



Optimum temperatures for soil respiration along a semi-arid elevation gradient in southern California

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ABSTRACT

Soil respiration (R) has not been adequately studied at temperatures above 35 °C, which are common temperatures for soils in the southwestern United States and may be important for C dynamics in semi-arid regions. While frequently excluded from ecosystem models or set to 35 °C, the optimum temperature for soil R is poorly understood. Optimum temperatures are likely controlled by substrate availability, soil moisture content, and previous climate. To quantify the optimal temperature for soil R and hypothesized relationships, we collected soils from beneath and between plant canopies at three sites along a semi-arid elevation gradient. Processed soil samples were incubated at three soil moisture contents and soil R was measured at 6 temperatures, successively (25–55 °C). From these data, an activation energy for reaction kinetics and deactivation energy for enzyme functionality model was used to generate soil R curves from which two parameters were derived: R_{\max} , the maximum rate of soil R and T_{opt} , the optimum temperature for soil R . R_{\max} was significantly greater for soils at the highest elevation and at medium soil moisture content. T_{opt} was greater than 35 °C at all locations. In addition, T_{opt} was significantly greater for soils with greater amounts of SOM but not significantly different along the elevation gradient or at different moisture contents. These results support inclusion of much higher optimum temperatures than currently used in many ecosystem and land-surface models and provide support for explaining variation in T_{opt} as regulated by substrate quantity within a site and general insensitivity across climate differences.

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1. Introduction

Understanding the rate at which terrestrial carbon cycling occurs is critical for determining the role of soil as a potential positive feedback mechanism for the greenhouse effect and resulting climate changes (Kirschbaum, 2006; Raich and Schlesinger, 1992; Schimel et al., 2001). The temperature dependence of decomposition and respiration of CO₂ by soil microorganisms is one principal controlling relationship (Kirschbaum, 2006). However, the interactions between temperature and soil metabolic activity have primarily been evaluated within 0–35 °C range, with few studies characterizing CO₂ efflux rates above 35 °C (Davidson et al., 2006; Fang and Moncrieff, 2001; Lloyd and Taylor, 1994). As a reflection of this lack of information, terrestrial ecosystem models of soil R typically do not include any negative

effect of temperature or the optimal temperature is assumed to be near 35 °C (Cable et al., 2011; Fang and Moncrieff, 2001; Lloyd and Taylor, 1994; Shen et al., 2008). However, soil temperatures in the lowlands of southern California and other warm drylands frequently exceed 35 °C from June through September (Barron-Gafford et al., 2011; Boyd-Deep Canyon Desert Research Center). In observational studies of diel changes in soil respiration, maximum rates of soil respiration have been observed above 35 °C (Barron-Gafford et al., 2011; Parker et al., 1983). Thus, determining the rate and variation of soil R at temperatures greater than 35 °C is important for understanding and modeling terrestrial carbon cycling in a warming world, particularly for soils within hyper-thermic temperature regimes.

Two key dependent variables describe soil R at optimal temperatures: the temperature of maximum respiration (T_{opt}) and the rate of maximum respiration (R_{\max}). The regulation of T_{opt} and R_{\max} may respond differently to environmental conditions. Similar to factors influencing soil R within the 0–35 °C range, we hypothesized variation around optimal temperatures would be

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dependent on soil moisture content, substrate supply, and the adjustment of soil microbes to local climatic conditions (Davidson and Janssens, 2006; Fierer et al., 2005; Scott-Denton et al., 2003; Waldrop and Firestone, 2006). Soil moisture content affects soil R by controlling soil water films, water potentials inside soil microorganisms, and the diffusion of O_2 (Ilstedt et al., 2000; McLatchey and Reddy, 1998; Šimůnek and Suarez, 1993; Stres et al., 2008). Generally, a soil moisture content around 50% of water-holding capacity (WHC) allows for maximum soil R (Ilstedt et al., 2000; Jin et al., 2008), although the effect on optimum temperature for soil R is unclear.

In addition to soil moisture, C substrate supply has been shown to directly influence soil R rates (Davidson et al., 2006) and strongly regulate temperature dependence of soil R (Davidson et al., in press). At low substrate concentrations, the delivery rate of C substrate to microbes may limit peak fluxes at the temperature associated with these fluxes. C substrate is primarily supplied to soil by adjacent vegetation in the form of detritus. The rate of soil organic matter (SOM) accumulation in soil is dependent on the vegetation type and climate (Berg and Meentemeyer, 2002; Raich and Tufekcioglu, 2000).

