VEGETATION AND ENVIRONMENTAL CONTROLS ON SOIL RESPIRATION IN A PIÑON-JUNIPER WOODLAND

BY

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B.S., ENVIRONMENTAL ENGINEERING, NEW MEXICO TECH, 2006

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

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ABSTRACT

Soil respiration (R_S) responds to changes in plant and microbial activity and environmental conditions. In arid ecosystems of the southwestern USA, soil moisture exhibits large fluctuations because annual and seasonal precipitation inputs are highly variable, with increased variability expected in the future. Patterns of soil moisture, and periodic severe drought, are often cited as a principal control on ecosystem processes such as R_S. To understand the influence of temperature, soil moisture, and other environmental variables on R_S, we compared R_S and micro-meteorological data from a piñon-juniper woodland at the Sevilleta LTER in central New Mexico during August 2006 to August 2007 and compared four models applied to the data. We measured autochamber soil respiration ($R_{S\text{-}A}$) using 8 high frequency automated chambers that each measured 20 times per day and ecosystem soil respiration ($R_{S\text{-}E}$) using a LICOR LI-6200 to measure 108 spatially distributed measurements each month. Ecosystem soil respiration sampling included soil between trees (interspace) and under the canopies of

piñon (*Pinus edulis*) and juniper (*Juniperus monosperma*) while R_{S-A} measured only interspace and piñon sub-canopy. Annual R_{S-E} was highest under piñon (491 ± 28.9 g C m^{-2} yr^{-1}) followed by juniper (448 ± 26.4 g C m^{-2} yr^{-1}) and interspaces (361 ± 38.9 g C m^{-2} yr^{-1}). Ecosystem soil respiration was scaled up to plot-level R_S (401 ± 34.0 g C m^{-2} yr^{-1}) using percent ground cover. Under piñon, R_{S-A} increased with soil temperature, while interspaces showed a positive trend for low temperatures below 25.8 °C and negative trend for temperatures above 25.8 °C. The soil temperature range was smaller under piñon than in interspaces. During the dry period, R_{S-A} under piñon decreased for increasing soil moisture indicating soil moisture was not limiting R_{S-A} under dry conditions. Under piñon and in interspace, R_{S-A} response did not differ for pulses smaller than 3 mm ($P = 0.64$), while R_{S-A} response under piñon was greater than in interspaces for pulses over 3 mm. The best fit models for R_{S-A} under piñon ($r^2 = 0.83$) and in interspace ($r^2 = 0.86$) contained the following variables: soil temperature; soil moisture; photosynthetically active radiation; and vapor pressure deficit. Changes in soil moisture and soil temperature had the biggest impact on modeled R_{S-A}. Predicting how climate change will affect this expansive ecosystem will require an understanding of the complex R_S responses in this ecosystem.

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CHAPTER 1 INTRODUCTION

Soil carbon makes up the largest carbon pool in terrestrial ecosystems (Post *et al.*, 1982; Dixon *et al.*, 1994). Soil respiration (R_S), the efflux of CO_2 from soil to the atmosphere, offsets gross primary production and aboveground respiration, a small factor, to determine net ecosystem exchange of CO_2 (Lavigne *et al.*, 1997; Goulden *et al.*, 1996; Law *et al.*, 1999a; Curtis *et al*., 2005), which is a key process in the global carbon cycle (Schlesinger, 1991; Schimel, 1995; Raich *et al.*, 2002). The main environmental factors controlling R_S in current models are soil temperature and precipitation (reflected in soil moisture) (Zhou *et al*., 2007; Vargas & Allen, 2008; Jin *et al*., 2008), both of which are predicted to change in the future (IPCC, 2007; Coops & Catling, 2002; Cook *et al.*, 2004). Since changes in model variables will be reflected in predicted R_S (Raich *et al.*, 2002). It is important that models of R_S in arid and semiarid ecosystems correctly incorporate the empirically determined relationships between environmental variables and R_S.

Water, the limiting factor in arid environments, occurs as precipitation pulses that vary in duration and magnitude (Austin *et al*., 2004). Precipitation pulses are important for heterotrophic and autotrophic organisms in semiarid ecosystems (Noy-Meir, 1973), which respond differently to pulse sizes, frequency, and on different time scales (Austin *et al.*, 2004; Huxman *et al.*, 2004; Weltzin *et al.*, 2003). Microbes in surface soils respond to small pulse events (Austin *et al.*, 2004; Schwinning & Sala, 2004), while plants are more responsive to larger pulse events (Huxman *et al.*, 2004). Precipitation increases soil moisture, while the depth of infiltration is mainly controlled by soil texture

(Austin *et al.*, 2004) and overland flow in the form of runoff and runon (Loik *et al.*, 2004; Sponseller & Fisher, 2008) and cover type (Bhark & Small, 2003). Soil evaporation is a function of microclimate and soil texture, and coarse textured soils dry down faster than fine-textured soils (Austin *et al.*, 2004). Microbial activity, which is known to exist in the top few centimeters (Garcia-Pichel & Belnap, 1996; West & Skujins, 1978), is limited under low soil moisture conditions (Fierer *et al.*, 2003), when access to C substrates becomes limited (Grant & Rochette, 1994). In contrast, high soil moisture limits oxygen diffusion and decreases aerobic decomposition (Jassal *et al.*, 2008). Precipitation events result in a variety of ecosystem conditions that influence R_S.

Studies have shown that R_S responds to changes in soil temperature (e.g. Lloyd & Taylor, 1994; Kirshbaum, 1995; Moncrieff & Fang 1999; MacDonald *et al.*, 1995; Rochette *et al.*, 1991; Dioumaeva *et al.*, 2002), soil moisture (e.g. Davidson *et al.*, 2000; Law *et al.*, 1999b; Reichstein *et al.*, 2002), and photosynthesis (e.g. Tang *et al.*, 2005a; Jassal *et al.*, 2008; Högberg *et al.*, 2001; Curiel Yuste *et al.*, 2007). Responses of R_S on spatial and temporal scales are complex (Hanson *et al.*, 1993). Many studies have modeled R_S as a function of soil temperature using an exponential relationship (e.g. Zhou *et al.*, 2007; Jin *et al.*, 2008; Savage & Davidson, 2003). Soil temperature and R_S are highly correlated due to temperature effects on microbial activity, root respiration, and diffusion (Jassal *et al.*, 2008). Soil moisture affects microbial activity (Orchard and Cook, 1983) as well as plant growth and respiration. Photosynthetically active radiation controls photosynthesis affecting root respiration and production of root exudates, which in turn affects microbial respiration (Fang & Moncrieff, 2001). In addition to light, vapor pressure deficit also affects photosynthesis through its effects on stomatal control (Nobel,

2005; McDowell *et al.*, 2008a). Such fundamental interaction may improve modeling of autotrophic respiration and thus help understand the controls on soil respiration.

Spatial heterogeneity is characteristic of semiarid environments due to the patchy distribution of resources, organisms, microclimate, and topography (Schlesinger & Pilmanis, 1998; Xu & Wan, 2008; Sponseller, 2007; Sponseller & Fisher, 2008). Furthermore, soil respiration varies at temporal scales ranging from hourly to annually (Savage & Davidson, 2003). Coupling automated chambers with monthly spatially distributed ecosystem soil respiration ($R_{S\text{-}E}$) measurements (located across the site is recommended to capture the ecosystem temporal and spatial variation (Savage & Davidson, 2003; Ryan & Law, 2005).

Piñon-juniper woodlands consist of about 22.5 million hectares in the Southwest, USA (Laycock, 1997). Headwater forests in the Middle Rio Grande watershed experienced 40 to 95% mortality of piñon-pine (*Pinus edulis*) along with a 2-25% mortality of juniper (*Juniperus monosperma*) in 2002 and 2003 (Breshears *et al.*, 2005; Shaw *et al.*, 2005). The mortality occurred in response to drought (Ogle *et al.*, 2000) and bark beetle infestations that extirpated piñon in some areas and left juniper woodlands (Breshears *et al.*, 2005). Impacts of this mortality on ecosystem respiration remain unknown. Soil respiration has been less studied in semiarid ecosystems than other regions (Raich & Schlesinger, 1992), and only a handful of R_S studies have been conducted in semiarid woodlands (e.g. Conant *et al.*, 2000). Soil respiration has not previously been measured using temporal and spatial techniques in piñon-juniper woodlands.

The piñon mortality prompted design of an experiment to examine baseline R_S rates under piñon canopies and in intercanopies (hereafter referred to as interspaces), which include grasses and bare soil, to predict R_S in this woodland and how it may change with mortality and climate change. We measured high frequency autochamber soil respiration (R_{S-A}) and low frequency spatially distributed, ecosystem soil respiration (R_{S-E}) along with accompanying soil temperature and soil moisture to capture the temporal and spatial differences across cover types. We compared our data to four different models driven by environmental data to investigate which variables and functions best predicted R_{S-A} in this semiarid woodland. In addition, we considered whether the controls over R_S in this woodland ecosystem are similar to those in forest and grassland ecosystems.

