2013-01-01

Carbon Emissions From Soil Respiration in the Northern Chihuahuan Desert Shrubland

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CARBON EMISSIONS FROM SOIL RESPIRATION IN THE NORTHERN CHIHUAHUAN DESERT SHRUBLAND

by

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THESIS

Presented to the Faculty of the Graduate School of

The University of Texas at El Paso

in Partial Fulfillment

of the Requirements

for the Degree of

MASTER OF SCIENCE

Department of Geology

THE UNIVERSITY OF TEXAS AT EL PASO

AUGUST 2013

Acknowledgements

I am grateful that throughout the fulfillment of this thesis I was surrounded by numerous wonderful people that cared as much as I did about this project. My advisor and mentor, Vanessa Lougheed allowed me to become a part of her lab, even when this project was an outlier, different from her research expertise, she gave me the liberty of researching what I love, and for that I am deeply grateful. I have always admired her and will forever strive to be the best scientist that I can because of her amazing influence. I could have not successfully completed my field sampling without the Systems Ecology Lab, especially Craig Tweedie, I am grateful that he took me under his wing, taught me, allowed me to research his site, and let me hitch a ride to the Jornada week after week. Support from my committee member, Lixin Jin was crucial, she provided me with a geologic perspective from the very beginning of this project, her input helped me obtain a multidisciplinary outlook.

I would like to also acknowledge the personal funding that I received for the completion of this project, from the NSF funded GK-12 fellowship. I learned, I listened, and I developed patience. I grew as a result of that. I will never forget the impact that GK-12 had on me and I would like to thank Dr. Aaron Velasco, Dr. Bill Robertson, Dr. Vanessa Lougheed, and Cynthia Ramirez for giving me the opportunity of serving as a Scientist in Residence.

I would also like to thank the Aquatic Ecology Lab, Marianna Vargas, Nicole Miller, and Gabriela Contreras for all of you love, friendship, and jokes. Thank you to Jeannette Olivarez for picking up my slack and being a wonderful friend and lab-field assistant, Ector Martell, Jennifer Ramos, Christian Andreson, Isa Valdez, Marisela Montelongo, and Aracelly Tellez for your countless hours of company in the lab.

Thank you to the Jornada Team all for keeping me company and awake during so many trips out to the research site, Naomi Luna for having my back, Aline Jaimes and Christine Laney for the intriguing science chats.

I would like to thank God for strength, my parents, Manuel Ortiz and Alicia Calvo, for all of their love and patience, my brother Christian Ortiz and sister, Marianna Ortiz, for their unwavering support. I would also like to thank Edgar Trejo, for loving me and dealing with me when I was most stressed.

Funding for this project came from the Cyber-ShARE Center of Excellence, the UTEP Graduate School Dodson Research Grant and NIH grant #5G12RR008124.

Abstract

The United States Department of Agriculture's Jornada Experimental Range (JER), is located in the northern Chihuahuan Desert in southern New Mexico and historically functioned as an experimental rangeland for cattle grazing. Historical grazing in the US Southwest has been identified as a leading, but not the sole, factor that has led to the conversion of pristine grasslands to shrublands, such has been the case on the JER. The estimated increased variability in precipitation intensity and frequency that is predicted to occur with climate warming will likely affect ecosystem responses from ecological processes including primary productivity, microbial decomposition, and thus respiration. This reinforces the importance of improving our understanding of ecosystem properties and processes that control uptake and release of CO_2 in desert rangelands. The contribution of CO_2 flux originating from soils in desert shrublands is largely unknown, yet may contribute substantially to ecosystem level fluxes. Soil flux plots were situated along a soil litter gradient around the dominant shrub species (*Prosopis glandulosa* and *Larrea tridentata)* and lichen crusts and were measured weekly or bi-weekly between August 2012 and May 2013 for soil temperature (5cm cm depth), soil volumetric water content, and C flux using an INNOVA 1312 Photoacoustic Analyzer. Seasonal composite samples from soil plots were taken to assess microbial functional diversity with the Biolog Ecoplate assays. Flux data was analyzed with ANOVA, ANCOVA, regression tree analysis, and NMS. Community-level physiological profiling (CLPP) determined microbial functional diversity with NMS. Soil total organic carbon (TOC) was measured with Lachat IL 550 TOC-TN analyzer from each plot seasonally. We found soil respiration ranging from 20-154.7 mg CO_2 m^{-2} hr^{-1}. Abiotic environmental factors such as temperature, solar radiation and barometric air pressure were found to have a significant effect on carbon efflux seasonally. Significant differences among or between shrub species and lichen crusts were not found and did not have an effect on carbon efflux. CLPP was found to depend on TOC concentrations available and showed unique functional diversity within and between shrub and lichen crust soils. Therefore, the

release of carbon to the atmosphere during the dry season was not attributed to microbial activity, rather to abiotic environmental effects. The completion of biweekly soil carbon efflux measurements spanning a full year in Chihuahuan Desert shrublands is an important research component to an ongoing study that is focused on further understanding the patterns and controls carbon budgets in desert landscapes.

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Introduction

In desert ecosystems, the contribution of soil respiration (SR) to total ecosystem respiration has been estimated to be 80-100% of the soil carbon efflux (Cable and Huxman 2004). Arid and semi-arid regions of the world currently cover over 40% of terrestrial land mass (UNDDD 2012). Thus, understanding processes that control the overall uptake and release of CO_2 in arid desert landscapes is imperative, yet poorly understood (Wohlfahrt, Fenstermaker, & Arnone Iii, 2008). The Chihuahuan Desert, which is arguably the largest North American desert, encompasses 174,000 km^2 in the United States (Ruhlman et al 2012) , and has an approximate grassland/shrublands ecoregion cover of 95.6+/- 2.3 percent (Ruhlman et al 2012) (Image 1). Investigating soil respiration in these shrublands will provide a much needed specific profile of carbon cycling for the region. Climate change models for the Chihuahuan Desert, suggest an increase in the intensity and frequency of precipitation events (National Assessment Team, 2010); furthermore, increased frequency in drought is expected for arid and semiarid regions globally (Seager et al., 2007). Such changes can result in alterations in plant community composition as well as changes in soil moisture and chemistry (Jimenez Aguilar, et al., 2009; Raich and Schlesinger, 1992). Further exacerbating global desertification, which is a process strongly associated with soil degradation and vegetation change from grassland to shrubland (Herman, Provencio, Herrera-Matos, & Torrez, 1995, Peters et al., 2013), sporadic precipitation events that govern water availability in deserts and particularly control microbial activity (Fernandez et al. 2006), face impending transformations as climate change threatens to alter precipitation patterns. These shifts are likely to impact microbial biomass and diversity and the uptake or release of CO_2 (Anderson, 2011), leading to changes in how different carbon sources are metabolized by soil microbes, hence impacting overall desert carbon budgets (Clark et al. 2008).

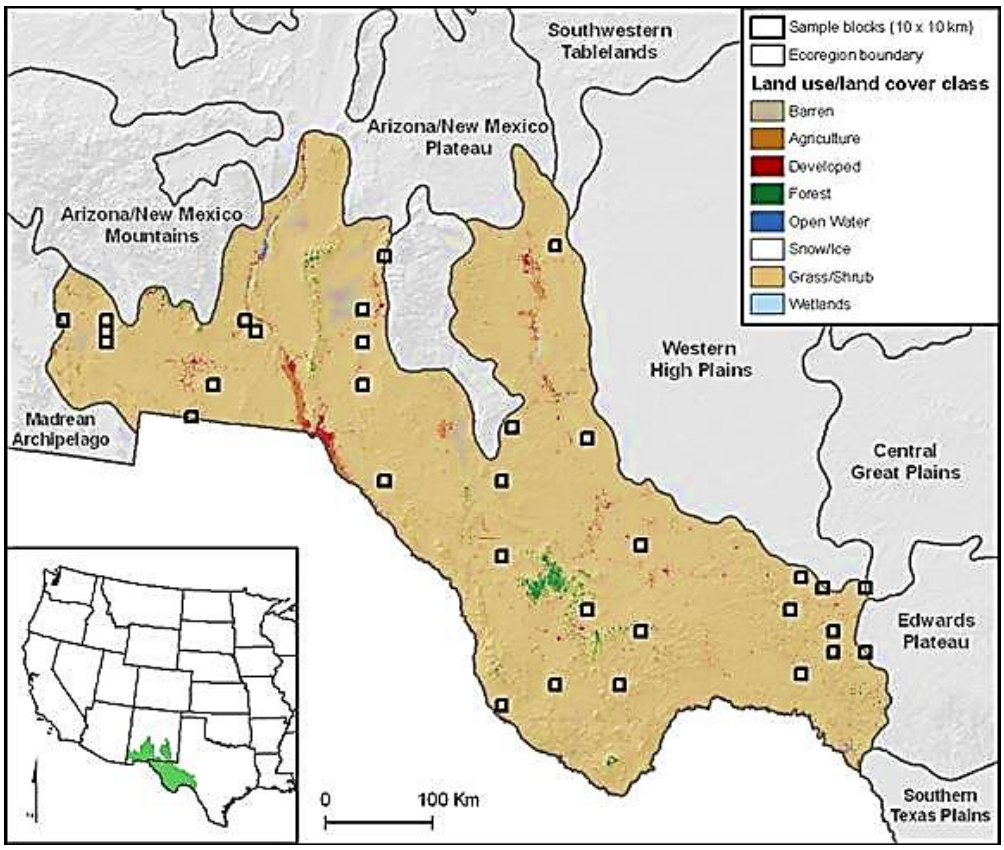

Image 1. USGS map of Chihuahuan Desert ecoregions, where ~95% is grasslands/shrubland.