An alternate hypothesis believed to control the temperature response of soil R is climate acclimation or adaptation of soil microorganisms. An early study of the temperature dependence of soil R by Koepf (1953) hypothesized local temperature regime was a dominant variable influencing the temperature sensitivity of soil R . Recent experiments have shown soil R acclimation to long term (>77 days) thermal environment (Bradford et al., 2010). Furthermore, soil microorganisms have been found to be phylogenetically clustered with respect to elevation (Bryant et al., 2008). Pietikäinen et al. (2005) hypothesized climate acclimation of soil microbial communities would occur with prolonged exposure to temperatures > 35 °C. Therefore, it may be possible that soil microorganisms are physically adapted to their climate and would exhibit a greater or lesser adaption to respire at elevated temperatures depending on their original climate.

To understand the variation in optimum temperature for soil R , we conducted laboratory incubations at elevated temperatures (>35 °C) using soils collected from contrasting plant canopy and interplant microenvironments along a 2500 m elevation gradient in southern California. The resulting data for each soil sample were coupled with a process-based model of metabolism that includes temperature sensitivity in both the activation energy required for respiration and the deactivation energy associated with enzyme degradation. We used this data-model combination to identify T_{opt} and R_{max} . The combination of elevation gradient and microenvironments were used to evaluate the potential influence of substrate and climate adaptation on the optimum temperature for soil R . This analysis was repeated at three different moisture contents to evaluate the role of moisture on soil R at elevated temperatures. The

climate adaptation hypothesis leads to a prediction that T_{opt} and R_{max} will be greatest at the low elevations and in open microenvironments compared to higher elevations and underneath plant canopy microenvironments. In contrast, substrate supply hypotheses predict T_{opt} and R_{max} will be greatest at high elevations and underneath plant canopy microenvironments as both have higher organic matter contents than either low elevations or the plant interspaces. Similar to soil R patterns within the 0–35 °C, the moisture availability hypothesis predicts T_{opt} and R_{max} will be highest under intermediate moisture content. The resulting data will provide some of the first estimates of soil R patterns near their thermal optimums and inform understanding of soil R dynamics in response to projected global warming.

2. Materials and methods

2.1. Soil sampling and site characterization

Soil samples were collected along a 2500 m elevation gradient of Mt. Santa Rosa in Riverside County, California, during August of 2009. The month was chosen to reflect the condition of the soil during the warmest temperatures of the year. Soil was collected using hand trowels from surface mineral horizons at 0–15 cm depth. Three sites were chosen along the elevation gradient: Base (289 m), Mid (1829 m) and Summit (2489 m) (Table 1). Along the elevation gradient from Base to Summit, the mean annual air temperature decreases from 24 to 10 °C and the mean annual precipitation increases from 80 to 524 mm (Table 1) (Kelly and Goulden, 2008). The three sites are located at three distinct landform positions: alluvial fan, rolling hills, and mountain Summit (Table 2). At each of the three sites, soil samples were collected from two contrasting microenvironments: five from beneath the canopy of the dominant vegetation species and five from the open spaces between the canopies, for a total of 30 field replicated samples. The dominant vegetation at Base, Mid, and Summit sites are *Larrea tridentata*, *Adenostema fasciculatum*, and *Pinus jefferyi*, respectively.

2.2. Sample preparation and analysis

Samples were air dried and sieved with a 2 mm mesh sieve. Sieving alters soil samples by reducing the soil pore volume and removes aggregates stabilized by soil microorganisms. The porosity would not have been dramatically impacted as volume reduction effects are minor for sandy textured soils. The use of sieved soil prevented coarse root biomass from influencing CO_2 measurements while retaining particulate organic matter < 2 mm in the samples. Where feasible, investigations should incorporate the use of intact soils to facilitate comparisons with intact organic horizons and field conditions. Subsamples were used for the determination

Table 1
Geographic location and climatic parameters, of Base, Mid, and Summit sites located along 2500 m elevation gradient of Santa Rosa Mountain located near Palm Springs, Riverside County, California, USA.

