12-1-2015

QUANTIFYING TEMPERATURE SENSITIVITY OF SOIL RESPIRATION ACROSS A RANGE OF SEMI-ARID BIOMES

Michelle Nuanez

Michelle Nuanez

Candidate

Biology

Department

This thesis is approved, and it is acceptable in quality and form for publication:

Approved by the Thesis Committee:

Marcy Litvak , Chairperson

Robert Sinsabaugh

Scott Collins

QUANTIFYING TEMPERATURE SENSITIVITY OF SOIL RESPIRATION ACROSS A RANGE OF SEMI-ARID BIOMES

by

MICHELLE NUANEZ

B.S. BIOLOGY

THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science
Biology

The University of New Mexico
Albuquerque, New Mexico

December, 2015

QUANTIFYING TEMPERATURE SENSITIVITY OF SOIL RESPIRATION ACROSS A RANGE OF SEMI-ARID BIOMES

by

Michelle Nuanez

B.S., Biology, University of New Mexico, 2013

Abstract

Soils in semi-arid regions store approximately 10% of earth's soil organic carbon, the substrate which microbes oxidize, resulting in the largest source of carbon to the atmosphere from terrestrial ecosystems. Semi-arid regions are expected to experience increased temperatures and altered precipitation regimes over the next 100 years, altering soil temperature and water, the two predominant drivers in soil respiration processes. In this study we quantify the temperature sensitivity of soil respiration in five semi-arid biomes ranging from desert grassland to ponderosa pine forest along an elevational/climate gradient in central New Mexico. We measured statistically similar temperature sensitivities in 4 of 6 biomes ranging from 3-7 % with a mean of 5± 0.9 % increase in soil respiration (R_s) per degree increase in soil temperature. Temperature sensitivity at the desert shrubland site was an exception with a minimal 1% increase, and we measured no significant relationship in the ponderosa pine forest. The integration of water into the response models yielded minimal change in the sensitivities between sites except at the juniper savanna site where SWC was the

dominant abiotic factor regulating R_S. Potential mechanisms driving this convergence of temperature sensitivity are the multi-year temporal scale of our measurements which dampen out any short-term responses, as well as mediation due to interacting co-varying controls on temperature sensitivity , and selection pressures for microbial populations that maximize growth under prevailing resource and temperature conditions across our gradient. Implications for global models are discussed.

Table of Contents

List of Figures

List of Tables

Introduction

Semi-arid biomes cover approximately 30% of the terrestrial surface, contain an estimated 159-191 billion tons of soil organic carbon (SOC) (Lal, 2004), and are a key contributor in the exchange of carbon between terrestrial ecosystems and the atmosphere at the global scale (Poulter et al. 2014; Ahlstrom et al. 2015). Carbon dynamics in semi-arid biomes are inherently dynamic, and variability in the exchange of carbon between semi-arid biomes and the atmosphere accounts for 57% of the inter-annual variability in global CO_2 exchange (Ahlstrom et al., 2015). Climate models suggest that mid-latitude regions, where most semi-arid biomes are found, will experience increased temperature coupled with increased variability in precipitation regimes in the next century (IPCC, 2014; Gutzler & Robbins, 2010). Given the importance of these biomes to global CO_2 exchange, it is crucial to understand how these predicted changes in climate will alter both the photosynthetic and respiration processes in these biomes.

Soil respiration (R_s), the summation of below ground autotrophic (plant root and mycorrhizal) respiration and microbial decomposition of SOC (Raich & Schlesinger, 1992), is the largest source of carbon to the atmosphere from terrestrial ecosystems (Schlesinger, 1997). Rates of R_s are controlled by several factors including temperature, moisture, photosynthetic inputs through above ground primary productivity (GPP), substrate availability (SOC), nutrient availability, vegetation cover, disturbance and land use history (Conant et al., 2004; Fang & Moncrieff, 2001; Lloyd & Taylor, 1994; Raich & Schlesinger, 1992; Schlesinger & Andrews, 2000). GPP, in particular, contributes by directly providing substrate for decomposition from above-ground litter input, and below ground root shedding and root exudate excretion (Kuzyakof & Domanski, 2000). Soil respiration components have been extensively studied over the past century (Ginsburg 1925; Vargas et al. 2011), with temperature sensitivity gaining coverage in the past few decades (Bradford, 2013; Conant et al., 2011; Fierer et al., 2005; Lutzow & Kogle-Knabner, 2009; Reichstein et al., 2003). We still lack a comprehensive understanding of large scale temperature sensitivity of R_s, however, as most studies focus on a single biome (Boon et al., 1998; Fierer et al., 2005; Thomey et al., 2011; Vargas et al., 2008a; Vargas et al., 2011) or are based on laboratory incubations which eliminate key factors such as temporal dynamics, vertical soil structure and above-ground interactions (Chatterjee & Jenerette, 2011; Conant et al., 2004; Richardson et al., 2012). In addition, very few of these studies have focused specifically on semi-arid biomes. In-situ, long term measurement data are required not only in semi-arid biomes, but across multiple biomes to address key questions regarding R_s temperature sensitivity (Conant et al. 2004; Davidson & Janssens, 2006b; Mahecha et al., 2010), and to understand how biome-specific these responses are likely to be.

The primary objective of this study was to quantify the temperature sensitivity of R_s across an elevation and climatic gradient of distinct semi-arid biomes using long term, in-situ soil CO_2 measurements. These biomes include a low elevation desert grassland and creosote shrubland, middle elevation juniper savanna and piñon-juniper woodland, and a high elevation ponderosa pine forest, all of which vary distinctly in climate, GPP, vegetation cover (Anderson-Teixera et al. 2011). Individual factors such as GPP, seasonality, quality of substrate, presence of roots, vegetation cover, soil texture and composition, and water availability individually alter R_s temperature sensitivity (Boon et al., 1998; Chatterjee and Jenerette, 2011; Davidson & Jannesson, 2006; Fierer et al., 2005; Song et al., 2014; Zahng et al., 2014). Interactions of these factors, as regularly seen in natural systems, can moderate the overall influence of any one factor, within and across biomes (Chatterjee and Jenerette, 2011). In addition, when R_s temperature sensitivity is quantified over long time scales, many site or biome-specific differences are minimized (Mahecha et al. 2010; Davidson & Janssens, 2006b). My overall hypothesis was that the temperature sensitivity of R_s would be very similar across this distinct gradient of semi-arid biomes due to: 1) the multi-year time scale of this dataset, and 2) interaction between several factors that co-vary across the gradient that have mitigating effects on temperature sensitivity of R_s.

A secondary objective of this study was to assess the role water plays in modifying temperature sensitivity across this range of semi-arid biomes. The importance of water within semi-arid biomes is well studied at the ecosystem scale (Collins et al., 2014; Heisler-White et al., 2008; Schwinning & Ehleringer, 2001; Snyder & Tartowski, 2006) as well as specifically pertaining to soil respiration (Orchard & Cook, 1983; Huxman et al., 2004; Wan et al., 2007). However, it is not clear if it is necessary to integrate soil water availability in the modeling and calculation of temperature sensitivity as a co-dominant control on these processes, especially in semi-arid biomes (Chatterjee et al., 2011; Conant, 2004).

Methods

Site information:

We made our measurements in five established eddy covariance tower sites in the New Mexico Elevation Gradient which are part of the Ameriflux Core network: US-Seg and US-Ses, northern Chihuahuan desert grassland and creosote shrubland, respectively, both at 1596m; US-Wjs, a juniper savanna at 1926 m; US-Mpj, a piñon-juniper woodland at 2126 m, and US-Vcp, a ponderosa pine forest at 2486m (Anderson-Teixera et al. 2011; Figure 1). The advantage of using these sites to look at temperature sensitivity across biomes is that they vary in dominant vegetation, mean annual temperature (MAT), mean annual precipitation (MAP), SOC (Anderson-Teixera et al. 2011; Table 1) and are representative of dominant biomes that occur across elevation gradients in the Southwestern US.

