forest. *Catena*, 19(3-4), 345–361.
- Jacobsen, A. L., Davis, S. D., & Fabritius, S. L. (2004). Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. In: M. Arianoutsou & V. P. Panastasis (Eds.), *Ecology, Conservation and Management of Mediterranean Climate Ecosystems* (pp. 1–5). Rotterdam, Netherlands: Millpress.
- Jacobsen, A. L., & Pratt, B. R. (2018). Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. *New Phytologist*, 219, 489–504.
- Joffre, R., & Rambal, S. (2001). Mediterranean ecosystems. *Encyclopedia of Life Sciences* (pp. 1–7). New York, United States: Macmillan Publishers Ltd, Nature Publishing Group.
- Law, B. E., Turner, D., Campbell, J., Sun, O. J., Van Tuyl, S., Ritts, W. D., & Cohen, W. B. (2004). Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA. *Global Change Biology*, 10, 1429–1444.
- Luo, H., Oechel, W. C., Hastings, S. J., Zulueta, R., Qian, Y., & Kwon, H. (2007). Mature semiarid chaparral ecosystems can be a significant sink of atmospheric carbon dioxide. *Global Change Biology*, 13, 386–396.
- Martinez-Mena, M., Almagro, M., Garcia-Franco, N., de Vente, J., Garcia, E., & Boix-Fayos, C. (2019). Fluvial sedimentary deposits as carbon sinks: Organic carbon pools and stabilization mechanisms across a Mediterranean catchment. *Biogeosciences*, 16, 1035–1051.

- O'Donnell, J. A., Turetsky, M. R., Harden, J. W., Manies, K. L., Pruett, L. E., Shetler, G., & Neff, J. C. (2009). Interactive effects of fire, soil climate, and moss on CO₂ fluxes in black spruce ecosystems of Interior Alaska. *Ecosystems*, 12, 57–72.
- O'Neill, K. P., Kasischke, E. S., & Richter, D. D. (2002). Environmental controls on soil CO₂ flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. *Canadian Journal of Forest Research*, 32, 1525–1541.
- Orchard, V. A., & Cook, F. J. (1983). Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry*, 15(4), 447–453.
- Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, 44, 593–622.
- Pratt, B. R., Jacobsen, A. L., Ramirez, A. R., Helms, A. M., Traugh, C. A., Tobin, M. F., Heffner, M. S., & Davis, S. D. (2014). Mortality of resprouting chaparral shrubs after a fire and during a record drought: Physiological mechanisms and demographic consequences. *Global Change Biology*, 20, 893–907.
- Qu, Q., Wang, Z., Gan, Q., Liu, R., & Xu, H. (2023). Impact of drought on soil microbial biomass and extracellular enzyme activity. *Frontiers in Plant Science*, 14, 1221288.
- Reichstein, M., Subke, J., Angeli, A.C., & Tenhunen, J.D. (2005). Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biology*, 11, 1754-1767.
- Stark, N. M. (1977). Fire and nutrient cycling in a Douglas-Fir/Larch forest. *Ecology*, 58(1), 16–30.

- Storey, E. A., Stow, D. A., Roberts, D. A., O’Leary, J. F., & Davis, F. W. (2020). Evaluating drought impact on postfire recovery of chaparral across Southern California. *Ecosystems*, 24(4), 806–824.
- Storey, E. A., Stow, D. A., O’Leary, J. F., Davis, F. W., & Roberts, D. A. (2021). Does short-interval fire inhibit postfire recovery of chaparral across southern California? *Science of the Total Environment*, 751, 142271.
- Swinbank, W.C. (1951). The measurement of vertical transfer of heat and water vapor by eddies in the lower atmosphere. *Journal of Meteorology*, 8(3), 135.
- Toro Guerrero, F. J. D., Hinojosa-Corona, A., & Kretschmar, T. G. (2016). A comparative study of NDVI values between north- and south-facing slopes in a semiarid mountainous region. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 9, 5350–5356.
- Underwood, E. C., Safford, H. D., Molinari, N. A., & Keeley, J. E. (2018). Valuing chaparral: Ecological, socio-economic, and management perspectives. Cham, Switzerland: Springer.
- Venturas, M. D., MacKinnon, E. D., Dario, H. L., Jacobsen, A. L., Pratt, R. B., & Davis, S. D. (2016). Chaparral shrub hydraulic traits, size, and life history types relate to species mortality during California’s historic drought of 2014. *PLoS ONE*, 11(7), e0159145.
- Way, D.A., Cook, A., & Rogers, A. (2021). The effects of rising CO₂ concentrations on terrestrial systems: Scaling it up. *New Phytologist*, 229, 2383–2385.
- Wirth, C., Schulze, E. D., Luhker, B., Grigoriev, S., Siry, M., Hardes, G., Ziegler, W., Backor, M., Bauer, G., & Vygodskaya, N. N. (2002). Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant and Soil*, 242, 41–63.

- Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Sigut, L., Menzer, O., & Reichstein, M. (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences*, 15, 5015–5030.
- Yu, X., Orth, R., Reichstein, M., Bahn, M., Klosterhalfen, A., Knohl, A., Koepsch, F., Migliavacca, M., Mund, M., Nelson, J., Stocker, B.D., Walther, S., & Bastos, A. (2022). Contrasting drought legacy effects on gross primary productivity in a mixed versus pure beech forest. *Biogeosciences*, 19, 4315–4329.
- Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation change in response to extreme events: The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, 64(4), 809–818.

Chapter 2

Reduced productivity as a result of stand age and abnormal rainfall events shift an old-growth chaparral ecosystem to a CO₂ source

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Abstract

A key step to determining the role chaparral ecosystems play in restoring balance to the global carbon budget is identifying carbon sink strength in varying-aged chaparral ecosystems. Carbon dioxide (CO₂) flux and the meteorological drivers that control carbon flux in old-growth semiarid chaparral ecosystems remains under investigated. Carbon flux in old-growth chaparral stands compared to mature chaparral stands is also poorly understood. Using eddy covariance techniques, we measured CO₂ flux over an old-growth (~178-years old in 2024) *Adenostoma fasciculatum*-dominated chaparral stand during the hydrological years of 2006 to 2020 in Southern California. We then compared carbon flux measurements from the old-growth chaparral stand to a mature (~20-year-old) once-burned chaparral stand to determine the effects of stand age on CO₂ flux. The old-growth chaparral stand released 3 to 447 gCm⁻²yr⁻¹ during eleven of the fourteen-year study period. The old-growth chaparral stand acted as a carbon sink during the hydrological years of 2018 to 2019 sequestering -34 gCm⁻²yr⁻¹. Following a wildfire in July of 2003, the mature 20-year-old chaparral stand acted as a source of CO₂ emitting 202 gCm⁻²yr⁻¹ to 848 gCm⁻²yr⁻¹ from 2006 to 2014. The mature chaparral stand transitioned back to a carbon sink sequestering -343 gCm⁻²yr⁻¹ to -69 gCm⁻²yr⁻¹ from 2014 to 2020. Stand age appeared to have a significant effect on productivity with gross primary productivity (GPP) being

significantly lower in the old-growth chaparral stand when compared to the mature 20-year-old chaparral stand. Results from our study indicate that old-growth chaparral ecosystems can be significant carbon sinks under normal weather conditions. However, reduced productivity due to stand age coupled with prolonged drought can turn this sink of CO₂ to a prolonged source of CO₂.

Keywords: old-growth, chaparral, CO₂ flux, eddy covariance, stand age

Introduction

Increased concentrations of greenhouse gases such as carbon dioxide in the atmosphere has resulted in global warming. To alleviate rising temperatures a reduction in carbon emissions and an increase in carbon sequestration must occur (Dai et al., 2013). Terrestrial ecosystems can be significant carbon sinks absorbing 30% of annual CO₂ emissions (Way et al., 2021), though the role old-growth terrestrial ecosystems play in sequestering carbon and restoring balance to the global carbon budget has been widely debated. Many have argued that old-growth ecosystems remain in a carbon-neutral state in which photosynthetic uptake of CO₂ is balanced by ecosystem respiration (Odum, 1969; Salati and Vose, 1984; Tan et al., 2011). However, the idea of old-growth ecosystems being in a state of equilibrium has been called into question as recent studies have found that old-growth forests can be significant carbon sinks. Zhou and others reported an old-growth forest in southern China sequestered carbon at a significantly high rate from 1979 to 2003 (Zhou et al., 2006). A 300-year-old subtropical evergreen forest was a carbon sink in southwest China (Tan et al., 2011). While a 200-year-old Chinese broad-leaved Korean pine mixed forest was a net sink of carbon sequestering $-308 \pm 116 \text{ g C m}^{-2}$ (Zhang et al., 2006). Increased carbon sequestration by old-growth ecosystems may be attributed to continued growth as the stand reaches full maturity and variation in meteorological controls that

alter the balance between gross primary productivity (GPP) and ecosystem respiration (Dai et al., 2013).

Though studies have proven that old-growth ecosystems are not in a state of equilibrium and have the ability to sequester carbon, the value of old-growth ecosystems and their role in mitigating rising atmospheric CO₂ levels is often compared to younger-aged ecosystems. A >300-year-old hemlock-hardwood forest was reported to be a significantly smaller sink sequestering $-72 \pm 36 \text{ gCm}^{-2}\text{year}^{-1}$ in 2002 and $-147 \pm 42 \text{ gCm}^{-2}\text{year}^{-1}$ in 2003 compared to $-438 \pm 49 \text{ gCm}^{-2}\text{year}^{-1}$ to $-490 \pm 48 \text{ gCm}^{-2}\text{year}^{-1}$ sequestered by a 70-year-old mature hardwood forest (Desai et al., 2005). Recently disturbed and old-growth forests in North America were found to be carbon sources, while areas with middle-aged forests were carbon sinks (Deng et al., 2013). Reports have also indicated that GPP gradually declines with stand age and gross ecosystem productivity (GEP) and net ecosystem productivity (NEP) are higher in younger-aged ecosystems (Desai et al., 2005; Peichel et al., 2010). Rapid removal of atmospheric CO₂ by young regrowing ecosystems has caused some management practices to conserve young-aged ecosystems and promote prescribed burns in old-growth ecosystems. To ensure that these practices are effective long-term it is important to examine CO₂ flux in young and old-growth ecosystems that are not as widely investigated such as chamise-dominated chaparral ecosystems.

As carbon sequestration by old-growth ecosystems gains more attention, assessment of CO₂ uptake by old-growth chaparral ecosystems and the meteorological drivers that control carbon sequestration requires further consideration. To our knowledge, there are few studies that examine carbon sequestration in old-growth chaparral ecosystems. One of the few studies to do so was a study conducted by Luo and others which examined CO₂ uptake by a 100-year old-growth chamise-dominated chaparral ecosystem from 1996 to 2003. Results from the study

indicated the old-growth chaparral stand acted as a sink of CO₂ sequestering -96 gCm⁻²yr⁻¹ to -155 gCm⁻²yr⁻¹ under normal weather conditions (annual precipitation levels within ± 100 mm of the 60-year mean of 349 mm) (Luo et al., 2007). While a weak sink of -18 gCm⁻²yr⁻¹ and a source of 207 gCm⁻²yr⁻¹ were reported during a severe drought event (Luo et al., 2007). There still remains a need for studies that examine CO₂ flux in old-growth chaparral ecosystems that surpasses the average study period of five to ten years and that also compares source-sink strength to younger-aged chaparral ecosystems. Here we provide a nearly continuous data set of CO₂ flux spanning 14 years from a 178-year-old old-growth chamise-dominated chaparral ecosystem. As old-growth chaparral ecosystems become increasingly threatened by frequent fire, prolonged drought events, and urbanization, understanding the amount of carbon sequestered or emitted over time by these ecosystems is vital to management practices geared towards protecting old-growth chaparral. In this study, we quantified the net ecosystem exchange (NEE) of CO₂ during the hydrological years of 2006 to 2020 from a 178 year-old (in 2024) unburned old-growth (*Adenostoma fasciculatum*)-dominate chaparral stand (US-SO4-Unburned) in Southern California using eddy covariance techniques. We compared CO₂ flux collected from the investigated old-growth chaparral stand to CO₂ flux data from a once burned 20-year-old (as of July 2023) chaparral stand to determine the effects of stand age on carbon sequestration in chaparral ecosystems. We asked (1) how CO₂ flux from the investigated old-growth chaparral stand varies over the 14-year study period? (2) How does the magnitude of CO₂ sequestration or emission by the old-growth chaparral stand compare to the once burned mature 20-year-old chaparral stand? Based on findings from Luo and others in 2007, we hypothesized that the old-growth chaparral stand would act as a significant carbon sink under normal weather conditions with periods of drought reducing sink strength. We expected GPP levels to be higher in the 20-

year-old chaparral stand causing the younger stand to sequester CO₂ at significantly higher rates than the old-growth chaparral stand.