Site	Elevation (m)	Latitude	Longitude	MAT (°C)	MAP (mm)	Frost Free days	Vegetation Type	Soil Taxonomy
Base	289	33°14'19" N	116°22'15" W	24 ^a	80	290	Desert Scrub	Sandy-skeletal, mixed, hyperthermic Typic Torriorthents
Mid	1829	33°32'41.5" N	116°29'24.7" W	15	508	175	Chaparral	Loamy, mixed, thermic, shallow Typic Xerochrepts
Summit	2489	33°31'16.4" N	116°25'11.1" W	10 ^b	521	110	Coniferous Forest	Coarse-Loamy, Mixed, Mesic Ultic Haploxeroll

All climate data is from USDA Natural Resource Conservation Service: Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions. Available online at <http://soils.usda.gov/technical/classification/osd/index.html>. Accessed [10/17/2009].

^a Soil Temperatures regularly exceed 50 °C (0–10 cm).

^b Soils temperatures have not been observed above 25 °C (0–10 cm).

Table 2

Soil parent material and physico-chemical properties of Base, Mid and Summit sites located along 2500 m elevation gradient of Santa Rosa Mountain, Riverside County, California, USA.

Site	Soil pH ^a	Canopy SOM %	Inter-Canopy SOM %	DOC ^b	Soil Texture	Landform	Parent Material
Base	7.9 (±0.4)	1.9% (±0.2)	1.5% (±0.1)	17.5 (±3.1)	Sand	Alluvial fan	Alluvium derived from granite
Mid	6.6 (±0.2)	3.4% (±0.2)	2.9% (±0.1)	29.4 (±5.2)	Sandy Loam	Rolling Hills	Granodiorite Residuum
Summit	6.1 (±0.2)	7.4% (±1.4)	7.3% (±0.8)	34.5 (±3.5)	Sandy Loam	Mountain	Residuum weathered from granite

^a Soil pH measured with 1:2.5 soil:water extract.

^b DOC units values are (mg C per kg dry soil).

of physical and chemical properties of each soil (Table 1, Table 2). Soil particle size distribution was determined using the hydrometer method (Bouyoucos, 1962). SOM was measured by combustion method: soil samples were placed in a muffle furnace at 550 °C for 4 h and the mass lost per mass dry soil was reported. DOC measurements were made with 50 g of dry soil, incubated for 5 d at 40% WHC. A 1 M K₂SO₄ solution was used in a 1:1 extraction and vacuum filtered with 8 µm Whatman 40 filter papers (GE Healthcare UK Limited), then analyzed with a Shimadzu TOC 5000 Analyzer using high temperature combustion (Shimadzu Corporation). Soil WHC was measured by the gravimetric method for each field replicates. 50 g sub-samples were saturated with de-ionized water in funnels lined with Whatman 40 filter paper, allowed to drain for 2 h to a constant mass, and then dried at 105 °C for 24 h to determine the mass of water held in the soil. Soil pH measurements used a 1:2.5 soil:water extract at 25 °C with an Accumet AB15 pH meter (Fisher Scientific) (Table 2).

2.3. Preparative incubation and measurements of soil R

A preparative incubation time and temperature were chosen to favor the growth of the soil microbial community and avoid the commonly observed pulse of activity following initial rewetting (Fierer and Schimel, 2003; Chatterjee and Jenerette, 2011a). 50 g of sieved soil was placed in glass jars, wetted with de-ionized water to one of three designated percentages of WHC (20, 40, and 80%), capped, and incubated in the dark for five days at 25 °C. After the preparative incubation, the jars were opened to ambient conditions for an hour and fanned to remove any accumulated gases. Soil R was measured at 6 temperatures successively (25°, 35°, 40°, 45°, 50°, 55 °C) using an LI-7000 infrared CO₂ gas analyzer (Licor Biosciences, Lincoln, NE) and a water bath system for temperature regulation (Chatterjee and Jenerette, 2011a). The non-randomized thermal incubation method may have influenced the respiration in a manner difficult to quantify (Davidson et al., 2006), although previous applications of sequential warming over short durations have suggested at short time-scales the problem is minimized (Fang et al., 2005). The short intervals were used to examine the current microbial community's temperature sensitivity before physiological adjustments occur (Bradford et al., 2010). The change in CO₂ concentration for a 90 s time interval was fit to a linear regression model to determine the flux of µmol CO₂ day⁻¹ kg dry soil⁻¹ (Yuste et al., 2007; Chatterjee and Jenerette, 2011a). The sequential heating incubations were completed within 8 h for every sample. A 30–40 min heating and stabilization interval between measurements was adequate to thoroughly heat the sample to the required temperature. The 30 field samples were analyzed at three different soil moisture contents (20, 40, and 80% WHC) for a total of 90 samples. This follows previous soil R studies that used slightly moist, intermediate, and near saturation soil water contents (Fang and Moncrieff, 2001; Reichstein et al., 2005). Soil water content was maintained throughout the incubation by the addition of de-ionized water to replace water lost. Soil CO₂ efflux estimates tend to underestimate soil R immediately following application of water (Bouma and Bryla, 2000). For this