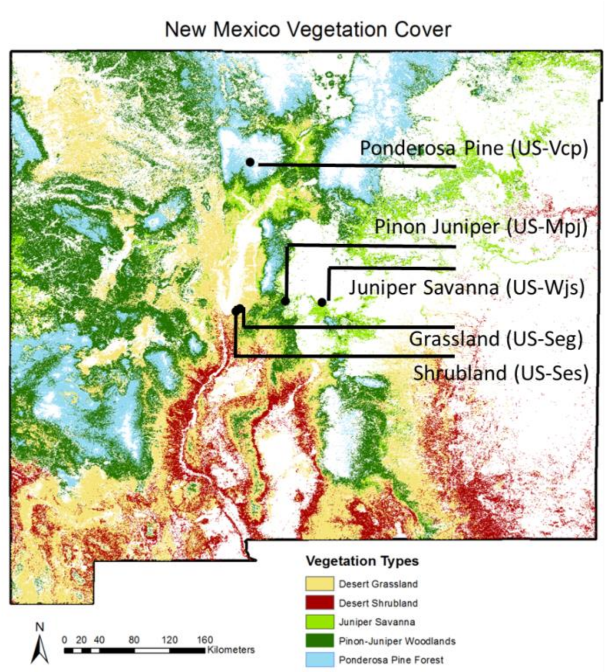

Figure 1: New Mexico land area covered by vegetation classes/biomes included in this study with research sites shown.

Table 1

Site Name	Biome	Location	Elevation	MAT (°C)	MAP (mm)	Dominant species	Mortality/ Disturbance history
Grassland (US-Seg)	Northern Chihuahuan Grassland	Sevilleta NWP LTER	1596	17.7	250	C4 grasses *(Bouteloua gracilis, B. eriopoda, Sporobolis spp., Hilaria jamesii, Muhlenbergia spp.)*	Cattle grazing prior to 1973
Shrubland (US-Ses)	Desert shrubland	Sevilleta NWP LTER	1605	17.7	250	*Larrea* (Creosote bush), C4 grasses *B. eriopoda, Sporobolis spp., Hilaria jamesii, Muhlenbergia spp.*	
Juniper Savanna (US-Wsj)	Juniper Savannah	Appx 25 Km S of Willard, NM	1926	15.2	361	*Juniperus monosperma* and C4 grasses (*Bouteloua gracilis)*	Sporadic but not intensive cattle grazing before 2010, but since exclosure has prevented grazing
Piñon-Juniper (US-Mpj)	Piñon-Juniper woodland	Appx 25 km S of Mountainair, NM	2126	14.8	418	*Juniperus monosperma* and *Pinus edulus* overstory with C4 grass understory (*Bouteloua gracilis*	Bark beetle outbreak, ~50% piñon mortality in 2013.
Ponderosa Pine (US-Vcp)	Ponderosa pine forest	Valles Caldera National Preserve, Jemez Mountains, NM	2486	9.8	550	*Pinus ponderosa* overstory, *Quercus gambelii and C3 grass and forbe understory*	

Soil respiration, water, and temperature measurements

We made continuous soil CO_2 measurements between 2009 and 2014, with various start dates of collection depending on study site (Table 2). At each site, soil CO_2 concentrations were measured using Vaisala CARBOCAP CO_2 solid state sensors (models GMM 221 and GMM 222)(Vaisala Group, Finland) in 3 pits directly under the dominant plant cover type. Sensors were originally placed at 5, 10, 20, and 40 cm depth at US-Mpj and 5, 10, 20, and 50 cm depths at US-Seg and US-Ses (Table 2). These depths were standardized in 2013 to 5, 10, and 30 cm at all sites with an additional 60 cm depth at US-Vcp to reflect deeper rooting patterns of the dominant species. We removed the deepest probes from the lower elevation sites in 2013 after determining that the 40/50 cm depth contributed minimally to R_s. Soil temperature (Campbell Scientific T107) and volumetric soil moisture (Campbell Scientific CS616) was measured simultaneously in all pits, at all depths.

Table 2

Site	Total Number of CO_2 probes	Probes depths (cm)	n	Cover vegetation
US-Seg	12 9	2011-2013: 5, 10, 20, 50 2014: 5, 10, 30	3 3	C4 grasses
US-Ses	12 9	2011-2013: 5, 10, 20, 50 2014: 5, 10, 30	3 3	*Larrea tridentata*
US-Wsj	9	5, 10, 30	3	*Juniperus monosperma*
US-Mpj	10 12	2009-2013: 5, 10, 20, 50 2014: 5, 10, 30	6 2	*Pinus edulis* *Juniperus monosperma*
US-Vcp	12	5, 10, 30, 60	3	*Pinus ponderosa*

We installed CO_2 sensors similar to Vargas and Allen (2008), using ¾ inch PVC housing and PVC caps sealed with a rubberized sealant to prevent interaction with above ground gasses, and covered each probe in a protective, semi-porous Teflon sleeve made by International Polymer Engineering (model 200-07-S-2). Soil CO_2 PVC housings were placed using a hand core whenever possible to minimize disturbance to the soil community and structure. In certain areas, soil structure (e.g. sand dominated soils) did not allow for this coring and a small hole was dug by hand. We calibrated the probes in the lab every 6 months with reference gasses according to manufacturer guidelines. Additionally, soil CO_2 data was temperature and pressure corrected according to manufacturer guidelines and the ideal gas law:

$$p\ (t,p) = p\ (25\ C, 1013hPa) * \frac{P}{1013} * \frac{298}{273 + t}$$

Where $p\ (t,p)$ is the corrected CO_2 measurement (ppm) is, p is the uncorrected CO_2 measurement (ppm), P is ambient pressure measured by infrared gas analyzer (LI-7500, Licor) at each site, and t is soil temperature (°C).

Data filtering and preparation:

Data filtering and quality analysis was done using R 3.2.0. Soil CO_2 and soil temperature data were smoothed using window size = 10 to maintain diurnal patterns while soil water data was smoothed using window size = 50 (R package RobFilter), and gaps were filled using an ensemble-learning model based imputation algorithm, or random forest modeling (R package missForest). This method has previously been used to fill environmental and flux data (Darrouzet-Nardi, *in prep*), and is an effective and accurate imputation technique (Stekhoven & Buhlmann, 2012). SWC, soil temperature and soil CO_2 data required 8%, 9%, and 22% gap filling, respectively.

R_s calculation from CO_2 *concentration measurements:*

We calculated R_s from the soil CO_2 profiles in each pit using the flux gradient method (Vargas & Allen 2008; Vargas et al., 2010). This method is based on Fick's law of diffusion, where the efflux of CO_2 from the soil can be calculated from the differential equation:

$$F = -Ds \frac{\partial C}{\partial z}$$

where F is the flux of CO_2 from the soil surface (µmol m^{-2} s^{-1}), D_s is the gaseous diffusion coefficient of CO_2 in the soil (m^2 s^{-2}), and $\frac{\partial C}{\partial z}$ is the rate of change of the molar concentration of CO_2 within the soil (C) at depth (z). The diffusion coefficient, D_s, takes into account soil temperature and atmospheric pressure according to the ideal gas law, SWC, soil porosity and soil texture. D_s accounts for values of the percentage of sand silt and clay where sand + silt + clay = 1, and sand + silt (S) is given as a value between 0 and 1. Porosity, or the percentage of air filled space in a soil sample, is also given as a decimal between 0 and 1. S for these sites ranged from 0.64 to 0.81 and porosity values ranged from 0.33 to 0.60 (see Table 3 for specific site and depth attributes). Silt and porosity values were measured by the US Forest Service at all sites in 2009 for all sites. The S-value for US-Wsj was determined using a publicly available soil properties report published by the USDA (USDA, 2015), using the mean of the regional clay percent value.