The calculated global SR rates range from 50-60 Pg C yr^{-1} with an efflux in desert shrubland of approximately 224 ± 38 g C m^{-2} yr^{-1} (Raich and Schlesinger 1992). Studies in other North American deserts report values ranging from 0.39-1.49, to 110-476.6 and 167-708 mg CO_2 m^{-2} hr^{-1} in the Mojave, Sonoran and Chihuahuan deserts respectively (Parker, L.W., Miller & Steinberger, 1983; Schaeffer, Billings, & Evans, 2003; Sponseller, 2007). SR can be driven by both biotic and abiotic factors.

Microbial activity regulates nutrient cycling through the decomposition of organic matter (Austin et al., 2004; Fernandez, Neff, Belnap, & Reynolds, 2006);Liu et al., 2010,Sherman & Steinberger, 2012) and increases nutrient availability in soil. Biotic SR can be attributed to five processes that include: microbial decomposition of organic matter or basal respiration, microbial decomposition of plant

residues and roots, microbial decomposition of dead plant matter, rhizomicrobial respiration, and root respiration, (Kuzyakov, 2006; Parker et al. 1983). Microbial CO_2 contributions are reliant on environmental factors such as rainfall, soil temperature, and soil moisture dynamics (Anderson, 2011; Austin et al., 2004; Cable & Huxman, 2004; Liu, Fu, Zheng, & Liu, 2010)). Rapid desiccation of these organisms subsequent to a wetting event results in a reduction of their capacity to osmoregulate carbon (Darby et al. 2011). According to Darby and others (2011), arid regions can thus produce significant amounts of volatile organic carbon (VOC) gases after desiccation. Similarly, cell lysis and the release high SR rates following rewetting can also significantly affect, microbial function, and contributions to CO_2 efflux (Austin et al., 2004; Birch, 1959; Sponseller, 2007; Tang, Misson, Gershenson, Cheng, & Goldstein, 2005), by releasing CO_2 magnitudes higher than prior to rehydration. In addition to expected shifts in precipitation patterns, different trophic levels such as primary producers and primary consumers, like microbial heterotrophs, which have different precipitation pulse needs and water activation depths (Griffiths, E. and Birch, H., 1961; Susanne Schwinning & Sala, 2004) will likely also shift their activities in response to water availability (Cable & Huxman, 2004). Previous studies highlight the effect that pulse magnitude can have in environmental responses and the release of carbon. For example, Wohlfahrt et al. (2008) showed different magnitudes of precipitation pulses in the Mojave Desert affect different ecosystem users, where precipitation events of lower magnitude activate only surface biota such as lichen crusts, cyanobacteria, mosses and heterotrophic microorganisms. Larger carbon efflux responses only occur when rain magnitude is large enough to reach plant root systems (Wohlfahrt, et al. 2008). Variation in water availability determined by precipitation pulse size affects organic litter availability and determines the pulse users, thus defining the functional diversity of the microbial communities present in soils (Austin et al., 2004; Manzoni, Schimel, & Porporato, 2012; Muldavin, et al., 2008; Schwinning, et al.,2004).

Other than soil moisture and precipitation events, other abiotic factors such as temperature, solar radiation, and barometric pressure have also been found to control production and diffusion of soil gases. In particular, temperature has been found to positively correlate with SR (Anderson-Teixeira, et al., 2011; Gu, Jia et al., 2006; Post, & King, 2004; Ross, Kelliher, & Tate, 1999; Thomas, Hoon, & Dougill, 2011). Austin and Vivanco (2006) and Gallo and others (2006) found organic litter decomposition driven by solar radiation, specifically UV radiation. Finally, 'pressure pumping' is the effect that atmospheric changes in barometric pressure and wind turbulence have on the diffusion of soil gasses, with a lowering of pressure allowing gas diffusivity into the atmosphere (Serrano-ortiz, Pérez-priego, & Sánchez-cañete, 2006; Takle et al., 2003, 2004; Paw-U et al., 2006). The investigation of such factors' effects on SR and its diffusion needs to be closely assessed to understand seasonal impacts on CO_2 efflux.

Historical grazing in the US Southwest has been identified as a leading cause in the conversion of desert grasslands to shrublands (Archer, Schimel & Holland, 1995; Okin et al., 2009, Yanoff & Muldavin, 2008). Grazing and trampling by range animals have led to the ecosystem transformations, such as plant community structural change (Brodie et al. 2002, Brown 1993, Hansen 2007, Liu et al 2010, Yergeau et al. 2007), which can indirectly affect microbial community structure (Raich and Schlesinger 1992). These changes to plant communities, such as increases in plant inter-space and modification of vegetation cover (Bird et al., 2002), can contribute to changes in soil organic carbon availability and soil moisture, altering biologic soil organic matter (SOM) decomposition and limiting SR (Sponseller 2007). However, little is known about the relationship between microbial community profiling and plant litter composition (Sherman and Steinberger 2011). Further understanding the controls and processes of desert shrubland SR, therefore, will likely be a valuable contribution to desert ecosystem science and enhance research focused on understanding the patterns and controls of land-atmosphere carbon efflux in desert ecosystems.

In particular, the cause of large losses of carbon following the initiation of the summer monsoon is unknown and may potentially be related to soil respiration. The overall objective of this project is to estimate the relative contribution of soil respiration to land-atmosphere efflux Chihuahuan Desert scrublands at the JER. In order to extrapolate to the landscape level, efflux data will be taken from representative sites along a gradient of organic litter cover, including soil biologic crusts. The gradient will provide insight on different factors contributing to soil respiration.

This proposal aims to test the following hypothesis:

- We expect that soils with high organic content, especially those with biologic crusts, will have higher carbon emissions after precipitation events; this will be a function of higher heterotrophic microbial functional diversity in organic soils. Soil microbial emission contributions will be a function of precipitation pulses; soil with higher water content will be active CO_2 producers.

Methods and Materials

Site Description

This study was conducted at the USDA Jornada Experimental Range (JER), which hosts the Jornada Long Term Ecological Research (LTER) program. The JER is located in Doña Ana County, New Mexico in the northern Chihuahuan Desert, and historically functioned as an experimental rangeland for cattle grazing.

The study site is dominated by shrubs including creosote bush (*Larrea tridentata)* and honey mesquite (*Prosopis glandulosa).* Temperatures commonly range from a monthly average of 36˚C in the summer to 13˚C in the winter, with precipitation averages of 241 mm yr^{-1} (Havstad et al., 2000).

Experimental Design

Fourteen soil microsites were located within a 200 m^2 study area and were classified according to both litter cover and plant species. Sites were characterized with respect to litter quantity as: 1) interspaces (containing 0-5% litter cover), 2) canopy edge (>15-25%), and 3) near the shrub crown (>25%). Two replicates of each litter type located in areas dominated by either creosote bush (*Larrea tridentata*) or honey mesquite (*Prosopis glandulosa*). At least 20m separated each selected plant used in the study. Two sites with >25% lichen crust cover were also selected.

Soil Sampling

Seasonal composite soil samples were taken from the top 5cm in a site adjacent to chamber plots and measured for total organic carbon (TOC) content. Each sample was measured using the Lachat IL 550 TOC-TN analyzer. TOC samples were first digested with 10% HCl to remove all inorganic carbon, then dried at 60°C as directed by the Lachat IL500 TOC-TN user manual.

Field emission measurements

Precipitation, barometric pressure and solar radiation were measured every five minutes by a HOBO U30 Station located about 50m from our study site.

Aluminum chamber bases 30 x 30 x 5 cm (l x w x h), were carefully pressed into the top 5cm at each plot. A sealed system was created between the bases and a custom built acrylic chamber (~8,550 cm^3) containing a small fan for air circulation and pressure equalizing tubing using a water seal (*sensu* Lin, 2012). Chambers were connected to a California Analytical INNOVA 1312 Photoacoustic IR Analyzer. Measurements from permanent plots were taken weekly around solar noon (± 2 hours) throughout summer, fall, spring, and winter, from August 2012 to July 2013. The INNOVA was used to measure CO_2 concentrations (ppm) in the dark for 5 minutes. Dark measurements allow the determination of Respiration (R), which is the release of CO_2 by heterotrophic microbiota. . Data for each duplicate site type (litter and plant treatments) were averaged prior to analysis. Data were transformed as required to meet the assumptions of normality; respiration (SR) required a square root transformation. All results relating to plot-level soil temperature were collected at 5cm depth.

Microbial Community-Level Physiological Profiling

Microbial functional diversity was examined seasonally from composite samples using community-level physiological profiling (CLPP) measured with Biolog Ecoplates. CLPP analysis was conducted for composite soil samples taken from the surface to a depth of 5cm. Samples were extracted during the summer dry season (late June) and after precipitation events (early August), then seasonally for the winter season in early December, and in the spring season in early May. Samples were blended thoroughly, sieved through a 500μm soil sifter, and ground in a mortar. Soil samples were stored at 4˚C until analysis. Soils were rehydrated to40% water content for 24 hours prior to inoculation because previous attempts to use air dried samples did not stimulate microbial activity. Dilutions of soil with Bacto-agar saline solution of 10 -2 g L-1 for each microsite per season were created to inoculate the Ecoplates. Plates were incubated in the dark at 37˚ C for 24 hours, until wells were visibly purple. EcoPlates hold three replicates of 31 common organic carbon substrates found in soil ecosystems. As soil microbes grew and metabolized the carbon source, a tetrazolium dye in the well was oxidized and

developed a purple color. The plates were repeatedly read in the Versa Max microplate reader until all plates reach an average well color development (AWCD) of 0.4 - 0.6nm. Differences in microbial functional diversity were analyzed using Nonmetric Multidimensional Scaling (NMS) where sites with similar communities group together in an NMS bi-plot. Differences in community activity among sites were analyzed by determining average well color development (AWCD) following 24 hours of incubation. Diversity was calculated in substrate wells with an absorbance value >0.10nm at 24 hours (Zak et al., 1994).