CHAPTER 2 METHODS

Site Description

The study site is located in piñon-juniper woodland on the eastern slope of the Los Pinos mountains on the Sevilleta National Wildlife refuge in central New Mexico, USA (N34 24' W106 32') ~1900 m asl. Mean annual precipitation near the site is 370 mm (Moore, 2008; Shulka et al., 2006) with a distribution typical of an arid monsoonal climate, where most of the summer rainfall occurs in late summer (July through September). Typically, about 45% of annual rainfall occurs during the monsoon season (Bowen, 1996), however in the defined monsoon period for 2006 presented here (DOY 182-275), only 26.5% of the yearly total was recorded and additional precipitation (71.2 mm in three days) occurred within 10 days after this period ended. This study was conducted from August 2006 to August 2007, during which the site received 348 mm of rainfall.

This project was part of a larger effort to determine the overall response of a piñon-juniper woodland to rainfall manipulations, but the study presented here was conducted prior to installation of the rainfall manipulations. The site consisted of 12 square plots, each 40 m on a side, arranged in 3 blocks of 4 plots. One block is nearly flat and has deeper soils. A second block is north, northeast facing, while the third block is southeast facing. Soil characteristics at the site ranged from silty loam to sandy loam, and there is a minimum of 40 cm of soil above bedrock across the plots. The soils contained 9.2% clay (±5.5 stdev; n = 50), 14.9% fine silt (±3.8 stdev; n = 50), 34.5% coarse silt (±13.1 stdev; n = 50), and 41.3% sand (±16.9 stdev; n = 50).

Piñon pine (*Pinus edulis*) and one seed juniper (*Juniperus monosperma*) are the dominant tree species at the site, with little ground vegetation cover under canopies. Blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eriopoda*) are the dominant grasses, which are located primarily in interspaces where they have about 30% ground cover. Other interspace vegetation include scrub oak (*Quercus turbinella*) (Dick-Peddie, 1993), cactus (prickly pear, *Opuntia polyacantha*; and cholla, *Opuntia impricata*), and *Yucca baccata*.

In order to scale up soil respiration to the plot-level, we estimated the percentage aerial canopy cover of each species to calculate a weighted flux based on the relative cover of each species. Percentage canopy cover was estimated by measuring the basal diameter of all piñon and all juniper individuals present in the plots and applying local allometric equations that predicted aerial canopy cover based on tree basal diameter. Based on this approach, the overall percentage canopy covers were 9.8% for piñon, 31% for juniper, and 59.2 % as interspace.

Spatially Distributed, Ecosystem Soil Respiration (R_{S-E}) Measurements

To capture the spatial heterogeneity of ecosystem soil respiration (R_{S-E}), we made monthly measurements of spot collars on all plots. Nine soil collars (3 collars under piñon canopy, 3 collars under juniper canopy, and 3 collars in tree canopy interspaces) were measured on each of the 12 plots using a gas exchange system (LI-6200; Li-Cor, Lincoln, NE USA) plumbed in a closed loop. The LI-6200 was connected using 6.4 mm bev-a-line tubing to a 200 mm inside diameter PVC cap. Soil collars had a 305 mm outer diameter to minimize edge effects, and were buried at least 20 mm in the ground to

obtain a soil seal. The cap, collar, and tubing contained an average volume of 5.8 L of air at room temperature. Soil moisture and soil temperature were measured adjacent to each collar during each measurement. Soil moisture (% per volume) was measured with a handheld water content reflectometer using 120 mm rods (Hydrosense, Campbell Scientific, Logan, UT USA). Soil temperature (^{o}C) was measured using a handheld controller (HH509; Omega Engineering, Stamford, CT USA) and Omega temp sensor (type E). Air temperature (^{o}C) was measured on site at a centrally located meteorological station and 10-300 m from the plots. Collars were deployed in a single installation a week before the first measurements in September 2006 and were not relocated during the duration of the study. A few collars were re-adjusted at their local spot as needed if dislodged by erosion or other disturbances. In these instances, collars were reset at least 24 hours before measurement to minimize root injury or soil disturbance influences on the measurements. In addition, dark measurement conditions allowed for living vegetation to be left intact in order to minimize root injury and/or decomposition error in measurements. The monthly measurements were not conducted when snow was present (late December 2006 and January 2007) or when the ground was too soft to conduct measurements without disturbing the soil surface (February 2007).

Multiple R_{S-E} measurements were made at each collar and averaged to calculate the final R_{S-E} value. Each measurement of CO_2 accumulation in the closed chamber system over time consisted of four points, each taken over a 4 ppm change in CO_2 concentration for a total change of 16 ppm. Ecosystem soil respiration was calculated in accordance with Rochette *et al*. (1997). In December when respiration rates were low, three points were recorded each over a 3 ppm CO_2 change (9 ppm total). This adjustment

was done to allow all 108 collars to be measured during the same day. Spatial, ecosystem measurements did not start until two hours after dawn (sunrise) and stopped two hours before dark (sunset) due to quick temperature changes during those time periods.

High Frequency Autochamber Soil Respiration ($R_{S\text{-}A}$) Measurements

A high frequency, nearly continuous automated system was employed to capture the temporal dynamics of R_S (henceforth referred to as autochamber soil respiration, $R_{S\text{-}A}$). The automated system was based on the design of Wayson *et al.* (2006). The system used a closed chamber design and was equipped with a LI-800 (LI-COR Lincoln, NE USA) infrared gas analyzer (IRGA) and 8 chambers located 20 to 70 m from the IRGA. The automated system cycled through all 8 chambers every 1.2 hours and each chamber cycled in 10 min, which yielded 20 cycles per day. The 10 min measurement cycle started with a 3 min expunge period with the lid open and was followed by a 7 min measurement period with the lid closed. During the measurement period, CO_2 was recorded as it increased above ambient, and the slope (change in $[CO_2]$ over time) was calculated using least squares regression (Rochette *et al.*, 1997). This system did not scrub below ambient before the measurement period. Each chamber consisted of a 254 mm diameter clear lexan cylinder that penetrated about 25 mm into the soil, stood 191 to 203 mm above the soil, and contained about 22 L of air at room temperature (including tubing to chamber). A ring of 12.7 mm tubing with a row of holes, spaced one centimeter apart, was positioned parallel to the ground and 5 mm from the soil surface to allow air from the IRGA back into the chamber. A single open 12.7 mm tube centered in the upper half of the chamber served as the air intake from the chamber to the IRGA, which was

similar to the method used by Goulden and Crill (1997) to minimize chamber dead space. A pneumatic piston opened and closed the lid, and held the lid in both the closed and open positions. The lid also had a counterbalance, which kept it open if the pneumatic system malfunctioned. A datalogger (CR10X, Campbell Scientific, Logan, UT, USA) controlled the automated chamber lids as well as sampling lines and data collection.

A standard addition cycle allowed calculation of the effective chamber volume daily for each chamber. Standard addition was run during the fourth cycle of each day that took place at about 3:00 am local time. To calculate the effective volume, we used a 200 ppm CO_2 addition to the measurement lines at known rate (set between 5 and 10 mL min^{-1}). The standard addition was tested in the laboratory using a water seal and implemented using the method described in Goulden and Crill (1997). We used the average effective volume for 2006 for each chamber to calculate the respiration rates for the study period and corrected for pressure and air temperature, which were measured near the IRGA. The IRGA was calibrated with standard CO_2 gas (775 ppm) every two months, which was sufficient to keep the IRGA from drifting significantly between calibrations.

One chamber was located under piñon canopy and one in tree interspace (bare ground) for each of 4 plots. No automated chambers were located under juniper canopy because the limited number of available chambers would not permit minimum replication across 3 cover types. The automated system ran during and after snow events. However, data impacted by these events were excluded during analysis since snow can alter $R_{S\text{-}A}$ compared to the actual rate due to storing CO_2 as well as increased sensitivity to pressure gradients and snow melt (Ryan & Law, 2005). Data was excluded from analysis when

vegetation cover occurred in the chambers and four days after vegetation removal. Vegetation was removed from the clear-sided autochambers to minimize the influence of photosynthesis and root growth and decay on the measurements. This only occurred in one chamber during the 2006 rainy season.

Starting January 03, 2007 (DOY), daily soil moisture was measured at 5-10 cm depth near each high frequency, R_{S-A} and low frequency, R_{S-E} measurements with EC-20 probes (Decagon, Pullman, WA, USA). Air temperature was measured 30.5 cm above the soil near the IRGA, while soil temperature at 5 cm depth was measured at each chamber. Photosynthetically active radiation (LI1905B-L; Li-Cor), rain (TE525WS-L Texas Electronics), air temperature (HMP 45C-L,Campbell Sci.), and relative humidity (HMP 45C-L,Campbell Sci.) were measured 1.2 m above the ground at 30-minute intervals. Air temperature and relative humidity were used to calculate vapor pressure deficit (the difference between saturation vapor pressure at leaf temperature - here air temperature - and atomospheric vapor pressure).

