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

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

by

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B.S. BIOLOGY

THESIS

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

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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.
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<td>Table 9</td>
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</tbody>
</table>
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 CO₂ 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 CO₂ 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 (Rₛ), 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 Rₛ 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 Rs, 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 Rs 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
Rs across an elevation and climatic gradient of distinct semi-arid biomes using long term,
in-situ soil CO2 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 1596 m; 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 2486 m (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>
<thead>
<tr>
<th>Site Name</th>
<th>Biome</th>
<th>Location</th>
<th>Elevation</th>
<th>MAT (°C)</th>
<th>MAP (mm)</th>
<th>Dominant species</th>
<th>Mortality/ Disturbance history</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>Northern Chihuahuan</td>
<td>Sevilleta NWP LTER</td>
<td>1596</td>
<td>17.7</td>
<td>250</td>
<td>C4 grasses (<em>Bouteloua gracilis</em>, <em>B. eriopoda</em>, <em>Sporobolis</em> spp., <em>Hilaria jamesii</em>, <em>Muhlenbergia</em> spp.)</td>
<td>Cattle grazing prior to 1973</td>
</tr>
<tr>
<td>Shrubland</td>
<td>Desert shrubland</td>
<td>Sevilleta NWP LTER</td>
<td>1605</td>
<td>17.7</td>
<td>250</td>
<td><em>Larrea</em> (Creosote bush), C4 grasses <em>B. eriopoda</em>, <em>Sporobolis</em> spp., <em>Hilaria jamesii</em>, <em>Muhlenbergia</em> spp.</td>
<td></td>
</tr>
<tr>
<td>Juniper Savanna</td>
<td>Juniper Savannah</td>
<td>Appx 25 Km S of Willard, NM</td>
<td>1926</td>
<td>15.2</td>
<td>361</td>
<td><em>Juniperus monosperma</em> and C4 grasses (<em>Bouteloua gracilis</em>)</td>
<td>Sporadic but not intensive cattle grazing before 2010, but since exclosure has prevented grazing</td>
</tr>
<tr>
<td>Piñon-Juniper</td>
<td>Piñon-Juniper woodland</td>
<td>Appx 25 km S of Mountainair, NM</td>
<td>2126</td>
<td>14.8</td>
<td>418</td>
<td><em>Juniperus monosperma</em> and <em>Pinus edulis</em> overstory with C4 grass understory (<em>Bouteloua gracilis</em>)</td>
<td>Bark beetle outbreak, ~50% piñon mortality in 2013.</td>
</tr>
<tr>
<td>Ponderosa Pine</td>
<td>Ponderosa pine forest</td>
<td>Valles Caldera National Preserve, Jemez Mountains, NM</td>
<td>2486</td>
<td>9.8</td>
<td>550</td>
<td><em>Pinus ponderosa</em> overstory, <em>Quercus gambelii</em> and C3 grass and forbe understory</td>
<td></td>
</tr>
</tbody>
</table>
Soil respiration, water, and temperature measurements

We made continuous soil CO\textsubscript{2} measurements between 2009 and 2014, with various start dates of collection depending on study site (Table 2). At each site, soil CO\textsubscript{2} concentrations were measured using Vaisala CARBOCAP CO\textsubscript{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\textsubscript{s}. Soil temperature (Campbell Scientific T107) and volumetric soil moisture (Campbell Scientific CS616) was measured simultaneously in all pits, at all depths.

Table 2

<table>
<thead>
<tr>
<th>Site</th>
<th>Total Number of CO\textsubscript{2} probes</th>
<th>Probes depths (cm)</th>
<th>n</th>
<th>Cover vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>12</td>
<td>2011-2013: 5, 10, 20, 50 2014: 5, 10, 30</td>
<td>3 3</td>
<td>C4 grasses</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>9</td>
<td>5, 10, 30</td>
<td>3 3</td>
<td>Juniperus monosperma</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td></td>
<td></td>
<td>Juniperus monosperma</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>12</td>
<td>5, 10, 30, 60</td>
<td>3 3</td>
<td>Pinus ponderosa</td>
</tr>
</tbody>
</table>
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:

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

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**

<table>
<thead>
<tr>
<th>Site</th>
<th>Soil porosity values</th>
<th>Sand + Silt value(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>5 cm = 0.4725</td>
<td>10 cm = 0.3924</td>
</tr>
<tr>
<td>US-Ses</td>
<td>5 cm = 0.4994</td>
<td>10 cm = 0.4589</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>5 cm = 0.3507</td>
<td>10 cm = 0.3507</td>
</tr>
<tr>
<td>US-Mpj</td>
<td>5 cm = 0.5663</td>
<td>10 cm = 0.5815</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>5 cm = 0.5024</td>
<td>10 cm = 0.4417</td>
</tr>
</tbody>
</table>

The calculation of surface flux assumes constant production of CO₂ within the soil profile, as well as increasing CO₂ 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 CO₂ 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 (April 1 - 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 $10^\circ C$ 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°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).

![Graphs showing soil water content, soil temperature, and $R_s$ measurements from 2009 to 2015 for all sites. Shaded areas indicate the time frames when data was omitted from analysis due to season (January 1 to March 31 and October 2 to December 31).](image)

*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).*
Temperature sensitivity of $R_s$ across biomes

The rate of $R_s$ at $0^\circ C$ (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).