Statistical Analyses

Nonmetric Multidimensional Scaling (NMS) was used to describe soil microbial communities. NMS axes scores were correlated with environmental factors such as TOC, soil temperature, barometric pressure, soil moisture, and SR, across a seasonal gradient in order to determine any associations between organic carbon consumption and abiotic variables. Regression tree analysis on NMS axis scores and environmental variables was also used to determine non-parametric associations with data such as barometric pressure and soil moisture. Additionally, regression tree analysis was utilized to determine relationships between carbon efflux and environmental parameters such as soil temperature, soil moisture, barometric pressure, solar radiation, and soil carbon. The statistical software R 2.15.1, PC-ORD 5.0, and JMP 10.0.2 were used to analyze data.

Results

Seasonal trends

The following are results for data collected from August 21st 2012 to June 1st 2013.

Seasonal trends in efflux can be observed for SR (Figure 1), were the highest rates of SR occurred between May and September. Similar trends were observed for all plant and litter types. SR values ranged from 21-154, 24-149 and 20-103 mg CO_2 m^{-2} hr^{-1} for creosote, mesquite, and soil crusts, respectively.

Temperatures were also highly driven by seasonality, with warmer temperatures observed from May to September. Peaks in VWC were driven by precipitation pulse events in the monsoon season (August-September), as well as an additional large precipitation event in the winter (Figure 2).

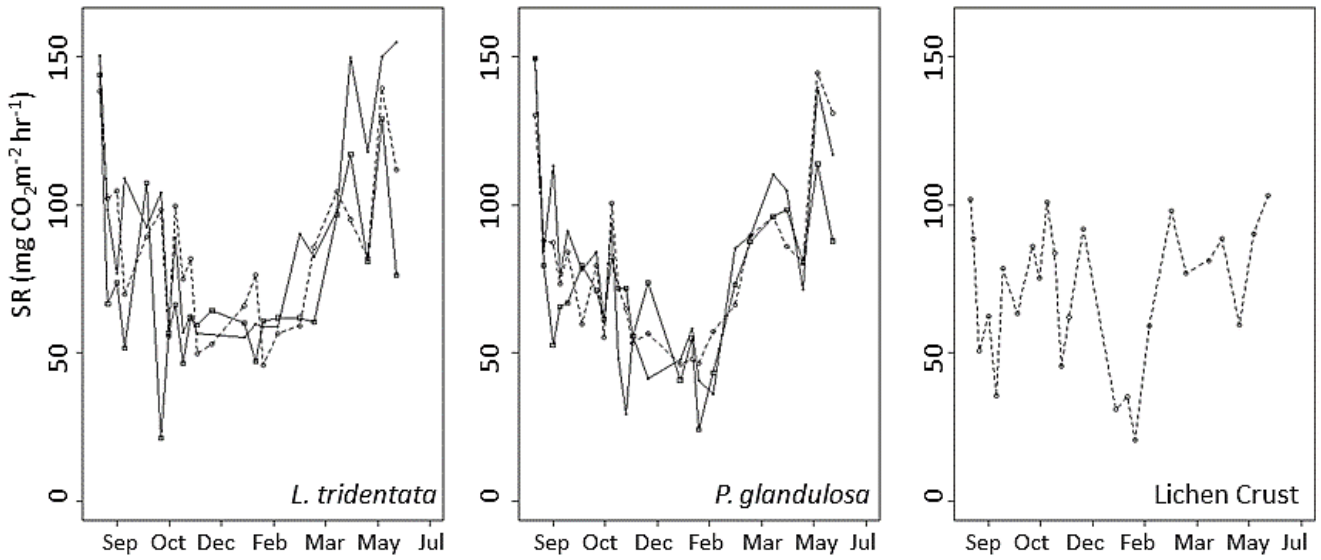

Figure 2. Soil Respiration (SR) for all plant and litter treatments. Left graph is for creosote (*L.tridentata*) soils, the middle graph is for mesquite soils (*P. glandulosa*), and the right is for soil crusts. Closed squares are for Shrub Crown soils, closed circles are for Canopy Edge soils, open circles are for Plant Interspace soils.

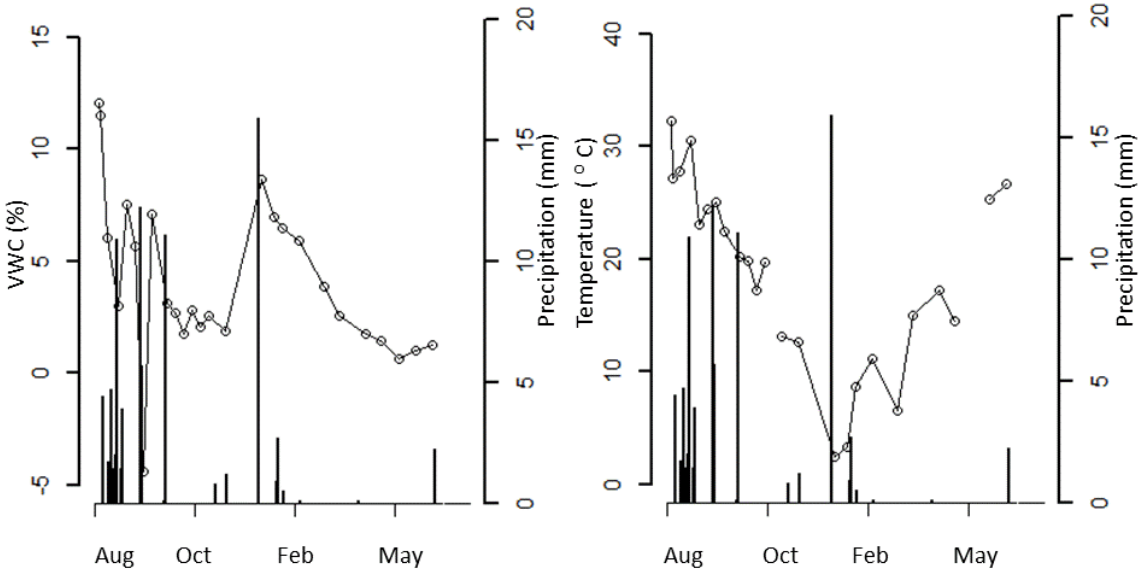

Figure 3. Trends through time for soil Volumetric Water Content % (VWC) and Precipitation (mm) (Left) and soil temperature at 5cm (°C) and Precipitation mm (Right).

Effect of plant type and litter quantity on soil respiration

There were little difference in CO_2 efflux among the different litter treatments surrounding each shrub species; only marginally significant differences were found for Creosote Crown (>25% litter cover) compared with Creosote Canopy Edge (15-25% litter cover) (p-value=0.0537, Two Sample t-test) and Mesquite Crown (>25% litter cover) compared with Creosote Canopy Edge (15-25% litter cover) (p-value=0.0586, Two Sample t-test). SR showed no significant differences among sites with different litter quantities (Figure 3, Table 1) (ANOVA, p-value>0.05). Because there were no significant effect of plant or litter on SR, site data from all plant and litter treatments were averaged for subsequent analyses.

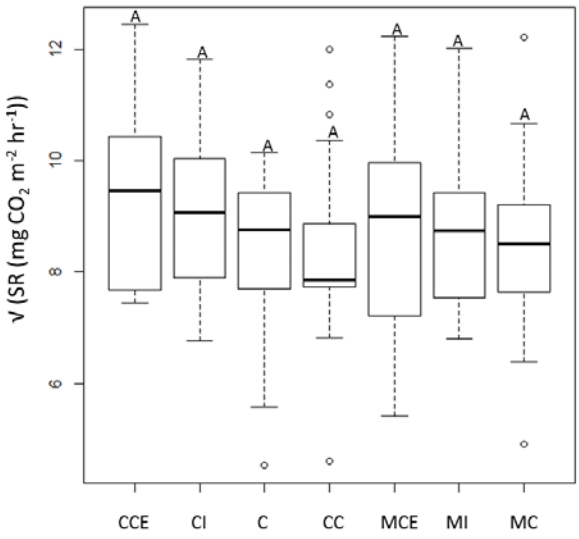

Figure 4. ANOVA and Tukey HSD on Soil Respiration (SR in mg CO_2 m^{-2} h^{r-1}, where Creosote Canopy Edge is CCE, Creosote Interspace is CI, Lichen Crust is C, Creosote Crown is CC, Mesquite Canopy Edge is MCE, Mesquite Interspace is MI and Mesquite Crown is MC.

Table 1. ANOVA on Soil Respiration with litter gradients.

Analysis of Variance

Table

(Soil Respiration) $^{-1/2}$

	Df	**SS**	**MS**	**F value**	**Pr(>F)**
Litter	6	23.9	3.976	1.571	0.159
Residuals	158	399.8	2.531		

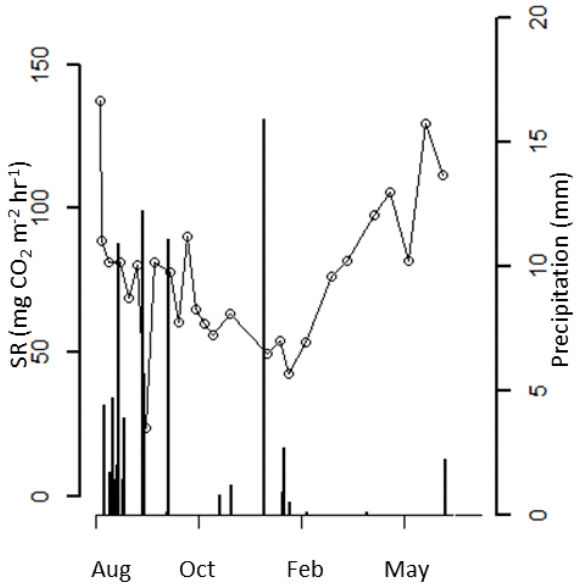

Figure 45. Trend through time for Soil Respiration (SR) in mg CO_2 m^{-2} $hr^{-1}$and Precipitation in mm.