Statistical Analysis

Data analysis was structured using periods with common climatic characteristics that corresponded with seasonal temperature and precipitation regimes. A cold period, corresponding with winter, was defined by daily minimum air temperature below 0 °C. The warming period (spring season) was defined as the transition between winter and summer. Summer was broken into two periods, (1) a dry period defined by high daytime air temperature and low soil moisture and (2) a monsoon, rainy, period when air temperature was high but convective storms increase soil moisture. The cooling period

was the transition between summer and winter when the soils start to dry out after the monsoons and maximum air temperature decreases. The following Julian day ranges (from 2006 to 2007) define these periods: (1) cold period 326-65; (2) warming period 66-148; (3) dry period 149-181; (4) monsoon 182-276; and (5) cooling period 277-325. Due to autochamber equipment malfunctions, there were insufficient R_{S-A} data to include the cooling season in the cross-season comparisons. Data collected during cooling season, however, were included in the full year data set for modeling R_{S-A}.

All statistical analyses were conducted using the Analyst program in SAS (SAS Institute Inc., Cary, NC USA) version 9.1.3. Repeated measures ANOVA was used to test differences across seasons and cover types using an alpha level of 0.05. Model fitting used multivariate linear regression of linearized models [Eqns (1-4) below] to examine controls on R_{S-A}. We used root mean squared error (RMSE) and r^2 values to select the best two statistical models, which were used for further comparisons. For the purpose of modeling, gaps in the soil moisture record, which was available on daily time scale, were filled using linear interpolation. Soil temperature and R_{S-A} were averaged by cover type before analysis. Autochamber soil respiration data under juniper were modeled using multivariate linear regression. To estimate annual and seasonal R_S, highly replicated R_{S-E} measurements were linearly interpolated by plot and cover type. The percent of annual R_S released in response to rain (pulse) events was calculated by comparing annual R_{S-A} with (complete data set) and without pulses using linear interpolation to fill gaps generated by removing pulse R_{S-A} values. Ecosystem soil respiration was scaled to the plot-level using a weighted mean based on percent ground area covered by measurements for piñon, juniper, and interspace conducted at the site.

Modeling

We examined different empirical models of $R_{S\text{-}A}$. The four different model forms are as follows: Eqn (1) - soil temperature and soil moisture exponential and power functions respectivley (Xu & Qi, 2001; Chen *et al.*, 2003); Eqn (2) - exponential soil temperature and soil moisture functions (Reiners, 1968; Tufekcioglu *et al.*, 2001); Eqn (3) - power functions for vapor pressure deficit and photosynthetically active radiation added to Eqn (1) because they directly influence physiological parameters; and Eqn (4) - Eqn (3) with soil temperature modified to a second order exponential function.

$$R_{S-A} = ae^{(bT_S)} * SM^{c} \quad (1)$$

$$R_{S-A} = ae^{(bT_S)}e^{(cSM)} \quad (2)$$

$$R_{S-A} = ae^{(bT_S)} * SM^{c} * VPD^{f} * PAR^{g} \quad (3)$$

$$R_{S-A} = ae^{(bT_S + dT_S^2)} * SM^{c} * VPD^{f} * PAR^{g} \quad (4),$$

where $R_{S\text{-}A}$ is autochamber soil respiration (μmol m^{-2} s^{-1}), T_S is soil temperature at 5 cm (°C), *SM* is soil moisture (volumetric water content) measured across 5-10 cm (%), *VPD* is vapor pressure deficit (kPa), *PAR* is photosynthetically active radiation (μmol m^{-2} s^{-1}), and *a*, *b*, *c*, *d*, *f*, and *g* are coefficients.

Models similar to Eqn 3 have been used in Mediterranean ecosystems (Xu *et al.*, 2004; Tang *et al.*, 2005b; Tang *et al.*, 2005c) and a mixed conifer forest (Vargas & Allen, 2008). Eqn (3) was designed to incorporate the climate parameters shown to influence soil respiration in previous studies, and Eqn (4) added a temperature curve. We compared model performance based on RMSE and r^2 values and used the best model(s) in further analyses.

Since the high frequency automated system did not sample under juniper canopies, it was also necessary to develop a model of daily R_S under juniper based on other empirical data collected on site. We modeled R_S under juniper using multivariate linear regression of monthly $R_{S\text{-}E}$ under juniper and $R_{S\text{-}A}$ and soil temperature under piñon. The relationship between mean $R_{S\text{-}E}$ under juniper averaged by plot and corresponding $R_{S\text{-}A}$ and soil temperature under piñon was as follows:

$$jR_{S-E} = 0.524 * pR_{S-A} + 0.116 * pT_S - 0.776 \quad (5),$$

where $jR_{S\text{-}E}$ is ecosystem soil respiration under juniper, $pR_{S\text{-}A}$ is daily autochamber soil respiration under piñon (μmol m^{-2} s^{-1}), and pT_S is soil temperature at 5 cm depth under piñon (°C).

CHAPTER 3 RESULTS

Environmental Controls

High frequency autochamber soil respiration (R_{S-A}) and ecosystem soil respiration (R_{S-E}) varied in response to seasonal and diurnal variation in soil temperature and soil moisture during our measurements (Fig. 1). Annual mean R_{S-A}, soil moisture, and soil temperature were greater under piñon canopies than in interspaces (Table 1, repeated measures ANOVA, $P < 0.01$). Soil temperature and R_{S-A} were lowest during the cold period and highest during the monsoon period when soil moisture was also high. Soil moisture increased with precipitation events, and R_{S-A} pulses corresponded to precipitation events. During the cold period, R_{S-A} under piñon was not different from R_{S-A} in interspaces ($P = 0.53$). Soil moisture ($P < 0.01$) and R_{S-A} ($P < 0.01$) were greater under piñon than in interspaces during the warming period, while soil temperature in interspace was greater than under piñon for the warming, dry, and monsoon periods ($P < 0.01$). For both the dry and monsoon periods, R_{S-A} under piñon was greater than in interspace ($P < 0.01$). Soil moisture dried down further in interspace than under piñon (minimum recorded values of 1.2% and 2.4%, respectively). R_{S-A} in interspace was lower than R_{S-A} under piñon ($P < 0.01$). A response to changes in environmental variables is not limited to R_{S-A} measurements.

Ecosystem soil respiration exhibited similar patterns across season and cover type reaching the highest rates during monsoon (August 2007) and the lowest values occurred during the cold period (February 2007) for all cover types (Table 1). Ecosystem soil respiration under piñon and juniper (Fig. 1) tracked each other over time with significant

differences found only for November ($P = 0.01$) and June ($P < 0.01$), where $R_{S\text{-}E}$ under piñon was greater than under juniper. Ecosystem soil respiration in interspace was lower than under both piñon and juniper during monsoon ($P < 0.01$), but $R_{S\text{-}E}$ in interspace was greater than under piñon and juniper during the warming period ($P < 0.01$), when forbs and some grasses were active.

The automated system allowed us to examine the response of soil respiration to precipitation pulses, which varied with rain event size (Fig. 2). For small rain events (≤3 mm), the percent increase in $R_{S\text{-}A}$ after the pulse ranged from 0-100% but did not differ between interspace or under piñon ($P = 0.64$). Before each pulse, $R_{S\text{-}A}$ under piñon was greater than $R_{S\text{-}A}$ in interspace ($P < 0.01$). Autochamber soil respiration increased in response to rain events larger than 3 mm, though the response was larger under piñon than in interspace ($P = 0.03$). Notably, $R_{S\text{-}A}$ decreased for both cover types after the largest recorded event (29 mm, April 13-14 2007, 8% of annual rainfall). The response of $R_{S\text{-}A}$ to precipitation pulses depends on the size of the pulse.

The impact of soil moisture on $R_{S\text{-}A}$ differed between piñon and interspace cover types (Fig. 3). In interspaces, $R_{S\text{-}A}$ was correlated with soil moisture during the monsoon ($P < 0.01$) but not during the warming ($P = 0.38$) or dry ($P = 0.40$) periods. Under piñon, $R_{S\text{-}A}$ was correlated with soil moisture during each period. Autochamber soil respiration under piñon was negatively correlated with soil moisture during the dry period ($P < 0.01$) and positively correlated with soil moisture during the warming period ($P = 0.04$). During the cold period, $R_{S\text{-}A}$ was positively correlated with soil moisture under piñon ($P < 0.01$) and interspace ($P = 0.02$).

The relationship between R_{S-A} and soil temperature differed for piñon and interspace cover types (Fig. 4). During dry and monsoon periods, mean soil temperature in interspace was 26.9 ± 0.20 °C and 24.6 ± 0.15 °C respectively, while mean soil temperature under piñon was 19.8 ± 0.09 °C and 20.5 ± 0.06 °C respectively. Maximum R_{S-A} in interspace occurred at 25.8 °C, with a positive relationship below the maximum and negative relationship above the maximum. Under piñon, R_{S-A} increased across all measured values of soil temperature but the maximum soil temperature under piñon may not have been high enough to observe a negative relationship as seen in interspace R_{S-A}.