Materials and Methods

Site description

This study was conducted at Sky Oaks Field Station in Southern California situated ~75 km east of the Pacific Ocean (Luo et al., 2007; Fig. 2.1). The old-growth chaparral stand (US-SO4-Unburned) has no record of fire. Ring analysis indicates that the stand is approximately 178 years old. The old-growth chaparral stand resides within the footprint of the eddy covariance tower (EC) US-SO4 (33° 23.075'N 116° 38.437'W, elevation: 1429m). The once burned 20-year-old chaparral stand (US-SO2-Burned Once) within the footprint of the EC tower US-SO2 (33° 22.433'N 116° 37.373'W, elevation: 1394m) was burned in July of 2003. Prior to the wildfire the stand was approximately 158 years old. The investigated chaparral stands are of a chamise (*Adenostoma fasciculatum*)-dominated chaparral ecosystem with *Adenostoma sparsifolium* being a major component of the ecosystem as well (Fig. 2.1). The chaparral ecosystems are characterized by a Mediterranean climate with cold, wet winters and hot, dry summers (Luo et al., 2007). Precipitation in the form of rain and snow falls between November and April. Average annual precipitation is around 550 mm. Soil types include Tollhouse (Entic Haploxeroll) and Sheephead (Ultic Haploxeroll) (Luo et al., 2007). Three seasons make-up the hydrological year: the dry season (July 1st to October 31st), winter season (November 1st to February 28th), and growing season (March 1st to June 30th) (Luo et al., 2007). The growing season is characterized by warm and moist conditions that promote plant growth (Luo et al., 2007). Low water availability and hot temperatures dominate the dry season (Luo et al., 2007).

Throughout the winter season radiation and temperature levels are low and water availability is adequate (Luo et al., 2007).

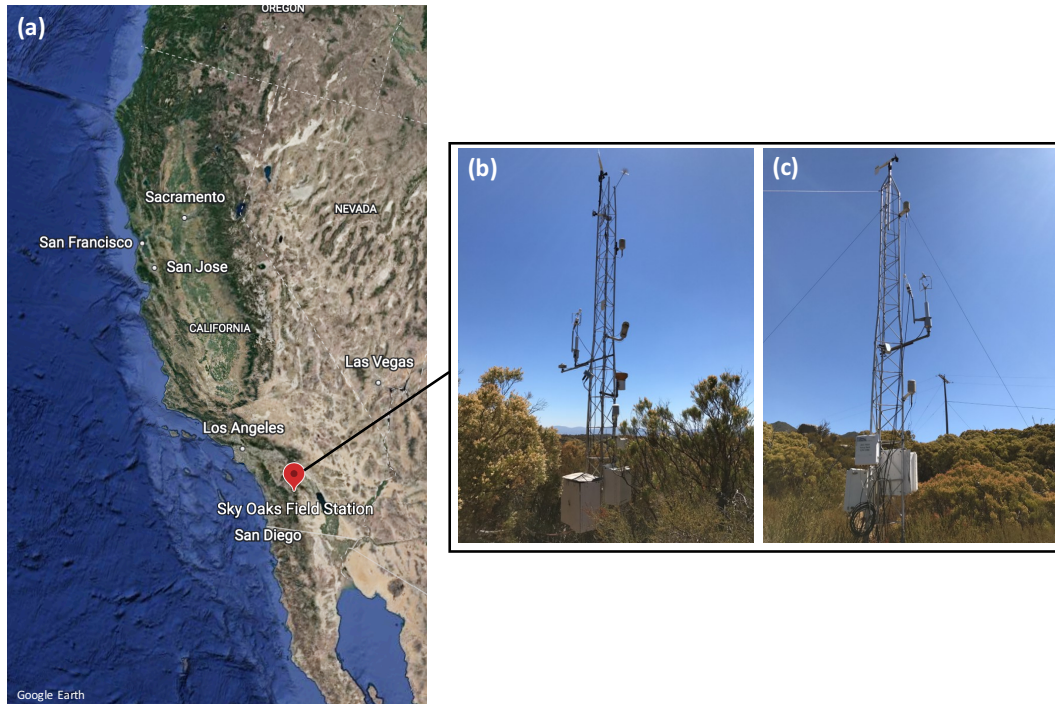


Fig. 2.1 Map of the location of the study site, (a) Sky Oaks Field Station, eddy covariance towers (b) US-SO4 (old-growth 178-year-old chaparral stand), and (c) US-SO2 (mature 20-year-old chaparral stand; burned once in 2003). Eddy covariance towers are labeled by their AmeriFlux designations.

Eddy covariance measurements

The net ecosystem exchange of CO₂ (NEE) was measured using eddy covariance techniques based on the conservation equation proposed by Swinbank in 1951 and Desjardins in 1972. The old-growth chaparral stand (US-SO4-Unburned) began collecting measurements in 2004. The EC tower, US-SO2 began collecting flux measurements over the once burned 20-year-old chaparral stand (US-SO2-Burned Once) in March of 1997 with a brief interruption in July of

2003 when the chaparral stand and EC tower were burned in the Coyote Wildfire (Luo et al., 2007). The footprints for US-SO₂ and US-SO₄ have a radius of approximately 400 meters. Eddy covariance measurements were collected and analyzed during the hydrological years of 2006 to 2020. A 10 Hz open-path infra-red gas analyzer was used to measure carbon dioxide fluctuations (LI-7500, Li-COR Inc.) (Luo et al., 2007). Half-hourly mean CO₂ fluxes were calculated as the covariance between vertical wind speed and the CO₂ mixing ratio using the post-processing software EddyPro (Bell et al., 2012). A three-dimensional sonic anemometer-thermometer was used to measure fluctuations in temperature, wind speed, and wind direction at 10 Hz (Windmaster Pro, Gill Instruments; Luo et al., 2007). The investigated micrometeorological variables (precipitation, relative humidity, air temperature, net radiation, photosynthetically active radiation (PAR), and soil moisture and temperature at depths of 2, 5, 10, 20, 30, and 40 cm) were collected every 10 seconds and recorded as 30-minute means through the use of a data logger (CR23X, Campbell Scientific Inc.; Luo et al., 2007).

Eddy covariance gap filling, post-processing, and statistical analyses

About 70% to 99% of the annual eddy covariance data over the fourteen-year study period was collected. Instrument calibration, computer, power or sensor failures, and quality assessment of data were the main sources of gaps within the data preventing 100% collection of the data. Prior to post-processing, fluxes were storage-corrected and checked for quality (QA/QC). The REdyProc package in R was used to post-process the flux data. Post-processing involved three steps, u^* filtering which identified and filtered periods with low turbulent mixing (Wutzler et al., 2018). The half-hourly flux data was then gap-filled to create a continuous data set (Wutzler et al., 2018). Lastly, NEE was partitioned into GPP and ecosystem respiration (R_{eco})

(Wutzler et al., 2018). NEE was partitioned according to the method of Reichstein et al. (2005) which estimates a respiration–temperature relationship from nighttime data (Wutzler et al., 2018). Ecosystem respiration is estimated from the temporarily varying R_{eco} -temperature relationship and GPP is calculated as the difference between ecosystem respiration and NEE (Wutzler et al., 2018). When the REddyProc package failed to gap-fill the flux data, the Random Forest method, which utilized the missForest package in R (version 3.4.3) filled the remaining gaps. A multiple linear regression was used to identify the meteorological variables controlling NEE from the old-growth chaparral stand during the hydrological years of 2006 to 2020. To identify significant environmental variables, the multiple regression model utilized a stepwise linear regression. NEE was summed and meteorological data was averaged by season for statistical analyses. Spearman’s rank and Shapiro-Wilk’s tests determined the amount of association between variables and ensured the assumption of normality was met. The data was normally distributed and did not require transformation.

Normalized Difference Moisture Index and Normalized Difference Vegetation Index

To assess vegetation water content over the fourteen-year study period the Normalized Difference Moisture Index (NDMI) and the Normalized Difference Vegetation Index (NDVI) were calculated seasonally. Landsat 8 Operational Land Imager (OLI) and Landsat 4-5 Thematic Mapper (TM) images containing a spatial resolution of 30 m were collected from USGS Earth Explorer. NDMI was calculated from reflectance measured in the short-wave infrared (SWIR) and near-infrared (IR) spectral bands corresponding to bands 5 and 4 of the TM sensor and bands 6 and 5 of the OLI sensor. NDMI values range from -1 to 1 with values greater than 0.4 indicating areas in which vegetation were under little to no water stress and negative values representing areas composed of vegetation suffering from high water stress.

$$\text{NDMI} = (\text{IR} - \text{SWIR}) / (\text{IR} + \text{SWIR})$$

NDVI was calculated from reflectance measured in the red (R) and near-infrared (IR) bands corresponding to bands 4 and 3 of the TM sensor and bands 5 and 4 of the OLI sensor. NDVI values below 0.1 indicated areas of bare land, sand, water, snow or rock (Toro Guerrero et al., 2016). NDVI values from 0.2-0.3 corresponded to grassland or shrubs while values between 0.6-0.8 represented agricultural or forested areas (Toro Guerrero et al., 2016).

$$\text{NDVI} = (\text{IR} - \text{R}) / (\text{IR} + \text{R})$$

The zonal statistics of NDMI and NDVI values for US-SO4-Unburned were calculated by averaging the index values within the footprint (400 m radius) of the EC tower for each satellite image using the ArcGIS zonal statistics tool (Toro Guerrero et al., 2016).

Results

Net ecosystem exchange of carbon in an Old-growth Chaparral Stand

The old-growth chaparral stand (US-SO4-Unburned) has not recently been exposed to fire and is approximately 178 years old. The old-growth chaparral stand acted as a source of CO₂ to the atmosphere during eleven of the fourteen years in which NEE measurements were collected. The stand acted as a carbon source emitting 304 gCm⁻²yr⁻¹ from 2006-2007, 319 gCm⁻²yr⁻¹ in 2007-2008, 239 gCm⁻²yr⁻¹ in 2008-2009, 17 gCm⁻²yr⁻¹ in 2011-2012, 118 gCm⁻²yr⁻¹ in 2012-2013, 63 gCm⁻²yr⁻¹ in 2013-2014, 130 gCm⁻²yr⁻¹ in 2014-2015, 447 gCm⁻²yr⁻¹ in 2015-2016, 139 gCm⁻²yr⁻¹ in 2016-2017, 53 gCm⁻²yr⁻¹ in 2017-2018, and 3 gCm⁻²yr⁻¹ in 2019-2020 (Fig. 2.2; Table 2.1). During the hydrological year of 2018 to 2019, the stand acted as a carbon sink sequestering -34 gCm⁻²yr⁻¹ (Fig. 2.2; Table 2.1). The stepwise

regression model indicated that seasonal net ecosystem exchange was significantly affected by NDMI (p-value = 0.048, $r^2 = 0.09$). NEE during the dry season was significantly affected by air temperature (p-value = 0.004, $r^2 = 0.14$), VPD (p-value = 0.016, $r^2 = 0.05$), relative humidity (p-value = 0.020, $r^2 = 0.03$), and NDMI (p-value = 0.015, $r^2 = 0.07$) while NEE during the growing and winter seasons were not significantly affected by the investigated meteorological variables.