reason, water was added approximately an hour before measurements. Soil R measurements were repeated in triplicate, and then averaged for a single sample value.

2.4. Soil R curve modeling

The temperature dependence of soil R_{max} was modeled using a modified Arrhenius equation as described by Leuning (2002), which is widely used in models of plant functioning (Misson et al., 2006; Barron-Gafford et al., in press), although to our knowledge it has not been applied to soil R.

$$R_{\max} = \frac{1 + \exp[(S_v T_0 - H_d)/(RT_0)] \exp[(H_a/RT_0)(1 - T_0/T_1)]}{1 + \exp[(S_v T_1 - H_d)/(RT_1)]} \quad (1)$$

Following Leuning (2002), the reference temperature was defined as T₀ = 298.2 K. H_a is the energy of activation (J, mol⁻¹) associated with enzyme mediated reactions, H_d is the energy of deactivation (J, mol⁻¹) which follows enzyme degradation. S_v is an entropy term (J, mol⁻¹ K⁻¹). This model allows for asymmetry in soil R surrounding the optimum temperature. Eq. (1) was able to model soil R curves for 87 of the 90 field replicates with R² ≥ 0.70 using Matlab (The MathWorks Inc., 2011). The remaining 3 samples did not exhibit characteristic temperature response function and were subsequently excluded from the analysis. The soil R curves, described by the modified Arrhenius equation, were used to empirically derive both T_{opt} and R_{max} for each of the 87 samples (Fig. 1). R_{max} and T_{opt} were calculated by differentiating each soil R curve to obtain the point of inversion. The optimum temperature (T_{opt}) was defined as the temperature (°C) on the soil R curve at which the maximum rate of soil R (R_{max}) occurred.

2.5. Statistical analysis

A three-way Analysis of Variance (ANOVA) was performed to determine the effect of site elevation, microenvironment, and water content on R_{max} and T_{opt}. To calculate the significance of differences between different levels, post-hoc unpaired two-sample t-tests were conducted with Tukey's Honestly Significant Difference test for confirmation. Correlative relationships between R_{max}, T_{opt}, SOM content, and DOC were investigated using multiple regression models. All regression modeling and analyses were conducted using Matlab.

3. Results

3.1. ANOVA analysis

The three-way ANOVA revealed R_{max} and T_{opt} varied with respect to elevation, microenvironment, and soil moisture content in different patterns (Table 3). T_{opt} was primarily affected by the microenvironment but not elevation or soil moisture. In addition, the ANOVA revealed significant interactions between elevation-microenvironment and elevation-soil moisture content (Table 3).