Modeling R_{S-A}

The models containing environmental variables linked to vegetation activity [Eqn (3 and 4)] were the best predictors of R_{S-A}. The two-variable models [Eqns (1 and 2)] had near equal r^2 and RMSE values for both cover types (Table 2). Adding vapor pressure deficit and photosynthetically active radiation to Eqn (1) [Eqn (3)] improved predictions of R_{S-A} by 3% in interspace ($r^2 = 0.77$; RMSE = 0.60) and 11% under piñon ($r^2 = 0.83$; RMSE = 0.49). The predicted values of R_{S-A} from Eqn (4) had the highest r^2 values and lowest RMSE in interspace ($r^2 = 0.86$; RMSE = 0.46) and under piñon ($r^2 = 0.83$; RMSE = 0.48). Using a second order exponential function (adding a squared soil temperature term) [Eqn (4)] incorporates the temperature curve trend seen in Fig. 4 and improved predictions of R_{S-A} by 9% in interspace and <1% under piñon. Since a temperature curve was not seen for R_{S-A} under piñon in Fig. 4 and adding the curve function explained <1% more data, Eqn (3) was used for further analysis of R_{S-A} under piñon, while Eqn (4) was used for further analysis of R_{S-A} in interspaces.

The accuracy of both equations [Eqn (3 and 4)] was largest during the monsoon (rainy) season. Both Eqns (3) and (4) predicted $R_{S\text{-}A}$ with more accuracy during the cold period when $R_{S\text{-}A}$ was low (Fig. 5). During the monsoon, when $R_{S\text{-}A}$ was high, the models for interspace and piñon cover types both showed large residual error. Residual $R_{S\text{-}A}$ under piñon and in interspace showed negative peaks that resembled pulse responses and aligned with precipitation events.

Soil moisture is the main driver of both multivariate, multiplicative models [Eqn (3 and 4)]. Since Eqns (3 and 4) contain four variables represented as either exponential functions or power functions in multiplicative association, all of the variables are directly related. Increasing soil temperature 1 °C causes a 28% increase in R_S in interspaces and a 26% increase in R_S under piñon when all other model variables remain constant. For soil moisture, vapor pressure deficit, and photosynthetically active radiation, the change in R_S is dependent on the initial value and the power coefficient, where R_S is most sensitive to changes in the variable with the largest coefficient. In both interspace [Eqn (4)] and piñon [Eqn (3)] cover type R_S models, soil moisture has the largest coefficient followed by photosynthetically active radiation and then vapor pressure deficit (Table 2). Due to multiplicative association in the models, predicted R_S is a function of the change in the interdependent variables.

Soil Respiration: Methods and Budget

Ecosystem soil respiration measurements showed similar trends to $R_{S\text{-}A}$ but did not capture the variation associated with changes in soil moisture on short time scales that were evident in the autochamber data. In both piñon and interspace, $R_{S\text{-}E}$ was correlated

with $R_{S\text{-}A}$ in all seasons except in interspace during the warming period (Fig. 6C, April-May) when $R_{S\text{-}E}$ was greater than both $R_{S\text{-}A}$ in interspace ($P < 0.01$, Fig. 6) and $R_{S\text{-}E}$ under piñon and juniper. In addition, $R_{S\text{-}E}$ under juniper was well correlated with the R_S values predicted by Eqn (5) ($r^2 = 0.64$). Despite the similar trends between $R_{S\text{-}E}$ and $R_{S\text{-}A}$, the two methods also show different trends.

Annual and seasonal $R_{S\text{-}E}$ varied across cover types and seasonal $R_{S\text{-}E}$ varied within cover types between seasons (Fig. 7). Seasonal $R_{S\text{-}E}$ under both juniper and piñon were not different between warming and dry periods ($P = 0.46$; $P = 0.44$ respectively) as well as cold and warming periods ($P = 0.97$; $P = 0.44$ respectively). Seasonal $R_{S\text{-}E}$ in interspace was not different between dry and monsoon periods ($P > 0.67$). Most $R_{S\text{-}E}$ occurred during monsoon, and the least during the cold period for all cover types. $R_{S\text{-}E}$ was not different across cover types during the cold and dry periods ($P > 0.13$; Table 1). $R_{S\text{-}E}$ in interspace was less than $R_{S\text{-}E}$ under both piñon and juniper, which did not differ ($P > 0.44$), for warming and monsoon periods ($P < 0.01$). Annual $R_{S\text{-}E}$ (Table 3) was highest under piñon (491 ± 28.9 g C m^{-2} yr^{-1}), closely followed by $R_{S\text{-}E}$ under juniper (448 ± 26.4 g C m^{-2} yr^{-1}), and lowest in interspaces (361 ± 38.9 g C m^{-2} yr^{-1}), which had the highest percent variation (47.4%). Under piñon, 41% (149 g C m^{-2} yr^{-1}) of annual $R_{S\text{-}E}$ was released in response to pulses and 22% (27 g C m^{-2} yr^{-1}) for annual $R_{S\text{-}E}$ in interspaces. Plot-level annual $R_{S\text{-}E}$ in this piñon-juniper woodland was 401 ± 34.0 g C m^{-2} yr^{-1}.

CHAPTER 4 DISCUSSION

Effects of Soil Moisture, Soil Temperature, and Precipitation on R_{S-A}

The relationship between R_{S-A} and soil moisture (Fig. 3) in this piñon-juniper woodland does not follow trends seen in many other forested ecosystems. Studies in a variety of ecosystems have identified thresholds of soil moisture above which increasing soil moisture decreased R_{S-A} (12% in temperate mixed hardwood forest Davidson *et al.*, 1998; 19% in ponderosa pine forest Xu & Qi, 2001; 60% in a marsh Jin *et al.*, 2008). The field capacity of our soils is 31%, thus, it is likely that our soils were too dry and/or coarse to observe this threshold behavior in R_{S-A} with respect to soil moisture except for brief periods during some rain events. Soil moisture under piñon during the dry period had a significant negative relationship with R_{S-A} (Fig. 3). This pattern was not seen during other periods and may indicate another factor not measured in this study was responsible for increased respiration at low soil moisture levels measured at 5-10 cm. A possible factor could be piñon root respiration from deeper soil layers or shallow root respiration responding to deep soil moisture when surface soils are dry. West *et al.* (2007) reported piñon water uptake could be from deep water sources during dry periods in Arizona. Also, solar radiation (in the form of ultraviolet light) has been shown to be an important factor in piñon and juniper litter decomposition especially under dry conditions (Gallo *et al.*, 2006). The unexpected negative trend between R_{S-A} and soil moisture under dry conditions indicates that when soil moisture is low other factors, such as soil temperature and ultraviolet light, drive R_{S-A}.

Autochamber soil respiration under piñon and in interspaces increased exponentially with increasing soil temperature across the cold and warming periods, but interspace $R_{S\text{-}A}$ exhibited a different trend during summer and monsoon periods. Under piñon and in interspaces, $R_{S\text{-}A}$ showed an exponential relationship for soil temperatures below 25.8 °C (Fig. 3), which corresponds with trends reported for many other ecosystems [e.g. (boreal forest) Gulledge & Schimel, 2000; (semi-arid) Carbone *et al.*, 2008; (grassland) Zhou *et al.*, 2007; (marsh) Jin *et al.*, 2008; and (temperate) Savage & Davidson, 2003]. Studies that used exponential trends for soil moisture in conifer forests had maximum soil temperatures ranging from 16 to 29 °C (Fang & Moncrieff, 2001; Saiz *et al.*, 2007; Tang *et al.*, 2005b; Tang *et al.*, 2005c; Vargas & Allen, 2008; Xu & Qi, 2001). Zhou *et al.* (2007) used an exponential soil temperature function in a temperate grassland that received 915 mm of mean annual rainfall and reached soil temperatures of about 40 °C. However, our site receives less annual precipitation (370 mm), and interspace $R_{S\text{-}A}$ decreased as soil temperatures increased above about 25 °C (during summer and monsoon periods). Enzymes begin to denature at high temperatures, which could cause R_S to be less responsive to high soil temperatures (Fang & Moncrieff, 2001). The combination of dry and hot conditions seen in this woodland may have caused the negative R_S trend in interspaces at high soil temperatures. This ecosystem experiences many combinations of environmental conditions that generate unexpected soil respiration responses and add complexity to R_S in this diverse woodland.

