Effects of Soil Temperature, Soil Water Content, and Rainfall on Soil Respiration and its Contribution to Ecosystem Respiration in Chaparral Shrublands

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Abstract

Soil respiration (Rs) is the second largest carbon dioxide (CO2) flux in terrestrial ecosystems, and it provides an average of 30-90% to ecosystem respiration (Reco). In semi-arid ecosystems, there is a considerable need to expand our knowledge on Rs trends. Chaparral, a semi-arid Mediterranean plant community in California, has the potential to act a sink, which is an essential ecosystem to mitigate climate change. However, Rs responses to meteorological variables remain uncertain in these regions and no studies have quantified how much Rs attributes to Reco in chaparral shrublands. Our study analyzed continuous field Rs data in chaparral shrublands, the effects of soil temperature (Ts) and soil water content (SWC), and its contribution to Reco.

Our study incorporated long-term Rs data collected by automated chambers and net ecosystem exchange (NEE) measurements collected by the eddy covariance technique from June 2020 to May 2021 in a chaparral stand in San Diego, California. The results suggest SWC was the strongest driver of Rs, whereas Ts was only a significant control when soil was wet, and temperatures were mild. Monthly Rs/Reco ratios, which described the contribution of Rs to Reco, were highest during the January and February, likely due to the reduced aboveground respiration. Whereas Rs/Reco ratios were lowest when SWC was the driest and Rs was reduced. The results from this study improve our understanding in Rs response to climatic conditions and emphasize the importance of Rs by quantifying its contribution to Reco in chaparral shrublands.

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Key Points:

- Soil respiration was primarily driven by soil water content year round.
- Soil temperature was only a significant control of soil respiration when soil water content was above 6%.
- Soil respiration contributed a substantial percentage to ecosystem respiration, being the highest during early winter and lowest during fall.

Abstract

Soil respiration (Rs) is the second largest carbon dioxide (CO_2) flux in terrestrial ecosystems, and it provides an average of 30-90% to ecosystem respiration (Reco). In semi-arid ecosystems, there is a considerable need to expand our knowledge on Rs trends. Chaparral, a semi-arid Mediterranean plant community in California, has the potential to act a sink, which is an essential ecosystem to mitigate climate change. However, Rs responses to meteorological variables remain uncertain in these regions and no studies have quantified how much Rs attributes to Reco in chaparral shrublands. Our study analyzed continuous field Rs data in chaparral shrublands, the effects of soil temperature (Ts) and soil water content (SWC), and its contribution to Reco.

Our study incorporated long-term Rs data collected by automated chambers and net ecosystem exchange (NEE) measurements collected by the eddy covariance technique from June 2020 to May 2021 in a chaparral stand in San Diego, California. The results suggest SWC was the strongest driver of Rs, whereas Ts was only a significant control when soil was wet, and temperatures were mild. Monthly Rs/Reco ratios, which described the contribution of Rs to Reco, were highest during the January and February, likely due to the reduced aboveground respiration. Whereas Rs/Reco ratios were lowest when SWC was the driest and Rs was reduced. The results from this study improve our understanding in Rs response to climatic conditions and emphasize the importance of Rs by quantifying its contribution to Reco in chaparral shrublands.

1 Introduction

Atmospheric carbon dioxide (CO_2) concentrations have increased since pre-industrial times because of anthropocentric activities. Human development, deforestation, agriculture, and the burning of fossil fuels have dramatically impacted the global carbon cycle (Intergovernmental Panel on Climate Change [IPCC], 2022). Soil is an important terrestrial carbon (C) reservoir, storing 1500 to 2500 PgC, which is twice as much carbon as in the atmosphere (Bispo et al., 2017; Scharlemann et al., 2014). Therefore, soil C storage could potentially offset anthropogenic CO_2 emissions, whereas soil C emitted to the atmosphere could exacerbate climate change (Rustad et al., 2000). The process of CO_2 release from soil to the atmosphere is referred to as soil respiration (Rs), which includes autotrophic (roots and rhizosphere) and heterotrophic (decomposing microbes) respiration (Hanson et al., 2000; Hogberg & Read, 2006). Rs is the second largest CO_2 flux (after gross photosynthesis) between terrestrial ecosystems and the atmosphere (Brændholt et al., 2017), supplying 30-90% to ecosystem respiration (Reco) and producing approximately 20-40% of total annual emitted CO_2 (Raich et al., 2002; Schimel et al., 2001). Moreover, small changes in Rs can significantly affect Reco, leading to changes in global CO_2 emissions (Ryan & Law, 2005; Sun, Wang, et al., 2018).

Quantifying spatial and temporal variability in Rs can be challenging to achieve (Phillips et al., 2016). Soil is highly heterogeneous due to the variable nutrients, minerals, organic compounds, and microorganisms it contains. These soil segments, and their interactions with biological mechanisms, can drive different responses to meteorological conditions, resulting in an immense variability of Rs (Rubio & Detto, 2017). Therefore, it is necessary to make studies on Rs across various ecosystems to develop precise global carbon budget estimations (Zeng et al., 2018). While there are extensive studies on Rs in regions with wetlands, peatlands, and permafrost (Davidson & Janssens, 2006; Scharlemann et al., 2014), there is a considerable lack of knowledge on Rs in semi-arid ecosystems (Schimel, 2010), how it responds to climatic changes (Anjileli et al., 2019; Zhong et al., 2016), and its contribution to Reco (Baldocchi et al., 2001; Jian et al., 2021). As they cover ~40% of global terrestrial surface and 24% of global soil organic carbon, arid and semi-arid ecosystems play an important role in global terrestrial cycling (Ahlström et al., 2015). And, given their vulnerability to projected droughts and rising temperatures, semi-arid ecosystems contribute to inter-annual variation in the global C cycle (Poulter et al., 2014). Consequently, as Rs is an important component of the terrestrial C cycle, it is specifically important to study Rs in semi-arid ecosystems to make better predictions of potential effects of climate change.

In many regions where water is non-limiting, soil temperature (Ts) is the strongest driver of Rs, which has a positive exponential or linear response to Ts (Luo et al., 2001; Zhang et al., 2015). However, in semi-arid ecosystems, Rs response to Ts is highly influenced by soil water content (SWC) (Muñoz-Rojas et al., 2016). When conditions are extremely dry, Rs response to Ts may be non-linear or non-significant (Carbone et al., 2011; Meena et al., 2020) since low water availability can limit C substrate and inhibit microbial activity (Moyano et al., 2013). Nevertheless, increasing SWC at higher temperatures can result in high Rs trends (Anjileli et al., 2019). Also, big pulses of Rs can occur when SWC increases, most likely due to rainfall events. Rainwater can push out the CO_2 accumulated inside soil pore spaces and stimulate root and microbial activity (usually dormant during dry periods) (Yan et al., 2014). Though Rs pulses after rainfall events may be short, it is important to analyze the aftereffects. Rs response to rainfall varies according to the season and can depend on Ts and SWC changes during rain events (Zhu et al., 2020). Thus, it is crucial to understand the seasonal Rs responses to rainfall, especially in semi-arid ecosystems, where we can expect higher variability in the intensity and frequency of rainfall (Diffenbaugh et al., 2008), as well as high seasonal Ts variation.