Table 3

Site	Soil porosity values	Sand + Silt value(s)
US-Seg	5 cm = 0.4725 10 cm = 0.3924 30 cm = 0.3384	0.81
US-Ses	5 cm = 0.4994 10 cm = 0.4589 30 cm = 0.3697	0.81
US-Wsj	5 cm = 0.3507 10 cm = 0.3507 30 cm = 0.3964	0.69
US-Mpj	5 cm = 0.5663 10 cm = 0.5815 30 cm = 0.5706	5 cm = 0.68 10 cm = 0.68 30 cm = 0.65
US-Vcp	5 cm = 0.5024 10 cm = 0.4417 30 cm = 0.4697	0.73

The calculation of surface flux assumes constant production of CO_2 within the soil profile, as well as increasing CO_2 concentration with depth (i.e. depth a will be less concentrated than depth b, depth b will be less concentrated than depth c and so on). This assumption was not always met, particularly during periods of rapid increase of CO_2 production, often following precipitation events, and these periods were removed.

Data Analysis:

We calculated daily means from thirty minute R_s fluxes during the growing season of each year (April1-October 1). Days with less than 75% of the day measured were eliminated to minimize bias of the data due to known diurnal cycles. SWC and soil temperature values were averaged across all depths measured given that the entire soil profile was used to calculate surface flux.

We examined site-specific responses of R_s to soil temperature using univariate linear regressions. Soil water content (SWC) was then incorporated by utilizing multiple linear regressions that included the fixed effects of soil moisture, soil temperature, site, as well as the interaction between site and soil moisture/temperature.

We used the natural log transformed R_s versus temperature relationship at each site to produce an absolute measure of temperature sensitivity which simultaneously minimized bias from other confounding factors (Sierra, 2012). The relationship between the natural-log transformed rate of R_s and temperature of the system produces a linear, stable value of sensitivity as a fractional change in R_s per degree change temperature, over the entire range of temperature. Temperature sensitivity of R_s is conventionally quantified by calculation of a Q_{10} value, or the rate of change in a chemical reaction, given a 10^{o}C change in temperature (Lloyd, 1994). This approach may not be ideal in quantifying the temperature sensitivity of R_s measurements due to its relative measure of increase rather than indicative of an absolute increase, which can lead to biased or relative estimates of temperature sensitivity that vary with temperature (Davidson &

Jannesson, 2006a). While the Q_{10} method may work well for comparing enzymatic limitation over small ranges in temperatures, it is less ideal for assessing temperature sensitivity of ecological systems that can range 40^{o}C. Alternatively, the Arrhenius equation assesses temperature sensitivity as a constant or absolute coefficient by linearizing the relationship between temperature and R_s (Sierra, 2012). Although this yields intrinsic activation energy for the system, this method confounds independently temperature sensitive reactions (such as V_{max} and K_m) as well as other thermodynamic assumptions, resulting in skewed intrinsic activation energy values (Davidson & Janessens, 2006).

We compared differences in sensitivity to temperature (slope) and the R_s rate at 0°C (y-intercept) between sites for both models in a post-hoc analysis adjusting for multiple comparisons following Hothorn et al. (2008) using the glht function in the R package multcomp. We used temperature and SWC weighted averages of the measurements in each pit, taking into account the entire profile contributed to the R_s flux. R_s and soil temperature were natural log transformed to meet linearity and homoscedasticity of model assumptions.

Results

Patterns in R_s across the gradient

In all sites, R_s varied on a seasonal scale, with peak efflux occurring during the monsoon period of each year when both soil temperature and SWC are high (Figure 2). R_s rates were highest at the piñon juniper site (higher under juniper than piñon), followed by the ponderosa pine site (p-value <0.001). We measured approximately 15 fold lower R_s rates at the US-Wsj, US-Ses and US-Seg sites with each of these sites being significantly similar to each other but significantly different than the higher elevation sites (p-value <0.001) (Figure 3).

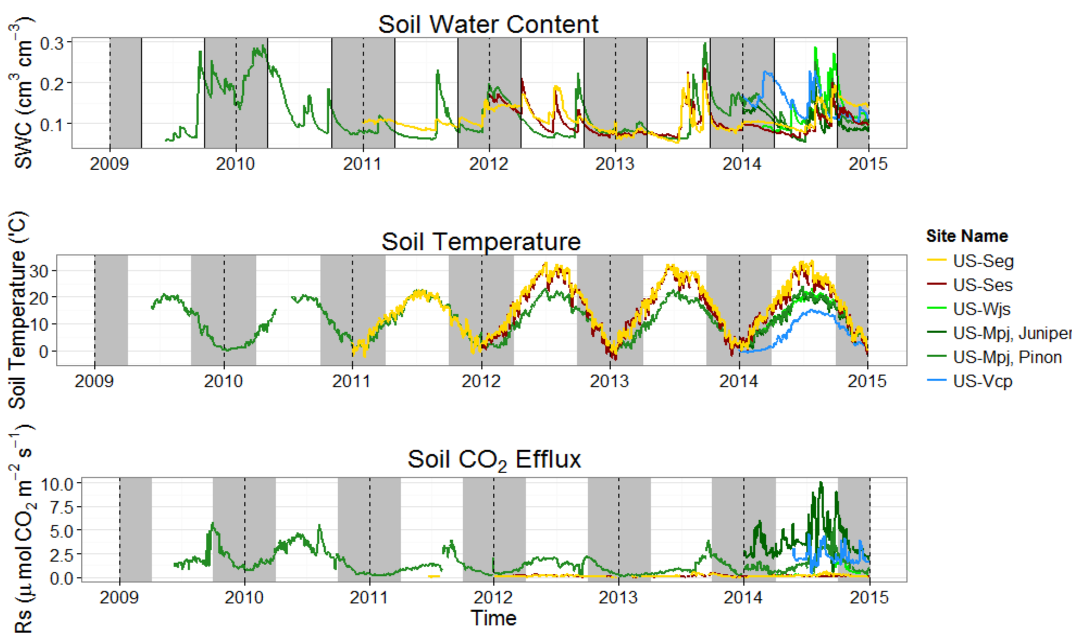

Figure 2: *Soil water content (top), soil temperature (middle) and R_s measurements from 2009 thru 2015 for all sites. Shaded area shows time frames which data was omitted from analysis because of season (Jan 1-March 31 and October 2-December 31 omitted).*