Small pulses create similar percent response in $R_{S\text{-}A}$ under piñon and in interspaces as a result of different conditions. Pulses smaller than 5 mm are probably unavailable to deep-rooted plants (trees), and thus CO_2 sources are limited to microbial

respiration and pore space CO_2 replacement (Huxman *et al.*, 2004). Interception leads to dryer conditions under piñon than in interspaces. Owens *et al.* (2006) found only 55% of rainfall reached soils under juniper (*Juniperus ashei*) canopies. Which was due to canopy interception and rainfall redirection. Piñon sub-canopies have different types and generally larger populations of microbes than in interspaces (Kuske *et al.*, 2002). Small pulses result in dryer conditions for piñon sub-canopies than in interspaces. These different conditions lead to similar percent $R_{S\text{-}A}$ increase microbial activity under piñon and in interspaces.

For larger pulses, when plants were able to respond, R_S under piñon and in interspaces diverged with a larger response under piñon (Fig. 2). Piñon generate thin O horizons from canopy litterfall (Davenport *et al.*, 1996), a horizon that has been shown to contribute 30-40% of R_S in forested areas (Buchmann, 2000; Bowden *et al.*, 1993; Davidson *et al.*, 2006). In addition, microbial activity in soils under plants is often higher than in adjacent bare soil (Herman *et al.*, 1995; Kieft *et al.*, 1997), which could account for lower interspace $R_{S\text{-}A}$ response to precipitation pulses > 3 mm.

Although our data captured only a limited number of large storms (> 25 mm), they suggest soil respiration inhibition (Fig. 2). Inhibition of $R_{S\text{-}A}$ might be due to reduced gas exchange caused by soil pore flooding in the upper soil layers. In one study, microbial R_S peaked when the pore space of coarse-textured soils were 60% water-filled (Linn & Doran, 1984). Jassal *et al.* (2008) suggested that very wet soils lead to low oxygen environments and decreased aerobic microbial respiration. The effects of rewetting on $R_{S\text{-}A}$ responses and associated carbon losses may be elucidated through experimentally controlled wetting pulses (Sponseller, 2007). The effect of pulse size is

difficult to quantify because of variation in pulse characteristics (size, intensity, prevailing temperature and humidity, etc) and antecedent soil moisture. Because daily precipitation at the study site, ranges from 0 – 60+ mm with similar variation in rainfall intensity, a longer term dataset encompassing a larger number of storms is required to characterize pulse response characteristics with greater certainty.

Cover and Spatial Effects on $R_{S\text{-}E}$ and $R_{S\text{-}A}$

Ecosystem soil respiration measurements revealed heterogeneity not captured in $R_{S\text{-}A}$ measurements in interspaces. However, since $R_{S\text{-}E}$ and $R_{S\text{-}A}$ were well correlated under piñon, autochambers under piñon likely represented the spatial heterogeneity well. Ecosystem soil respiration in interspaces, which are largely bare soil with grass and other herbaceous plants, was less than under piñon or juniper except for two collections (Figs. 1 and 6). The large number of $R_{S\text{-}E}$ measurements gave a better representation of the spatial heterogeneity present in interspaces, which did not occur under piñon or juniper canopies (Savage & Davidson, 2003; Raich *et al.*, 1990; Dugas, 1993). Differences in $R_{S\text{-}A}$ under juniper and piñon in November and June may be attributed to differences in tree water use. Direct measurement of $R_{S\text{-}A}$ under juniper canopies are needed to compare high frequency measurements of $R_{S\text{-}A}$ under the dominant species. Davenport *et al.* (1996) found only 2 of 17 measured soil properties differed across piñon, juniper and interspace cover types in northern New Mexico, which suggests that soil texture is not a major contribution to R_S differences across cover types in these woodlands. The differences between cover types and between measurement methods reflect complexity in this woodland ecosystem.

Annual R_{S-E} in this study did not generally correspond to reported values from other ecosystems. Plot-level annual R_{S-E} is slightly above the range of values reported by Raich and Schlesinger (1992) for woodlands and boreal forests (332 ± 31 g C m^{-2} yr^{-1}), and as expected plot-level annual R_{S-E} is below the ranges reported for Mediterranean woodlands (713 ± 88 g C m^{-2} yr^{-1}), temperate conifer forests (681 ± 95 g C m^{-2} yr^{-1}) (Raich & Schlesinger, 1992), and a ponderosa pine plantation (Xu & Qi, 2001). Conant *et al.* (2000) measured annual R_S rates under P*inus edulis* (511 ± 40 g C m^{-2} yr^{-1}), under *Juniperus monosperma* (529 ± 51g C m^{-2} yr^{-1}), and in interspaces (347 ± 24 g C m^{-2} yr^{-1}), where R_S measured both in interspaces and under piñon are similar to this study. However, annual R_{S-E} under juniper in this study was lower than the value reported by Conant *et al.* (2000). Interspace respiration is in the lower range for temperate grasslands (442 ± 78 g C m^{-2} yr^{-1}) and above the range for desert scrub (224 ± 38 g C m^{-2} yr^{-1}) reported by Raich and Schlesinger (1992). Precipitation varies on a yearly basis in semi-arid and arid environments (Knapp & Smith, 2001) including piñon-juniper woodlands (Conant *et al.*, 1998). Inter-annual variability in R_{S-E} has been observed in many ecosystems (e.g. Irvine *et al.*, 2008; Polley *et al.*, 2008; Zhou *et al.*, 2007), which is attributed to variability in precipitation in a grassland ecosystem (Zhou *et al.*, 2007). Future research at this site will investigate inter-annual variability and R_S drivers in this ecosystem.

R_{S-A} Model Drivers and Predictions

The two models [Eqn (3 and 4)] that produced the highest r^2 and RMSE when predicted R_{S-A} was compared with R_{S-A} both contained parameters linked to the

autotrophic contribution to R_S. Soil respiration has been previously correlated with photosynthetically active radiation (Liu *et al.*, 2006; Vargas & Allen, 2008) with variable lag times due to the synthesis of sugars and its influence on root respiration (Tang *et al.*, 2005a) and microbial respiration through root exudates (Liu *et al*., 2006). Liu *et al*. (2006) did not find significant lag times, and we made the simplifying assumption that lag times were negligible in order to linearize the models for purposes of analysis. Evaluation of lags in this system would add confidence to the R_S models.

In addition to photosynthetically active radiation, vapor pressure deficit also influences plant processes. Piñon close their stomata in response to drought (high vapor pressure deficit) before juniper. When stomata are closed, CO_2 uptake is limited, and photosynthesis is consequently down regulated (Nobel, 2005). Although vapor pressure deficit is correlated with R_S in some forests (Vargas & Allen, 2008), the impacts of vapor pressure deficit on R_S are poorly understood, and future research should be conducted to evaluate the importance of vapor pressure deficit on R_S. Plant contributions to R_S are important (e.g. Ryan & Law, 2005; Tang *et al.*, 2005a; Jassel *et al.*, 2008) and complex due to the wide range of vegetation cover (from bare soil to tree canopy) within this woodland.

Using a second order exponential function for soil temperature leads to different model predictions for R_S than using a first order exponential function under hot, dry conditions. Only a handful of studies have modeled R_S using second order exponential function for soil temperature (e.g. Hunt, 1977; O'Connell, 1990; Fang & Moncrieff, 2001). Hunt (1977) first used a second order exponential [Eqn (3)] to describe temperature effects on soil decomposition, which is an important component of soil

respiration (Brady & Weil, 2000). If the squared soil temperature coefficient is positive, then the equation limit goes to infinity. However, if the squared soil temperature coefficient is negative, then the limit goes to 0 via a parabolic curve. The equations used by O'Connell (1990) and Hunt (1977) had a negative coefficient for thea squared soil temperature term, as did our study (Table 2), and their measured soil temperatures reached between 38 and 40 ºC. Fang and Moncrieff (2001) reported a maximum soil temperature of about 32 ºC in Scotland, and their equation used a positive squared soil temperature coefficient. The Scotland climate (Fang & Moncrieff, 2001) likely too wet to observe a negative R_S trend at high soil temperatures seen in this and other studies. If temperatures increase and droughts become more frequent with climate change, in the future, R_S may be overestimated in arid and semiarid climates by using a positive first order exponential function for soil temperature.

Soil temperature and soil moisture each limit R_S in piñon-juniper woodlands. Conant *et al.* (2000) found that increased R_S in response to increasing soil temperature was constrained by soil moisture in a piñon-juniper woodland. At low soil moisture, decomposition rates from microbial activity decrease (Hunt, 1977), but in nearby grassland and shrublands, ultraviolet light aids breaking down litter under dry conditions comparable to microbial activity alone (Gallo *et al.*, 2006). Low soil moisture conditions exist in combination with high soil temperatures during the dry period and at the beginning of the monsoon period. Soil respiration showed negative trends during these periods in response to decreasing soil moisture and increasing soil temperature in interspaces, where litterfall rates are insignificant compared to piñon and juniper sub-canopies. Piñon sub-canopies had higher soil moisture and lower soil temperatures than

in interspaces, which offer an explanation as to why the parabolic trend was not observed under piñon. Since soil moisture is predicted to be variable in the future due to changes in precipitation, R_S is likely to be more variable in the future.