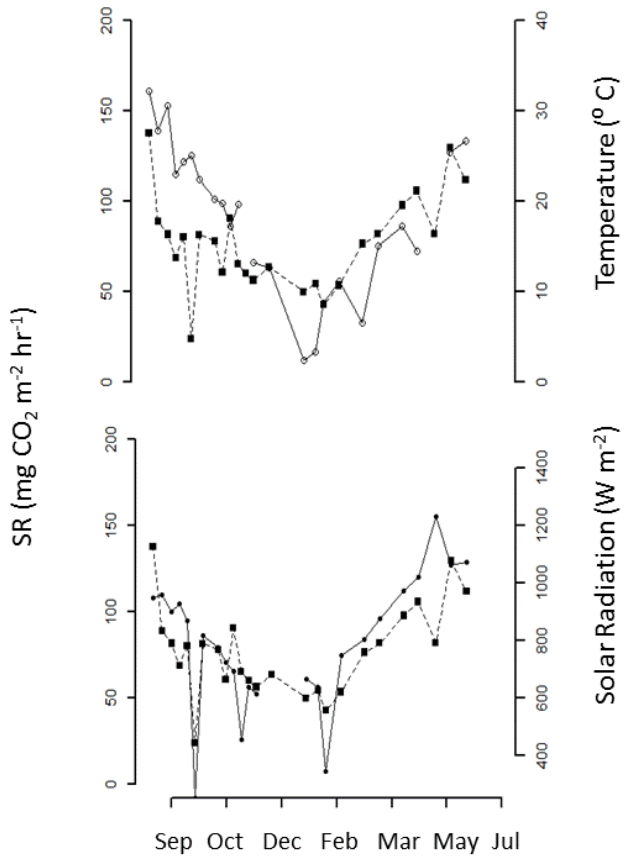

Figure 6. Trends through time for Soil Respiration (closed circle, dashed line in for Soil Temperature (^{0}C) (open circle, full line) (Top) and Solar Radiation (W m^{-2}) (Bottom) (closed circle, full line).

Abiotic drivers of soil respiration

A comparison of trends in SR and precipitation events indicated increased respiration at the late monsoon season (August-October 2012) (Figure 4); however, the largest precipitation event in the winter season (15mm in December) was not associated with increased SR. Furthermore, little to no precipitation events occurred in subsequent months (February- May 2013), but these Spring data displayed comparably high fluxes relative to the late monsoon season. Solar radiation and soil temperature trends through time also tend to co-vary with SR (Figure 5).

Average soil temperature had a significant effect on SR (simple linear regression, $p<0.001$, Figure 6), were higher temperatures led to higher SR. The SR- soil temperature relationship did not appear to differ among litter quantities or plant type (ANCOVA; see Appendix A). A similar effect on carbon efflux was found with solar radiation ($W\ m^{-2}$) (simple linear regression, $p<0.0001$, Figure 7). Significantly higher radiation occurred during the spring, while summer had the highest temperatures and winter the lowest (Table 2, ANOVA, $p<0.05$, Figure 8). Not surprisingly, temperature and solar radiation were highly correlated; high soil temperatures co-occurred with high levels of radiation (Figure 9).

Table 2. ANOVA table for Solar radiation and soil temperature by seasons.

Analysis of Variance

Table

Solar Radiation

	Df	SS	MS	F value	Pr(>F)
Season	3	4340745	1446915	99.02	<2e-16***
Residuals	154	2250340	14613		

Temperature

	Df	SS	MS	F value	Pr(>F)
Season	3	7672	2557.4	132.7	<2e-16***
Residuals	141	2718	19.3		

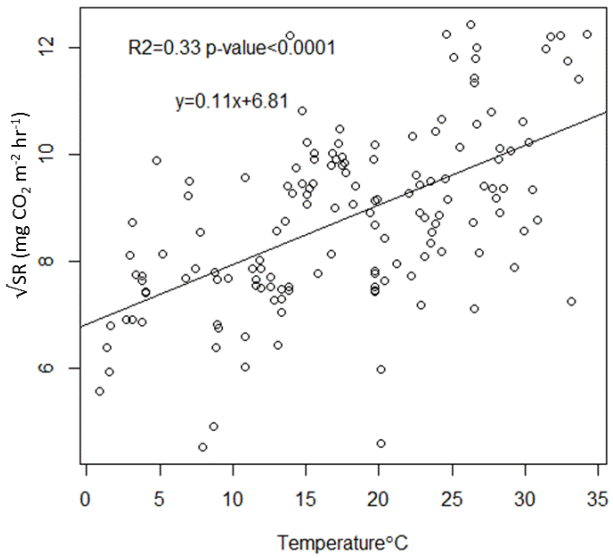

Figure 7. Linear Regression model (solid line) for soil respiration (SR) (mg CO_2 m^{-2} hr^{-1}) against soil temperature ^0C, R^2=0.37 and p-value<0.0001

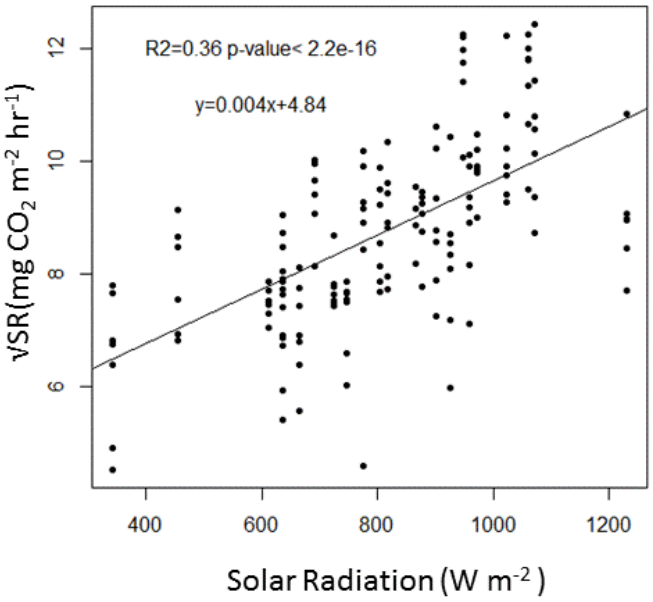

Figure 8. Linear regression for Soil Respiration (SR) mg CO_2 m^{-2} hr^{-1} against Solar Radiation (W m^{-2}), both relationships are significant.

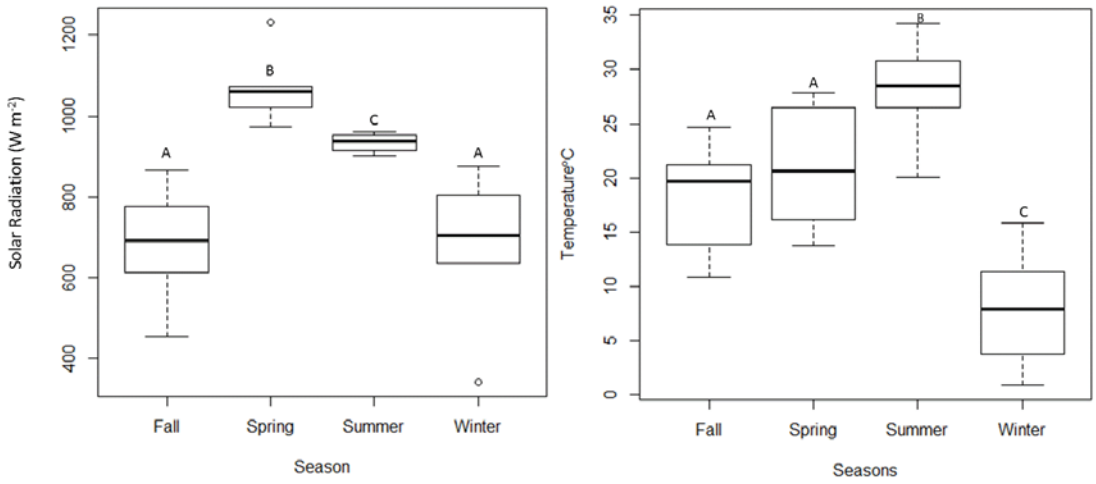

Figure8. Solar radiation (W m-2) and soil temperature (^{0} C) over 2012-13 sampling. Highest solar radiation occurred in the spring and higher temperatures in the summer.

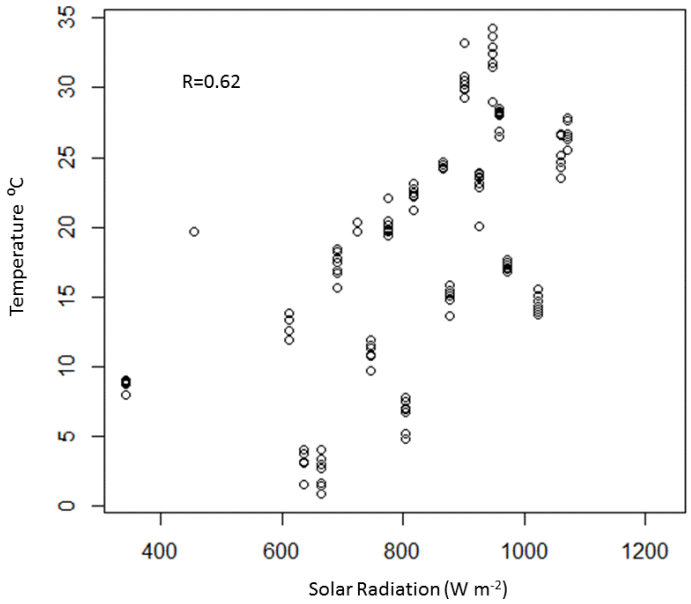

Figure 9 Temperature and Solar Radiation correlation R=0.62, increasing radiation increases soil temperatures.