Net ecosystem exchange of carbon in a Mature Chaparral Stand

While the old-growth chaparral stand acted as a source of CO₂ during eleven years of the fourteen-year study period, the mature 20-year-old chaparral stand (US-SO₂-Burned Once) released 395 gCm⁻²yr⁻¹ in 2006-2007, 355 gCm⁻²yr⁻¹ in 2007-2008, 325 gCm⁻²yr⁻¹ in 2008-2009, 848 gCm⁻²yr⁻¹ in 2009-2010, 415 gCm⁻²yr⁻¹ in 2010-2011, 240 gCm⁻²yr⁻¹ in 2011-2012, 397 gCm⁻²yr⁻¹ in 2012-2013, and 202 gCm⁻²yr⁻¹ in 2013-2014 (Fig. 2.2). The stand reverted back to a carbon sink sequestering -69 gCm⁻²yr⁻¹ in 2014-2015, -315 gCm⁻²yr⁻¹ in 2015-2016, -294 gCm⁻²yr⁻¹ in 2016-2017, -343 gCm⁻²yr⁻¹ in 2017-2018, -196 gCm⁻²yr⁻¹ in 2018-2019, and -144 gCm⁻²yr⁻¹ in 2019-2020 (Fig. 2.2). The mature chaparral stand was a carbon sink for six years sequestering up to -343 gCm⁻²yr⁻¹ compared to only one year of uptake (-34 gCm⁻²yr⁻¹) by the old-growth chaparral stand (Fig. 2.2).

Gross Primary Productivity and Ecosystem Respiration

The once burned mature chaparral stand was significantly more productive than the old-growth chaparral stand with GPP during the growing season reaching -666 gCm⁻²season⁻¹ compared to -264 gCm⁻²season⁻¹ sequestered by US-SO₄-Unburned (Fig. 2.3). Ecosystem respiration was significantly higher in the mature chaparral stand reporting a release of 600 gCm⁻²season⁻¹ compared to a release of 242 gCm⁻²season⁻¹ by the old-growth chaparral stand

(Fig. 2.3). The mature chaparral stand was significantly more productive on an annual scale with GPP reaching $-1417 \text{ gCm}^{-2}\text{yr}^{-1}$ compared to $-423 \text{ gCm}^{-2}\text{yr}^{-1}$ reported by the old-growth stand. US-SO2-Burned Once reported a significantly higher annual ecosystem respiration of $1223 \text{ gCm}^{-2}\text{yr}^{-1}$ compared to a release of $584 \text{ gCm}^{-2}\text{yr}^{-1}$ by US-SO4-Unburned.

Table 2.1 Total annual NEE and precipitation, and annual averages of meteorological variables collected during the hydrological years of 2006 to 2020 from US-SO4-Unburned.

Year	NEE ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Precipitation (mm yr^{-1})	PAR ($\mu\text{mol m}^{-2}$)	Net Radiation (W m^{-2})	Relative Humidity (%)	Air Temperature ($^{\circ}\text{C}$)	Soil Temperature ($^{\circ}\text{C}$)	VPD (kPa)	Soil Moisture ($\text{m}^3 \text{ m}^{-3}$)
2006-2007	304	196	449	179	39	15	15	0.63	14
2007-2008	319	387	477	137	39	16	18	0.62	21
2008-2009	239	304	454	103	44	15	18	0.69	21
2009-2010	ND								
2010-2011	ND								
2011-2012	17	170	414	90	40	15	16	0.63	25
2012-2013	118	204	411	135	42	15	17	0.68	19
2013-2014	63	259	415	95	38	15	17	0.6	18
2014-2015	130	222	410	126	41	16	18	0.68	19
2015-2016	447	281	431	115	43	15	17	0.67	30
2016-2017	139	531	447	78	42	15	16	0.64	30
2017-2018	53	125	429	38	38	16	18	0.63	29
2018-2019	-34	459	420	229	46	14	18	0.7	23
2019-2020	3	342	457	301	38	17	18	0.65	25

Negative values of NEE indicated ecosystem carbon sink of CO_2 from the atmosphere. Positive values of NEE indicated ecosystem carbon source of CO_2 to the atmosphere. Limited data availability prevented the calculation of NEE in 2009-2010 and 2010-2011 (ND).

Table 2.2 Multiple regression and stepwise regression of total seasonal NEE and average seasonal soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, NDVI, NDMI, and total seasonal precipitation from US-SO4-Unburned.

Multiple Regression				Stepwise Regression			
Environmental Parameters	r ²	Coefficient	P-value	Environmental Parameters	r ²	Coefficient	P-value
Precipitation		1.18e ⁻⁰¹	0.587	Precipitation		8.73e ⁻⁰¹	0.295
Soil Temperature		1.52	0.872	Soil Temperature		-6.17e ⁰¹	0.367
Soil Moisture		-2.44	0.371	Soil Moisture		3.09e01	0.247
Air Temperature	0.266	1.06e ⁰¹	0.570	Air Temperature	0.821	-3.87e ⁰¹	0.393
PAR		8.57e ⁻⁰²	0.729	--			
Net Radiation		-1.58e ⁻⁰¹	0.387	Net Radiation		-1.06	0.269
VPD		-6.09e ⁰¹	0.827	VPD		-3.21e ⁰³	0.156
Relative Humidity		1.50	0.830	--			
NDVI		6.94e ⁰¹	0.840	NDVI		1.52e ⁰²	0.267
NDMI		-1.85e ⁰²	0.176	NDMI		1.18e ⁰³	0.048

Table 2.3 Multiple regression and stepwise regression of total dry season NEE and average dry season soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, NDVI, NDMI, and total dry season precipitation from US-SO4-Unburned.

Multiple Regression				Stepwise Regression			
Environmental Parameters	r ²	Coefficient	P-value	Environmental Parameters	r ²	Coefficient	P-value
Precipitation		8.92e ⁻⁰¹	0.629	Precipitation		1.07	0.054
Soil Temperature		2.32e ⁰¹	0.897	--			
Soil Moisture		1.27	0.933	--			
Air Temperature	0.229	1.85e ⁰²	0.779	Air Temperature	0.799	2.66e ⁰²	0.004
PAR		-9.46e ⁻⁰¹	0.633	PAR		-1.08	0.113
Net Radiation		-1.03e ⁻⁰¹	0.914	--			
VPD		-2.63e ⁰³	0.772	VPD		-3.70e ⁰³	0.016
Relative Humidity		6.68e ⁰¹	0.758	Relative Humidity		9.18e ⁰¹	0.020
NDVI		9.10e ⁰²	0.653	NDVI		1.02e ⁰³	0.085
NDMI		-5.08e ⁰²	0.337	NDMI		-5.06e ⁰²	0.015

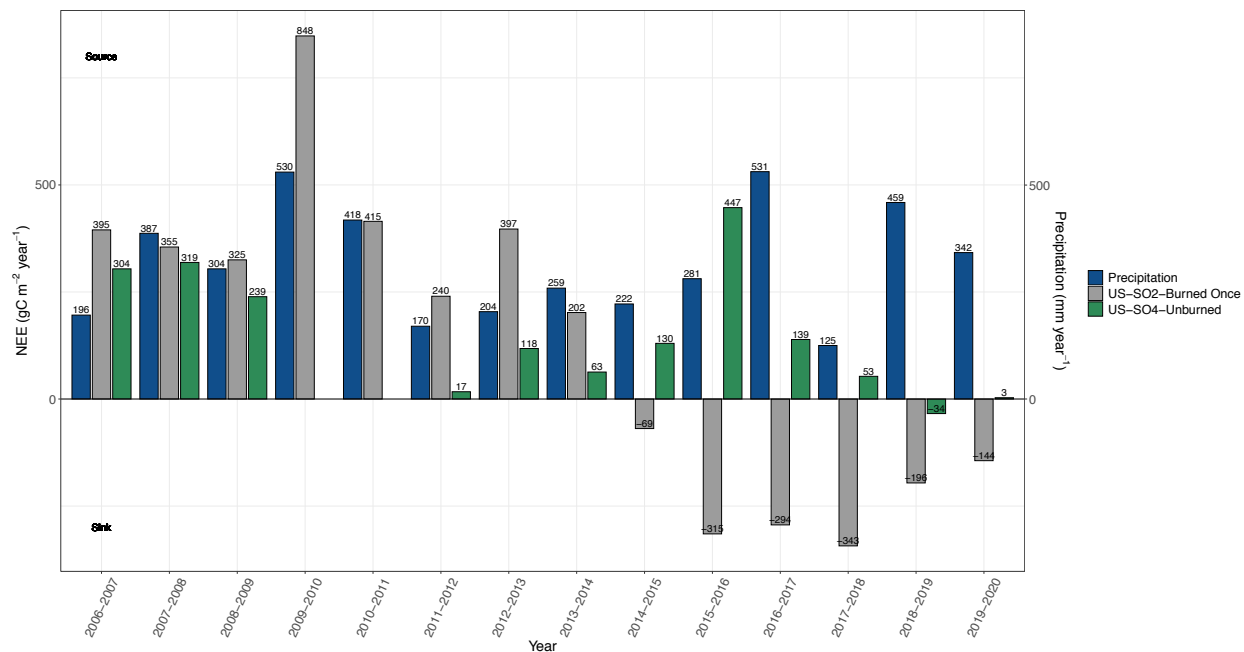


Fig. 2.2 Total annual precipitation and net ecosystem exchange (NEE) from US-SO₂-Burned Once (20-years-old; burned in 2003) and US-SO₄-Unburned (178-years-old) during the hydrological years of 2006 to 2020. Limited data availability prevented the calculation of NEE in 2009-2010 and 2010-2011 for US-SO₄-Unburned.



Fig. 2.3 Total seasonal net ecosystem exchange (NEE), gross primary productivity (GPP), and ecosystem respiration during the measurement period of 2006 to 2020 from US-SO4-Unburned and US-SO2-Burned Once. Dry season (July 1st-October 31st) denoted by the letter *D*, growing season (March 1st-June 30th) denoted by the letter *G*, and winter season (November 1st-February 28th) denoted by the letter *W*. Lack of GPP and respiration data was due to the inability of the REdDyProc package to properly gap-fill and partition NEE resulting in utilization of the missForest package to gap-fill missing data. Limited data availability prevented the calculation of NEE in 2009-2010 and 2010-2011 for US-SO4-Unburned.

Discussion

Contrary to the claims that old-growth ecosystems are in a carbon-neutral state, the investigated old-growth 178-year-old chaparral stand released $3 \text{ gCm}^{-2}\text{yr}^{-1}$ to $447 \text{ gCm}^{-2}\text{yr}^{-1}$ during eleven of the fourteen-year study period (Odum, 1969; Salati and Vose, 1984; Tan et al.,

2011). The old-growth stand demonstrated its ability to sequester CO₂ during the hydrological year of 2018-2019 absorbing -34 gCm⁻²yr⁻¹. For much of the study period, ecosystem respiration outpaced GPP leading to the release of CO₂ by the old-growth chaparral stand (Fig. 2.3). High autotrophic respiration levels have been observed in old-growth ecosystems to maintain accumulating biomass, which may explain the large-scale release of CO₂ by US-SO4-Unburned (Litvak et al., 2003). The release of CO₂ throughout the study period appeared to occur during periods of abnormally low and high precipitation levels. Low rainfall, high light, and increased temperatures may have resulted in a reduction in GPP, leading to the release of CO₂ as ecosystem respiration outpaced GPP (Yu et al., 2022). Surges in precipitation may have led to a rise in soil microbial activity and decomposition rates resulting in an increase in ecosystem respiration and a release of CO₂ to the atmosphere by the old-growth chaparral stand (Orchard and Cook, 1983).