Modeling pulse events remains unresolved in this and other ecosystems. Neither Eqn (3) nor Eqn (4) captured soil respiration during monsoon season, the period that is perhaps most important in understanding pulse dynamics in this woodland since 41% of annual $R_{S\text{-}A}$ under piñon and 22% annual $R_{S\text{-}A}$ in interspace was released in response to pulses. Xu *et al.* (2004) found, in general, R_S responds to pulses with a quick peak followed by exponential decay and return to the initial R_S value. The R_S pulse response is also dependent on antecedent conditions, where the R_S pulse response was larger when preceded by low soil moisture conditions than wet conditions (Xu *et al.*, 2004; Cable *et al.*, 2008). It is also likely that antecedent soil temperature also influences R_S pulse response since soil temperature is known to influence R_S processes (e.g. Lloyd & Taylor, 1994; Moncrieff & Fang, 1999; Rochette *et al.*, 1991). This study lays the foundation for future modeling efforts in this woodland. With precipitation expected to become more variable, modeling both pulse dynamics as well as other environmental responses will be of increasing importance in the future.

Other Implications for Piñon-juniper Woodlands

Soil respiration and its components have been shown to differ across cover types. Within interspaces microbial communities are vastly different between soil crusts, under grasses, and between grass species (Kuske *et al.*, 2002). Tree sub-canopy environments add another level of complexity. For example, during this study, $R_{S\text{-}A}$ under piñon

released in response to pulses was over five times (149 g C m^{-2} yr^{-1}) the amount of R_{S-A} released in interspaces (27 g C m^{-2} yr^{-1}). In addition, mycorrhyzal fungi populations, which aid in water and nutrient uptake and contribute to R_S, have been found to be different under piñon and juniper trees (Hawkes *et al.*, 2008). Ryan and Law (2005) reported that respiration from roots and mycorrhizal fungi make up about half of soil respiration. Hawkes *et al.* (2008) found that increasing temperature increased respiration from roots and fungi and carbon losses to the atmosphere. Thus, the change in temperature regime associated with the loss of tree canopy cover during piñon mortality will have a large influence on the ecosystem (Haskins & Gehring, 2005). Since climate change is expected to exacerbate the frequency and severity of future droughts throughout southwestern USA (Coops & Catling, 2002), mortality events of similar or greater magnitude are likely in the future (McDowell *et al.*, 2008b). Because plot-level R_S is a function of the cover types that comprise the ecosystem, plot-level soil respiration is likely to decrease in the long term if piñon cover decreases due to bark beetle infestations and drought.

CHAPTER 5 CONCLUSIONS

The piñon-juniper woodland ecosystem presents challenges to measuring R_S because it is a mosaic of cover types with tree sub-canopy environments adjacent to sparsely vegetated interspaces containing grasses and forbs. Soil respiration in this complex woodland ecosystem is a function of cover type as well as soil temperature, soil moisture, and plant processes. Surprisingly, $R_{S\text{-}A}$ decreased with high soil temperature, which suggests that R_S may not continue to increase without limit as climate temperatures increase. Negative relationships between R_S and both soil moisture and soil temperature under low soil moisture and high soil temperature conditions have not been observed in other ecosystems to our knowledge and further studies are needed to evaluate the extent of this relationship in other ecosystems. Annual $R_{S\text{-}E}$ in interspace was less than $R_{S\text{-}E}$ under both juniper and piñon, which were not different despite the broad spatial sampling. Under piñon, $R_{S\text{-}A}$ was higher than in interspaces, which suggests that, on a long term scale, piñon mortality may lead to a decrease in R_S scaled to the plot-level if piñon are replaced by interspace vegetation. Including a proxy for photosynthesis such as photosynthetically active radiation and vapor pressure deficit improved model predictions of R_S under piñon and in interspaces. Model predictions of R_S leave room for improvement in explaining precipitation event dynamics, which has been seen in other arid and semiarid systems and contributed 22 – 41% of annual $R_{S\text{-}E}$ in this piñon-juniper woodland. Future work is needed to focus on better modeling of R_S pulses given that environmental conditions are expected to be more variable in the future.

FIGURES AND TABLES IN ORDER OF REFERENCE

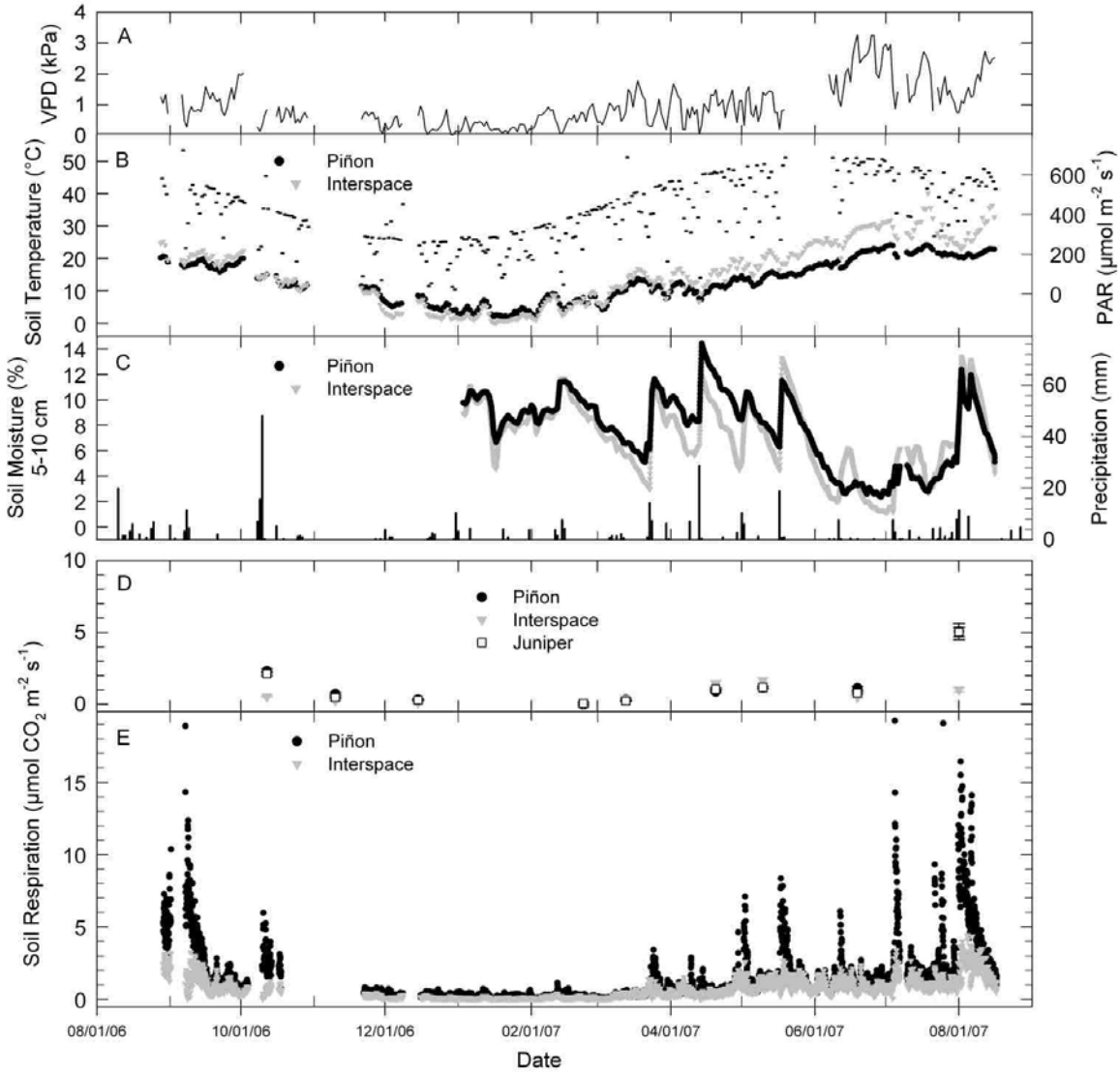

Figure 1 Environmental variables along with soil moisture and soil respiration (R_S). Panel contents are as follows: A) Vapor pressure deficit (VPD, solid black line) daily mean; B) Photosynthetically active radiation (PAR, black rectangles) daily mean, soil temperature (5 cm depth) in interspaces (gray triangles) and under piñon (black circles) daily mean; C) soil moisture (5-10 cm) in interspaces (gray triangles) and under piñon (black circles) and precipitation (black vertical bars); D) Ecosystem R_S (R_{S-E}) under piñon (black circles), in interspaces (gray triangles), and under juniper (open squares) with standard error bars shown; and E) Autochamber R_S (R_{S-A}) under piñon (black circles) and in interspaces (gray triangles) complete data set.