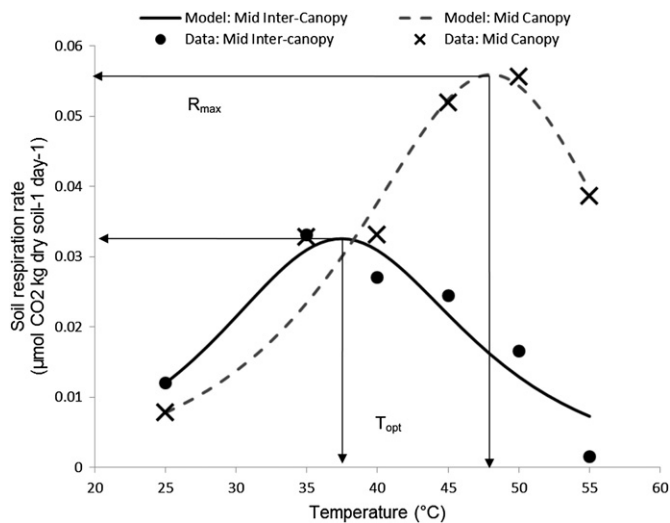


Fig. 1. An example of the modified Arrhenius equation fit to respiration data. 87 of the 90 total field replicates were accurately described with R^2 values ≥ 0.70 . The optimum temperature (T_{opt}) was defined as the temperature ($^{\circ}\text{C}$) at which the maximum rate of CO_2 efflux (R_{max}) occurred on the modeled soil R graph.

Post-hoc two-sample t -tests identified significant variation in T_{opt} with respect to elevation, soil moisture, and microenvironment between samples. The T_{opt} values for Base and Mid canopy samples were significantly greater than Base and Mid between canopies samples ($P < 0.05$) (Fig. 2, Table 4). Overall, T_{opt} values for soil beneath canopies (44.1 ± 0.6 S.E. $^{\circ}\text{C}$) were significantly greater when compared to inter-canopy soils (42.4 ± 0.9 S.E. $^{\circ}\text{C}$) ($P < 0.05$) (Table 4). In addition, the Summit inter-canopy T_{opt} value was significantly greater than the Base and Mid values ($P < 0.05$). However, when samples were regrouped with respect to elevation and soil moisture content, T_{opt} did not vary significantly as hypothesized (Table 3).

R_{max} varied conversely with T_{opt} with respect to elevation, soil moisture, and microenvironment. From the ANOVA, R_{max} was significantly affected by elevation and soil moisture content but not microenvironment (Table 3). Fig. 3 depicts the variation of R_{max} for each elevation at the three soil moisture contents. R_{max} at Mid site (32 ± 2.9 S.E. $\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$) were significantly less than Base (63.4 ± 6.5 S.E. $\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$) and Summit (77.7 ± 8.5 S.E. $\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$) (Fig. 3, Table 4). As expected, the soil moisture content significantly affected soil R in a similar manner as with previous studies. 40% WHC was significantly greater with an R_{max} value of 81.4 ± 8.5 S.E. ($\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$) compared to 20% WHC and 80% WHC ($P < 0.05$) (Fig. 3, Table 4). Furthermore, 20% WHC was significantly less than 80% WHC with R_{max} values of 34.6 ± 3.1 S.E.

Table 3

Three-way ANOVA for T_{opt} and R_{max} with respect to elevation, microenvironment, and soil moisture content are displayed for 87 samples.

	Optimal Temperature for soil Respiration (T_{opt})	Maximum rate of soil respiration (R_{max})
Elevation (E)	0.051	<0.001***
Microenvironment (M)	<0.05*	0.342
Soil moisture (S)	0.144	<0.001***
E \times M	<0.05*	0.436
E \times S	<0.05*	<0.05*
M \times S	0.369	<0.001***
E \times M \times S	<0.001***	0.571

* and *** denote significant differences of $P < 0.05$ and $P < 0.001$, respectively.

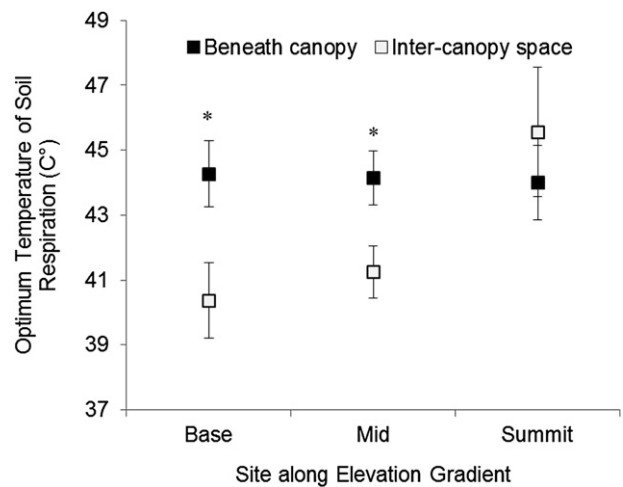


Fig. 2. The optimum temperature for soil R is shown for the three elevations at two different microenvironments. The mean values for the 87 T_{opt} values are displayed with standard error bars. * denotes a significant difference when compared between canopy and inter-canopy samples ($P < 0.01$).