The eight-year release of CO₂ by the once burned mature chaparral stand (US-SO2-Burned Once) may be attributed to altered decomposition rates due to changes in soil temperature, soil moisture, and microbial community composition following the wildfire in July of 2003, coupled with increased decomposition of belowground and partially burned aboveground biomass (Fritze et al., 1994; Imeson et al., 1992; O'Donnell et al., 2009; O'Neill et al., 2002; Stark, 1977; Bissett and Parkinson, 1980). Ecosystem respiration has been shown to significantly increase post-fire reducing CO₂ sink strength (Grau-Andres et al., 2019). During this period of release, GPP may have been suppressed due to fire-induced mortality of the vegetation reducing leaf area and below normal rainfall causing respiration to outpace GPP (Yu et al., 2022). Similar to the old-growth stand, surges in precipitation may have led to an increase in microbial activity and decomposition rates resulting in a release of CO₂ from 2006 to 2014 by

US-SO₂-Burned Once (Orchard and Cook, 1983). Once US-SO₂-Burned Once recovered from the wildfire it reverted back to a carbon sink sequestering -69 gCm⁻²yr⁻¹ to -343 gCm⁻²yr⁻¹ from 2014 to 2020 (Fig. 2.2). Site location may also be a contributing factor to increased carbon sequestration by the mature 20-year-old chaparral stand. Continuous carbon sequestration during the last six-years of the study period by US-SO₂-Burned Once may be correlated to exportation of carbon from a nearby slope and lateral transport of soil organic carbon into nearby alluvial deposits, ponds, and lakes (Martinez-Mena et al., 2019).

The old-growth chaparral stand was on average less productive than the mature 20-year-old stand with annual gross primary productivity reaching -423 gCm⁻²yr⁻¹ compared to a GPP of -1417 gCm⁻²yr⁻¹. A reduction in productivity may be related to stand age as old-growth ecosystems have shown to be less productive than younger-aged ecosystems (Desai et al., 2005). Desai and others in 2005 found that gross ecosystem production was lower in a >300-year-old hemlock-hardwood forest compared to a 70-year-old mature hardwood forest resulting in decreased sink strength. It has long been observed that net primary productivity (NPP) increases as the stand reaches maturity and gradually declines as the stand continues to age (Tang et al., 2014).

Conclusion

By examining the effects of stand age on CO₂ flux in chaparral ecosystems we found that old-growth chaparral ecosystems are not in a carbon-neutral state and under normal weather conditions can be carbon sinks. To our knowledge, our study is one of few that have examined carbon sink strength in an old-growth and mature chaparral ecosystem over a fourteen-year study period. We found that the investigated old-growth 178-year-old chaparral stand was not in a state

of equilibrium and instead was releasing CO₂ to the atmosphere for eleven of the fourteen-year study period. The old-growth chaparral stand proved to be a carbon sink during the hydrological year of 2018 to 2019 sequestering -34 gCm⁻²yr⁻¹. The old-growth stand was also significantly less productive than the investigated mature 20-year-old chaparral stand. This study has shown old-growth chaparral ecosystems are not in a carbon-neutral state and their ability to sequester or release carbon is affected by rainfall events. We found that abnormally high and low rainfall levels can cause old-growth chaparral ecosystems to switch from a carbon sink to a long-term source of CO₂ to the atmosphere. Findings from this study show the importance of understanding how stand age and abnormal precipitation levels can affect carbon sequestration in old-growth chaparral ecosystems. With chaparral being the most extensive biotic community in California, old-growth stands, which have proven to be significant pools of carbon, should be considered in management practices geared towards restoring balance to the global carbon budget.

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Author Contributions Statement

Conceptualization of the manuscript and formulation of the experimental design was achieved by Andrea Fenner and Dr. Walter Oechel. Andrea Fenner collected the data, restructured and re-formatted the data, created code to interpret the data, performed the measurements *in situ*, and interpreted the results. Funding acquisition and resources were provided by Dr. Walter Oechel. Andrea Fenner drafted and revised the manuscript under recommendations from the co-author and committee.

References

- Baret, A., Pepin, S., & Pothier, D. (2018). Hydraulic limitations in dominant trees as a contributing mechanism to the age-related growth decline of boreal forest stands. *Forest Ecology and Management*, 427, 135-142.
- Bell, T.W., Menzer, O., Troyo-Diequez, E., & Oechel, W.C. (2012). Carbon dioxide exchange over multiple temporal scales in an arid shrub ecosystem near La Paz, Baja California Sur, Mexico. *Global Change Biology*, 18, 2570-2582.
- Bissett, J., & Parkinson, D. (1980). Long-term effects of fire on the composition and activity of the soil microflora of a subalpine, coniferous forest. *Canadian Journal of Botany*, 58(15), 1704-1721.
- Bond, B.J. (2000). Age-related changes in photosynthesis of woody plants. *Trends in plant science Reviews*, 5(8), 349-353.
- Dai, L., Jia, J., Yu, D., Lewis, B.J., Zhou, L., Zhou, W., Zhao, W., & Jiang, L. 2013. Effects of climate change on biomass carbon sequestration in old-growth forest ecosystems on Changbai Mountain in Northeast China. *Forest Ecology and Management*, 300, 106-116.
- Deng, F., Chen, J.M., Pan, Y., Peters, W., Birdsey, R., McCullough, K., & Xiao, J. 2013. The use of forest stand age information in an atmospheric CO₂ inversion applied to North America. *Biogeosciences*, 10, 5335-5348.

- Desai, A.R., Bolstad, P.V., Cook, B.D., Davis, K.J., & Carey, E.V. 2005. Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. *Agricultural and Forest Meteorology*, 128, 33-55.
- Desjardins, R.L. (1972). A study of carbon-dioxide and sensible heat fluxes using the eddy correlation technique. PhD dissertation, Cornell University.
- Fritze, H., Smolader, A., Levula, T., Kitunen, V., & Malkonen, E. (1994). Wood-ash fertilization and fire treatments in a Scots pine forest stand: Effects on the organic layer, microbial biomass, and microbial activity.
- Grau-Andres, R., Gray, A., Davies, M.G., Scott, M.E., & Waldron, S. (2019). Burning increases post-fire carbon emissions in a heathland and a raised bog, but experimental manipulation of fire severity has no effect. *Journal of Environmental Management*, 233, 321-328.
- Hubbard, R.M., Bond, B.J., & Ryan, M.G. 1997. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology*, 19, 165-172.
- Imeson, A.C., Verstraten, J.M., van Mulligen, E.J., & Sevink, J. (1992). The effects of fire and water repellency on infiltration and runoff under Mediterranean type forest. *Catena*, 19(3-4), 345-361.
- Karatassiou, M., Karaiskou, P., Verykouki, E., & Rhizopoulou, S. (2022). Hydraulic Response of Deciduous and Evergreen Broadleaved Shrubs, Grown on Olympus Mountain in Greece, to Vapour Pressure Deficit. *Plants (Basel)*, 11(8), 1013.

- Litvak, M., Miller, S., Wofsy, S.C., & Goulden, M. 2003. Effect of stand age on whole ecosystem CO₂ exchange in the Canadian boreal forest. *Journal of Geophysical Research*. 108 (D3), 8225.
- Luo, H., Oechel, W.C., Hastings, S.J., Zulueta, R., Qian, Y., & Kwon, H. (2007). Mature semiarid chaparral ecosystems can be a significant sink of atmospheric carbon dioxide. *Global Change Biology*, 13, 386-396.
- Martinez-Mena, M., Almagro, M., Garcia-Franco, N., de Vente, J., Garcia, E., & Boix-Fayos, C. (2019). Fluvial sedimentary deposits as carbon sinks: organic carbon pools and stabilization mechanisms across a Mediterranean catchment. *Biogeosciences*, 16, 1035-1051.
- Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262-270.
- O'Donnell, J.A., Turetsky, M.R., Harden, J.W., Manies, K.L., Pruett, L.E., Shetler, G., & Neff, J.C. (2009). Interactive Effects of Fire, Soil Climate, and Moss on CO₂ Fluxes in Black Spruce Ecosystems of Interior Alaska. *Ecosystems*, 12, 57-72.
- O'Neill, K.P., Kasischke, E.S., & Richter, D.D. (2002). Environmental controls on soil CO₂ flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. *Canadian Journal of Forest Research*, 32, 1525-1541.
- Peichl, M., Arain, M.A., & Brodeur, J.J. 2010. Age effects on carbon fluxes in temperate pine forests. *Agricultural and Forest Meteorology*, 150, 1090-1101.

- Phillips, N., Bond, B.J., McDowell, N.G., Ryan, M.G., & Schauer, A. 2003. Leaf area compounds height-related hydraulic costs of water transport in Oregon White Oak trees. *Functional Ecology*, 17, 832-840.
- Reichstein, M., Subke, J., Angeli, A.C., & Tenhunen, J.D. (2005). Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biology*, 11, 1754-1767.
- Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J., Rambal, S., Miglietta, F., Peressottis, A., Pecchiari, M., Tirone, G., & Valentini, R. (2002). Severe drought effects on ecosystem CO₂ and H₂O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Global Change Biology*, 8, 999-1017.
- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., & Senock, R.S. 2004. An Experimental Test of the Causes of Forest Growth Decline with Stand Age. *Ecology Monographs*, 74(3), 393-414.
- Salati, E., & Vose, P.B. (1984) Amazon basin – a system in equilibrium. *Science*, 225, 129-138.
- Stark, N.M. (1977). Fire and Nutrient Cycling in a Douglas-Fir/Larch Forest. *Ecology*, 58(1), 16-30.
- Swinbank, W.C. (1951). The measurement of vertical transfer of heat and water vapor by eddies in the lower atmosphere. *Journal of Meteorology*, 8(3), 135.
- Tang, J., Luysaert, S., Richardson, A.D., & Janssens, I.A. (2014). Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences*, 111(24), 8856-8860.

- Tan, Z., Zhang, Y., Schaefer, D., Yu, G., Liang, N., & Song, Q. 2011. An old-growth subtropical Asian evergreen forest as a large carbon sink. *Atmospheric Environment*, 45, 1548-1554.
- Toro Guerrero, F.J.D., Hinojosa-Corona, A., & Kretschmar, T.G. (2016). A Comparative Study of NDVI Values Between North- and South-Facing Slopes in a Semiarid Mountainous Region. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, 9, 5350-5356.
- Way, D.A., Cook, A., & Rogers, A. (2021). The effects of rising CO₂ concentrations on terrestrial systems: scaling it up. *New Phytologist*, 229, 2383-2385.
- Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Sigut, L., Menzer, O., & Reichstein, M. (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences*, 15, 5015-5030.
- Zhang, J., Han, S., & Yu, G. 2006. Seasonal variation in carbon dioxide exchange over a 200-year-old Chinese broad-leaved Korean pine mixed forest. *Agricultural and Forest Meteorology*, 137, 150-165.
- Zhou, G., Liu, S., Li, Z., Zhang, D., Tang, X., Zhou, C., Yan, J., & Mo, J. 2006. Old-Growth Forests Can Accumulate Carbon in Soils. *Science (American Association for the Advancement of Science)*, 314 (5804), 1417-1417.

Chapter 3

Meteorological drivers of monthly, seasonal, and annual CO₂ flux in a south-facing twice burned chaparral ecosystem

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Abstract

Chaparral dominates the Mediterranean climate region of southern California and has the ability to sequester significant amounts of atmospheric CO₂ (Luo et al., 2007). This semi-arid ecosystem is characterized by a Mediterranean climate with cold, wet winters and hot, dry summers. CO₂ fluxes during these varying conditions and the environmental variables that control them may play a role in determining future CO₂ budgets. Here we report the meteorological controls of monthly, seasonal, and annual CO₂ flux from a twice burned 20-year old chamise (*Adenostoma fasciculatum*)-dominated south-facing chaparral ecosystem during the hydrological years of 2005 to 2020 using eddy covariance techniques. The chaparral stand acted as a source of CO₂ to the atmosphere for nine of the fifteen-year study period releasing 45 gCm⁻²yr⁻¹ to 830 gCm⁻²yr⁻¹ annually. A carbon sink was observed for five of the fifteen-year study period, sequestering -14 gCm⁻²yr⁻¹ to -1003 gCm⁻²yr⁻¹ annually. Changes in soil temperature and relative humidity were found to drive variations in seasonal NEE. CO₂ flux during the dry season was driven by changes in relative humidity. Changes in NEE during the growing season were significantly related to changes in air temperature, relative humidity, and VPD. The meteorological controls of monthly NEE were soil temperature, net radiation, and relative humidity. Continued changes in environmental controls on CO₂ flux in chaparral due to

climate change may affect the ability of chaparral ecosystems residing on south-facing slopes to sequester carbon in the future.