	Cover Type	Full year	Cold	Warming	Dry	Monsoon
% year		100.0	28.8	22.7	9.0	26.0
R_{S-E} (g C m^{-2} d^{-1})	Interspace	0.99 ± 0.11(37.3) a	0.54 ± 0.06(40.9) a	1.56 ± 0.25(56.3) a	1.14 ± 0.09(27.3) a	1.05 ± 0.08(26.7) a
	Juniper	1.23 ± 0.07(20.4) ab	0.55 ± 0.03(19.5) a	0.94 ± 0.04(14.9) b	1.08 ± 0.09(30.4) a	2.27 ± 0.26(39.1) b
	Piñon	1.35 ± 0.08(20.3) b	0.60 ± 0.02(12.3) a	0.93 ± 0.03(10.8) b	1.27 ± 0.07(19.4) a	2.52 ± 0.29(39.4) b
	Plot-level	1.10 ± 0.09(30.4)	0.55 ± 0.05(31.4)	1.30 ± 0.16(39.0)	1.13 ± 0.16(31.8)	1.57 ± 0.16(31.8)
R_{S-A} (µmol m^{-2} s^{-1})	Interspace	0.64 ± 0.01(102.1)	0.10 ± 0.001(64.3)	0.62 ± 0.01(69.5)	0.82 ± 0.01(45.1)	1.28 ± 0.02(59.1)
	Piñon	1.30 ± 0.02(145.0)	0.26 ± 0.003(55.4)	1.06 ± 0.03(98.5)	1.18 ± 0.03(57.8)	3.11 ± 0.07(90.1)
T_S (°C)	Interspace	15.2 ± 0.13(64.5)	4.2 ± 0.07(76.0)	15.8 ± 0.12(31.4)	26.9 ± 0.20(19.1)	24.6 ± 0.15(22.9)
	Piñon	12.9 ± 0.08(49.7)	5.7 ± 0.06(44.6)	12.2 ± 0.06(19.7)	19.8 ± 0.09(12.0)	20.5 ± 0.06(11.4)
SM_{5-10} (%)[a]	Interspace	7.3 ± 0.15(36.7)	7.9 ± 0.19(22.9)	7.7 ± 0.26(3.12)	3.3 ± 0.28(49.5)	7.3 ± 0.32(38.2)
	Piñon	8.3 ± 0.18(38.0)	8.9 ± 0.14(15.1)	9.1 ± 0.23(22.7)	3.9 ± 0.25(36.7)	7.0 ± 0.41(47.5)
VPD (kPa)	All	1.00 ± 0.01(94.5)	0.43 ± 0.01(77.7)	0.93 ± 0.02(70.6)	2.23 ± 0.06(56.7)	1.51 ± 0.03(69.8)
PAR (µmol m^{-2} s^{-1})	All	420.04 ± 7.72(138.8)	267.33 ± 9.55(157.4)	485.63 ± 16.35(129.0)	632.46 ± 33.72(116.0)	505.25 ± 16.66(125.8)

[a]collected once daily

Table 1 Temporal data in the form: mean ± standard error (coefficient of variation, %) by seasonal period, where R_S is soil respiration, T_S is soil temperature measured at 5 cm depth, SM is soil moisture, VPD is vapor pressure deficit, and PAR is photosynthetically active radiation.

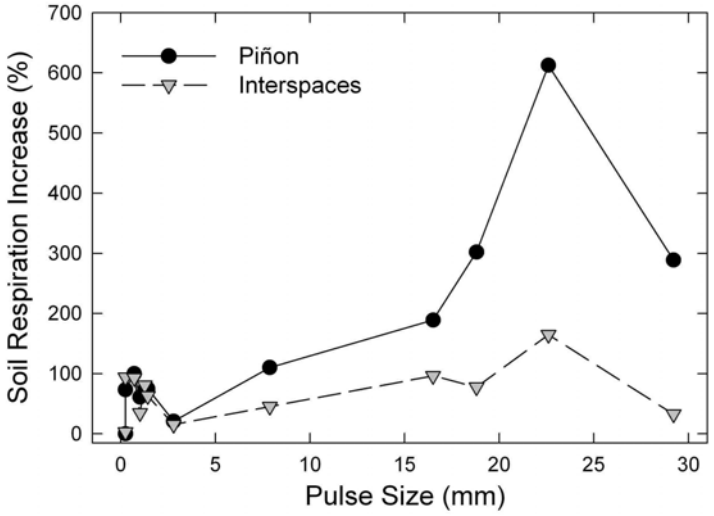

Figure 2 Autochamber soil respiration (R_{S-A}) percent increase after rain event (pulse) at the same time of day in interspaces and under piñon versus pulse size.

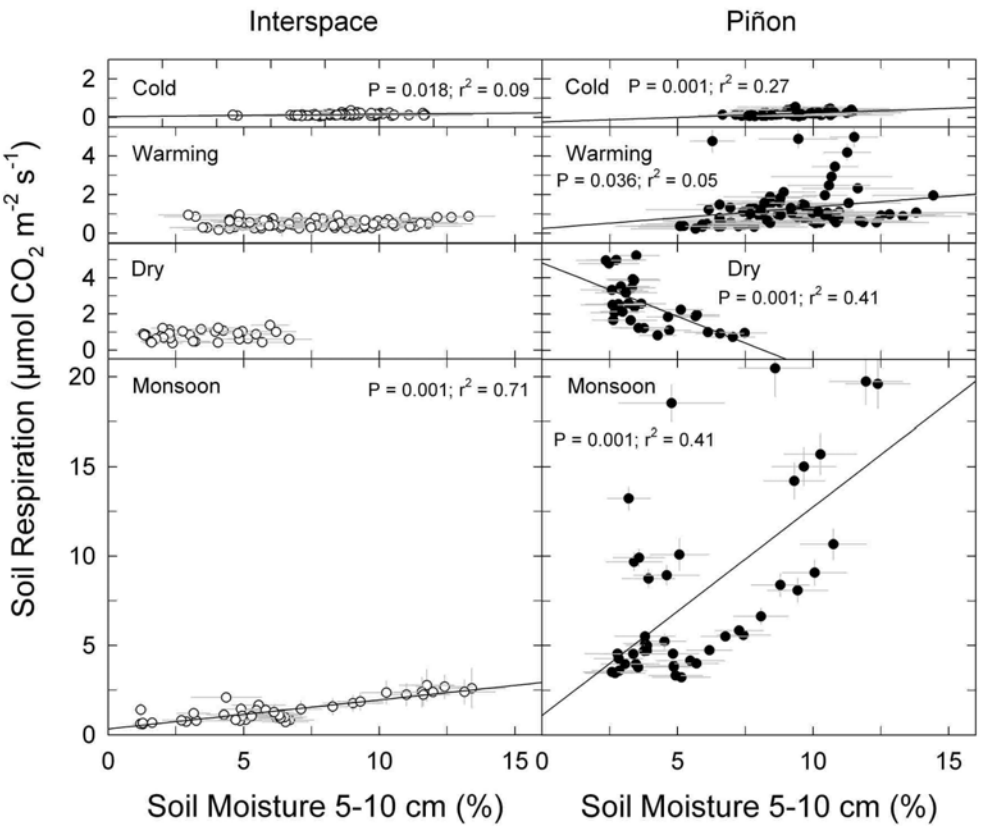

Figure 3 Autochamber soil respiration (R_{S-A}) versus soil moisture (5-10 cm) under piñon (right, solid circles) and in interspaces (left, open circles) for each time period. Data shown are daily values with standard error bars (x- and y-axis) and R_{S-A} values are corrected for temperature. Regression lines (solid lines), p-values, and r^2 values are shown for significant correlations ($P < 0.05$). Equations for interspace (yi) and piñon (yp) cover significant regressions are as follows: (Monsoon) yi= 0.16*x+0.34, yp= 1.17*x+1.08; (Warming) yp= 0.11*x+0.25; (Dry) yp= -0.59*x+4.82 and (Cold) yi= 0.01*x+0.04, yp= 0.05*x-0.24.