Besides environmental controls, spatial variations can also influence rates of Rs, especially in semi-arid shrublands, where landscapes consist of patchy vegetation with bare soil inter-canopy spaces (Loik et al., 2004). Hence, it is crucial to account for soil spatial variability to quantify Rs at a specific region. Using Rs field data representing the spatial heterogeneity can provide accurate proportions of Rs to Reco at a local scale. Reco can be determined with net ecosystem exchange (NEE) continuous data collected with a stationary tower using the eddy-covariance technique (Goulden et al., 1996). While, long-term in-situ Rs can be collected with automated chambers, which may be placed under the canopies of different plant species and inter-canopy spaces. Moreover, Rs can be upscaled accordingly to the land cover percentages of different soil microsites (Barron-Gafford et al., 2011; Qubaja et al., 2020). The upscaling of Rs can provide high spatial-temporal data and be compared with Reco to obtain accurate Rs/Reco ratios.

Within semi-arid ecosystems, the Mediterranean-type climate can be found worldwide, around the Mediterranean Basin in southern Europe, central Chile, California and Baja California, and South Africa. These regions are hotspots for diversity (Rundel et al., 2016). However, due to their mild weather and proximity to coasts, human activity often affects them, especially through agricultural intensification and urban development (Underwood et al., 2009). In California, chaparral is a native semi-arid Mediterranean plant community able to withstand periodic fires, extremely high temperatures, and droughts (Keeley & Safford, 2016). Chaparral makes up 9% of wildland vegetation in California, and 73% is covered by shrubs. Half of this chaparral is distributed in Southern California, with the largest area in San Diego County (Parker et al., 2016). Chaparral is particularly vulnerable to increased housing development (Syphard et al., 2018), altered fire regimes (Keeley & Safford, 2016), and conversion of native shrubs to non-native grasses (Hayhoe et al., 2004; Lenihan et al., 2003). These threats may reduce essential ecosystems services by chaparral, water provision (Riggan et al., 1986), habitat for wildlife (Quinn & Keely, 2006), and pollination (Kremen et al., 2004). Additionally, chaparral shrublands can store significant amounts of carbon above and belowground (Padgett & Allen, 1999; Pratt et al., 2012), and act a significant sink of CO_2 (Luo et al., 2007), which is an important ecosystem service to mitigate climate change. However, we need to understand the role of Rs and its responses to environmental variables in chaparral to gain knowledge about the C balance in this region and make future management recommendations that could enhance climate change mitigation services.

In this study, we collected hourly measurements of in-situ Rs by automated chambers for a year under the canopies of native chaparral shrubs *Adenostoma sparsifolium* and *Adenostoma fasciculatum*, and inter-canopy bare soil spaces. Continuous Ts (at the surface) and SWC (in the top 30 cm of soil) measurements were also collected for each chamber. We averaged Rs, Ts, and SWC and upscaled them using the percent cover of shrub and bare soil. We also incorporated Reco estimates collected by an eddy covariance tower on site and compared them with our upscaled Rs to improve our understanding of the seasonal variation of Rs/Reco ratios. The objectives of this study were to (1) upscale Rs accordingly to the shrub species and inter-canopy percentages of a chaparral stand in San Diego, (2) determine the controls of Ts, SWC, and rainfall on Rs, and (3) estimate the contribution of Rs to Reco.

2 Materials and Methods

2.1 Study Site and Species

This study was conducted in a ~ 20-year old chaparral stand burned by a fire in 2003, located at Sky Oaks Field Station (33°23′N, 116°38′W, 1420 m above sea level) in Southern California managed by San Diego State University. This region is characterized by a semi-arid Mediterranean climate with cold, wet winters and hot, dry summers. Mean temperature falls between 9.6°C in January and 25.4°C in July. Most precipitation events occur between November and April with a mean annual precipitation of 419 mm between the years 2015-2019. Moderate snow events may occur for a few days during winter, and occasional warm, arid Santa Ana winds may blow during late summer and fall. The soil in this field study is identified as loamy sand, Ultic Haploxeroll and has bulk density of 1.04g cm-3, with 32% rocks (Lipson et al., 2005).

This chaparral study stand is dominated by native shrubs Adenostoma fasciculatum H & A. (chamise) and Adenostoma sparsifolium Torr. (redshank). Both shrubs are drought tolerant and frost resistant, but chamise and redshank differ in height ranges (0.6-3.5 m and 2-6 m respectively) (Zammit & Zedler, 1993). Chamise, like many other chaparral plants, flowers in spring following the wet season, while redshank flowers between late July and early August (Wiens et al., 2012). Both shrubs have deep roots and can resprout after a fire (Parker, 1984).

2.2 Soil Respiration Measurements

Microsites were selected under three shrub canopies of redshank three shrub canopies of chamise and three inter-canopy spaces (bare) between shrubs. Nine polyvinyl chloride soil collars, each with a 20-cm diameter and 12-cm height, were inserted into the soil surface at each selected microsite. Soil collars were placed approximately 2 to 3 cm above soil surface. To avoid disruption effects caused by the installation, all collars were placed at least a day prior making measurements.

Long-term soil respiration measurements were collected with a LI-COR 8100 soil gas flux analyzer, nine LI-COR 8100-01 automated chambers, and one LI-COR 8150 multiplexed chamber array system (LI-COR Inc., Lincoln, Nebraska, USA). Soil respiration was measured every hour at each chamber from June 2020 to May 2021. The chambers mechanically closed and sealed the soil collars to measure soil respiration at every sampling point. There was a 30 sec dead band after each chamber closed to allow the pressure inside to stabilize. After the dead band period, soil respiration was measured every 10 sec for 2 minutes. After the 2 minutes, the chamber opened and remained opened until the next measurement in order to avoid modifying the ambient soil conditions, such as sunlight, precipitation, and litter exposure.

Concurrent with the long-term Rs measurements, Ts and SWC were measured with soil sensors (CS650, Campbell Scientific Inc., Logan, Utah, USA) installed next to each chamber. Ts was measured at 0 cm and the SWC was measured as an average of 0-30 cm. Both Ts and SWC data were continuously collected every 30 minutes and stored using a datalogger (CR1000, Campbell Scientific Inc.).

Upscaling of the collar measurements (Rs, Ts, and SWC) to the footprint covered by the EC tower was done by multiplying the fractional areas (Ø) of the microsites (redshank, chamise, and bare) by the average of the three replicates of each (Barron-Gafford et al., 2011; Qubaja et al., 2020):

$$Rs = Rs_{redshank} * \emptyset_{redshank} + Rs_{chamise} * \emptyset_{chamise} + Rs_{bare} * \emptyset_{bare}, \quad (2.1)$$

$$Ts = Ts_{redshank} * \emptyset_{redshank} + Ts_{chamise} * \emptyset_{chamise} + Ts_{bare} * \emptyset_{bare}, \quad (2.2)$$

$$SWC = SWC_{redshank} * \emptyset_{redshank} + SWC_{chamise} * \emptyset_{chamise} + SWC_{bare} * \emptyset_{bare}, \quad (2.3)$$

The percent cover of each microsite was determined by classifying unmated aerial systems (UAS) images of the research site. Survey flights using a DJI Phantom 4 Advanced Quadcopter with a FC6310 camera captured nadir, oblique and 20° images. The images were processed with ENVI 5.5.3 and classified into redshank, chamise, and bare with the maximum likelihood classification (**Figure 1).**