Keywords: chaparral, eddy covariance, CO₂ flux, semi-arid ecosystem

Introduction

Terrestrial vegetation can sequester 112-169 PgC of carbon annually potentially offsetting rising atmospheric carbon dioxide (CO₂) emissions (Sha et al., 2022). The most extensive terrestrial vegetation type in southern California, chaparral, has the potential for carbon sequestration as it has been reported to be a significant carbon sink (Luo et al., 2007). Carbon uptake in chaparral has proven to be affected by abiotic factors including temperature, radiation, and water and nutrient availability (Jacobsen and Pratt, 2018; Luo et al., 2007; Rundel & Parsons, 1980). How these abiotic factors vary in relation to topography particularly, slope-aspect, has also been examined in chaparral ecosystems. Increased soil moisture on north-facing slopes of chaparral compared to south-facing slopes explains greater density and vegetation cover on north-facing slopes (Ng and Miller, 1980). Reduced incoming solar irradiance was observed in a north-facing slope chaparral ecosystem compared to chaparral residing on a south-facing slope (Miller and Poole, 1980). Miller et al. (1983) reported lower soil moisture retention and higher solar insolation and evapotranspiration on south-facing slopes in southern California chaparral.

To our knowledge, little is known about the abiotic factors that control CO₂ flux on an annual, seasonal, and monthly scale in chaparral ecosystems residing on south-facing slopes. However, meteorological drivers of CO₂ exchange over multiple temporal scales in varying ecosystems has been widely examined. It has been reported that in an arid shrub ecosystem precipitation was the controlling factor of annual net ecosystem exchange (NEE) of CO₂,

photosynthetically active radiation (PAR) and soil temperature controlled seasonal NEE, and soil moisture controlled monthly NEE (Bell et al., 2012). In two temperate deciduous forests variations in air temperature, soil temperature, global radiation, and VPD controlled winter, spring, and summer net ecosystem productivity (Tamrakar et al., 2018). Winter CO₂ flux in a sagebrush-steppe ecosystem was correlated to changes in soil temperature, wind speed, and snow depth (Gilmanov et al., 2004). Changes in annual precipitation, air temperature, soil water content, and evapotranspiration were the important factors controlling net ecosystem CO₂ exchange over a temperate *Stipa krylovii* steppe (Wang et al., 2008). Though it appears there has been interest in understanding the meteorological controls of CO₂ flux over different temporal scales in various ecosystems worldwide, the climatic drivers of annual, seasonal, and monthly CO₂ flux in chaparral ecosystems remains under investigated. To fill this gap, we provide a long-term analysis of CO₂ flux from a twice burned south-facing chaparral ecosystem to identify meteorological controls that may help explain interannual, seasonal, and monthly variability in carbon dioxide exchange. Identifying and understanding the factors that contribute to the temporal variability in CO₂ flux in chaparral residing on south-facing slopes is crucial for understanding the ability of chaparral in complex terrains to sequester carbon.

In this study, we report the net ecosystem exchange (NEE) of CO₂ in a 20-year old chamise (*Adenostoma fasciculatum*)-dominated south-facing chaparral stand during the hydrological years of 2006 to 2020 using eddy covariance techniques. The chaparral stand was exposed to a prescribed burn in 1992 and a wildfire in July of 2003. Average historical fire frequency for chaparral is 25 to 65 years with mature canopies establishing within 10 years post-fire (Luo et al., 2007; Storey et al., 2021). The objective of this study was to identify the environmental controls on monthly, seasonal, and annual NEE of CO₂ in a twice burned 20-year

old south-facing chaparral ecosystem in southern California. We hypothesized that the meteorological variables significantly affected by slope-aspect would have a significant effect on CO₂ flux. We believed the south-facing orientation of the chaparral stand would cause frequent increases in air temperature, soil temperature, net radiation, vapor pressure deficit (VPD), and photosynthetically active radiation (PAR) and a decrease in precipitation, relative humidity, and soil moisture reducing carbon sequestration during these conditions.

Materials and Methods

Site description

This study was conducted at Sky Oaks Field Station in southern California located about 75 km east of the Pacific Ocean at an elevation of approximately 1420 m (Luo et al., 2007; Fig. 3.1). Net ecosystem exchange of CO₂ from a 20-year-old (as of July 2023) chaparral stand referred to as US-SO3 (33° 22.634'N 116° 37.360'W, elevation: 1429m) within the footprint (400 meters) of the eddy covariance (EC) tower US-SO3 was investigated. The chaparral stand was burned twice within the past 30 years. In 1992, the chaparral stand was subject to a prescribed burn and the Coyote Wildfire in July of 2003. The chaparral stand is a chamise (*Adenostoma fasciculatum*)-dominated chaparral ecosystem with *Adenostoma sparsifolium* present as well (Fig. 3.1). This semi-arid ecosystem is characterized by a Mediterranean climate with hot, dry summers and cold, wet winters (Luo et al., 2007). Precipitation primarily falls between November and April in the form of rain and snow with an average annual precipitation of around 550 mm (Luo et al., 2007). Chamise is a drought tolerant sclerophyllous evergreen shrub that historically burns on average every 25 to 65 years (Luo et al., 2007). Soil types at the study site include Tollhouse (Enthic Haploxeroll) and Sheephead (Ultic Haploxeroll) (Luo et al., 2007). The hydrological year encompasses three seasons: the dry season (July 1st to October 31st),

winter season (November 1st to February 28th), and growing season (March 1st to June 30th) (Luo et al., 2007). During the growing season, weather conditions are favorable for growth with warm and moist conditions promoting plant growth (Luo et al., 2007). The dry season is characterized by low water availability and hot temperatures (Luo et al., 2007). During the winter season, radiation and temperature levels are low with adequate water availability (Luo et al., 2007).

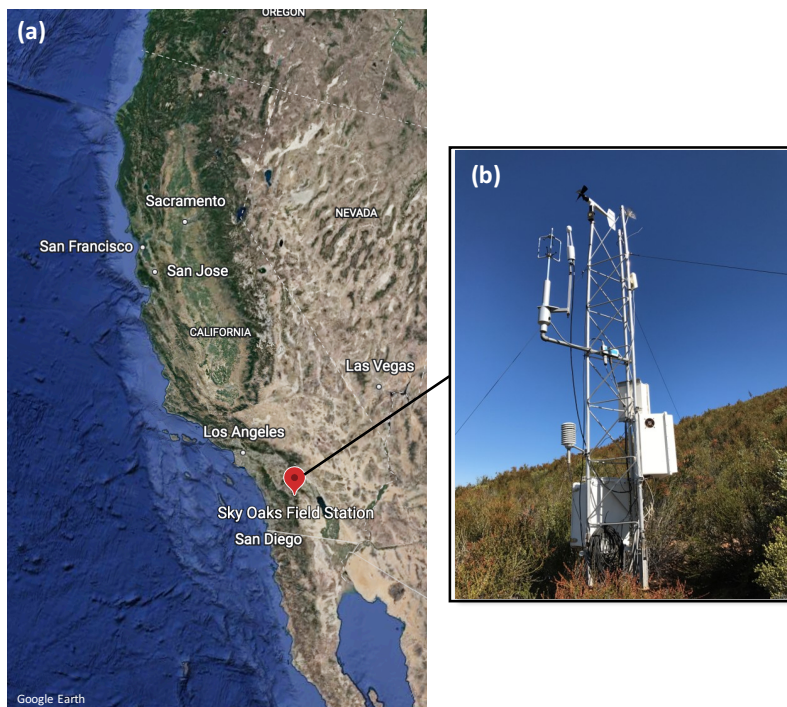


Fig. 3.1 Map of the location of the study site, Sky Oaks Field Station (a) and eddy covariance tower (b) US-SO3 (burned in 1992 and 2003). Eddy covariance tower is labeled by its AmeriFlux designation.

Eddy covariance measurements

The eddy covariance techniques based on the conservation equation proposed in the micrometeorological theory by Swinbank in 1951 and Desjardins in 1972 provided the framework for interpreting and quantifying NEE and other micrometeorological flux measurements. Eddy covariance measurements for US-SO3 began in March of 1997 with a brief

interruption in July of 2003 when a natural wildfire burned the stand consuming the established eddy covariance tower (Luo et al., 2007). The footprint for the eddy covariance tower has a radius of approximately 400 meters. The period of eddy covariance measurements under investigation were the hydrological years of 2006 to 2020. Carbon dioxide fluctuations were measured using a 10 Hz open-path infra-red gas analyzer (LI-7500, Li-COR Inc.) (Luo et al., 2007). Half-hourly mean CO₂ fluxes were calculated as the covariance between the CO₂ mixing ratio and vertical wind speed using the post-processing software EddyPro (Bell et al., 2012). Using a three-dimensional sonic anemometer-thermometer, fluctuations in temperature, wind direction, and wind speed were measured at 10 Hz (Windmaster Pro, Gill Instruments; Luo et al., 2007). Micrometeorological variables (relative humidity, wind vector, air temperature, net radiation, incident solar radiation, precipitation, photosynthetically active radiation (PAR), soil moisture and temperature at depths of 2, 5, 10, 20, 30, and 40 cm, atmospheric pressure, and ground heat flux) were collected every 10 seconds and reported as 30-minute means through the use of a data logger (CR23X, Campbell Scientific Inc.; Luo et al., 2007).

Eddy covariance gap filling and post-processing

Over the fifteen-year measurement period on average 70% to 99% of the eddy covariance data was collected. Instrument calibration, computer, power or sensor failures, and quality assessment of data prevented 100% collection of the eddy covariance data. Prior to post-processing, fluxes were quality checked (QA/QC) and storage-corrected. Post-processing was carried out by the REddyProc package in R. Post-processing followed three steps the first being u^* filtering used to identify and filter periods with low turbulent mixing (Wutzler et al., 2018). Secondly, gap filling missing data in the half-hourly flux data was implemented (Wutzler et al.,

2018). Lastly, partitioning NEE into GPP and ecosystem respiration (R_{eco}) was conducted (Wutzler et al., 2018). NEE was partitioned according to the method of Reichstein et al. (2005) which estimates a respiration–temperature relationship from nighttime data (Wutzler et al., 2018). Ecosystem respiration is estimated from the temporarily varying R_{eco} -temperature relationship and GPP is calculated as the difference between ecosystem respiration and NEE (Wutzler et al., 2018). When the REddyProc package failed to gap-fill missing flux data, gaps in NEE were filled by using the Random Forest method, which utilized the missForest package in R (version 3.4.3).

Statistical Analyses

A multiple linear regression (R, version 4.0.3) was used to identify the monthly, seasonal, and annual meteorological drivers of CO_2 flux during the hydrological years of 2006 to 2020. The multiple linear regression model used a stepwise linear regression to identify significant meteorological variables on varying temporal scales. NEE and precipitation were aggregated into monthly, seasonal, and annual totals. Meteorological variables were aggregated into monthly, seasonal, and annual averages. Spearman's rank and Shapiro-Wilk's tests were utilized to test the assumption of normality and determine the amount of association between variables. Transformations were applied to seasonal and monthly NEE values to ensure a normal distribution of CO_2 flux.