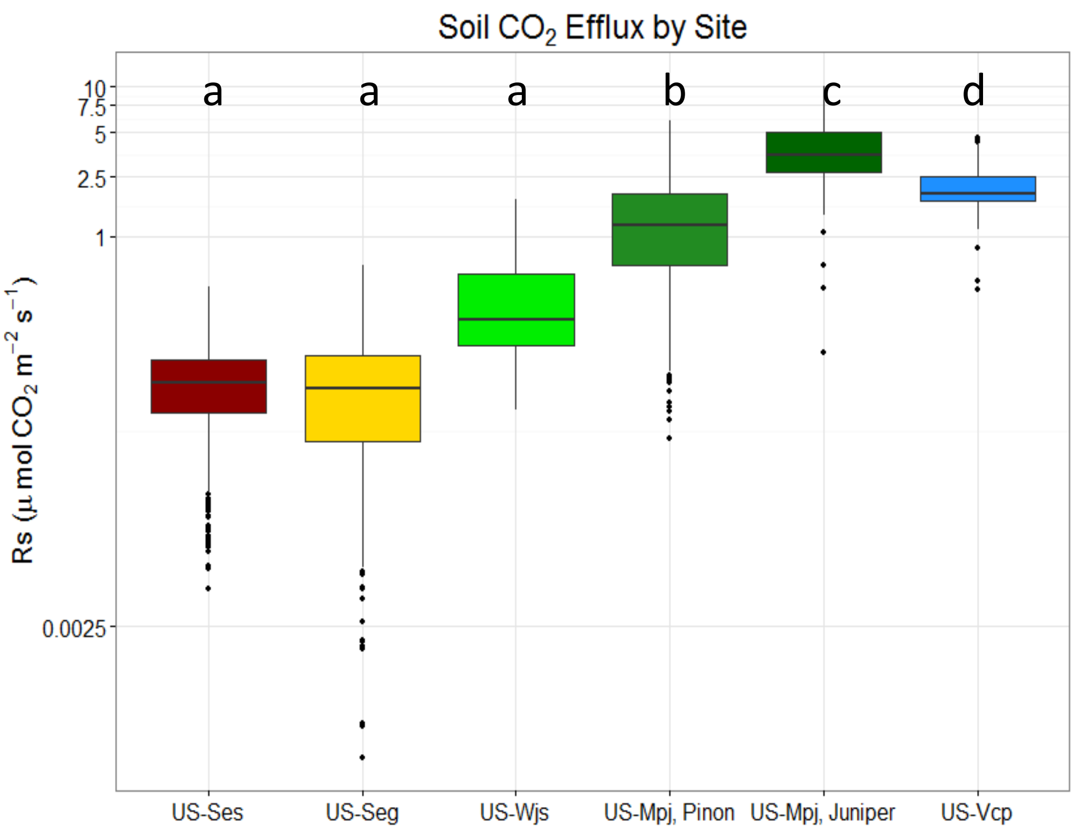

Figure 3: *Daily average rates of Rs by site. Y axis is natural log transformed to show extreme differences in the rates of Rs across the gradient. Letters indicate statistically similar pairings.*

Temperature sensitivity of R_s *across biomes*

The rate of R_s at 0^oC (y-intercept) or what we call the "basal R_s rate" showed extreme differences between sites with a 100 fold increase between the minimum (US-Seg) and maximum (US-Vcp) across the biome gradient. A pair-wise comparison revealed that all sites have different basal R_s values, except US-Ses and US-Wjs which were statistically similar (Figure 3).

Correlations of temperature and R_s were positive and significant for all sites (Table 4), except for US-Vcp, which was not significantly correlated (r^2 <0.001, p-value = 0.94), thus US-Vcp was not included in further analysis or across site comparisons. The sensitivity of R_s to temperature, indicated by the slope of the relationship between log transformed R_s and temperature, was not statistically different at US-Seg, US-Wjs, and US-Mpj under both piñon and juniper canopy. The slopes of the relationship in all statistically similar sites ranged from 3-7% (mean = 5 ± 0.9%; Figure 4, Table 5), and suggests a convergence in R_s temperature sensitivity for 4 out of 6 of our biomes/cover types. The slope of the relationship in US-Ses, was statistically different from the other sites, exhibiting minimal sensitivity to temperature (1.5 ± 0.5%) (Figure 4, Table 5).

Table 4

Site	Slope (Temp. sensitivity)	Basal R_S Rate (non-ln transformed)	r^2	Temp. sensitivity specific p-value
US-Seg	0.069489	0.023199	0.229	<0.001
US-Ses	0.014642	0.084466	0.022	<0.01
US-Wsj	0.052815	0.094175	0.125	<0.001
US-Mpj-P	0.027937	0.92599	0.031	<0.001
US-Mpj-J	0.050795	1.733792	0.115	<0.001
US-Vcp	-0.002191	2.169782	<0.001	0.94

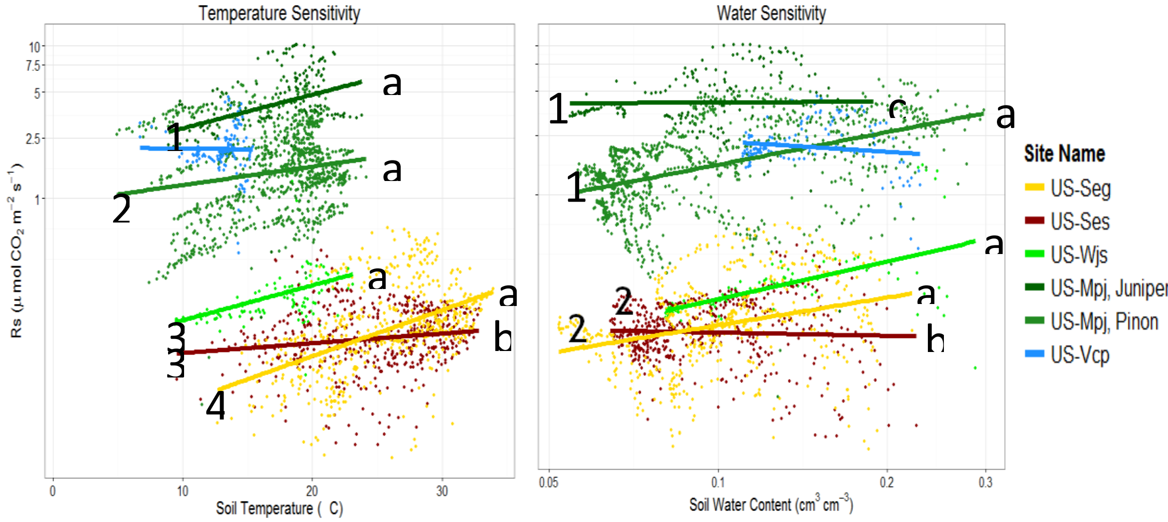

Figure 4: *Rs temperature sensitivity (left) and water response (right) assessed as univariate linear regressions. Y-axis (rate of Rs) has been natural log transformed as has soil water content. Letters indicate statistically similar slopes while numbers indicate statistical similar groupings of basal Rs values.*

Table 5

Site	Slope (Water. sensitivity)	Water specific basal R_s rate	r^2	Univariate linear regression p-value
US-Seg	0.61314	-0.588	0.0809	<0.001
US-Ses	-0.06949	-2.273	<0.001	0.41
US-Wsj	0.83965	0.333	0.35	<0.001
US-Mpj-P	0.72253	2.130	0.235	<0.001
US-Mpj-J	0.01975	1.469	<0.001	0.88
US-Vcp	-0.23476	0.287	0.0127	0.29

Univariate regressions of R_s and SWC indicate that R_s in only US-Seg, US-Wjs and US-Mpj under piñon canopy is statistically responsive to water. Between these sites which were statistically responsive to water, all three sites had similar sensitivities to one another (61-83%; Figure 4). The linear fit for these models was generally poor, with r^2 values of <0.01 in 4 of the 6 sites/cover types. "Basal R_s value" in this case referred to the rate of soil respiration at extremely dry soil conditions (~2% water by volume). These basal respiration rates varied widely, however, and showed similarities between the lower elevation sites. When sites with statistically significant correlations were compared to each other, the driest of the three sites, US-Wjs site and US-Seg sites were similar while the US-Mpj under piñon was significantly different from the other two (Figure 4).