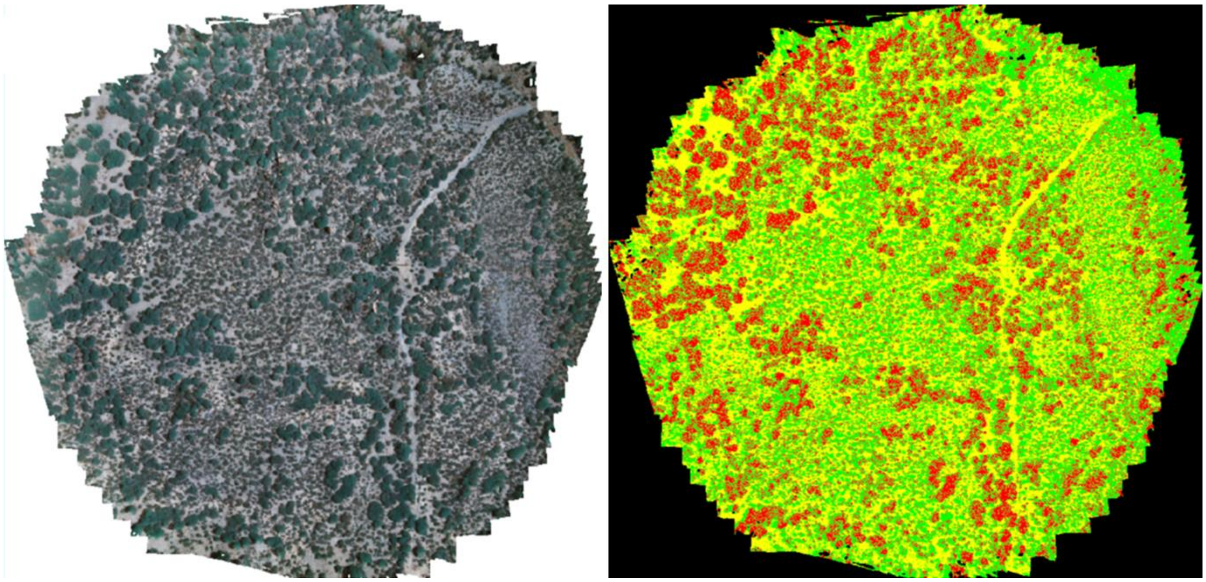

Figure 1. Chaparral stand before and after supervised maximum classification. Image was captured by unmanned aerial system.

2.3 Soil Respiration Processing

Soil CO_2 fluxes were calculated with exponential curves using Licor 8100 FileViewer software (Version 3.00, LI-COR Inc. 2004-2006) for each measurement. Outliers were removed if the coefficient of variation was less than 2 or if the exponential R^2 fit was less than 97%. On occasion, there were power losses or equipment malfunctioning on site resulting in gaps in Rs. Only data when at least two chambers for each microsite were functioning was included. When one chamber for each microsite did not function, it was filled with the average of the other two chambers (Mauritz & Lipson, 2021).

2.4 EC Measurements and Flux Partitioning

An EC tower located at our site collected terrestrial-atmosphere gas exchange at ecosystem level (Goulden et al.,1996). The instruments of the EC technique included an open-path infrared gas (CO_2/H_2O) analyzer (LI-7500, Li-COR Inc.) and a 3-axis ultrasonic anemometer (WindMaster Pro, Gill Instruments Ltd, Hampshire, England). The instruments were installed at 4.5 m above ground and 2.5 m above mean height of vegetation. Half-hourly measurements of raw data were collected in a datalogger (CR1000X23X, Campbell Scientific Inc.). NEE was calculated from the raw data using the EddyPro data processing software (LI-COR Inc., USA). Two corrections were applied for the anemometer, including the “w-boost” correction to fix the bug which causes underestimation of vertical wind speed and “angle of attack” correction due to the imperfect sine and cosine response using units affected by “w-boost” bug (Nakai & Shimoyama, 2012).

Data quality control procedures included the removal of outlier NEE measurements when they were less than -15 or greater than 15 CO_2 µmol m^2 s^{-1}. Spikes can often occur in EC measurements due to the quick changes in air turbulence, sensor interference, or weather conditions. Half-hourly NEE measurements were determined as a spike following the methodologies in Papale et al. (2006), with a threshold value of 5.5. Data processing followed the ReddyProc package in R (https://cran.rproject.org/web/packages/REddyProc/index.html). Friction velocity thresholds were as determined seasonally using ReddyProc, following Reichstein et al. (2005). Observations at friction velocities less than the seasonal threshold were removed prior to gap-filling and partitioning. Gap-filling was conducted using a random forest model with a maximum time period of 1.5 months (Breiman, 2001) with environmental predictors, including: vapor-pressure deficit (VPD), air temperature (HMP45C, Vaisala Inc., Helsinki, Finland), soil moisture (CS615, Campbell Scientific Inc.), incoming global radiation (LI-200R Pyranometer, Li-COR Inc.), photosynthetic active radiation (PAR; LI-190SB, Li-COR Inc.), net radiation (Q*7.1, Radiation Energy Balance Systems (REBS) Inc., Seattle, WA, USA), wind speed and wind direction (RM Young Wind Sentry, R. M. Young Company, Traverse, MI, USA). NEE was partitioned into GPP and Reco by extrapolating night-time data based on temperature similar to that done in Reichstein et al. (2005). Additionally, precipitation was collected as 30-min averages with a tipping bucket rain gauge connected to the EC tower (TR-525M, Li-COR Inc.).

2.5 Models with Soil Temperature and Soil Water Content

When analyzing Rs as a univariate function of Ts, the exponential formula was used:

$$Rs = e^{\beta_0 + \beta_1 Ts}, \tag{2.4}$$

The single effect of Ts and SWC, respectively, was analyzed with the quadratic formula (Liu et al., 2018):

$$Rs = \beta_0 + \beta_1 Ts + \beta_2 Ts^2 \text{ or } \beta_0 + \beta_1 SWC + \beta_2 SWC^2, \tag{2.5}$$

Moreover, due to the irregularity of the data, the effect of SWC was also analyzed with the cubic polynomial formula (Sun, Zhao, et al., 2018):

$$Rs = \beta_0 + \beta_1 SWC + \beta_2 SWC^2 + \beta_3 SWC^3, \tag{2.6}$$

In all formulas, β represents the parameters of Ts and SWC.

2.6 Soil Respiration Before and During Rainfall

The relative change of soil respiration as a response to rainfall was determined following the formula similar to Zhu et al. (2020), where Rsbefore and Rsduring represent Rs before and during rainfall days, respectively:

$$\text{Relative change of soil respiration} = (Rs_{during} - Rs_{before}) / Rs_{before}, \tag{2.7}$$

The daily average of upscaled soil respiration was used for the day prior and during rainfall events.

2.7 Statistical Analyses

All statistical analyses were carried out in open-source statistical software R version 4.1.1 (R Core Team, 2021). Spatial heterogeneity between the three chamber replicates of each microsite was considered weak if CV % ≤10, moderate if 10% CV % ≤ 100%, and high if CV %

> 100%. Seasons were grouped based on the change of temperature and rainfall resulting in two seasons being considered: dry (Jun 1, 2020 – Nov 8, 2020) and wet (Nov 9, 2020 – May 21, 2021). 5-day averages were calculated to diminish the daily variability of upscaled Rs and to analyze the effects of Ts and SWC. The model fits of Rs response to Ts and SWC (including linear models and equations 2.4, 2.5 and 2.6) were compared and the best fit was selected based on reducing the Akaike information criterion (AIC) (Guthery et al., 2003). Differences in daily averages of Rs before and during rainfall were determined with linear mixed models (lme4 package in R: Bates et al., 2015) with date of rainfall event as random effect and timing of rainfall (before or during) as a fixed effect. To observe the seasonal variation of Rs/Reco ratios (the contribution of Rs to ecosystem respiration), monthly means of Rs were divided by Reco. 5-day averages of Rs/Reco ratios were calculated to understand the effects of SWC, Ts, and air temperature. Only days with observed NEE data available were included to compare Reco to Rs and no gap-filled data was included in these statistical analyses.