Results

Meteorological controls of annual variability in CO₂ fluxes

On average the twice burned south-facing chaparral stand acted as source of CO₂ emitting 424 gCm⁻²yr⁻¹ during the hydrological year of 2006-2007, 447 gCm⁻²yr⁻¹ in 2007-2008, 45 gCm⁻²yr⁻¹ in 2008-2009, 259 gCm⁻²yr⁻¹ in 2012-2013, 830 gCm⁻²yr⁻¹ in 2015-2016, 548 gCm⁻²yr⁻¹ in 2016-2017, 408 gCm⁻²yr⁻¹ in 2017-2018, 237 gCm⁻²yr⁻¹ in 2018-2019, and 108 gCm⁻²yr⁻¹ in 2019-2020 (Fig. 3.2; Table 3.1). The chaparral stand acted as a carbon sink absorbing -14 gCm⁻²yr⁻¹ in 2005-2006, -15 gCm⁻²yr⁻¹ in 2010-2011, and -195 gCm⁻²yr⁻¹ in 2011-2012, -942 gCm⁻²yr⁻¹ in 2013-2014, and -1003 gCm⁻²yr⁻¹ in 2014-2015 (Fig. 3.2, Table 3.1). Annual NEE was not significantly affected by the investigated meteorological variables. Although, not statistically significant increases in precipitation, soil moisture, net radiation, and relative humidity led to an increase in annual NEE.

Table 3.1 Total annual NEE and precipitation and annual averages of meteorological variables collected during the hydrological years of 2005 to 2020 from US-SO3.

Year	NEE (g C m ⁻² yr ⁻¹)	Precipitation (mm yr ⁻¹)	PAR (μmol m ⁻²)	Net Radiation (W m ⁻²)	Relative Humidity (%)	Air Temperature (°C)	Soil Temperature (°C)	VPD (kPa)	Soil Moisture (m ³ m ⁻³)
2005-2006	-14	244	480	106	46	13	16	0.70	21
2006-2007	424	196	483	104	38	15	21	0.62	13
2007-2008	447	387	503	55	43	15	20	0.53	27
2008-2009	45	304	462	103	41	15	18	0.69	19
2010-2011	-15	418	578	127	35	22	26	0.70	19
2011-2012	-195	170	512	4	41	15	19	0.66	20
2012-2013	259	204	484	26	41	15	19	0.64	18
2013-2014	-942	259	501	-69	38	16	20	0.75	19
2014-2015	-1003	222	492	-62	41	16	21	0.58	21
2015-2016	830	281	480	-57	41	17	20	0.71	22
2016-2017	548	531	525	-64	43	16	20	0.69	24
2017-2018	408	125	489	-112	38	13	17	0.53	19
2018-2019	237	459	476	99	48	14	18	0.73	26
2019-2020	108	342	508	154	43	15	18	0.65	25

Positive values of NEE indicated ecosystem carbon source of CO₂ to the atmosphere. Negative values of NEE indicated ecosystem carbon sink of CO₂ from the atmosphere.

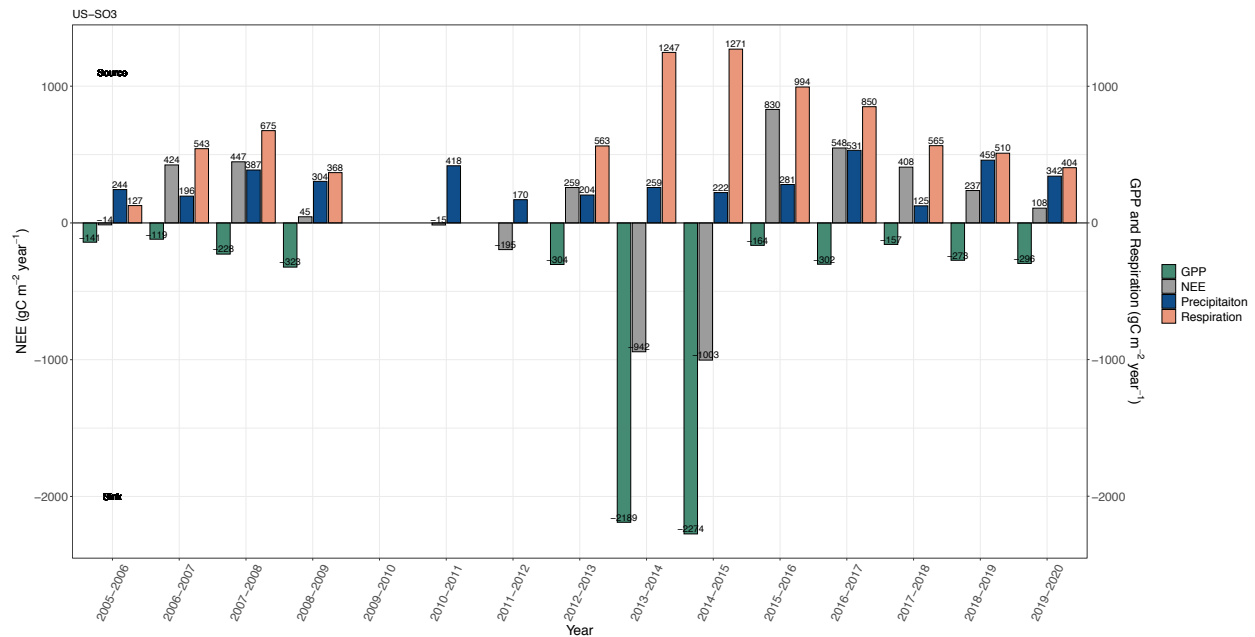


Fig. 3.2 Total annual net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration, and precipitation during the hydrological years of 2005 to 2020 collected

from US-SO3. Limited data availability prevented the calculation of NEE and precipitation in 2009-2010. NEE was unable to be partitioned into GPP and ecosystem respiration for the hydrological years of 2010 to 2012.

Meteorological controls of seasonal variability in CO₂ fluxes

On a seasonal scale NEE appeared to be increasingly sensitive to climate variability. Soil temperature (p-value = 0.001) and relative humidity (p-value = 0.024) were the most significant factors controlling seasonal NEE (Fig. 3.3, Table 3.2). Periods of increased soil temperature and reduced relative humidity led to a significant rise in seasonal NEE (Fig. 3.3). During the growing season NEE was significantly affected by changes in air temperature (p-value = $4.79e^{-04}$), relative humidity (p-value = $8.97e^{-04}$), and VPD (p-value = $2.42e^{-05}$) (Fig. 3.3). Relative humidity (p-value = 0.045) had a significant effect on NEE during the dry season (Fig. 3.3). Although, variations in NEE during the winter season were observed, the investigated meteorological variables had no statistically significant effect on NEE.

Table 3.2 Multiple and stepwise regression of total seasonal NEE and average seasonal soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, and total seasonal precipitation.

Multiple Regression				Stepwise Regression			
Environmental Parameters	r ²	Coefficient	P-value	Environmental Parameters	r ²	Coefficient	P-value
PAR	0.132	-1.47e ⁻⁰³	0.933	--	0.310	--	--
Soil Temperature		1.09	0.204	Soil Temperature		6.66e ⁻⁰¹	0.001
Precipitation		-2.60e ⁻⁰³	0.779	--		--	--
VPD		1.54	0.945	--		--	--
Relative Humidity		3.83e ⁻⁰¹	0.244	Relative Humidity		3.88e ⁻⁰¹	0.024
Air Temperature		-5.43e ⁻⁰¹	0.685	--		--	--
Soil Moisture		-2.17e ⁻⁰²	0.915	--		--	--
Net Radiation		-1.62e ⁻⁰²	0.217	Net Radiation		-1.56e ⁻⁰²	0.124

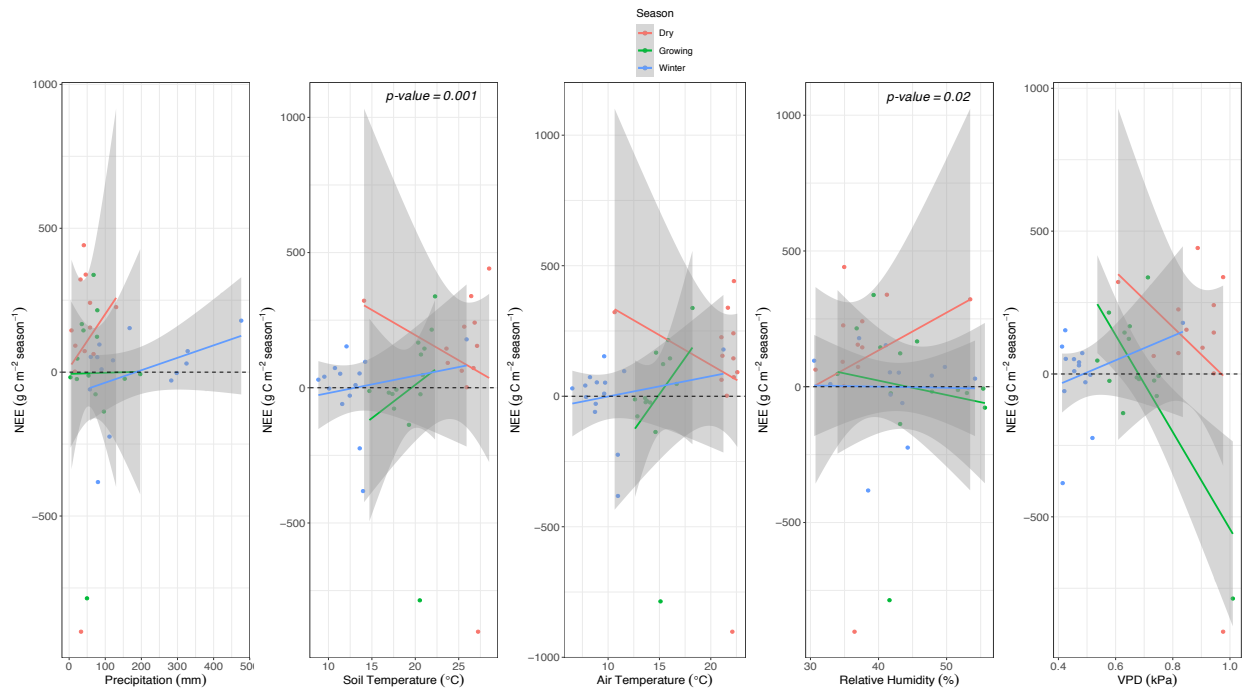


Fig. 3.3 Relationship of total seasonal NEE with average soil temperature, air temperature, relative humidity, VPD, and total seasonal precipitation during the hydrological years of 2005 to

2020 collected by US-SO3. Ecosystem carbon source denoted by positive NEE values and ecosystem carbon sink denoted by negative NEE values.

Meteorological controls of monthly variability in CO₂ fluxes

On a monthly scale multiple meteorological factors controlled CO₂ flux. NEE showed a positive relationship with soil temperature (p-value = 1.09e⁻⁰⁶) and net radiation (p-value = 3.87e⁻⁰⁴) (Fig. 3.4, Table 3.3). An increase in monthly NEE was observed due to an increase in soil temperature and net radiation (Fig. 3.4). A negative relationship was reported between monthly NEE and relative humidity (p-value = 3.33e⁻⁰³). An increase in relative humidity caused a decrease in monthly NEE (Fig. 3.4).

Table 3.3 Multiple and stepwise regression of average monthly NEE, soil temperature, soil moisture, air temperature, PAR, net radiation, VPD, relative humidity, and total monthly precipitation.