Biome-specific patterns in R_s as a function of both soil temperature and water content

The variability (scatter) in the temperature sensitivity regression was far better explained by the inclusion of SWC in the analysis, evident by increased r^2 values at all sites except US-Ses (Table 6). US-Vcp showed poor fit in both regression analyses and lacked correlation to either variable, thus US-Vcp was not included in site comparisons. This analysis also revealed a notable decrease in the temperature sensitivity of R_s at US-Wjs while conversely suggesting this site was highly responsive to water. This analysis suggests that SWC better explains R_s at this site than temperature. However, all other sites except US-Ses were explained by both variables (Table 7, Figure 5), indicating a multifactor control on R_s at these sites. R_s at the US-Ses site was not statistically correlated to either variable, suggesting neither SWC nor temperature alone regulate R_s at this site.

Table 6

Site	Univariate model temp. sensitivity	Std Error	r^2	Multivariate model temp. sensitivity	Std Error	r^2
US-Seg	0.0695	0.005	0.229	0.0725	0.005	0.330
US-Ses	0.0146	0.005	0.022	0.0144	0.005	0.018
US-Wsj	0.0528	0.016	0.125	0.0012	0.017	0.344
US-Mpj-P	0.028	0.005	0.031	0.060	0.004	0.115
US-Mpj-J	0.051	0.011	0.115	0.055	0.011	0.379
US-Vcp	-0.002	0.026	<.001	0.009	0.027	0.007

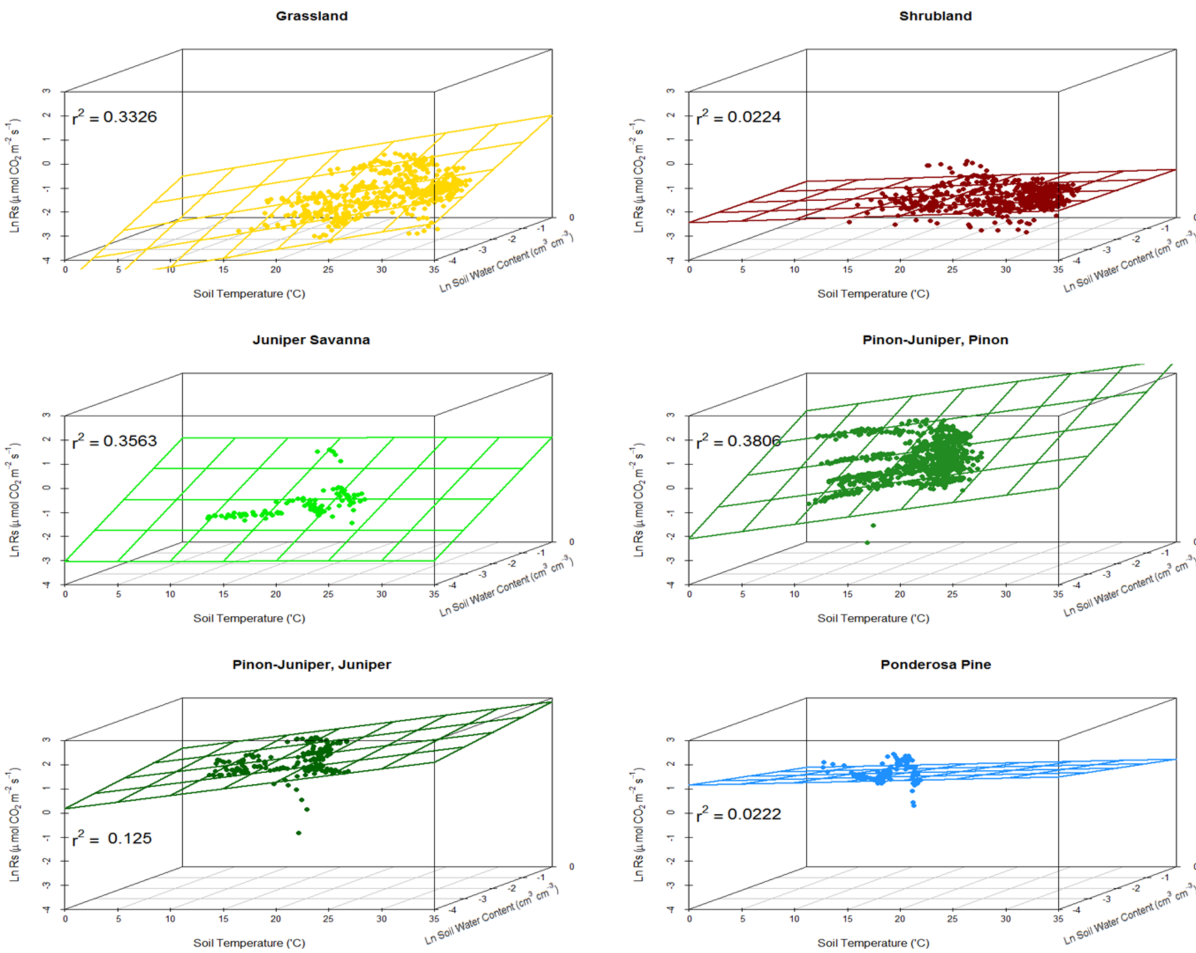

Figure 5*: multivariate regression models for the interaction of temperature and water at all sites.*

Table 7

Site	Temp sensitivity (slope)	Temp sensitivity p-value	SWC sensitivity (slope)	SWC sensitivity p-value	r^2
US-Seg	0.072470	<0.001	0.682001	<0.001	0.330
US-Ses	0.014412	0.003	-0.016803	0.83012	0.018
US-Wsj	0.001204	0.944	0.833033	<0.001	0.344
US-Mpj-P	0.060427	<0.001	0.886859	<0.001	0.115
US-Mpj-J	0.054619	<0.001	0.182395	0.14877	0.379
US-Vcp	0.009463	0.725	-0.260823	0.21733	0.007

Discussion

We used *in situ* continuous soil respiration measurements to quantify temperature sensitivities for multiple semiarid biomes. The sites, which range from desert grassland to ponderosa pine forest, exhibited large difference in basal R_s rates (0.2 – 2.0 μmol m^{-2} s^{-1}), which were linked to plant community structure, including GPP, above-ground biomass, leaf area index ,and edaphic characteristics including soil organic carbon (Anderson-Teixera et al. 2011; Kuzyakof & Domanski, 2000). Despite these structural differences among biomes across the elevation gradient, the temperature sensitivity of basal R_s rates across this gradient were statistically similar for 4 of our 6 cover types.

Expressed as Q_{10} ratios, temperature sensitivity in our biomes ranged from 1.5 to 2.0, with a mean value of 1.57. These values are comparable to those reported in other studies and syntheses (Bahn et al., 2010; Conant et al., 2004; Peng et al., 2008; Song et al., 2014; Vargas et al., 2012) and approximate the global temperature sensitivity of Q_{10} =1.4, proposed by Mahecha et al. (2010). These Q_{10} values are lower than those reported for short-term biochemical and organismal responses which range from 2 to 3 (Brown et al. 2004). The difference between the Q_{10} of R_s in more theoretical idealized systems and Q_{10} of soil respiration can be explained, in part, by the mediation of temperature sensitive reactions with insensitive reactions (e.g. mycorrhizal respiration) (Langley et al., 2005). In addition, the attenuated long term temperature responses of ecological communities compared to those of fundamental biochemical reactions is often attributed to a combination of thermal adaptation on the part of communities and conflation of temperature gradients with resource gradients.