3 Results

3.1 Spatial Variations and Upscaling Collar Measurements

The spatial variations in collar measurements across microsites (redshank, chamise, and bare) are presented in Table S1. Overall, the collar measurements showed weak to moderate spatial variability, with Rs lowest in bare soil and higher below plant canopies, with redshank microsites having slightly higher Rs than chamise. To upscale collar measurements of Rs, Ts, and SWC, we followed formulas 2.1, 2.2, and 2.3, respectively. The three replicates of bare, chamise-dominated, and redshank-dominated were averaged and multiplied by the percentage of land cover being 47.1%, 24%, and 28.9%, respectively. These upscaled estimates are in Table S1.

3.2 Seasonal Patterns of Rs

Upscaled mean annual Rs was 1.30 ± 0.04 g C $m^{-2}d^{-1}$, ranging from the lowest in October (0.53 ± 0.03 g C $m^{-2}d^{-1}$), and the highest in April (2.27 ± 0.07 g C $m^{-2}d^{-1}$). SWC was highest during March (17.91 ± 0.45%) and lowest during October (4.69 ± 0.02%). Ts peaked during July and August, averaging 26.1 ± 0.37 and 27.1 ± 0.50 °C respectively, and it was the coldest during January (6.01 ± 5.93 °C). Mean annual air temperature was 16.9 °C, and it followed the same trends as Ts; however, it seemed air cooled faster than soil during the dry season. Few rainfall events happened during the dry season, whereas frequent and intense rainfall fell during the wet season, resulting in 87% of the 210 mm total annual precipitation (Figure 2).

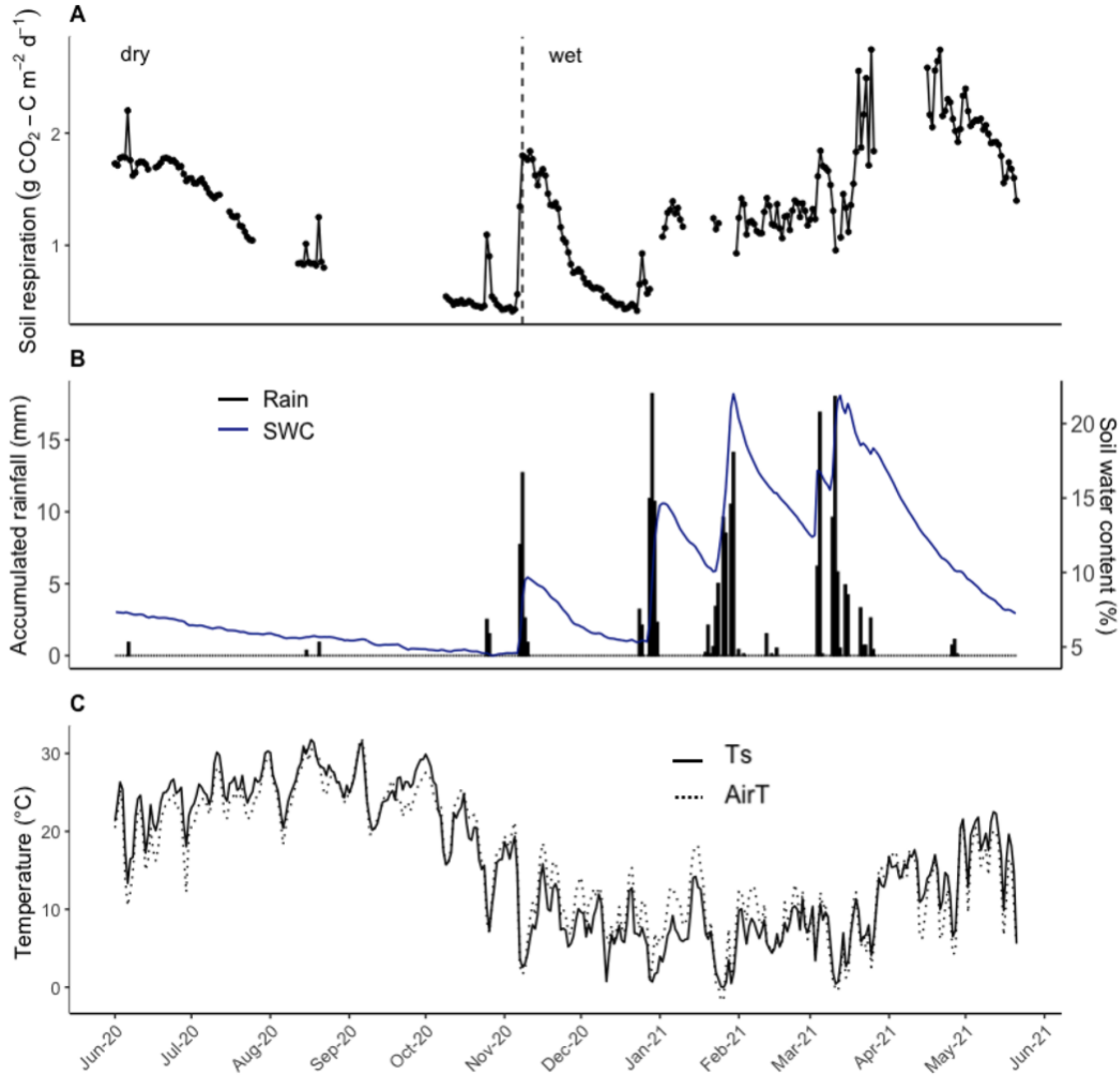

Figure 2. Daily averages of (a) Rs with dotted vertical line indicating each season, (b) rainfall and SWC, and (c) soil and air temperature.

3.3 Effect of Ts and SWC under Different Thresholds

Because Ts effects on Rs depend on SWC, the effect of Ts as a single-factor was investigated by grouping the data by SWC levels from wet to dry: >9%, 6 – 9%, and 4 – 6%. Under moist conditions (>9% SWC) Ts had a strong positive linear (R^2=0.43, p<0.01) and an exponential effect (R^2=0.43, p<0.01) on Rs (Figure 3a and Table S2). Under moderate SWC (6-9%), Ts was found to be significant with the best fit using a quadratic function (R^2=0.83, p<0.0001). Importantly, under the driest conditions (4-6% SWC), there was no effect of Ts on Rs. Conversely, the effect of SWC as a single-factor was visualized by grouping the data by Ts levels from hottest to coldest: >20 °C, <=20 – >10 °C, and <=10 °C. SWC was found have significant positive linear and non-linear effects on Rs at all Ts levels (R^2=0.74-0.99) (Figure 3b and Table S3), and there was no difference among Ts levels when SWC was very low.