Individual linear regressions indicated significant effects of temperature on SR for all seasons ($p<0.05$). The strongest relationship between temperature and SR was observed during the summer ($R^2=0.45$, $p<0.05$), while less than 15% of the variation in SR was explained by temperature in all other seasons (Table 3). The slope of the line describing SR versus temperature in summer was significantly different from that in all other seasons (Table 3, ANCOVA, interaction p-value<0.05), indicating that summer SR tended to be lower a low temperatures, but greater at higher temperatures (Figure 10). While the slopes of the lines for spring, fall and winter were identical, (ANCOVA, $p<0.05$) there was a significant effect of season, indicating that the magnitude of SR was significantly greater in spring for similar temperatures observed in fall and winter.

Conversely to the effects of temperature, individual linear regressions per season did not show significant effects of solar radiation. In particular, there was no effect of radiation on spring and summer SR ($p<0.01$). Slopes of the lines for SR versus radiation in fall and winter were identical, with a significant effect of season (Table 6, ANCOVA, $p<0.05$. Similarly, the slopes of the SR versus solar

radiation relationships were not significantly different in fall and winter, but the magnitude of efflux was higher in fall. Additional differences among summer and other seasons might be observed once additional 2013 summer data, with a wider temperature range, are analyzed.

Table 3. Illustrates linear regression parameters for individual season Soil Respiration (SR) against soil temperature (^{0} C).

Season	R^2	P-value	Y=mx+b
Spring	0.1432	0.04711	Y=0.07x+8.91
Summer	0.4453	7.69e-05	Y=0.30x+0.80
Fall	0.1001	0.03217	Y=0.09x+6.79
Winter	0.1394	0.01488	Y=0.10x+6.80

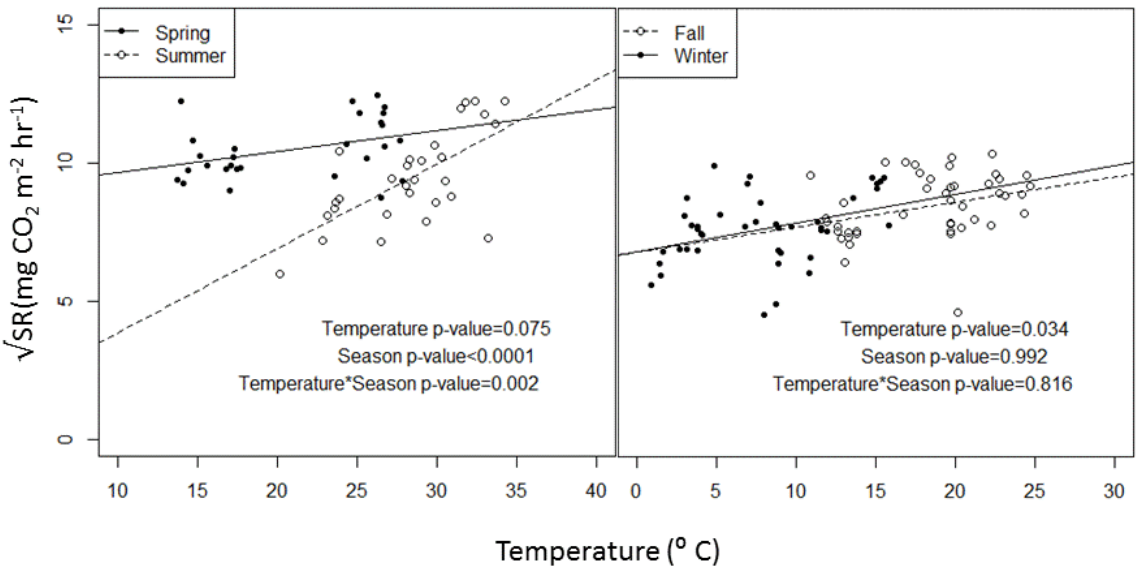

Figure 10. (Left) ANCOVA for spring and summer SR explained by soil temperature. Summer individual R^2 0.445, p-value<0.001, y=0.305x+0.802; spring R^2 0.143. p-value<0.05, y=0.075x+8.912. (Right) ANCOVA for fall and winter SR explained by Temperature. Fall individual R^2 0.106, p-value<0.05, y=1.525x+44.904; winter R^2 0.152, p-value<0.05, y=1.632x+46.837

Table 4 ANCOVA summary for all Seasonal Soil Respiration comparisons. Bonferroni corrected alfa is <0.0083 (*p-value<0.008; p-value<0.05).

Season	**Effect**	**P-value**	
Spring v. Summer	Temperature	0.197	
	Season	1.42e-06	*
	Temp*Season	0.002	*
Spring v. Fall	Temperature	3.34e-06	*
	Season	2.99e-09	*
	Temp*Season	0.783	
Spring v. Winter	Temperature	1.48e-15	*
	Season	0.0004	*
	Temp*Season	0.6073	
Summer v. Fall	Temperature	2.54e07	*
	Season	0.1543	
	Temp*Season	0.0051	*
Summer v. Winter	Temperature	1.42e-10	*
	Season	0.0427	.
	Temp*Season	0.0095	.
Fall v. Winter	Temperature	7.36e-06	*
	Season	0.628	
	Temp*Season	0.817	

Table 5. ANCOVA results for Soil Respiration (SR) defined by solar radiation per season

Season	Effect	P-value
Fall v. Winter	Solar Radiation	3.02e-7
	Season	0.002
	Solar Radiation*Season	0.309

As expected, given the previous analysis (Figure 11 and Table 7), there was a significant effect of season on soil respiration (ANOVA, Tukey HSD, $p<0.0001$). Statistically similar efflux within the cooler and warmer seasons were observed (Table 7). Summer and spring seasons, which had mean temperatures ranging from 20-28 °C, emitted 92 and 105 mg CO_2 m^{-2} hr^{-1}, respectively, in comparison to the cooler seasons of fall and winter, which had mean temperatures of 7 and 18°C, and average SR of 70 and 59 mg CO_2 m^{-2} hr^{-1}..

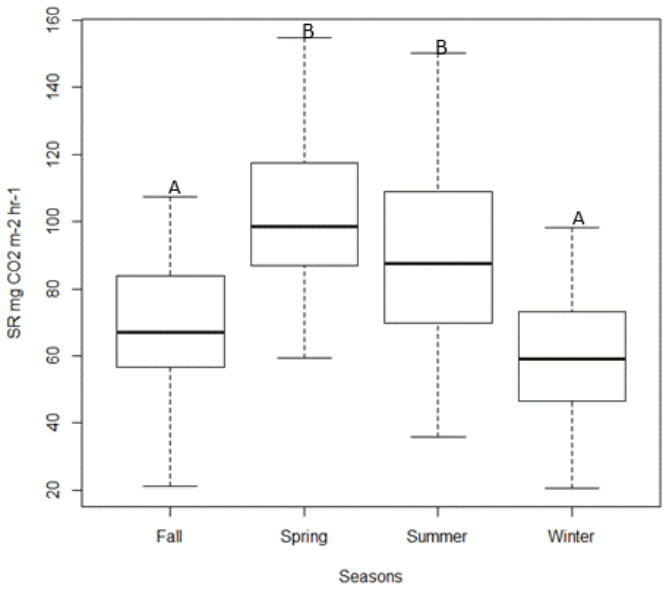

Figure 11. ANOVA on season and Soil Respiration (SR) with Tukey HSD post hoc test and Seasons.

Table 7. ANOVA on Soil Respiration (SR) by seasons

Analysis of Variance Table

(Soil Respiration) $^{-1/2}$

	Df	**SS**	**MS**	**F value**	**Pr(>F)**
Season	3	152.89	50.962	30.298	1.388e-15***
Residuals	161	270.81	1.682		

Regression tree analysis showed soil temperature to be the primary environmental driver of carbon efflux (Figure 12). Initial partitions in the data suggest thresholds in SR occurred when temperature rose above 13°C. The highest mean SR (117.9 mg CO_2 m^{-2} hr^{-1}, n=12) occurred at temperatures between 24-26 °C. The lowest SR (50.6 mg CO_2 m^{-2} hr^{-1}, n=13) was observed at temperatures lower than13°C, and with VWC greater than 6.8%. The model also depicted a partition (n=40) for soils within a temperature range of 19-24 °C where soils with only 1.84% VWC or less, emit a mean of 20 mg CO_2 m^{-2} hr^{-1}, illustrating the importance that high temperatures and low soil moisture availability have on carbon release. Interestingly, when air pressure (mbar) was added to the analysis, it explained spring and summer SR better than any other environmental variable. The highest mean SR (111.05 mg CO_2 m^{-2} hr^{-1}, n=36) occurred when barometric pressures were less than 862.3 mbar, contrary to fall and winter SR, which responded primarily to temperature and VWC. In cool season soils, the lowest SR occurred at temperatures less than 14 °C (56.22 mg CO_2 m^{-2} hr^{-1}, n=49). The highest fall and winter SR occurred at temperature thresholds higher than 14 °C and were co-limited by VWC greater than or equal to 2.89% (80.79 mg CO_2 m^{-2} hr^{-1}, n=28). Regression tree analysis including solar radiation (not shown) overpowered responses by any other environmental variable (R^2=0.54), with continuous partitions on radiation.