Although our results show a similar temperature sensitivity of R_s across multiple biomes (similar to Conant et al, 2004; Mahecha et al., 2010, Table 8), it is by no means a universal result. Other studies report a range of biome- or site-specific temperature sensitivity of R_s (e.g. Chen and Tian, 2005; Boone et al., 1998; Chatterjee and Jenerrette, 2010; Fierer et al., 2005; Peng et al., 2008; Song et al., 2014; Zahng et al., 2014; Zheng, et al., 2009, Tables 8, 9). Potential mechanisms that might explain the convergence in temperature sensitivity we observed in 4 of the 6 sites across our gradient are: 1) the temporal scale of this study, 2) mitigating interactions among temperature and resource constraints, and 3) selection of microbial communities that are thermally adapted both to site-specific resources and thermal regimes. Each of these potential mechanisms are discussed below.

Temporal scale is an important component to consider when comparing temperature sensitivity. For physiological adaptation, four weeks might be considered “long term” (Chen and Tian, 2005). However, seasonal, and inter-annual variation combined with disturbance may introduce changes in temperature sensitivity on multiple time scales (Conant et al., 1998; Vargas et al., 2012). Although short-term variability in the temperature sensitivity of respiration processes was evident in all of our sites, the multi-year length of record for this study, may have attenuated short-term responses, contributing to convergence in the temperature sensitivity of R_s, similar to what was observed between diverse biomes at a global scale (Mahecha et al., 2010). The shorter data record at two of our sites, US-Wjs and Us-Vcp, may explain why these sites exhibited greater temperature sensitivity of R_s than the other sites.

Table 8

Cross Biome Studies				
Study	**Convergence seen?**	**Proposed mechanisms**	**Methods**	**Biomes included**
Chen and Tian, 2005	No	Vegetation, amount of relative heterotrophic and autotropic respiration occurring and soil fauna vary between sites and alter temperature sensitivity	Meta analysis of 38 "long term" (>4 weeks) studies using unspecified soil respiration data	Boreal, temperate and tropical/subtropical Non-water limited sites specified
Conant et al., 2004	Yes	Differences in carbon and quality of litter minimize differences between sites	Laboratory incubations	Semi-arid ranging from desert shrubland to ponderosa pine forest
Chatterjee and Jenerrette, 2010	No	Elevation, microclimate and associated vegetation alter temperature sensitivity	Laboratory incubations	Semi-arid desert scrubland , evergreen shrubland and evergreen woodland
Mahecha et al., 2010	Yes	Temporal scale offsets individual factors	Ecosystem level FLUXNET network eddy-covariance data from 60 sites which were mathematically normalized for temporal scale	Plant functional types indicated range from croplands to evergreen needle-leaf
Peng et al., 2008	No	MAP and MAT predict R_s temperature sensitivity Grassland and desert biomes limited by carbon availability	Meta analysis of 52 previously published field based (otherwise unspecified) Q10 data	Alpine tundra, temperate forest, desert, cropland, and various forested biomes Desert system was minimally included due to lack of data
Song et al., 2014	No	Soil water availability alters temperature sensitivity across biomes	Ecosystem level FLUXNET eddy-covariance network data from 163 sites	Boreal to temperate to wetlands No semi-arid biomes indicated
Zheng, et al., 2009	No	Climate, vegetation and ecosystem type all moderate temperature sensitivity	Ecosystem level ChinaFlux network non-continuous soil level data from 10 sites	Temperate, subtropical and alpine forests, croplands and grasslands

Manipulations in single-biome studies suggest temperature sensitivity of R_s varies based on factors such as water availability, vegetation cover, root density, type and quality of carbon substrate (Chaterjee & Jennerette, 2010; Conant et al., 2004; Fierer et al., 2005; Zhang et al., 2014) (Table 9). It is possible that the convergence of temperature sensitivity we observed across sites may be due to an interaction between several of these variables that co-vary across our sites (Conant et al. 2004). For example, from grassland to piñon-juniper woodland, water availability increases, which may increase temperature sensitivity (Conant et al. 2014). However, substrate quality (lability) should also increase from our low to mid and high elevation sites due to increased GPP and subsequent root exudates, which might decrease temperature sensitivity. Both of these resource available gradients have the potential to negatively interact with respect to their influence on the temperature sensitivity of biome-specific R_s across our gradient.

Table 9

Single Site/Manipulation Studies					
Study	**Manipulated Variable**	**Methods**	**Biomes**	**Affect variable has on temp. sensitivity**	**Proposed Mechanisms**
Boone et al., 1998	Presence and density of roots	Manipulation field study using non-continuous soil measurements	Temperate deciduous forest	Roots increase temperature sensitivity	Roots increase labile carbon (root exudates) in the soil
Chatterjee and Jenerrette, 2010	Frequency of soil wetting	Laboratory incubation	Semi-arid desert scrubland and evergreen woodland	Frequent wetting increases temperature sensitivity	Carbon sources are depleted with frequent wetting, leaving more recalcitrant substrate with each wetting event
Fierer et al., 2005	Quality of carbon source (labile vs. recalcitrant)	Laboratory incubation	Non-specific	Temperature sensitivity increases as substrate becomes more recalcitrant (low-quality)	Recalcitrant carbon requires higher activation energy for oxidation
Langley and Koch, 2005	Presence and absence of Mycorrhizal fungi	Single species, greenhouse, inoculation study	N/A, greenhouse experiment	None	Mycorrihizal respiration is temperature insensitive
Vargas et al., 2012	Fire disturbance Precipitation frequency and magnitude	In-situ, continuous soil measurements	Semi-arid grassland	Fire minimally effects temperature sensitivity, but only for a short duration (< 1 year) Decreased water stress increases temperature sensitivity	Fire alters the soil microbial and plant communities, but only temporarily
Zahng et al., 2014	Vegetation cover	R_s chamber measurements	Desert shrubland	Temperature sensitivity increases with water availability Vegetation cover alters temperature sensitivity	Environmental conditions and soil properties associated with different vegetation influence sensitivity

Finally, convergence of temperature sensitivity of R_s across multiple biomes that span both an elevation and climate gradient may be due to the long-term selection of microbial communities adapted to both the resources availability and thermal regime. Short-term physiological responses to resource availability can alter temperature sensitivity of R_s. But over decadal time scales, microbial community composition might be expected to be reflect the prevailing climate regime and local resource dynamics which often masks the temperature sensitivity of fundamental biochemical reactions. Such long term selection pressures could explain the convergence of temperature sensitivity of R_s we observed.

Inclusion of SWC in temperature sensitivity assessment

The modeled interaction of temperature and water showed the co-limitation of water and temperature and at the US-Seg and US-Mpj sites under both canopy types while other sites showed varying degrees of responsiveness to both factors. The inclusion of SWC in our linear model reduced the variance in our respiration data at all sites except for US-Vcp and US-Ses. At US-Wsj, water is a better predictor of R_s than temperature. The ponderosa pine site, US-Vcp, the least water stressed site, was excluded from this analysis due to the short duration of measurements. It is possible that with continued measurements, response and sensitivity to abiotic factors may emerge at this site as well.

R_s in the US-Ses (creosote shrubland), although statistically significant in its response to temperature, increased only 1% per degree change in temperature and was not responsive to SWC. The lack of response to either soil water content or temperature at this site suggests a limiting factor for R_s not addressed in this study. The creosote shrubs are less responsive (in terms of carbon uptake) to these drivers than C3 forb and C4 grasses at the nearby grassland site (US-Seg) (Petrie et al, 2014). Lower photosynthetic activity in the creosote may limit not only above ground inputs to SOC but also below ground root exudation, both of which would limit carbon/substrate available for R_s in this system. Secondarily, Breecker (2012) found that these shrubs may be preferentially allocating carbon to deeper soil horizons which may also contribute to the reduced sensitivity to temperature and water.