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

<table>
<thead>
<tr>
<th>Site</th>
<th>Slope (Temp. sensitivity)</th>
<th>Basal $R_s$ Rate (non-ln transformed)</th>
<th>$r^2$</th>
<th>Temp. sensitivity specific p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>0.069489</td>
<td>0.023199</td>
<td>0.229</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Ses</td>
<td>0.014642</td>
<td>0.084466</td>
<td>0.022</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>0.052815</td>
<td>0.094175</td>
<td>0.125</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Mpj-P</td>
<td>0.027937</td>
<td>0.92599</td>
<td>0.031</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Mpj-J</td>
<td>0.050795</td>
<td>1.733792</td>
<td>0.115</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>-0.002191</td>
<td>2.169782</td>
<td>&lt;0.001</td>
<td>0.94</td>
</tr>
</tbody>
</table>
Table 5

<table>
<thead>
<tr>
<th>Site</th>
<th>Slope (Water. sensitivity)</th>
<th>Water specific basal Rs rate</th>
<th>$r^2$</th>
<th>Univariate linear regression p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>0.61314</td>
<td>-0.588</td>
<td>0.0809</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Ses</td>
<td>-0.06949</td>
<td>-2.273</td>
<td>&lt;0.001</td>
<td>0.41</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>0.83965</td>
<td>0.333</td>
<td>0.35</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Mpj-P</td>
<td>0.72253</td>
<td>2.130</td>
<td>0.235</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>US-Mpj-J</td>
<td>0.01975</td>
<td>1.469</td>
<td>&lt;0.001</td>
<td>0.88</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>-0.23476</td>
<td>0.287</td>
<td>0.0127</td>
<td>0.29</td>
</tr>
</tbody>
</table>

**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.
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

<table>
<thead>
<tr>
<th>Site</th>
<th>Univariate model temp. sensitivity</th>
<th>Std Error</th>
<th>$r^2$</th>
<th>Multivariate model temp. sensitivity</th>
<th>Std Error</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>0.0695</td>
<td>0.005</td>
<td>0.229</td>
<td>0.0725</td>
<td>0.005</td>
<td>0.330</td>
</tr>
<tr>
<td>US-Ses</td>
<td>0.0146</td>
<td>0.005</td>
<td>0.022</td>
<td>0.0144</td>
<td>0.005</td>
<td>0.018</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>0.0528</td>
<td>0.016</td>
<td>0.125</td>
<td>0.0012</td>
<td>0.017</td>
<td>0.344</td>
</tr>
<tr>
<td>US-Mpj-P</td>
<td>0.028</td>
<td>0.005</td>
<td>0.031</td>
<td>0.060</td>
<td>0.004</td>
<td>0.115</td>
</tr>
<tr>
<td>US-Mpj-J</td>
<td>0.051</td>
<td>0.011</td>
<td>0.115</td>
<td>0.055</td>
<td>0.011</td>
<td>0.379</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>-0.002</td>
<td>0.026</td>
<td>&lt;.001</td>
<td>0.009</td>
<td>0.027</td>
<td>0.007</td>
</tr>
</tbody>
</table>
Figure 5: multivariate regression models for the interaction of temperature and water at all sites.
Table 7

<table>
<thead>
<tr>
<th>Site</th>
<th>Temp sensitivity (slope)</th>
<th>Temp sensitivity p-value</th>
<th>SWC sensitivity (slope)</th>
<th>SWC sensitivity p-value</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>US-Seg</td>
<td>0.072470</td>
<td>&lt;0.001</td>
<td>0.682001</td>
<td>&lt;0.001</td>
<td>0.330</td>
</tr>
<tr>
<td>US-Ses</td>
<td>0.014412</td>
<td>0.003</td>
<td>-0.016803</td>
<td>0.83012</td>
<td>0.018</td>
</tr>
<tr>
<td>US-Wsj</td>
<td>0.001204</td>
<td>0.944</td>
<td>0.833033</td>
<td>&lt;0.001</td>
<td>0.344</td>
</tr>
<tr>
<td>US-Mpj-P</td>
<td>0.060427</td>
<td>&lt;0.001</td>
<td>0.886859</td>
<td>&lt;0.001</td>
<td>0.115</td>
</tr>
<tr>
<td>US-Mpj-J</td>
<td>0.054619</td>
<td>&lt;0.001</td>
<td>0.182395</td>
<td>0.14877</td>
<td>0.379</td>
</tr>
<tr>
<td>US-Vcp</td>
<td>0.009463</td>
<td>0.725</td>
<td>-0.260823</td>
<td>0.21733</td>
<td>0.007</td>
</tr>
</tbody>
</table>
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 $\mu$mol 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

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

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

\textit{Implications and suggested continued work}

The convergence of a similar sensitivity of R\textsubscript{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


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Song W, Chen S, Wu B et al. (2012) Vegetation cover and rain timing co-regulate the responses of soil CO2 efflux to rain increase in an arid desert ecosystem. Soil Biology & Biochemistry, 49, 114-123.


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.