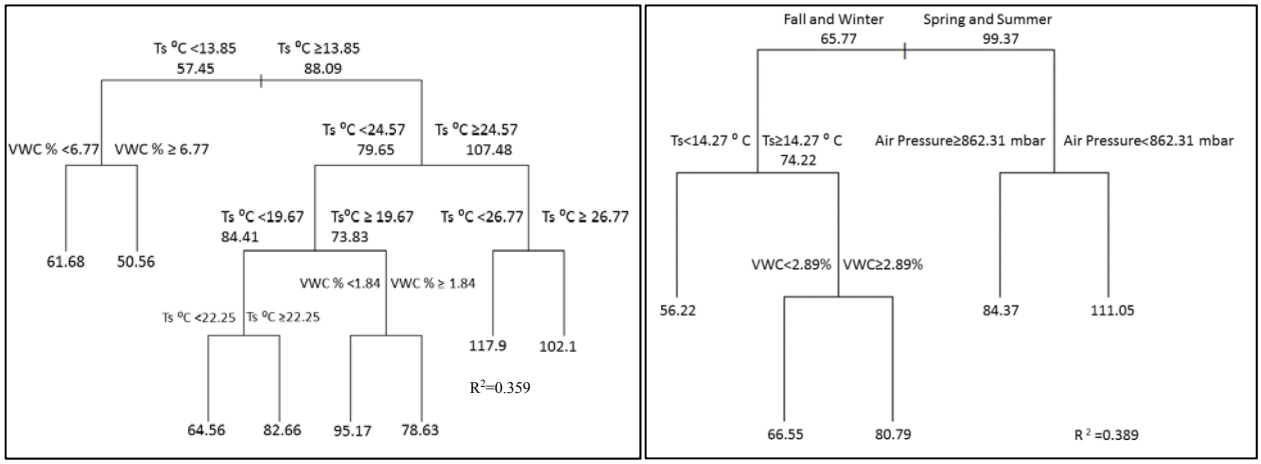

Figure 12. Regression Tree model for Soil Respiration (mg CO_2 m^{-2} hr^{-1}), explained by soil temperature ^0C (Ts), and Volumetric Water Content (VWC %) with R^2 of 0.359, n=158 (Left) and SR explained by Seasons, Air Pressure (mbar), Temperature ^0C (Ts), and Volumetric Water Content (VWC %) with R^2 of 0.389, n=165 (Right)

Using the temperature and moisture thresholds identified through regression tree analyses, we divided the data into groups of cool and moist soils (CM), cool and dry soils (CD), warm and moist (WM) and warm and dry soils (WD) (Table 8). Significant differences between CD and CM with WD and WM soils was found (Table 9, ANOVA, Tukey HSD, p-value<0.0001), where mean SR for CD and CM are 61.85 and 50.87 mg CO_2 m^{-2} hr^{-1} respectively and 100.40 and 88.75 for WD and WM mg CO_2 m^{-2} hr^{-1}, respectively (Figure 13).

Table 8. Soil temperature and moisture threshold categories used in the following ANOVA, defined by regression tree partition classifications.

	Temperature ^0C	**VWC %**	**N**
CD	<13.85 ^0C	<6.77%	30
CM	<13.85 ^0C	>6.77%	20
WD	>13.85 ^0C	<1.84%	29
WM	>13.85 ^0C	>1.84%	66

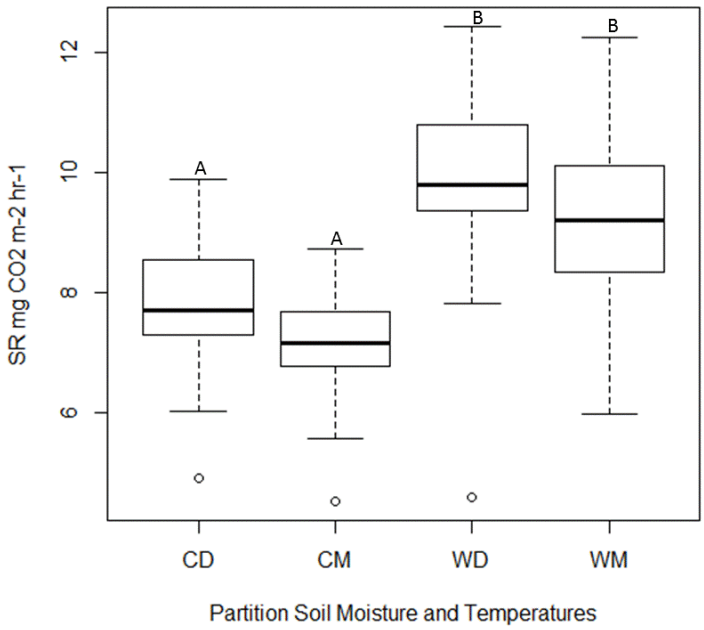

Figure 13. ANOVA and Tukey HSD on partition soil moisture and soil temperatures, where cool and dry (CD) and cool and moist (CM) soils have lower SR from warm and dry (WD) and warm and moist (WM) soils.

Table 9. ANOVA table for partition levels of soil moisture and soil temperature thresholds.

Analysis of Variance Table

(Soil Respiration) $^{-1/2}$

	Df	**SS**	**MS**	**F value**	**Pr(>F)**
Partition Soil Moisture and Temperatures	3	143.2	47.74	27.1	6.71e-14***
Residuals	141	248.4	1.76		

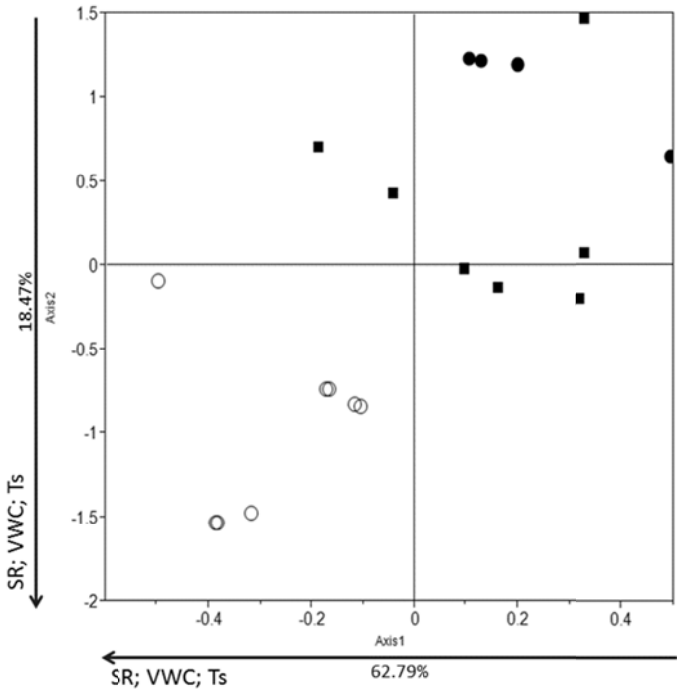

Figure 14. NMS on Environmental Variables: Total Organic Carbon (TOC), Ts (soil temperature), VWC (Volumetric Water Content), and Soil Respiration (SR), where open circles are summer efflux, and closed circles and square are winter and fall season efflux.

NMS (Stress=3.77, first 2 axes explain 62.79 and 18.47% of variance, 2-dimensional solution) of the same environmental variables included in the RT further supports these trends (Figure 14). Sites are grouped by season, where summer is plotted in the bottom left quadrant and the remaining samples tend to be in the upper right. Summer conditions were associated with higher levels of SR, temperature and VWC, as opposed to fall and winter soils.

Community-Level Physiological Profiling

Nonmetric Multidimensional Scaling (NMS) (Stress=18.02, first 2 axes explain 26.49 and 13.06% of variance, 2-dimensional solution) on 32 different environmental organic carbon substrates across seasons showed a broad range of functional diversity between replicates suggesting that all soils had a unique soil microbial composition (Figure 15). Soils with 0-5% plant litter cover had no response

to the Biolog Ecoplate assay, likely due to the overwhelmingly low bacterial counts. There were no obvious seasonal patterns in the carbon substrate use by soil microbes.

In general, each NMS axis was associated with a unique combination of carbon compounds. There were twice as many compounds associated with Axis 1 than with Axis 2, including five more carboxylic acids, four more amino acids, two more carbohydrates, one less "Miscellaneous" compound, one more amine/amide. Both axes had one polymer. Both axes had a variety among chemical guild counts with the lack of similarities among axes demonstrating the broad use of 24 different organic compounds by microbial communities.

The primary driver of carbon substrate use appeared to be soil TOC, which was significantly related to NMS axis 1 ($R^2=0.30$, $p<0.05$) (Figure 16). Linear regressions with between NMS axis scores (Table 10) and other environmental variables such as soil temperature (Ts), VWC, and SR showed no relationship.

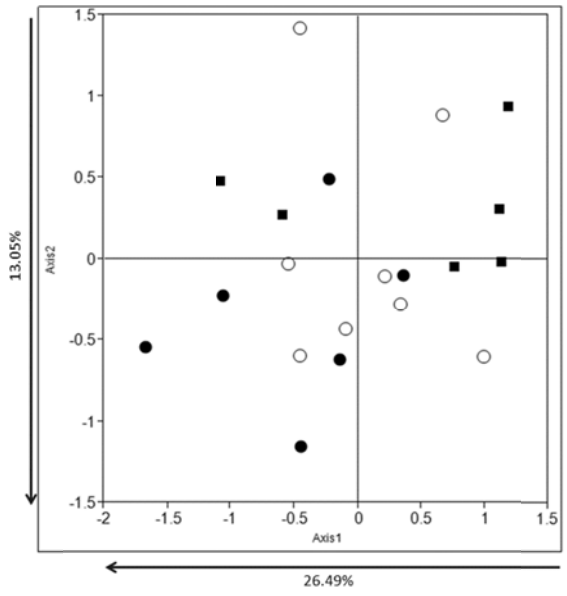

Figure 15. NMS for 32 environmentally available organic compounds across seasons, where closed circles are winter, closed squares are fall, and open circles are summer soils.