Multiple Regression				Stepwise Regression			
Environmental Parameters	r ²	Coefficient	P-value	Environmental Parameters	r ²	Coefficient	P-value
PAR		-4.78e ⁻⁰⁵	0.584	--			
Soil Temperature		4.10e ⁻⁰³	0.144	Soil Temperature		7.45e ⁻⁰³	1.09e ⁻⁰⁶
Precipitation		-2.75e ⁻⁰⁴	0.198	Precipitation		-3.44e ⁻⁰⁴	0.076
VPD	0.214	4.18e ⁻⁰²	0.548	--	0.238		
Relative Humidity		2.32e ⁻⁰³	0.050	Relative Humidity		2.48e ⁻⁰³	0.003
Air Temperature		4.54e ⁻⁰⁴	0.899	--			
Soil Moisture		-4.63e ⁻⁰²	0.752	--			
Net Radiation		-2.22e ⁻⁰⁴	0.001	Net Radiation		-2.12e ⁻⁰⁴	0.000

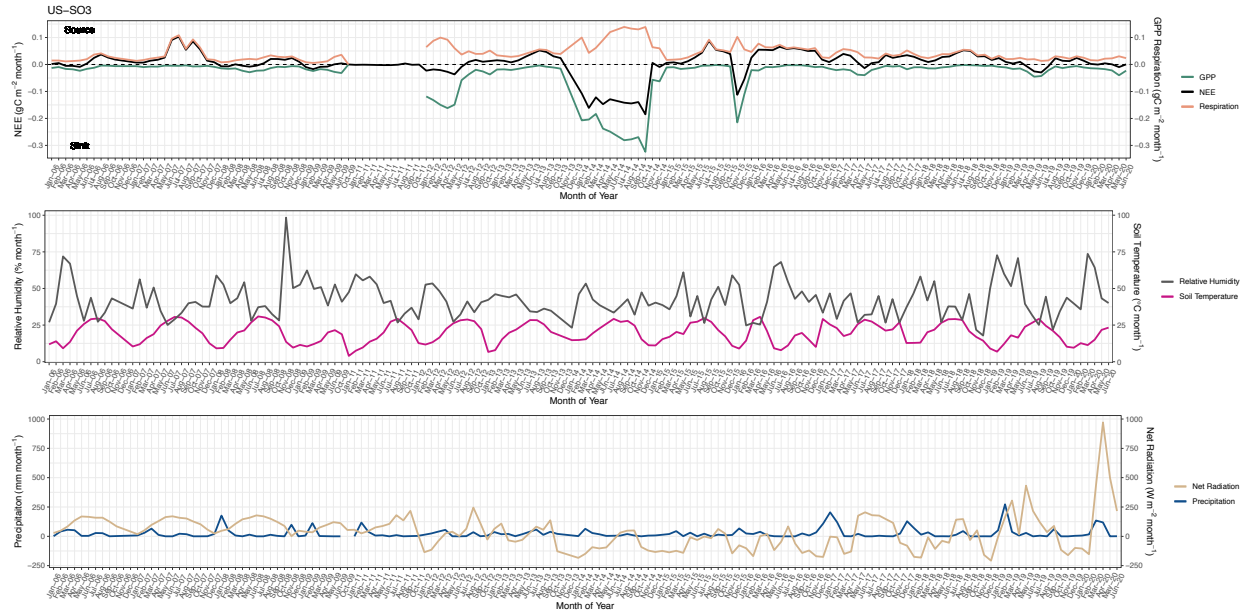


Fig. 3.4 Average monthly net ecosystem exchange (NEE), gross primary productivity (GPP), ecosystem respiration, soil temperature, relative humidity, net radiation, and total monthly precipitation during the hydrological years of 2005 to 2020 collected from US-SO3.

Discussion

Meteorological controls of annual, seasonal, and monthly CO₂ fluxes

The 20-year old twice burned south-facing chaparral stand was an annual source of CO₂ for nine of the fifteen-year study period. The stand released 45 gCm⁻²yr⁻¹ to 830 gCm⁻²yr⁻¹ annually (Fig. 3.2). The chaparral stand acted as a carbon sink for five years sequestering -14 gCm⁻²yr⁻¹ to -1003 gCm⁻²yr⁻¹ (Fig. 3.2). Annual NEE was not significantly affected by the investigated meteorological variables. Seasonal patterns of CO₂ flux were controlled by seasonal variations in soil temperature and relative humidity. Soil temperature and relative humidity were the significant meteorological factors controlling overall seasonal NEE. Increased soil temperature led to an increase in seasonal NEE (reduced carbon sequestration) causing the stand

to release CO₂ to the atmosphere (Fig. 3.3). While a reduction in relative humidity resulted in an increase in NEE (Fig. 3.3). The observed increase in release of CO₂ during periods of elevated soil temperature may be attributed to increased rates of soil respiration as soil respiration has been positively correlated to soil temperature (Tang et al., 2019). Increased soil temperature is often associated with higher rates of soil respiration due to accelerated rates of carbon cycling via autotrophic and heterotrophic respiration (Tang et al., 2019). Similar findings were observed in a mixed deciduous forest and alpine meadow with daily CO₂ flux increasing with increasing soil temperature (Peterjohn et al., 1994 & Saito et al., 2009).

We also observed a strong sensitivity of NEE during the growing season to changes in air temperature, VPD, and relative humidity. Periods of elevated air temperature and low relative humidity and VPD resulted in an increase in NEE during the growing season (Fig. 3.3). The observed increase in NEE may be a result of stomatal closure in response to elevated temperatures and reduced relative humidity and VPD levels to maintain plant water status (Moore et al. 2021). Stomatal closure during periods of elevated air temperature and low relative humidity and VPD decreases photosynthesis rates allowing ecosystem respiration to outpace GPP potentially, explaining periods of increased NEE during the growing season (Moore et al. 2021). The meteorological factor controlling NEE during the dry season was relative humidity. An increase in relative humidity during the dry season resulted in an increase in NEE (Fig. 3.3). Increased relative humidity increases microbial activity and decomposition rates potentially contributing to an increase in ecosystem respiration causing respiration to outpace GPP during the dry season (Stark and Firestone, 1995). The reduction in carbon sequestration during the dry season may also be attributed to the stand's ability to assimilate carbon during periods of increased water stress (Green et al., 2019). Dry conditions reduced evaporation resulting in increases in

temperature leading to vegetation stomatal closure and a decrease in photosynthesis, increasing the ratio of respiration to gross primary productivity (Green et al., 2019). In two temperate deciduous forests similar findings were reported as spring and summer fluxes were controlled by air temperature, soil temperature, and global radiation (Tamrakar et al., 2018).

Monthly variations in CO₂ flux were controlled by changes in soil temperature, net radiation, and relative humidity. Increases in soil temperature and net radiation led to an increase in monthly NEE (Fig. 3.4). A reduction in monthly carbon sequestration during periods of elevated soil temperature and net radiation may have been attributed to partial stomatal closure to prevent water loss reducing growth and productivity (Khairi and Hall, 1970). Periods of low relative humidity leading to a decrease in monthly NEE may partially be due to a decrease in soil moisture and microbial activity reducing respiration and the ratio of ecosystem respiration to GPP (Orchard and Cook, 1983; Fig. 3.4). Low water availability and relative humidity can reduce soil microbial activity by decreasing intracellular water potential limiting enzyme activity and hydration (Stark and Firestone, 1995). A reduction in respiration during periods of low soil moisture and drier conditions was observed in an annual grassland and a community of varying grasses and forbs (Suseela et al., 2012; Xu et al., 2004). With the investigated chaparral stand residing on a south-facing slope it is exposed to more sunlight and warmer and drier conditions (Maren et al., 2015). As expected, seasonal and monthly NEE were significantly affected by increased air temperature, soil temperature, net radiation and reduced relative humidity and VPD resulting in a reduction in carbon sequestration.

Conclusion

From this study, we have identified that CO₂ flux from chaparral ecosystems residing on south-facing slopes are significantly influenced by variations in abiotic factors including temperature, moisture, and radiation. Warmer and drier conditions reduced seasonal and monthly carbon sequestration. Through this research we found that carbon storage by chaparral with a south-facing slope aspect are sensitive to changing climatic conditions and therefore might be expected to be affected by global warming. To our knowledge, our study is one of the first to identify the meteorological controls of NEE on an annual, seasonal, and monthly scale from a south-facing chaparral stand spanning a fifteen-year period. These results highlight the need for further management practices that focus on further examining the meteorological drivers of CO₂ flux on varying temporal scales to quantify the ability of chaparral ecosystems in complex terrains to sequester carbon. Given its extensive geographic range and ability to cover a variety of terrain, semi-arid chaparral ecosystems should be considered in management plans to secure its role in restoring balance to the global carbon budget.

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Author Contributions Statement

Conceptualization of the manuscript and formulation of the experimental design was achieved by Andrea Fenner and Dr. Walter Oechel. Andrea Fenner collected the data, restructured and re-formatted the data, created code to interpret the data, performed the measurements *in situ*, and interpreted the results. Funding acquisition and resources were provided by Dr. Walter Oechel. Andrea Fenner drafted and revised the manuscript under recommendations from the co-author and committee.

References

- Baldocchi, D.D., Hicks, B.B., & Meyers, T.P. (1988). Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology*, 69, 1331-1340.
- Bell, T.W., Menzer, O., Troyo-Diequez, E., & Oechel, W.C. (2012). Carbon dioxide exchange over multiple temporal scales in an arid shrub ecosystem near La Paz, Baja California Sur, Mexico. *Global Change Biology*, 18, 2570-2582.
- Desjardins, R.L. (1972). A study of carbon-dioxide and sensible heat fluxes using the eddy correlation technique. PhD dissertation, Cornell University.
- Green, J.K., Seneviratne, S.I., Berg, A.M., Findell, K.L., Hagemann, S., Lawrence, D.M., & Gentine, P. (2019). Large influence of soil moisture on long-term terrestrial carbon uptake. *Nature*, 565(7740), 476-479.
- Gilmanov, T.G., Johnson, D.A., Saliendra, N.Z., Svejcar, T.J., Angell, R.F., & Clawson, K.L. (2004). Winter CO₂ fluxes above sagebrush-steppe ecosystems in Idaho and Oregon. *Agricultural and Forest Meteorology*, 126, 73-88.
- Jacobsen, A.L., & Pratt, B.R. (2018). Extensive drought-associated plant mortality as an agent of type-conversion in chaparral shrublands. *New Phytologist*, 219, 489-504.
- Khairi, M.M., & Hall, A.E. (1976). Temperature and Humidity Effects on Net Photosynthesis and Transpiration of Citrus. *Physiologia plantarum*, 36(1), 29-34.

- Luo, H., Oechel, W.C., Hastings, S.J., Zulueta, R., Qian, Y., & Kwon, H. (2007). Mature semiarid chaparral ecosystems can be a significant sink of atmospheric carbon dioxide. *Global Change Biology*, 13, 386-396.
- Maren, I.E., Karki, S., Prajapati, C., Yadav, R.K., & Shrestha, B.B. (2015). Facing north or south: Does slope aspect impact forest stand characteristics and soil properties in a semiarid trans-Himalayan valley? *Journal of Arid Environments*, 121, 112-123.
- Miller, P.C., & Poole, D.K. (1980). Partitioning of Solar and Net Irradiance in Mixed and Chamise Chaparral in Southern California. *Oecologia*, 47(3), 328-332.
- Moore, C.E., Meacham-Hensold, K., Lemonnier, P., Slattery, R.A., Benjamin, C., Bernacchi, C.J., Lawson, T., & Cavanagh, A.P. (2021). The effect of increasing temperature on crop photosynthesis: from enzymes to ecosystems. *Journal of Experimental Botany*, 72(8), 2822-2844.
- Ng, E., & Miller, P.C. (1980). Soil Moisture Relations in the Southern California Chaparral. *Ecology*, 61(1), 98-107.
- Orchard, V.A., & Cook, F.J. (1983). Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry*, 15(4), 447-453.
- Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., Bowles, F.P., & Aber, J.D. (1994). Responses of Trace Gas Fluxes and N Availability to Experimentally Elevated Soil Temperatures. *Ecological Applications*, 4(3), 617-625.

- Reichstein, M., Subke, J., Angeli, A.C., & Tenhunen, J.D. (2005). Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biology*, 11, 1754-1767.
- Rundel, P.W., & Parsons, D.J. (1980). Nutrient Changes in Two Chaparral Shrubs Along a Fire-Induced Age Gradient. *American Journal of Botany*, 67(1), 51-58.
- Saito, M., Kato, T., & Tang, Y. (2009). Temperature controls ecosystem CO₂ exchange of an alpine meadow on the northeastern Tibetan Plateau. *Global Change Biology*, 15, 221-228.
- Sha, Z., Bai, Y., Li, R., Lan, H., Zhang, X., Li, J., Liu, X., Chang, S., & Xie, Y. (2022). The global carbon sink potential of terrestrial vegetation can be increased substantially by optimal land management. *Communications earth & environment*, 3(8), 1-10.
- Stark, J.M., & Firestone, M.K. (1995). Mechanisms for Soil Moisture Effects on Activity of Nitrifying Bacteria. *Applied and Environmental Microbiology*, 61(1), 218-221.
- Storey, E.A., Stow, D.A., O'Leary, J.F., Davis, F.W., & Roberts, D.A. (2021). Does short-interval fire inhibit postfire recovery of chaparral across southern California? *Science of the Total Environment*, 751, 142271.
- Suseela, V., Conant, R.T., Wallenstein, M.D., & Dukes, J.S. (2012). Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology*, 18, 336-348.
- Swinbank, W.C. (1951). The measurement of vertical transfer of heat and water vapor by eddies in the lower atmosphere. *Journal of Meteorology*, 8(3), 135.