Implications and suggested continued work

The convergence of a similar sensitivity of R_s to temperature across our gradient of biomes, in addition to the results from Mahecha et al. (2010), support the use of a single global temperature sensitivity coefficient for long term, global carbon and climate models. Several of these models currently use static temperature sensitivity coefficients (Frank et al., 2010) to predict future carbon budgets, ranging from 1.25 to 3.63 (Lenton and Huntingford, 2003) with many models using a universal value of 2 (Frank et al., 2010; Mahecha et al., 2010). These models also neglect water as a covariate (Frank et al., 2010) which we show is an important component to the calculation of temperature sensitivity in semi-arid ecosystems. These currently used coefficients are higher than the suggested converged upon coefficients from this study and Mahecha el al. (2010). This difference between currently used and recently assessed values suggests that current land surface models may be overestimating the sensitivity of soil carbon fluxes to temperature, and thus might be overestimating the amount of carbon released from the terrestrial soil carbon pool as global temperatures increase.

In this study *in situ*, long term soil level carbon, temperature and water data were assessed to quantify temperature sensitivity between biomes. However, we suggest that there is an outstanding need for continued long-term monitoring using these methods in the context of natural ecosystems to gain a full view of the sensitivities of these systems. Furthermore, as disturbance in natural systems continues to be prevalent, comparing disturbed and undisturbed ecosystems over long temporal scales is of high importance.

Conclusions

Across a range of semi-arid ecosystems, the sensitivity of R_s to temperature converged at a mean value of 1.57, comparable to a previously suggested global coefficient of 1.4. The similarities in temperature sensitivity between the range of disparate sites across our gradient is likely the result of the multi-year temporal scale of our measurements which dampen out any short-term responses, as well as mediation due to interacting co-varying controls on temperature sensitivity, and selection pressures for microbial populations that maximize growth under prevailing resource and temperature conditions across our gradient of biomes. The integration of SWC into this assessment increased our ability to explain the variability in R_s compared to a univariate analysis of temperature sensitivity alone. However, the degree to which water explains R_s was variable across our gradient. Long term, *in situ*, measurements for analysis of R_s temperature sensitivity are required to further test hypotheses related to convergence of temperature sensitivities across ecosystems, especially in semi-arid biomes. Quantifying temperature sensitivity following disturbances such as pathogens, fire and drought is also proposed as an outstanding need in this research.

References

Ahlstrom A, Raupach Mr, Schurgers G *et al.* (2015) The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. Science, **348**, 895-899.

Allen Mf, Vargas R, Graham Ea *et al.* (2007) Soil sensor technology: Life within a pixel. Bioscience, **57**, 859-867.

Anderson-Teixeira Kj, Delong Jp, Fox Am, Brese Da, Litvak Me (2011) Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. Global Change Biology,**17**, 410-424.

Bahn M, Reichstein M, Davidson Ea *et al.* (2010) Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes. Biogeosciences, **7**, 2147-2157.

Balogh J, Foti S, Pinter K, Burri S, Eugster W, Papp M, Nagy Z (2015) Soil CO_2 efflux and production rates as influenced by evapotranspiration in a dry grassland. Plant and Soil, **388**, 157-173.

Boone Rd, Nadelhoffer Kj, Canary Jd, Kaye Jp (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature, **396**, 570-572.

Bradford Ma (2013) Thermal adaptation of decomposer communities in warming soils. Frontiers in Microbiology, **4**.

Breecker Do, Mcfadden Ld, Sharp Zd, Martinez M, Litvak Me (2012) Deep Autotrophic Soil Respiration in Shrubland and Woodland Ecosystems in Central New Mexico. Ecosystems, **15**, 83-96.

Brown Jh, Gillooly Jf, Allen Ap, Savage Vm, West Gb (2004) Toward a metabolic theory of ecology. Ecology, **85**, 1771-1789.

Carbone Ms, Vargas R (2008) Automated soil respiration measurements: new information, opportunities and challenges. New Phytologist, **177**, 295-297.

Chatterjee A, Jenerette Gd (2011) Changes in soil respiration Q(10) during drying-rewetting along a semi-arid elevation gradient. Geoderma, **163**, 171-177.

Chen H, Tian Hq (2005) Does a general temperature-dependent Q(10) model of soil respiration exist at biome and global scale? Journal of Integrative Plant Biology,**47**, 1288-1302.

Collins Sl, Belnap J, Grimm Nb *et al.* (2014) A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems. Annual Review of Ecology, Evolution, and Systematics, Vol 45, **45**, 397-419.

Conant Rt, Dalla-Betta P, Klopatek Cc, Klopatek Ja (2004) Controls on soil respiration in semiarid soils. Soil Biology & Biochemistry, **36**, 945-951.

Conant Rt, Klopatek Jm, Malin Rc, Klopatek Cc (1998) Carbon pools and fluxes along an environmental gradient in northern Arizona. Biogeochemistry, **43**, 43-61.

Cross Af, Schlesinger Wh (1999) Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. Plant Ecology, **145**, 11-25.

Cueva A, Bahn M, Litvak M, Pumpanen J, Vargas R (2015) A multisite analysis of temporal random errors in soil CO_2 efflux. Journal of Geophysical Research-Biogeosciences, **120**, 737-751.

Davidson Ea, Janssens Ia (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature, **440**, 165-173.

Davidson Ea, Janssens Ia, Luo Yq (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). Global Change Biology, **12**, 154-164.

Fang C, Moncrieff Jb (2001) The dependence of soil CO_2 efflux on temperature. Soil Biology & Biochemistry, **33**, 155-165.

Fierer N, Craine Jm, Mclauchlan K, Schimel Jp (2005) Litter quality and the temperature sensitivity of decomposition. Ecology, **86**, 320-326.

Frank Dc, Esper J, Raible Cc, Buentgen U, Trouet V, Stocker B, Joos F (2010) Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. Nature,**463**, 527-U143.

Ginsburg Jm (1925) A modified respiration apparatus for plant and soil studies. Soil Science, **19**, 411-415.

Gutzler Ds, Robbins To (2011) Climate variability and projected change in the western United States: regional downscaling and drought statistics. Climate Dynamics, **37**, 835-849.

Heisler-White Jl, Knapp Ak, Kelly Ef (2008) Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia, **158**, 129-140.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical Journal, **50**, 346-363.

Huntingford C, Lowe Ja, Booth Bbb, Jones Cd, Harris Gr, Gohar Lk, Meir P (2009) Contributions of carbon cycle uncertainty to future climate projection spread. Tellus Series B-Chemical and Physical Meteorology, **61**, 355-360.

Huxman Te, Snyder Ka, Tissue D *et al.* (2004) Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia, **141**, 254-268.

Knorr W, Prentice Ic, House Ji, Holland Ea (2005) Long-term sensitivity of soil carbon turnover to warming. Nature, **433**, 298-301.

Krishnan P, Meyers Tp, Scott Rl, Kennedy L, Heuer M (2012) Energy exchange and evapotranspiration over two temperate semi-arid grasslands in North America. Agricultural and Forest Meteorology, **153**, 31-44.

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. Journal of Plant Nutrition and Soil Science-Zeitschrift Fur Pflanzenernahrung Und Bodenkunde, **163**, 421-431.

Lal R (2004) Soil carbon sequestration to mitigate climate change. Geoderma, **123**, 1-22.

Langley Ja, Johnson Nc, Koch Gw (2005) Mycorrhizal status influences the rate but not the temperature sensitivity of soil respiration. Plant and Soil, **277**, 335-344.

Lloyd J, Taylor Ja (1994) ON THE TEMPERATURE-DEPENDENCE OF SOIL RESPIRATION. Functional Ecology, **8**, 315-323.

Mahecha Md, Reichstein M, Carvalhais N *et al.* (2010) Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level. Science, **329**, 838-840.