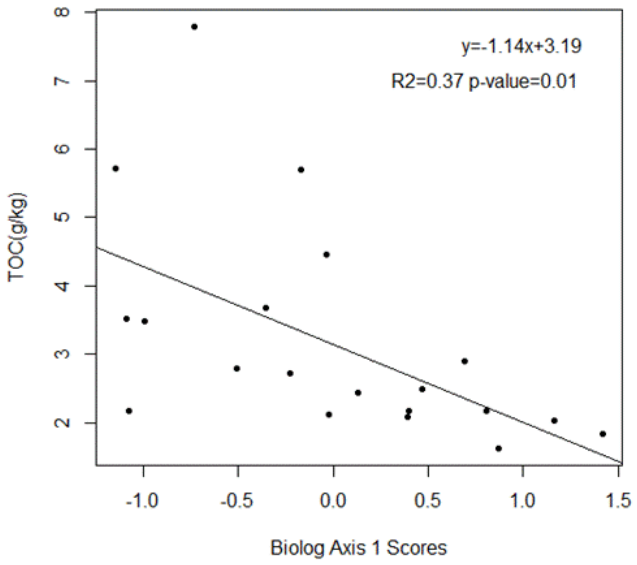

Figure 126. Linear regression models TOC (g/kg) against Biolog NMS Axis 1 scores.

Table 10. Summary of organic carbon substrates, their pairwise correlation factors, P-values, and Chemical Guilds.

Axis #	Substrate	Correlation	N	P-value	Chemical Guild
Axis1	AKTBA	-0.56669	20	0.00918	Carboxylic Acid
Axis1	BMDG	-0.49743	20	0.025641	Carbohydrate
Axis1	DGAL	-0.69325	20	0.000701	Carboxylic Acid
Axis1	DGLA	0.48765	20	0.029177	Carboxylic Acid
Axis1	DGLP	-0.63829	20	0.002457	Miscellaneous
Axis1	DMAL	-0.58753	20	0.006449	Carboxylic Acid
Axis1	DMAN	0.816389	20	1.13E-05	Carbohydrate
Axis1	DYXL	0.449349	20	0.046853	Carbohydrate
Axis1	FHBA	-0.52612	20	0.01718	Carboxylic Acid
Axis1	GLGA	0.603352	20	0.004856	Amino Acid
Axis1	LARG	-0.51112	20	0.021268	Amino Acid
Axis1	LASP	-0.64801	20	0.002003	Amino Acid
Axis1	LPEHN	0.620287	20	0.003525	Amine/Amide
Axis1	LTHRE	0.706672	20	0.000495	Amino Acid
Axis1	PHEM	0.577716	20	0.007638	Amine/Amide
Axis1	PUT	0.692508	20	0.000714	Amine/Amide
Axis1	TWEE	0.481448	20	0.031612	Polymer
Axis1	YHBA	-0.50301	20	0.02378	Carboxylic Acid
Axis2	DGAYL	0.667277	20	0.001308	Miscellaneous
Axis2	DGLP	0.464556	20	0.039053	Miscellaneous
Axis2	GLGA	-0.56905	20	0.008831	Carboxylic Acid

Axis2	GLYCO	-0.59852	20	0.005304	Polymer
Axis2	LPHEN	-0.44637	20	0.04851	Amine/Amide
Axis2	LSER	-0.49802	20	0.025439	Amino Acid
Axis2	NADG	0.57611	20	0.007848	Carbohydrate
Axis2	PHEM	-0.70775	20	0.000481	Amine/Amide
Axis2	YHBA	0.461961	20	0.040307	Carboxylic Acid

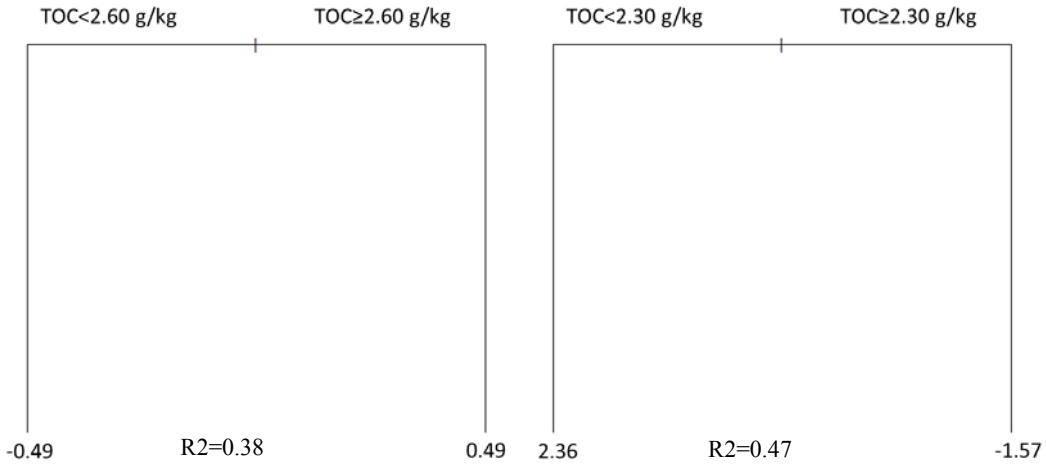

Figure 137. Regression tree analysis for NMS axis score 1 (Left) and NMS axis score 2 (Right) explained by environmental variables of Soil Respiration (SR), Total Organic Carbon (TOC), Temperature ^{0}C (Ts) and barometric air pressure (mbar); however, only TOC best explained both axis (n=20)

Regression tree analysis for Biolog Ecoplate NMS axis scores explained by SR, temperature, TOC, VWC, and barometric air pressure were best explained by total organic carbon (Figure 17, R^2= 0.38 and 0.47, Axis1 and 2, respectively). TOC less than 2.60 g/kg usually resulted in the consumption of mainly carboxylic acids, with select carbohydrates and amino acids for Axis 1. TOC concentrations greater than 2.60 g/kg resulted in the consumption of amines/amides, amino acids, and carbohydrates.

For NMS Axis 2, if TOC concentrations were lower than 2.30 g/kg, then microbial consumption of organic compounds was limited to amines/amides, amino acids, carboxylic acids, and polymers. If TOC was greater than 2.30 g/kg, then mostly “miscellaneous” and other carbohydrates and carboxylic acids were consumed (Table 10).

Discussion

Within the Chihuahuan Desert, grasslands/shrublands cover 95.6+/-2.3 percent of the area (Ruhlman, Gass, & Middleton, 2012), thus, results presented here, could be useful in modeling carbon effluxes in the region, particularly due to abiotic environmental variables.

Previous studies have found that soil respiration in the Chihuahuan Desert ranged from 167 to 708 mg CO2 m-2 hr-1 under summer precipitation events, which is higher than for some forest ecosystems (Parker, L.W., Miller & Steinberger, 1983). In the Sonoran Desert, soil respiration beneath the plant canopy ranged from 183.3-476.6 mg CO2 m-2 hr-1 and was 110 to 256.66 mg CO2 m-2 hr-1 for plant interspace soils under artificial re-wetting (Sponseller, 2007). In the Mojave, SR from soils fertilized with nitrogen and carbon ranged from 0.39-1.49 mg CO2 m-2 hr-1 (Schaeffer et al., 2003). In this study, SR ranged from 20-154.7 mg CO2 m-2 hr-1, and was well within the range of SR reported, even though the SR from preceding studies were largely derived from artificial rewetting or fertilization experiments. A wider range of SR from our site may become available as the annual dataset is completed.

We established that seasonal dynamics were critical in explaining carbon released from desert soils into the atmosphere with SR minima of 20 mg CO2 m-2 hr-1 in the winter and spring maxima of 154.7 mg CO2 m-2 hr-1. Similar results have been observed in studies focused on different arid habitats, where seasonal SR changes were controlled by soil moisture and temperature variability (Cable et al., 2012; Fernandez et al., 2006; Raich, J.W. and Schlesinger, 1992; Tang, Baldocchi, & Xu, 2005). In particular, higher SR was observed in warmer seasons, as opposed to cooler seasons, which is similar to trends found by Fernandez et al. (2006) and Jassal et al. (2005). SR was most strongly related to temperature during the late summer season. Such a relationship could be the result of microbial decomposition, due to the compounded effect that frequent precipitation pulses and high temperatures have on microbial activity.

Comparison of seasonal trends in efflux and precipitation showed that late summer monsoon season spikes in SR were often a result of precipitation events. However, regression tree analyses indicated that during periods of warmer temperatures, including spring and summer, temperature alone was a more important predictor of SR. Conversely, VWC played a more important role in explaining efflux during the colder seasons. In previous works in the cold desert by Fernandez et al. (2006) higher soil moisture also produced higher SR in cool seasons. Similarly, in the present study, the occurrence of higher VWC yielded higher respiration in the cold seasons. Such responses could be the result of soil water becoming too cold for microbial metabolism activation; therefore, decreasing efflux. However, warmer season efflux did not show such a complex co-dependency. Seasonal analyses found an air pressure-specific response for warmer seasons.

Barometric pressure was an important driver of SR during the warmer seasons and was associated with the highest observed SR values ranging from 84-111.05 mg CO2 m-2 hr-1. Changes in atmospheric pressure brought on by wind currents, referred to as pressure pumping, have been found to have a positive effect on the release of trace gases, such as CO2, from soils (Takle et al., 2004). Kimbal and Lemon (1971-1972) and Paw-U and others (2004) reported similar phenomena, where wind turbulence increased pressure pumping, forcing soils to emit CO2. We found a threshold for barometric pressure at 862.31 mbar, where higher air pressures yielded lower efflux and lower pressures generated higher efflux. This suggests that abiotic processes, specifically atmospheric pressure and wind currents, were responsible for controlling soil gas diffusivity, but at a very specific threshold. Further research on eddy-covariance turbulence, which was collected during a related study, and wind velocity is likely to further explain the relationships between barometric air pressure and SR during the summer season. Soil efflux measured from March to May was some of the highest SR measured, despite having no antecedent precipitation pulses and low VWC. Emmerich (2003) debated that in such conditions, microbial respiration cannot be considered an important contributor to SR, because of the absence of

significant VWC. Rather, the dissolution of CaCO3 or UV radiation litter decomposition would better explain carbon effluxes in such situations (Austin & Vivanco, 2006; Emmerich, 2003; Stevenson & Verburg, 2006). Work by Stevenson and Verburg (2006), showed 20-30% of SR to be a result of CaCO3 dissolution from sterile soils. Such results may explain why there was no difference between warm and moist and warm and dry soil observed in the present study. CO2 efflux during the Warm and Dry seasons could be the result of inorganic carbon losses (Eq. 1 below). Emmerich (2003) showed that warm and dry CaCO3 rich soils with lower water content, similar to the soils found at the research site, release higher volumes of CO2.