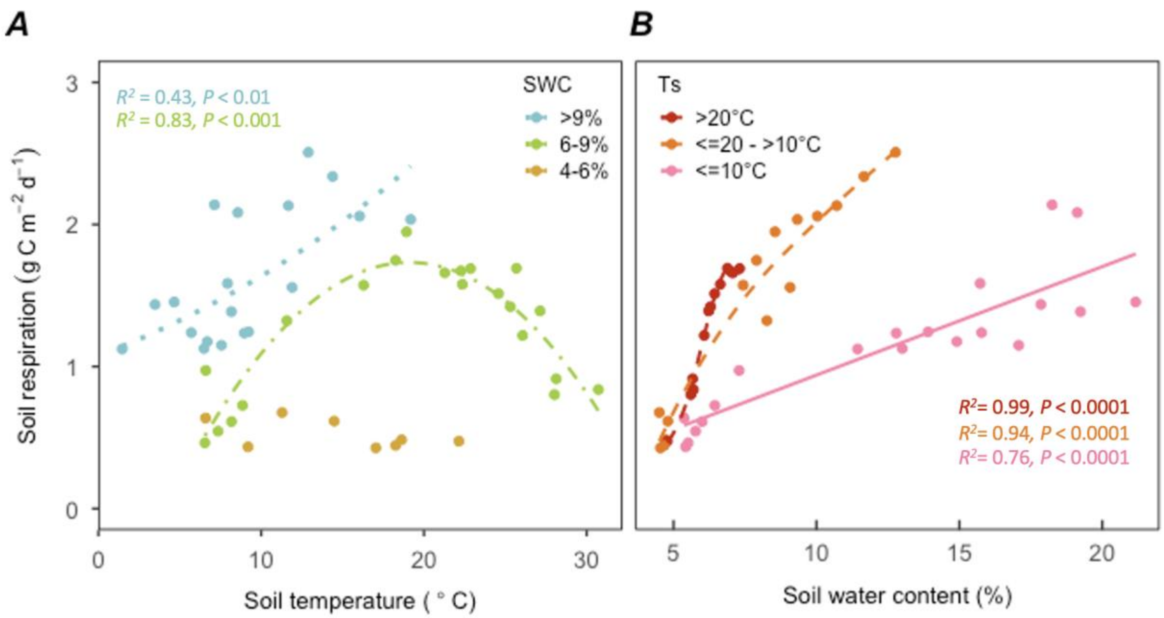

Figure 3. 5-day means of Rs predicted by (a) Ts grouped by SWC levels and, (b) SWC grouped by Ts levels. Only the best significant relationships were included accordingly to the AIC values. Solid, dotted, dot-dashed, and dashed lines represent linear, exponential, quadratic, and cubic.

3.4 Diurnal Rs Response to Ts

There was as significant response of diurnal Rs to Ts that varied by month (Table S4). The slopes of diurnal Rs responses to Ts were higher during wetter months, except for December, than during drier months (Figure 4). During most of the months in the dry season, Ts explained 51-89% of total variation in diurnal Rs, except during June, when Ts did not have a significant effect. However, during months in the wet season, Ts explained 82-98% of total variation in diurnal Rs, with generally stronger effects of Ts on Rs, illustrated by stepper slopes during the wet season in Figure 4.

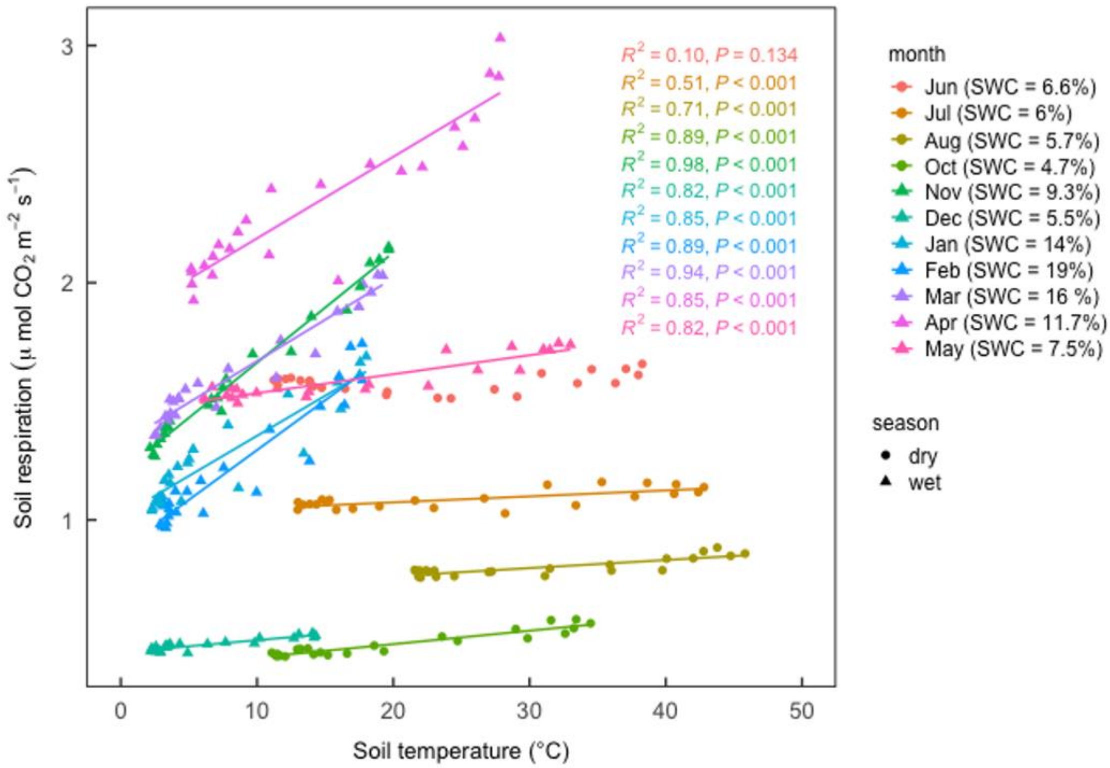

Figure 4. Diurnal relationship between Rs and Ts during 5-day periods for each month (except September). Colors and shape denote month and season, respectively. Solid lines represent significant linear effect (<0.05) of Ts on Rs. Only days without rainfall were included. The 5-day periods for each month were: Jun 26 – 30, 2020, Jul 18 – 22, 2020, Aug 14 – 18, 2020, Oct 10 – 14, 2020, Nov 11 – 15, 2020, Dec 12 – 16, 2020, Jan 4 – 8, 2021, Feb 1 – 5, 2021, Mar 5 – 9, 2021, Apr 17 – 21, 2021, and May 16 – 20, 2021. The SWC% averages for the 5-day periods were included inside parentheses.

3.5 Rs during Rainfall

SWC as a single factor explained 81% of total variation in Rs during days with rainfall in the dry season but had no significant effect in the wet season (Figure 5a). No effect of Ts on Rs during days with rainfall was found in the dry and wet season. Accumulated rainfall accounted for 74% of total variation in Rs during days with rainfall in the dry season, while no effect was found in the wet season (Figure 5b). Daily means of Rs during rainfall were significantly higher than before rainfall in the dry season (Table S5). Whereas there was no significant difference in Rs between before and during rainfall in the wet season (Figure S1 and Table S5). Moreover, the relative change of daily Rs during rainfall compared to before rainfall was consistently positive in the dry season, while it varied from negative to positive in the wet season (Figure 6).