($\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$) and 56.1 ± 6.3 S.E ($\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$), respectively ($P < 0.05$) (Fig. 3, Table 4).

3.2. Chemical and physical soil properties

SOM% differed significantly by elevation and microenvironment. Summit SOM% was significantly greater than both Base and Mid samples ($P < 0.01$) (Table 2). SOM% was higher for soils beneath plant canopies for Base and Mid samples ($P < 0.05$). However, SOM% was similar for both microenvironments at the Summit site. These patterns are consistent with previous extensive sampling of spatial variation in soil properties along this transect (Chatterjee and Jenerette, 2011b). At 40% WHC, linear regression analysis revealed SOM% content was positively correlated with greater T_{opt} values ($P < 0.05$) ($R^2 = 0.183$) (Fig. 4) and with greater R_{max} values ($P < 0.05$) ($R^2 = 0.348$) (Fig. 4). The equations for the linear regressions for SOM% with T_{opt} and R_{max} are:

$$T_{opt} = 1.002 \cdot \text{SOM}\% + 40.14 \quad (2)$$

$$R_{max} = 9.556 \cdot \text{SOM}\% + 41.92 \quad (3)$$

SOM% and DOC were positively correlated with each other ($P < 0.05$). Soil pH was negatively correlated with SOM% and DOC ($P < 0.05$). Soil pH was significantly higher for Base samples when compared to Mid samples ($P < 0.01$) and for Mid samples compared to Summit samples ($P < 0.05$) (Table 2). Soil pH between microenvironments was not significantly different.

Table 4

T_{opt} and R_{max} values by microenvironment, soil water content, and elevation. The mean values (\pm standard errors) are displayed for the 87 samples.

	T_{opt} ($^{\circ}\text{C}$)	R_{max} ($\mu\text{mol CO}_2 \text{ day}^{-1} \text{ kg dry soil}^{-1}$)
Canopy	44.1 (± 0.6)	54.2 (± 5.5)
Inter-Canopy	42.4 (± 0.9)	60.5 (± 6.3)
20% WHC	42.3 (± 0.9)	34.6 (± 3.1)
40% WHC	44.3 (± 1.2)	81.4 (± 8.5)
80% WHC	43.2 (± 0.4)	56.1 (± 6.3)
Base	42.3 (± 0.8)	63.4 (± 6.5)
Mid	42.7 (± 0.6)	32.0 (± 2.9)
Summit	44.8 (± 1.2)	77.7 (± 8.5)

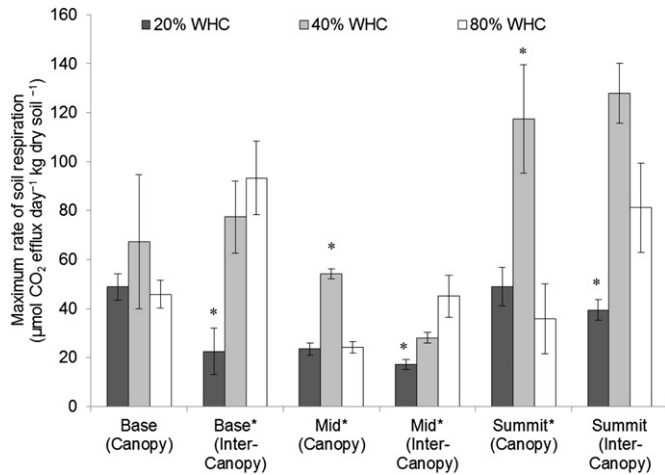


Fig. 3. Maximum soil respiration rate (R_{max}) at different soil moisture contents (20, 40, 80% of the total WHC) of soils from two microenvironments (canopy and inter-canopy) at Base, Mid, and Summit elevation positions. Mean values for 87 R_{max} are displayed with standard error bars. * indicates a significantly different R_{max} value within the same elevation and microenvironment ($P < 0.05$).