Equation1. $CaCO_3\ (s) + CO_2\ (g) + H_2O\ (l) \leftrightarrow Ca_2^+(aq) + 2HCO_3^-(aq).$

Increased water availability increases microbial activity, leading to significantly higher CO2 release (Jassal et al., 2005). However, in other studies, long-term exposure to solar radiation and decreased cloud cover have been found to explain more of the variation in aboveground soil litter decomposition than the presence of soil water alone (Austin & Vivanco, 2006). Clearly, a combination of multiple environmental factors contributes to higher CO2 efflux from soils.

In the present study, strong correlations between carbon efflux and solar radiation were found, where higher radiation led to higher efflux from soil. Through these results, we can conclude that even the lowest levels of radiation, and even those that are lower than the seasonal maxima, affect carbon efflux from soil. Though this might be the result of confounding effects of radiation and temperature, radiation has been reported to affect seasonal efflux of other carbon gases (Galbally, Kirstine, Meyer, & Wang, 2008). The absence of precipitation pulses from March to May, indicate that the high SR was likely due to the compound effect of solar radiation or temperature on decomposition and CaCO3 dissolution (Austin & Vivanco, 2006; Emmerich, 2003). Future laboratory experiments on litter decomposition under UV light radiation might be able determine and isolate the rate of carbon losses due solely to decomposition caused by solar radiation independent of other factors.

The effects of root respiration on SR and their temporal effects on efflux might explain higher efflux rates found in the spring season compared to the summer season which coincidentally had lower soil moisture than the summer season. Previous works have found that growing season root respiration dominates SR (Tang et al., 2005). Understanding plant phonological responses to weather and climate will allow us to specifically determine plant-soil and soil-atmosphere interactions related to plant growth, root respiration, and carbon uptake for photosynthates.

NMS analysis indicated that soil microbial carbon substrate use was related to TOC. These results suggest that microbial communities and their activity depend on the availability of labile carbon sources. This specificity could be the result of microbial ecological adaptations to present labile carbon (Zak, John C, Willing, Michael R., Moorhead, Daryl L., and Wildman, 1994). These results also indicate that TOC concentrations decrease when select amines/amides, amino acids, and carbohydrates were consumed. We can conclude that biologic carbon cycling by soil microbes occurred and that they consumed labile forms of carbon, even in dry seasons. Labile organic carbon decomposition depended on the quality of carbon, specific to chemical guilds available. However, NMS analysis found no similarities in microbial functional diversity among soils of the same plant type or litter gradients or within seasons. Unique microbial functional communities were ubiquitous among plants of the same type; spatial homogeneity found in SR, indicated that functional diversity of microbial communities had little impact on SR. Further analyses on exact quantification of microbial respiration with MicroResp assays could provide clues to its percent release from soils.

Previous publications have found spatial heterogeneity in SR and microbial functional diversity defined by plant types in arid ecosystems (Cable et al., 2012; Sponseller, 2007; Yu & Steinberger, 2012; Zak, John C, Willing, Michael R., Moorhead, Daryl L., and Wildman, 1994), however, we found no difference in SR among three dominant habitat types in Chihuahuan Desert shrublands. Our results do not support our initial hypothesis that soils with higher organic matter, especially soil crusts, would emit

the most CO2 from the three habitat types and that functional diversity would vary depending on plant types. The similarity among our sampling units may be due in part to the relatively constant plant sizes and water availability throughout our sampling area. Conversely, shrubs located closest to washes or "arroyos" would be greater in size but were not represented in this study. Similarly, islands of fertility, which define spatial regions particularly rich in organic matter and microbial activity, would increase in areas of enhanced water availability. Plant size, health and islands of fertility are interrelated factors, which have been shown to result in differential microbial composition and carbon efflux(Austin et al., 2004; Cable et al., 2012; Herman et al., 1995; Megías, Sánchez-piñero, & Hódar, 2011; Sponseller, 2007; White, Welty-Bernard, Rasmussen, & Schwartz, 2009). Similarity among different plant treatments may also be attributed to experimental design bias, since plots were chosen semi-haphazardly; additionally, treatments were only included 2 replicates, which decreased statistical power in the analyses performed.

These analyses and datasets are integral in providing key land-atmosphere interactions at the JER research site. Up-scaling and partitioning from ground level efflux to eddy tower measurements will now be possible. High percentage contributions from SR to the landscape level are expected, since other ecosystem efflux rates were within the ranges presented here. All analyses suggest warmer season soils have statically higher emissions, behave differently to cooler season soils and that SR were abiotically controlled by temperature, barometric air pressure, and VWC. Furthermore, microbial functional diversity among plant types appears to have no effect on carbon effluxes.

Future Research Directions

Future research priorities should focus on up scaling of ground-level fluxes to eddy covariance tower measurements in order to determine percent contributions of SR from soils to ecosystem level fluxes. The coupling of plant phenological data with ground based efflux will help determine the

relative contribution of root respiration resulting from precipitation pulses. Furthermore, the aluminum chamber bases used in this project may contribute to artificial heating within individual soil plots; a pilot study measuring temperature within and outside the aluminum bases should help define if any confounding effects exist. In the case that artificial heating occurs, PVC soil collars should be installed instead, as typically used by the soil science community. A larger set of bases should also be randomly placed in the area directly opposite of the eddy covariance tower for continuous monitoring with newer and more appropriate field technologies such as the Li-Cor 6400. As for microbial effects on litter decomposition, a study using litter bags to examine UV litter decomposition could help provide information on the contributions of other radiation effects on litter degradation. Soil flux partitioning of microbial, root, and inorganic SR are important and should be collected in order to complete a robust shrubland SR model. Furthermore, an increased number of microbial community physiological profiling replicates per mesquite and creosote soils, as well as other dominant vegetation species' soils such as bush muhly (*Muhlenbergi porter*) and tar bush (*Flourensia cernua*) should be conducted. Seasonal Microresp microbial assays and soil biomass analyses would provide microbial-specific contributions to SR and a better understanding of seasonal growth and activities. Finally, analyses on $CaCO_3$ dissolution rates need to be quantified to determine exact SR percent contributions from inorganic carbon.

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Appendix A

Table 6A. ANCOVA for Soil Respiration, Temperature and Litter, Bonferroni corrected alfa is 0.0025.

Litter	Effect	P-value
MI v. MC	Temperature	0.0002
	Litter	0.7665
	Temp*Litter	0.7532
MI v. MCE	Temperature	0.00025
	Litter	0.7064
	Temp*Litter	0.8873
MCE v. MC	Temperature	0.0025
	Litter	0.5087
	Temp*Litter	0.6528
CI v. CC	Temperature	0.0131
	Litter	0.2270
	Temp*Litter	0.5539
CI v. CCE	Temperature	0.0024
	Litter	0.43219
	Temp*Litter	0.9678
Cl v.MI	Temperature	3.76e-07
	Litter	0.390
	Temp*Litter	0.967
CI v. MCE	Temperature	5.32e-07
	Litter	0.669
	Temp*Litter	0.602
CI v. MC	Temperature	2.75e-05
	Litter	0.0894
	Temp*Litter	0.5923
CCE v. MI	Temperature	6.91e-06
	Litter	0.0859
	Temp*Litter	0.9009
CCE v. MCE	Temperature	7.55e-06
	Litter	0.192
	Temp*Litter	0.595
CCE v. MC	Temperature	0.0001
	Litter	0.0182
	Temp*Litter	0.6953
CC v. MI	Temperature	0.0001
	Litter	0.4397
	Temp*Litter	0.4548
CC v. MCE	Temperature	9.6e-05
	Litter	0.296
	Temp*Litter	0.281
CC v. MC	Temperature	0.0018
	Litter	0.9388
	Temp*Litter	0.8335
C v. CI	Temperature	0.0001

	Litter	0.9586
	Temp*Litter	0.8922
C v. CCE	Temperature	0.0004
	Litter	0.0187
	Temp*Litter	0.4890
C v. CC	Temperature	0.0048
	Litter	0.9049
	Temp*Litter	0.9291
C v. MI	Temperature	4.02e-14
	Litter	0.0863
	Temp*Litter	0.8493
C v. MCE	Temperature	4.44e-05
	Litter	0.214
	Temp*Litter	0.203
C v. MC	Temperature	0.0010
	Litter	0.9622
	Temp*Litter	0.7427

Vita

Anna Ortiz earned her Bachelor's Degree from the University of Texas at El Paso of Environmental Science in 2011. She then continued to pursue a Master's Degree under the supervision of Dr. Vanessa Lougheed in Environmental Science with a focus in soil ecology. Ms. Ortiz has received numerous awards and scholarships: 2nd Place 2013 UTEP Geology Colloquium Oral Presentation, NSF GRFP Honorable mention, and UTEP's Graduate School Dodson Research Grant. She has received travel awards to Indoor Air 2011, SACNAS 2011, fellowships from UTEP's NSF funded Undergraduate Research and Mentoring and GK-12. She has also attended the Jornada Centennial Symposium 2012 and ESA 2011. Ms. Ortiz also has publication as a result of an undergraduate internship from the proceeding of the 2011 Indoor Air Conference.

This thesis was typed by Anna Ortiz.