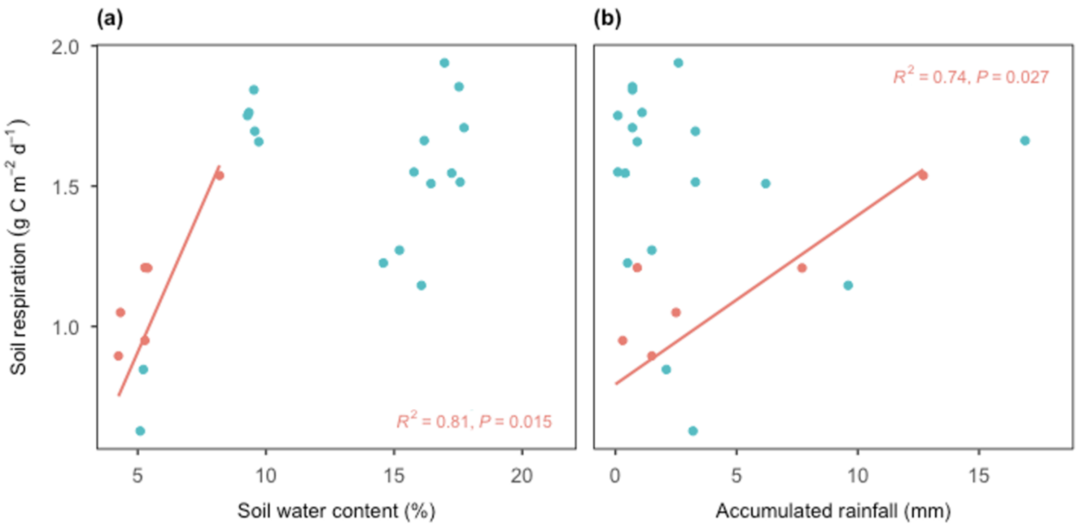

Figure 5. Daily means of Rs during rainfall responding to (a) soil water content and (b) accumulated rainfall. Colors denote season. Solid lines represent significant linear relationships (<0.05).

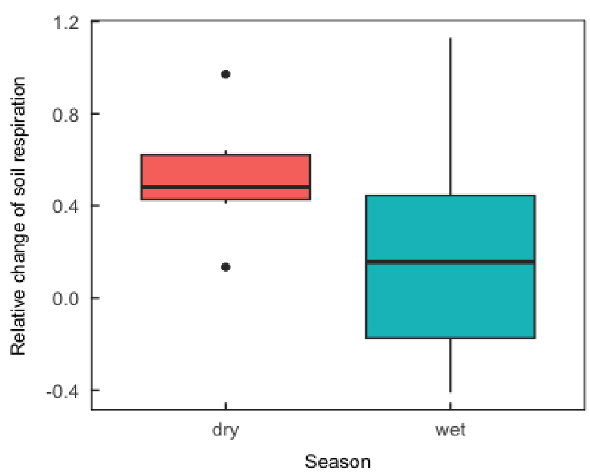

Figure 6. Relative change of Rs during rainfall in the dry and wet season.

3.6 Trends and Drivers of Rs and Reco

There were gaps in Reco data for September, November-December, and March-May due to technical issues with the EC tower, and Rs/Reco ratios were missing for large portion of the wet season. Monthly estimates of Rs and Reco from June to February indicated the Rs/Reco ratio ranged from 0.27 to 0.80, with a mean of 0.58 (Table 1). While Reco did not fluctuate a lot during the dry months of July-October, Rs steadily declined along with SWC levels (Figure 7), resulting in Rs to contribute the least during October when it was the driest (Table 1). Moreover, Rs attributed the most to Reco during January and February, when SWC was the highest (Figure 7 and Table 1). Considering all data, SWC had a significant non-linear effect on Rs/Reco ratio and explained 67% of total variation (Figure 8a). At a seasonal scale, during the dry season, SWC had a significant positive linear effect on Rs/Reco, explaining 62% of variability, whereas there was no significant effect found during the wet season (Figure 8b). Accumulated rainfall, Ts, and air temperature did not show any significant effect on Rs/Reco (Table S6). Yet, the difference between air and soil temperature was negatively corelated with Rs/Ratio during the dry season (Figure 9), meaning Rs contributed more to Reco when air cooled down faster than soil.

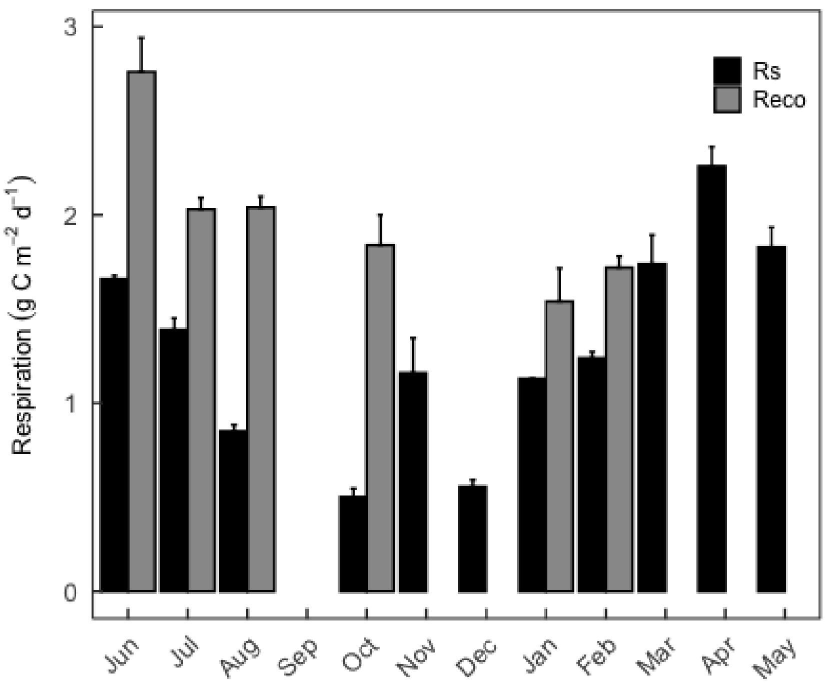

Figure 7. Monthly means of Rs and Reco with standard error bars.

Table 1. Monthly ratios of Rs and Reco and SWC.

Month	Ratio	SWC
Jun	0.63	7.01
Jul	0.67	6.13
Aug	0.43	5.65
Sep	NA	5.15
Oct	0.27	4.69
Nov	NA	7.41
Dec	NA	6.29
Jan	0.80	13.53
Feb	0.73	15.84
Mar	NA	17.91
Apr	NA	12.71
May	NA	8.41

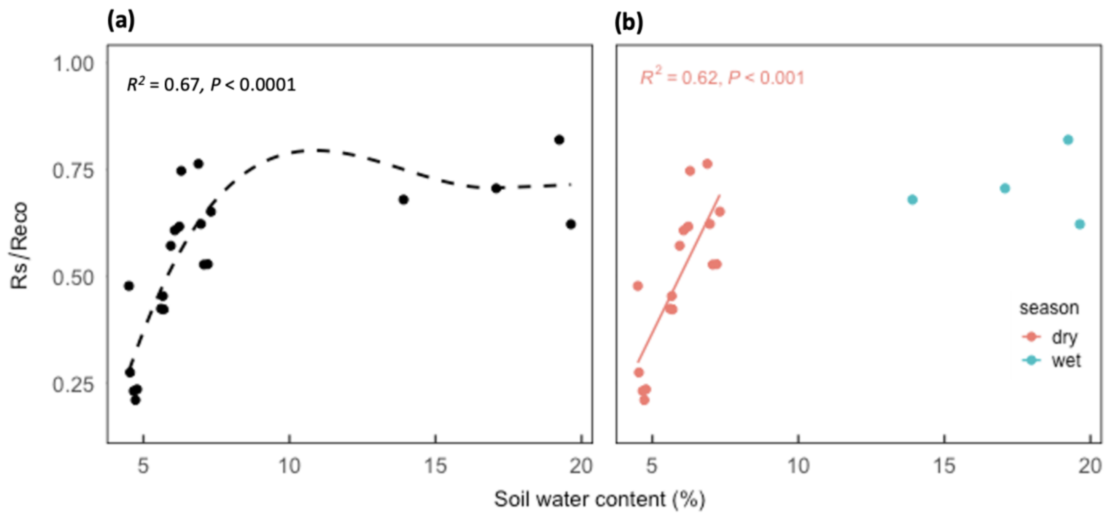

Figure 8. 5-day averages Rs/Reco ratio response to SWC, considering all data (a) and grouped by season (b). Only the best significant fit is shown accordingly to the AIC values. Solid and dashed lines represent linear and cubic fit, respectively.