- Tamrakar, R., Rayment, M.B., Moyano, F., Mund, M., & Knohl, A. (2018). Implications of structural diversity for seasonal and annual carbon dioxide fluxes in two temperate deciduous forests. *Agricultural and Forest Meteorology*, 263, 465-476.
- Tang, J., Bradford, M.A., Carey, J., Crowther, T.W., Machmuller, M.B., Mohan, J.E., & Todd-Brown, K. 2019. Chapter 8 - Temperature sensitivity of soil carbon. *Microbes, Vegetation, Fauna and Soil Biogeochemistry*. 175-208.
- Wang, Y., Zhou, G., & Wang, Y. (2008). Environmental effects on net ecosystem CO₂ exchange at half-hour and month scales over *Stipa krylovii* steppe in northern China. *Agricultural and Forest Meteorology*, 148, 714-722.
- Wutzler, T., Lucas-Moffat, A., Migliavacca, M., Knauer, J., Sickel, K., Sigut, L., Menzer, O., & Reichstein, M. (2018). Basic and extensible post-processing of eddy covariance flux data with REddyProc. *Biogeosciences*, 15, 5015-5030.
- Xu, L., Baldocchi, D.D., & Tang, J. (2004). How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Global Biogeochemical Cycles*, 18(4), 1-10.

Conclusion

The work presented here outlines the importance of understanding the patterns and controls of long-term CO₂ flux through wildfire and drought events in chaparral ecosystems. It also identifies the carbon storage capabilities of old-growth chaparral ecosystems exposed to drought conditions. Changes in fire frequency and rainfall events due to climate change can create variations in long-term CO₂ flux altering carbon sequestration in chaparral ecosystems.

I present evidence that exposure to increased and below normal rainfall can extend post-fire recovery in chaparral leading to a prolonged release of CO₂ for up to eight years post-fire. Altered soil temperature, soil moisture, and microbial community composition post-fire can change decomposition rates affecting long-term carbon source-sink dynamics (Fritze et al., 1994; Imeson et al., 1992; O'Donnell et al., 2009; O'Neill et al., 2002). Low rainfall during drought conditions can extend the rate of carbon removal as microbial activity and the breakdown of biomass and soil organic matter slows (Qu et al., 2023 and Deng et al., 2021). Suppression of gross primary productivity due to below normal rainfall coupled with reduced leaf area as a result of fire-induced mortality of vegetation may also lead to prolonged CO₂ release post-fire (Yu et al., 2022). During periods of abnormally high precipitation a rise in microbial activity and decomposition rates can occur causing ecosystem respiration to outpace GPP and release of CO₂ by the chaparral stand (Orchard and Cook, 1983). I also show that once the chaparral stand recovered, >10 years post-fire, it reverted back to a carbon sink due to its ability to tap into water reserves deep within the soil profile ensuring water demands were met and continued productivity (Luo et al., 2007). Site location may have also attributed to increased carbon sequestration with exportation of carbon from a nearby slope and lateral transport of soil organic carbon into nearby alluvial deposits, lakes, and ponds (Martinez-Mena et al., 2019). This work

highlights the need for further analysis of long-term CO₂ flux measurements through wildfires and drought events to accurately estimate carbon sequestration levels in chaparral ecosystems.

I show that old-growth chaparral ecosystems are not in a carbon neutral state and have the ability to release and sequester atmospheric CO₂. Carbon sequestration in old-growth chaparral ecosystems varies in response to rainfall events. Reduced GPP during periods of low rainfall, increased temperatures, and high light may have caused ecosystem respiration to outpace GPP causing the old-growth chaparral stand to act as a carbon source (Yu et al., 2022). Increased respiration may have also been attributed to periods of abnormally high precipitation levels resulting in an increase in microbial activity and decomposition rates (Orchard and Cook, 1983). Long-term release of CO₂ by the old-growth 178-year-old chaparral stand may be attributed to high autotrophic respiration levels to maintain accumulating biomass (Litvak et al., 2003). I also demonstrate that old-growth chaparral stands are significantly less productive than mature 20-year-old stands. Reduced productivity may be attributed to hydraulic limitation of water transport with increasing shrub height leading to a decrease in photosynthesis, GPP, and sink strength in old-growth chaparral ecosystems (Baret et al., 2018; Bond, 2000; Ryan et al., 2004). This outlines the importance of understanding how stand age affects CO₂ flux in old-growth chaparral ecosystems exposed to multiple drought events. Better understanding the carbon source-sink dynamics of old-growth chaparral ecosystems can help determine the role old-growth ecosystems play in restoring balance to the global carbon budget.

Finally, I identify the source-sink strength of a twice burned south facing ~20-year-old chaparral ecosystem and the annual, seasonal, and monthly meteorological controls of CO₂ flux. The chaparral stand was a source of CO₂ for nine of the fifteen-year study period and a carbon sink for five years. Seasonal patterns of CO₂ flux were controlled by increases in soil

temperature and a reduction in relative humidity. Growing season NEE was controlled by changes in air temperature, VPD, and relative humidity. Stomatal closure in response to increased temperatures and reduced relative humidity and VPD may have resulted in reduced GPP to maintain plant water status (Moore et al. 2021). Dry season NEE was controlled by relative humidity. An increase in microbial activity and decomposition rates due to increased relative humidity may explain the release of CO₂ by the chaparral stand during the dry season (Stark and Firestone, 1995). Monthly drivers of CO₂ flux were soil temperature, net radiation, and relative humidity. Reduced monthly carbon sequestration during periods of elevated soil temperature and net radiation may be attributed to reduced productivity due to stomatal closure (Khairi and Hall, 1970). A decrease in monthly NEE during periods of low relative humidity may be a result of reduced soil moisture and microbial activity causing GPP to outpace ecosystem respiration (Orchard and Cook, 1983). Findings from this work identified that carbon storage by chaparral with a south-facing slope aspect are sensitive to variations in abiotic factors including temperature, moisture, and radiation which are expected to continue to change due to climate change. This identifies the need to further examine the meteorological drivers of CO₂ flux on varying temporal scales to quantify the ability of chaparral ecosystems in complex terrains to store carbon.

With chaparral being the most extensive biotic community in California covering over 13 million acres and 13% of total land area they remain underrepresented in climate models. The source of variations in long-term CO₂ flux data through extreme weather events also remains under investigated (Norton et al., 2006; Luo et al., 2007). Failure to consider how CO₂ flux over multiple decades varies through abnormal fire and drought regimes can result in an inaccurate assessment of carbon sequestration by varying-aged chaparral ecosystems. This work addresses

these knowledge gaps regarding long-term source-sink dynamics in chaparral ecosystems exposed to fire and drought and can provide the framework for future research. Additional research can be done to further identify how fire and drought directly affect CO₂ flux in chaparral ecosystems. This work offers a significant contribution to understanding the patterns and controls of long-term CO₂ flux measurements from chamise-dominated chaparral ecosystems through fire and drought events. A deeper understanding of how extreme weather events directly affect carbon sequestration in chaparral ecosystems will help to identify their ability to mitigate rising atmospheric CO₂.

References

- Baret, A., Pepin, S., & Pothier, D. (2018). Hydraulic limitations in dominant trees as a contributing mechanism to the age-related growth decline of boreal forest stands. *Forest Ecology and Management*, 427, 135-142.
- Bond, B.J. (2000). Age-related changes in photosynthesis of woody plants. *Trends in plant science Reviews*, 5(8), 349-353.
- Deng, L., Peng, C., Kim, D., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shangguan, Z., & Kuzyakov, Y. (2021). Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. *Earth-Science Reviews*, 214, 103501.
- Fritze, H., Smolader, A., Levula, T., Kitunen, V., & Malkonen, E. (1994). Wood-ash fertilization and fire treatments in a Scots pine forest stand: Effects on the organic layer, microbial biomass, and microbial activity.
- Hanan, E.J., Tague, C., & Schimel, J.P. (2017). Nitrogen cycling and export in California chaparral: the role of climate in shaping ecosystem responses to fire. *Ecological Monographs*, 87(1), 76-90.
- Imeson, A.C., Verstraten, J.M., van Mulligen, E.J., & Sevink, J. (1992). The effects of fire and water repellency on infiltration and runoff under Mediterranean type forest. *Catena*, 19(3-4), 345-361.
- Khairi, M.M, & Hall, A.E. (1976). Temperature and Humidity Effects on Net Photosynthesis and Transpiration of Citrus. *Physiologia plantarum*, 36(1), 29-34.

- Litvak, M., Miller, S., Wofsy, S.C., & Goulden, M. 2003. Effect of stand age on whole ecosystem CO₂ exchange in the Canadian boreal forest. *Journal of Geophysical Research*. 108 (D3), 8225.
- Luo, H., Oechel, W.C., Hastings, S.J., Zulueta, R., Qian, Y., & Kwon, H. (2007). Mature semiarid chaparral ecosystems can be a significant sink of atmospheric carbon dioxide. *Global Change Biology*, 13, 386-396.
- Martinez-Mena, M., Almagro, M., Garcia-Franco, N., de Vente, J., Garcia, E., & Boix-Fayos, C. (2019). Fluvial sedimentary deposits as carbon sinks: organic carbon pools and stabilization mechanisms across a Mediterranean catchment. *Biogeosciences*, 16, 1035-1051.
- Moore, C.E., Meacham-Hensold, K., Lemonnier, P., Slattery, R.A., Benjamin, C., Bernacchi, C.J., Lawson, T., & Cavanagh, A.P. (2021). The effect of increasing temperature on crop photosynthesis: from enzymes to ecosystems. *Journal of Experimental Botany*, 72(8), 2822-2844.
- Norton, U., Horwath, W.R., & Norton, J.B. (2006). Fire Frequency Effects On Greenhouse Gas Emissions and Belowground C and N Processes in Chaparral Shrubland. *EOS*, 87(52), 593-595.
- O'Donnell, J.A., Turetsky, M.R., Harden, J.W., Manies, K.L., Pruet, L.E., Shetler, G., & Neff, J.C. (2009). Interactive Effects of Fire, Soil Climate, and Moss on CO₂ Fluxes in Black Spruce Ecosystems of Interior Alaska. *Ecosystems*, 12, 57-72.

- O'Neill, K.P., Kasischke, E.S., & Richter, D.D. (2002). Environmental controls on soil CO₂ flux following fire in black spruce, white spruce, and aspen stands of interior Alaska. *Canadian Journal of Forest Research*, 32, 1525-1541.
- Orchard, V.A., & Cook, F.J. (1983). Relationship between soil respiration and soil moisture. *Soil Biology and Biochemistry*, 15(4), 447-453.
- Qu, Q., Wang, Z., Gan, Q., Liu, R., & Xu, H. (2023). Impact of drought on soil microbial biomass and extracellular enzyme activity. *Frontiers in Plant Science*, 14:1221288.
- Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P., & Senock, R.S. 2004. An Experimental Test of the Causes of Forest Growth Decline with Stand Age. *Ecology Monographs*, 74(3), 393-414.
- Stark, J.M., & Firestone, M.K. (1995). Mechanisms for Soil Moisture Effects on Activity of Nitrifying Bacteria. *Applied and Environmental Microbiology*, 61(1), 218-221.
- Yu, X., Orth, R., Reichstein, M., Bahn, M., Klosterhalfen, A., Knohl, A., Koepsch, F., Migliavacca, M., Mund, M., Nelson, J., Stocker, B.D., Walther, S., & Bastos, A. (2022). Contrasting drought legacy effects on gross primary productivity in a mixed versus pure beech forest. *Biogeosciences*, 19, 4315-4329.