4. Discussion

4.1. General discussion

Our study provides experimental evidence that the optimal temperature of soil *R* is consistently higher than 35 °C across climates, vegetation types, and moisture contents. This conclusion was based on soil *R* measurements throughout an elevation gradient of nearly 2500 m, from contrasting microenvironments, and a 60% variation in soil moisture content. Across these different factors, the optimal temperature for soil *R* was influenced primarily by microenvironment, in which the highest optimum temperatures were observed from beneath plant canopies (Fig. 2). The maximum rate of soil *R* at the optimum temperature was primarily influenced by soil moisture content and the elevation gradient (Table 3). These findings correspond with the hypotheses of intermediate soil moisture and substrate supply dominance on soil *R* at elevated temperatures, however, the consistency in T_{opt} across the elevation transect is in contrast with expectations of climate induced acclimatization or adaptation of microbial communities.

There were no significant relationships between soil physical properties and the optimal temperature response of soil *R*. Soil texture was similar along the elevation gradient. There was no significant change in parent material, thus contributions of carbonates to CO_2 efflux were most likely low. The soil chemical properties yielded many relationships with the response of soil *R* to temperature. Soil pH was significantly correlated with SOM% due to organic acids as expected. The pH at the Base elevation was high and may have affected soil microbial community in structure and possibly its function (Bryant et al., 2008).

4.2. The effect of soil moisture content

As with previous studies (e.g. Ilstedt et al., 2000; Jin et al., 2008; Wilson and Griffin, 1975), our results demonstrate soil *R* is generally restricted at both high and low soil moisture contents (Fig. 3). At 20% WHC, limited moisture availability may have decreased R_{max} by reducing substrate transport and decreased internal soil microbe water potentials, which both may have limited microbial growth and their metabolic activities (Ilstedt et al., 2000; Orchard and Cook, 1983). At 80% WHC, the near saturating conditions may have reduced R_{max} by decreasing transport of oxygen and creating oxygen-limited conditions (E.g. Ilstedt et al., 2000; McLatchey and Reddy, 1998). In contrast to R_{max} , T_{opt} was not significantly affected by soil moisture content alone. The three-way factor ANOVA revealed a significant interaction among water content and elevation affecting T_{opt} ($P < 0.05$) (Table 3). This suggests components of the temperature response of soil microorganisms to temperatures > 35 °C were differentially dependent on moisture when at least 20% WHC is present.

4.3. The effect of soil organic matter

The substrate supply hypothesis, which predicts soils with the greatest substrate availability would have the greatest T_{opt} and R_{max} values, was supported for R_{max} but was less consistent for T_{opt} . The greatest R_{max} values were observed at the elevation and the microenvironment with the highest SOM% and DOC values. T_{opt} was greater for canopy microenvironments but similar across all elevations. The lack of correspondence with T_{opt} and general estimates of substrate supply across the elevation gradient could be indicative of changes in substrate quality from plant litter differences. Vegetation type may have directly influenced R_{max} by differences in the decomposability of the plant foliar tissue and the availability of labile carbon and nitrogen compounds such as non-

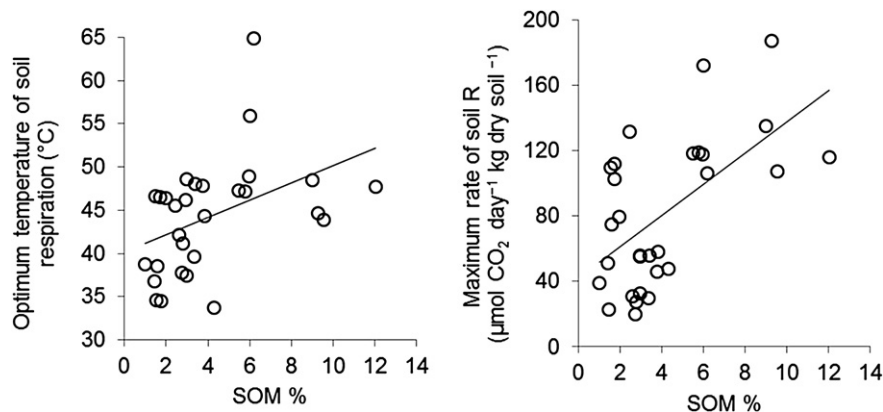


Fig. 4. (Left) The correlative relationship between optimum temperature (T_{opt}) for soil *R* and the SOM content at 40% WHC is displayed. The linear regression is significant at $P < 0.05$ with $R^2 = 0.183$. (Right) The correlative relationship between the maximum rate of soil *R* and the SOM content at 40% WHC. The linear regression is significant at $P < 0.001$ with $R^2 = 0.348$.