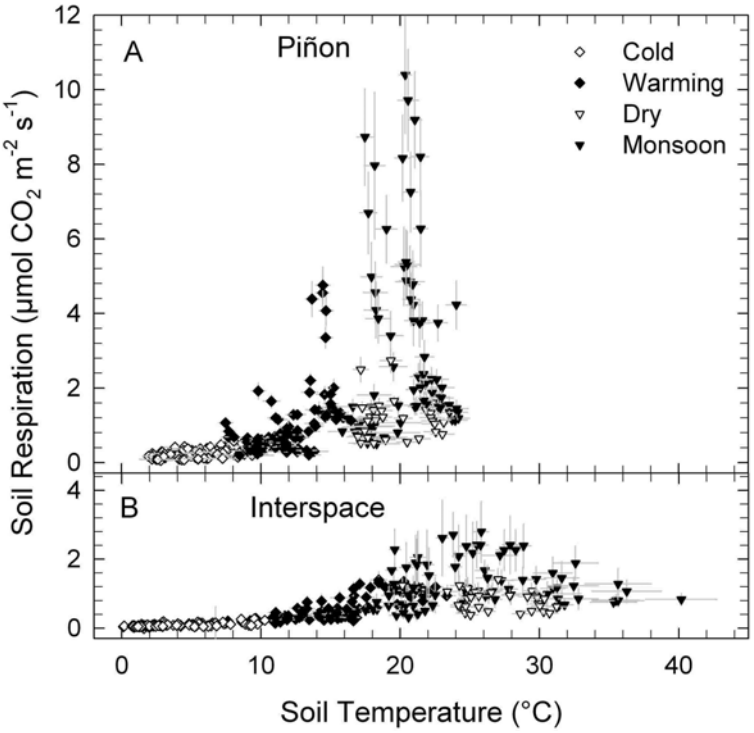

Figure 4 Autochamber soil respiration ($R_{S\text{-}A}$) versus soil temperature (5 cm depth) under piñon (A) and in interspaces (B). Time periods are depicted as follows: cold (open diamonds); warming (closed diamonds); dry (open triangles); and monsoon (closed triangles). Standard error bars (x- and y-axis) are shown for all data.

	a	*b*	*c*	*d*	*f*	*g*	r^2	RMSE
Interspace								
Equation 1	0.018	0.118	0.592				0.743	0.626
Equation 2	0.027	0.115	0.100				0.736	0.634
Equation 3	0.011	0.135	0.560		-0.272	0.050	0.774	0.596
Equation 4	0.008	0.254	0.394	-0.004	-0.308	0.060	0.864	0.462
Piñon								
Equation 1	0.007	0.184	1.134				0.711	0.614
Equation 2	0.015	0.182	0.183				0.719	0.606
Equation 3	0.003	0.229	1.097		-0.490	0.079	0.829	0.486
Equation 4	0.002	0.289	0.980	-0.002	-0.504	0.080	0.834	0.478

Table 2 Autochamber soil respiration ($R_{S\text{-}A}$) model coefficients, r^2, and root mean squared error (RMSE) values for interspace and piñon, which correspond to Eqns (1-4).

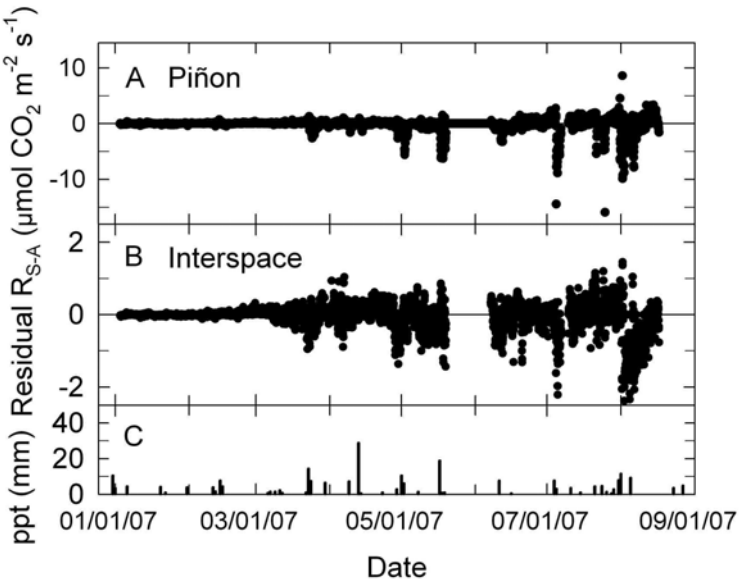

Figure 5 Eqn (3) (panel A, piñon) and Eqn (4) (panel B, interspace) model residuals for autochamber soil respiration (R_{S-A}) versus time, with precipitation bars (panel C). A line at 0 is plotted for each panel.

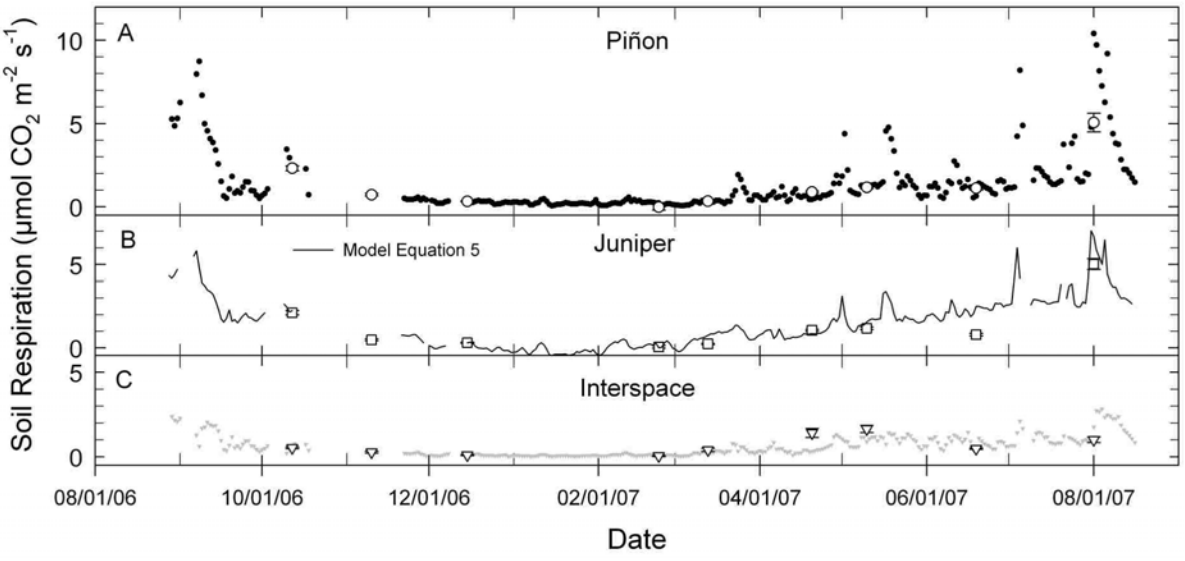

Figure 6 Autochamber and ecosystem soil respiration (R_{S-A} and R_{S-E}) by cover type. Panel contents are as follows: A) R_S under piñon for autochamber (solid circles) and ecosystem (open circles) measurements; B) ecosystem R_S measurements under juniper (open squares) and modeled R_S under juniper using Eqn (5) (solid line); C) R_S in interspaces for autochamber (gray triangles) and ecosystem (open triangles) measurements. Error bars on R_{S-E} data show standard error of the mean. Daily averages are shown for R_{S-A} (see Fig. 1 for full data).

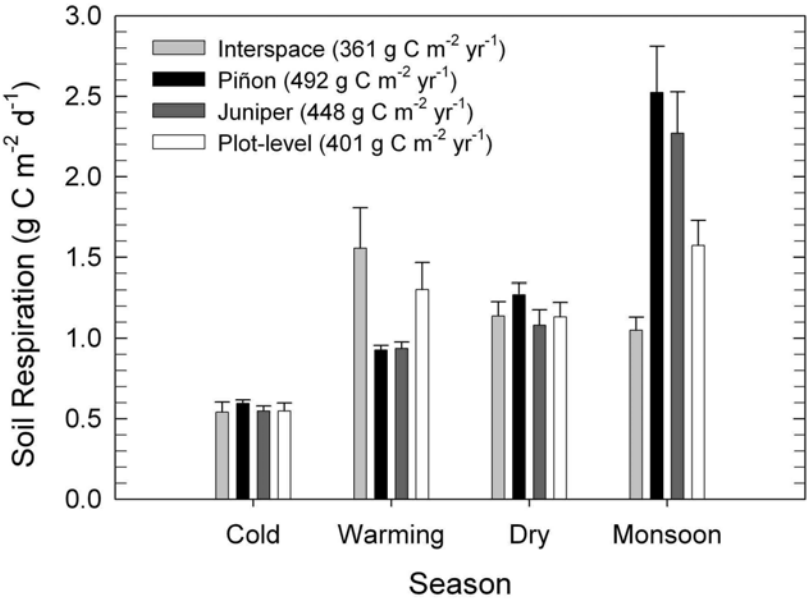

Figure 7 Ecosystem soil respiration (R_{S-E}) by seasonal period and cover type during measurement period averaged by plot with standard error bars for all data. Annual R_{S-E} values are given in key. Values were calculated using linear interpolation of R_{S-E} measurements by plot and cover type. Plot-level values represent annual R_{S-E} rates scaled by percent cover.

	Interspace	Juniper	Piñon	Plot-level
Annual R_{S-E} (g C m^{-2} $year^{-1}$)	361 ± 38.9	448 ± 26.4	491 ± 28.9	401 ± 34.0
Ground cover (%)	59.2	31.0	9.8	100.0
Weighted annual R_{S-E} (g C m^{-2} $year^{-1}$)	214 ± 23.0	138 ± 8.2	48 ± 2.8	489 ± 47.7

Table 3 Annual ecosystem soil respiration (R_{S-E}) with standard errors, percent ground cover, and weighted annual R_{S-E} by cover type.

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