Mahecha Md, Reichstein M, Carvalhais N *et al.* (2011) Response to Comment on "Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level". Science, **331**, 1265-+.

Meigs Gw, Donato Dc, Campbell Jl, Martin Jg, Law Be (2009) Forest Fire Impacts on Carbon Uptake, Storage, and Emission: The Role of Burn Severity in the Eastern Cascades, Oregon. Ecosystems, **12**, 1246-1267.

Nakano T, Nemoto M, Shinoda M (2008) Environmental controls on photosynthetic production and ecosystem respiration in semi-arid grasslands of Mongolia. Agricultural and Forest Meteorology, **148**, 1456-1466.

Nakano T, Shinoda M (2010) Response of ecosystem respiration to soil water and plant biomass in a semiarid grassland. Soil Science and Plant Nutrition, **56**, 773-781.

Nie M, Pendall E, Bell C, Gasch Ck, Raut S, Tamang S, Wallenstein Md (2013) Positive climate feedbacks of soil microbial communities in a semi-arid grassland. Ecology Letters, **16**, 234-241.

Peng S, Piao S, Wang T, Sun J, Shen Z (2009) Temperature sensitivity of soil respiration in different ecosystems in China. Soil Biology & Biochemistry, **41**, 1008-1014.

Raich Jw, Schlesinger Wh (1992) THE GLOBAL CARBON-DIOXIDE FLUX IN SOIL RESPIRATION AND ITS RELATIONSHIP TO VEGETATION AND CLIMATE. Tellus Series B-Chemical and Physical Meteorology, **44**, 81-99.

Reichstein M, Beer C (2008) Soil respiration across scales: The importance of a model-data integration framework for data interpretation. Journal of Plant Nutrition and Soil Science, **171**, 344-354.

Reichstein M, Rey A, Freibauer A *et al.* (2003) Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Global Biogeochemical Cycles, **17**.

Richardson J, Chatterjee A, Jenerette Gd (2012) Optimum temperatures for soil respiration along a semi-arid elevation gradient in southern California. Soil Biology & Biochemistry, **46**, 89-95.

Schlesinger Wh, Andrews Ja (2000) Soil respiration and the global carbon cycle. Biogeochemistry, **48**, 7-20.

Schwinning S, Ehleringer Jr (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. Journal of Ecology, **89**, 464-480.

Sierra Ca (2012) Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations. Biogeochemistry, **108**, 1-15.

Sierra Ca, Trumbore Se, Davidson Ea, Vicca S, Janssens I (2015) Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture. Journal of Advances in Modeling Earth Systems, **7**, 335-356.

Snyder Ka, Tartowski Sl (2006) Multi-scale temporal variation in water availability: Implications for vegetation dynamics in arid and semi-arid ecosystems. Journal of Arid Environments, **65**, 219-234.

Song B, Niu S, Luo R *et al.* (2014) Divergent apparent temperature sensitivity of terrestrial ecosystem respiration. Journal of Plant Ecology, **7**, 419-428.

Song W, Chen S, Wu B *et al.* (2012) Vegetation cover and rain timing co-regulate the responses of soil CO_2 efflux to rain increase in an arid desert ecosystem. Soil Biology & Biochemistry, **49**, 114-123.

Springsteen A, Loya W, Liebig M, Hendrickson J (2010) Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. Plant and Soil, **328**, 369-379.

Stekhoven Dj, Buehlmann P (2012) MissForest-non-parametric missing value imputation for mixed-type data. Bioinformatics, **28**, 112-118.

Stoy Pc, Richardson Ad, Baldocchi Dd *et al.* (2009) Biosphere-atmosphere exchange of CO_2 in relation to climate: a cross-biome analysis across multiple time scales. Biogeosciences, **6**, 2297-2312.

Tang Jw, Baldocchi Dd, Qi Y, Xu Lk (2003) Assessing soil CO_2 efflux using continuous measurements of CO_2 profiles in soils with small solid-state sensors. Agricultural and Forest Meteorology, **118**, 207-220.

Taylor Ja, Lloyd J (1992) SOURCES AND SINKS OF ATMOSPHERIC CO_2. Australian Journal of Botany, **40**, 407-418.

Thomey Ml, Collins Sl, Vargas R, Johnson Je, Brown Rf, Natvig Do, Friggens Mt (2011) Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. Global Change Biology, **17**, 1505-1515.

Vargas R, Allen Mf (2008a) Dynamics of fine root, fungal rhizomorphs, and soil respiration in a mixed temperate forest: Integrating sensors and observations. Vadose Zone Journal, **7**, 1055-1064.

Vargas R, Allen Mf (2008b) Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration. New Phytologist, **179**, 460-471.

Vargas R, Baldocchi Dd, Allen Mf *et al.* (2010a) Looking deeper into the soil: biophysical controls and seasonal lags of soil CO_2 production and efflux. Ecological Applications, **20**, 1569-1582.

Vargas R, Baldocchi Dd, Bahn M *et al.* (2011a) On the multi-temporal correlation between photosynthesis and soil CO_2 efflux: reconciling lags and observations. New Phytologist, **191**, 1006-1017.

Vargas R, Carbone Ms, Reichstein M, Baldocchi Dd (2011b) Frontiers and challenges in soil respiration research: from measurements to model-data integration. Biogeochemistry, **102**, 1-13.

Vargas R, Collins Sl, Thomey Ml, Johnson Je, Brown Rf, Natvig Do, Friggens Mt (2012) Precipitation variability and fire influence the temporal dynamics of soil CO_2 efflux in an arid grassland. Global Change Biology, **18**, 1401-1411.

Vargas R, Detto M, Baldocchi Dd, Allen Mf (2010b) Multiscale analysis of temporal variability of soil CO_2 production as influenced by weather and vegetation. Global Change Biology, **16**, 1589-1605.

Vargas R, Sonnentag O, Abramowitz G *et al.* (2013) Drought Influences the Accuracy of Simulated Ecosystem Fluxes: A Model-Data Meta-analysis for Mediterranean Oak Woodlands. Ecosystems, **16**, 749-764.

Vickers D, Thomas Ck, Pettijohn C, Martin Jg, Law Be (2012) Five years of carbon fluxes and inherent water-use efficiency at two semi-arid pine forests with different disturbance histories. Tellus Series B-Chemical and Physical Meteorology, **64**.

Wan S, Norby Rj, Ledford J, Weltzin Jf (2007) Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biology, **13**, 2411-2424.

Wang B, Zha Ts, Jia X, Wu B, Zhang Yq, Qin Sg (2014) Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. Biogeosciences, **11**, 259-268.

Whitford Wg, Anderson J, Rice Pm (1997) Stemflow contribution to the 'fertile island' effect in creosotebush, Larrea tridentata. Journal of Arid Environments, **35**, 451-457.

Yvon-Durocher G, Caffrey Jm, Cescatti A *et al.* (2012) Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature*,* **487**, 472-476.

Zeng X, Zhang W, Shen H, Cao J, Zhao X (2014) Soil respiration response in different vegetation types at Mount Taihang, China. Catena*,* **116**, 78-85.

Zhang Lh, Chen Yn, Zhao Rf, Li Wh (2010) Significance of temperature and soil water content on soil respiration in three desert ecosystems in Northwest China. Journal of Arid Environments*,* **74**, 1200-1211.

Zheng Z-M, Yu G-R, Fu Y-L, Wang Y-S, Sun X-M, Wang Y-H (2009) Temperature sensitivity of soil respiration is affected by prevailing climatic conditions and soil organic carbon content: A trans-China based case study. Soil Biology & Biochemistry*,* **41**, 1531-1540.