structural carbohydrates, phenolics, or amino acids (Berg and Meentemeyer, 2002; Quideau et al., 2000). These plant created microenvironments may have also led to altered microbial communities (Waldrop and Firestone, 2006), potentially causing compensating effects across the elevation transect. The amount of SOM accumulation in soil is dependent on the vegetation type and climate (Berg and Meentemeyer, 2002; Raich and Tufekcioglu, 2000). The effect of SOM supply across the elevation gradient on T_{opt} may have been masked by the change in quantity and distribution of SOM. In our transect, the dominant vegetation dramatically changed (Table 1) from *Larrea tridentata*, a desert shrub reaching up to 2 m in height, to *Pinus ponderosa*, a pine tree which may grow to 50 m in height. *Pinus ponderosa*, the dominant vegetation of the Summit site, deposits more needle leaves in a wider fashion covering both microenvironments with greater evenness than *Larrea tridentata*. This potentially explains of a why T_{opt} was not significantly different between microenvironments at the Summit elevation.

4.4. The effect of thermal acclimation or adaptation

The thermal acclimation or adaptation hypotheses suggested that T_{opt} and R_{max} will be greatest at the low elevations which regularly reach temperatures $> 35\text{ }^{\circ}\text{C}$ and in open microenvironments which have higher daily temperatures. Differences in the optimum temperature for maximum soil R due to existing climate had been hypothesized by Koepef (1953) based on a microbial thermal acclimatization mechanism. Furthermore, Pietikäinen et al. (2005) attributed an optimum temperature in soil R above $30\text{ }^{\circ}\text{C}$ to an adaptive response resulting from a shift in microbial community composition in response to higher temperatures. Thermal acclimation or adaptation hypotheses were derived from the potentially large variation in microbial communities and the assumption of their ability to respond to ambient temperatures. In contrast to these hypotheses, we observed no effect of elevation (Fig. 2), which constitutes large differences in mean annual temperature, maximum temperature, mean annual precipitation, and number of frost free days, on T_{opt} . The mean optimum temperatures for the Summit site were substantially higher than temperatures occurring in recent history at that elevation. Consequently, our observations suggest microorganisms capable of respiring at temperatures $>35\text{ }^{\circ}\text{C}$ are ubiquitous to all three climates examined. In contrast to the thermal acclimation hypothesis, plant created microenvironments had a higher T_{opt} than inter-canopy microenvironments only a few meters away (Fig. 2). At the Base site, T_{opt} varied by nearly $10\text{ }^{\circ}\text{C}$ between contrasting microenvironments. The localized microenvironment effect may result from the higher SOM under the plant canopies providing different soil microorganisms with sufficient substrates to support metabolic activity at higher temperatures. Evidence of a consistent T_{opt} across the elevation gradient and higher T_{opt} in the more moderated plant-canopy microenvironments than the warmer inter-canopy microenvironments both suggest climatic dependence of peak rate characteristics is minimal in this landscape.

4.5. Conclusion

The optimum temperature for respiration in soil has not received enough attention. Our results suggest revisions to current assumptions used in ecosystem and land-surface models used for future climate projections. T_{opt} was consistently higher than $35\text{ }^{\circ}\text{C}$ and varied not in response to regional climate variation but more with local vegetation effects. The co-variance of vegetation type and their respected detritus production along the elevation gradient may have indirect effects that interact with direct climate

effects on soil respiration temperature sensitivity. Short-term based measurements provide insight into the ubiquity of the complex temperature dependent response of soil respiration in the mineral soil at high temperatures. In-situ measurements along with incubation studies will further our knowledge in this area and lead to more accurate depictions of soil R in regions where soil temperatures regularly exceed $35\text{ }^{\circ}\text{C}$. With global annual temperatures expected to increase, more soils will experience temperatures nearer and above their optimums; extending ecosystem models and experiments to these higher temperature regimes are important research needs.

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