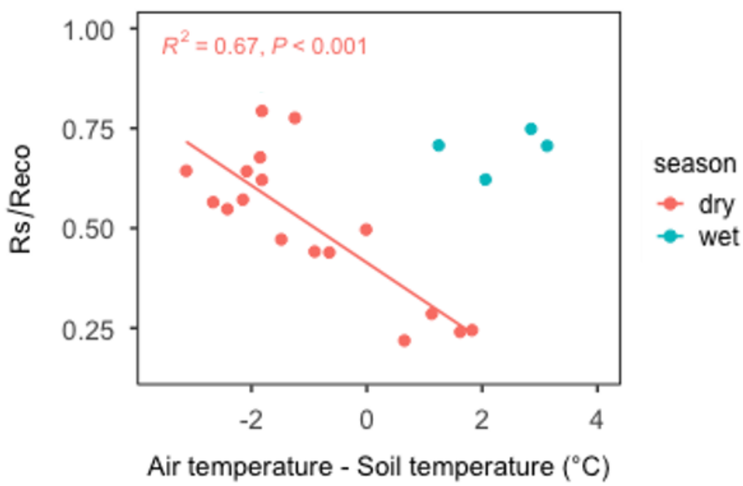

Figure 9. 5-day averages Rs/Reco ratio linear response to the difference between air and soil temperature grouped by season. Solid line represents significant linear fit (<0.05).

4 Discussion

Compared with previous values from other semi-arid ecosystems, our annual Rs estimates were lower than in pine forests with mixed-chaparral in USA (1.5-3.24 g C m^{-2} d^{-1}, Carbone et al., 2011) and semi-arid shrubland in Italy (1.5-5.2 g C m^{-2} d^{-1}, de Dato et al., 2009). However, our numbers were relatively close to other studies in semi-arid steppe ecosystems in Spain (0.84 – 1.77 g C m^{-2} d^{-1}, Rey et al., 2011) and China (0.87 – 1.04 g C m^{-2} d^{-1}, Yan et al., 2014). Moreover, our annual estimate was very similar to a study in xeric shrublands in Mexico (1.35 g C m^{-2} d^{-1}, Campuzano et al., 2021).

4.1 Co-limiting Effects of Ts and SWC

Ts has been shown to have a linear or exponential effect on Rs in various ecosystems (Bond-Lamberty & Thomson, 2010; Lloyd & Taylor, 1994). However, in arid and semi-arid ecosystems, relationships between Ts and Rs may be non-significant or non-linear and can be influenced by SWC (Carbone et al., 2011; Meena et al., 2020). In this study, Ts did not influence Rs under very dry soil conditions (6%), suggesting Rs did not increase with Ts due to lack of water availability (Figure 2A). Nevertheless, under moderately dry soil conditions (>6-9%), Rs had a quadratic response to Ts, increasing until it reached 20 °C. Rs response to Ts can have an optimal value, ranging from 20-35 °C, and once surpassed, microorganism growth and function ceases (Anjileli et al., 2019; Tuomi et al., 2008), resulting in Rs to decrease or not be affected by Ts under higher temperatures (Estruch et al., 2020; Huang et al., 2005). Additionally, our results found Rs to have exponential and linear responses to Ts under very wet soil conditions (>9%), suggesting Rs has a positive response to Ts when SWC is high enough and temperatures are not above the optimal value (Carbone et al., 2011; Rey et al., 2011).

The quadratic formula has been used to understand the effects of SWC on Rs and has suggested Rs increases with SWC until it reaches an optimal threshold, followed by decreased Rs (Anjileli et al., 2019; Liu et al., 2018). However, due to the irregularity of our data, the quadratic formula was not the best way to explain the effects of SWC. Instead, the cubic polynomial formula better explained annual Rs variation (Sun, Zhao, et al., 2018), possibly due to the gaps in our data. Under high temperatures (>20 °C), Rs responded strongly to SWC. In contrast, under cold temperatures (<=10 °C), SWC explained less of the total variation in Rs (Figure 2B). However, our results showed Rs to be reduced when SWC was low, regardless of the soil temperature levels, indicating the significant effect SWC has on Rs at all seasons. Moreover, when SWC is too high, soil pores are water-filled, and oxygen content is potentially reduced (Jiang et al., 2015), resulting in Rs to be inhibited. Whereas, when soil is too dry, there is limited substrate availability, and microbes can become dormant due to drought stress (Moyano et al., 2013). Our results showed an optimal SWC threshold of ~10%, lower than previously recorded values, between 12-20% (Rey et al., 2002; Tang & Baldocchi, 2005). However, Rs slightly increased when SWC was ~18%, during April 2021 when chamise bloomed, and temperatures were mild. It is important to note that our Ts and SWC values were recorded at 0 cm and as a 30 cm average, respectively, and measuring different layers could have given a more accurate representation of Rs response to Ts and SWC.

Diurnal monthly averages provided insight into Rs sensitivity to Ts at different SWC levels. Our results demonstrated that Ts strongly influenced diurnal variation, whereas SWC had no effect on diurnal Rs. Diurnal SWC has been shown to be constant or not change significantly to influence diurnal Rs variation (Gaumont-Guay et al., 2006), while it has also been suggested to be an important driver of diurnal Rs (Wang et al., 2014). In this study, Ts was a strong driver of diurnal Rs and had higher R^2 values during the wet months. Diurnal variation in Rs can be attributed to biological factors, such as root and photosynthetic activity. Hence, dry conditions may decrease the Rs sensitivity to Ts due to the decreased root activity, activated when soil becomes wet enough for water to reach the rhizosphere (Tang et al., 2005; Yan et al., 2014).

4.2 Seasonal Effects of Rainfall

Rainfall amount has been shown to be a seasonal control of Rs in arid and semi-arid ecosystems (Sponseller, 2007; Yan et al., 2014). In this study, the accumulated rainfall per rain day was significantly positively related to Rs during rainfall, but only in the dry season. Moreover, the relative change of Rs in response to rainfall in the dry season was consistently positive, whereas it varied from negative to positive changes in the wet season. Consequently, SWC influenced Rs during days with rainfall in the dry season only. In arid and semi-arid ecosystems, the "Birch effect" is likely to occur after periods without rainfall, by restoring microbial respiration and displacing CO_2 in air-filled pores to the atmosphere when water penetrates the soil (Birch, 1958). Conversely, negative relationships between Rs and SWC during rainfall days have suggested that excessive precipitation can inhibit or not affect Rs (Zhu et al., 2020).

SWC may vary at distinct soil depths, because rainwater can penetrate the soil layer at different rates, especially when the rainfall events are short and isolated. Our measurements may be limited due to the need for more data at different depths since short rainfall events may only impact the shallow soil layers in arid soils, benefiting the microbial activity at the surface (Austin et al., 2004; Wu et al., 2016). Also, there was missing data during the wet season, particularly during January when snow fell. Because of this, we are unable to determine Rs rates and the effects of SWC during periods with snow. We may have slightly overestimated Rs during January because snow can inhibit Rs (Tucker et al., 2016). Further work on the effect of snow on Rs in chaparral would provide valuable knowledge about seasonal variations in Rs since this has not been previously observed in this ecosystem. However, automated chambers do not work well under snow, and continuous long-term data would be challenging to collect during winter. Periodic survey campaigns could provide Rs measurements before, during, and after snowfall.

4.3 Seasonal Variation in Rs/Reco Ratio

This study demonstrates that Rs contributes a sizable proportion of Reco. Our mean estimate of Rs/Reco ratio was 0.58, comparable with previous studies in xeric shrublands (0.72, Campuzano et al., 2021), temperate and boreal forests (0.62, Davidson et al., 2005) and mixed forests (0.69, Janssens et al., 2001). Our results demonstrated that Rs contribution to Reco decreased from June to October as conditions became drier and Rs was reduced. Reco may have remained stable during the dry season despite Rs declining due to the plants ability to rely on groundwater deposits (Wiens et al., 2012) and their deep root systems (Redtfeldt & Davis, 1996). Additionally, the difference between air and soil temperature has been shown to influence Rs/Reco during autumn, similar to our results (Davidson et al., 2005). Air cooling down faster than soil may result in aboveground respiration declining quicker than Rs during the dry season, thus increasing Rs/Reco rations at this time.

Rs/Reco ratios were the highest during January and February, possibly due to the cold temperatures, low light intensity, and shorter days, resulting in plants photosynthesizing at a slower rate for a limited time (Ren et al., 2018) and reducing Reco while Rs was at intermediate levels. Also, drought conditions during the dry season may reduce photosynthetic activity in early winter because of the stress it has caused to the plants remains even after winter rains begin (Saunier et al., 2018). Due to the lack of available data from March to May, we are unable to determine the rates of Rs/Reco during spring. Increased temperatures, high SWC levels, and mobilization of stored carbohydrates can result in higher aboveground respiration than Rs during spring (Davidson et al., 2005). Hence, we assumed aboveground respiration increased and surpassed Rs between March and April, as chamise covers the largest section of our study site and it flowers at this time of the year.

4.4 Importance of Rs in Semi-arid Ecosystems and the Potential Effects of Changing Climate

Drought and increased precipitation can be a significant driver of Rs across various ecosystems (Morris et al., 2022). Previous studies in arid ecosystems suggest increased precipitation has a strong positive effect on Rs, whereas decreased precipitation lowers Rs. Moreover, arid and semi-arid regions have been shown to act as a sink during wet years due to increased rainfall influencing the growth and productivity of vegetation (Ahlström et al., 2015), which can balance out the CO_2 emitted from the soil after some time (El-Madany et al., 2018; Luo et al., 2020). However, the aridity of the location plays an essential role in the effect of increased or decreased precipitation, and it is crucial to make location-specific studies on Rs to understand the potential long-term effects of changing precipitation patterns in semi-arid ecosystems. In Southern California, Rs in semi-arid ecosystems will likely be impacted by climatic changes, specifically droughts, which have been worsening in the last decades (Robeson, 2015). In this study, we showed the importance of seasonality and how it influences the effects of rainfall on Rs in chaparral shrublands. Our results demonstrated the relative change of Rs during days with light rainfall days in the dry season to be consistently positive. While in the wet season, relative change of Rs during days with more substantial rainfall varied from positive to negative. Consequently, the timing of rainfall influences the effect it has on Rs (Yan et al., 2014; Zhu et al., 2020) and incorporating inter-annual analysis and observing the seasonal variation in Rs during years with high or low accumulated rainfall could enhance our understanding in the effects of rainfall on Rs in chaparral shrublands.

4.5 Challenges and Future Research

Field research can be challenging, and gaps are expected due to climatic conditions, equipment malfunction, or power loss. In this study, automated chambers were unable to operate under snowy conditions, resulting in gaps in our data during the wet season. Measurements with hand-held survey chambers could be an effective method to collect periodic Rs data before and after snow.

Our project was restricted to the amount of nine automated chambers, hence reducing our number of replicates. While instrumental for long-term field studies, automated chambers are also expensive and require a lot of maintenance to function properly. It is difficult to obtain spatial and temporal high-frequency Rs data, as there is a trade-off depending on the methodologies used. Survey measurements allow one to make more measurements at multiple locations; however, they require someone to make those measurements manually during a restricted timeframe, resulting in the potential over- or underestimation of Rs (Ryan & Law, 2005). Also, making measurements only during certain days would likely overlook immediate Rs pulses after rainfall events (Sotta et al., 2004). In contrast, automated chambers can be left in the field and collect continuous diurnal Rs measurements. Nevertheless, the number of replicates will be limited to the number of available automated chambers to use, and they are usually left permanently installed at chosen locations. The choice of equipment will depend highly on the priorities and research questions of the study.

Furthermore, different soil depths can experience distinct temperatures and moisture levels. Hence, it could have been helpful to incorporate sensors at various layers. Our Ts data was collected at 0 cm, and we lacked the observation at deeper layers. However, in previous studies done in similar semi-arid environments, Ts at the surface and at 2 cm depth have demonstrated to have the strongest relationship with Rs (Tucker et al., 2017; Yao et al., 2019). Moreover, we were unable to make observations at distinct soil depts since our SWC data was collected as 0-30 cm averages. It would be useful to know collect SWC at separate depts, especially during rainfall events, because water may penetrate the soil at different rates. Particularly, short rainfall events may only impact the shallow soil layers in arid soils, benefiting the microbial activity at the surface (Austin et al., 2004; Wu et al., 2016). Whereas changes in SWC at deeper layers of soil may respond at slower rate than shallow soil after rainfall.

Additionally, litter accumulation, litter quality, root biomass, and phenology affect microbial and root respiration accordingly to the plant species. Seasonal trends of Rs can be influenced by how microbial and root respiration respond to rainfall in semi-arid ecosystems (Carbone et al., 2011). Hence, it would be valuable to understand the contributions of microbes and roots to Rs to understand the seasonal biological drivers in chaparral shrublands.

5 Conclusion

Small changes in Rs can influence CO_2 emissions to the atmosphere, and due to soil's high spatial variability, it is necessary to quantify Rs in various ecosystems. Specifically, semi-arid ecosystems can be a source of variability in the global C budget due to prolonged dry spells and unpredictable rainfall patterns (Ahlström et al., 2015; Poulter et al., 2014). Chaparral provides many ecosystem services, including carbon sequestration, and it can be a significant sink of C, making it a vital element of the global carbon cycle (Jenerette et al., 2018; Luo et al., 2007). This comprehensive study upscaled Rs in a chaparral stand in San Diego, CA, determined the effects of Ts, SWC, and rainfall, and estimated the Rs contribution to Reco. Overall, the results demonstrated SWC to be the largest driver of Rs, while Ts influenced Rs when SWC was high and temperatures did not surpass their optimal value. Additionally, rainfall was important in explaining Rs, particularly during the dry season, when rain was light and sparse. Moreover, our comparisons between Rs and Reco suggested that soil respires more CO_2 than plants in colder and wetter conditions. Inter-annual long-term observations could provide a better understanding of the effects of rainfall on Rs/Reco ratios. This study improves our knowledge of Rs controls and how much CO_2 it provides to the atmosphere in chaparral shrublands. Yet, given the vulnerability chaparral faces to fires, droughts, and land-use changes, it is crucial to understand the underlying biological mechanisms driving CO_2 emitted from the soil.

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Open Research

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