



Changes in soil respiration Q_{10} during drying–rewetting along a semi-arid elevation gradient

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ABSTRACT

Wetting induced increases in soil CO_2 efflux (R) from dry soils have been repeatedly reported, however little is known about the sensitivity of the pulse to temperature. To address this knowledge gap changes in temperature sensitivity of soil CO_2 efflux (Q_{10}) during repeated drying–rewetting (DW) events were experimentally quantified for soils collected both under canopy and interspace microenvironments at three elevations on Santa Rosa Mountain in southern California. Five field-replicated surface soil samples for each location were incubated at 13, 19, 25 and 31 °C. At each temperature, three consecutive DW cycles were performed by adding water to 40% water holding capacity. Instantaneous R was measured immediately after wetting and repeatedly until the soils were dry (<2% of added water). Soil R responses were averaged above and below 20% WHC and considered as wet and dry fluxes, respectively. Wet and dry soil R responses were separately modeled using the Arrhenius equation and activation energy (E_i) was determined using non-linear mixed-level modeling. Soil R at 25 °C (flux25) increased with elevation gradient with a decrease in required E_i values. Negative relationship between flux25 and Q_{10} supported the carbon-quality hypothesis, whereas, Q_{10} values >2 supported a temperature sensitive metabolic pulse throughout repeated DW events for soils across the mountain. Including variation in Arrhenius temperature kinetics with precipitation patterns has the potential to improve predictions of the precipitation pulse induced C loss across large spatiotemporal scales.

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1. Introduction

Prolonged drying followed by rapid rewetting has a substantial influence on belowground C mineralization processes (Borken and Matzner, 2009; Fierer and Schimel, 2002; Jarvis et al., 2007). Changing climatic patterns may increase drying–rewetting (DW) events due to more variable precipitation regimes and greater evapotranspiration rates particularly for semiarid/arid soils (Weltzin et al., 2003). Previous studies of soil respiration and climate have primarily focused on either temperature (Davidson and Janssens, 2006; Fierer et al., 2006; Lloyd and Taylor, 1994) or moisture (Fierer and Schimel, 2003; Huxman et al., 2004; Sponseller, 2007) effects on soil CO_2 efflux (R) without explicitly examining their interaction for DW events.

Wetting of dry soils generally increases soil microbial activity within minutes and R is elevated manifold compared to dry states (Fierer and Schimel, 2003; Sponseller, 2007). The immediate increase in R is generally associated with changes in enzyme activity and

substrate supply through several candidate mechanisms (Curiel-Yuste et al., 2007; Davidson et al., 2006; Jenerette and Lal, 2005). The overall process has been hypothesized to cause a reduction in temperature sensitivity based on enzymatic activity theory where wetting effectively reduces the activation energy requirements for metabolic reactions through an associated release of labile substrate (Jenerette et al., 2008). Alternatively, temperature sensitivity of R may increase in response to wetting due to alleviation of substrate limitation kinetics as described by Michaelis–Menten dynamics and the canceling effect of the half saturation constant on the apparent or overall temperature sensitivity (Davidson et al., 2006).

Throughout drying after an initial wetting induced pulse the magnitude of R dramatically declines (Borken and Matzner, 2009) through multiple mechanisms including decreases in the diffusion of carbon substrates, extracellular enzymes and microbial mobility (Curiel-Yuste et al., 2003; Jenerette et al., 2008; Lee et al., 2002; Rey et al., 2002). The response of soil R to temperature over drying should reflect the coupled effects of direct temperature responses, reduced substrate availability, and moisture gradients (Fang and Moncrieff, 2001; Munson et al., 2010; Reichstein et al., 2005). Commonly, R responses to drying are modeled independently of temperature (Lamparter et al., 2009) using a form of $R = f(\text{moisture}) \times f(\text{temperature})$, where the temperature sensitivity is independent of soil

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moisture (Bauer et al., 2008; Davidson et al., 2000; Orchard and Cook, 1983). However, temperature sensitivity itself may also be affected by soil moisture through both direct effects on enzyme activity kinetics and indirect effects on substrate availability.

Repeated DW cycles have been widely shown to progressively reduce the wetting effect on R at a constant temperature due to (1) less organic matter available for the subsequent cycle (Birch, 1958), (2) soil aggregates increasing resistance to slaking and the physical protection of labile substrates preventing further microbial utilization (Borken and Matzner, 2009) and (3) microbial response to wetting gradually becoming less dramatic with successive rewetting events (Kim et al., 2010). These mechanisms suggest possible increases in temperature sensitivity of R due to proportionately less labile substrates as predicted from the activation energy hypothesis or less overall substrates as predicted from the substrate limitation hypothesis; whereas, decreases in temperature sensitivity may occur through increased enzyme effectiveness associated with microbial adaptation (Bradford et al., 2008; Davidson et al., 2006; Larionova et al., 2007).

Variation in organic matter quality, long-term climate, and microbial community are important components influencing temperature and moisture effects on R, but deciphering their relative control mechanisms is challenging (Davidson and Janssens, 2006). Topographic gradients provide opportunities for the comparative study of soil–plant relationships as temperature decreases and precipitation increases along the rise in elevation. The climatic changes correspond with large variations in plant communities and soil formation. Moreover, changes in vegetation community and canopy characteristics along the mountain introduce variable wetting intensities and alter R between microenvironments. According to Fierer and Schimel (2003), soils with less frequent DW events should exhibit larger R pulses following rewetting due to a greater proportion of C released from osmoregulatory solutes on rewetting and their subsequent use by growing microbes. In contrast, Miller et al. (2005) suggested soils experiencing less frequent DW cycles had lower R pulses than soils facing frequent DW cycles because of declines in microbial capacity to rapidly use dissolved organic C.

In this experiment, we examined a series of questions to better understand the changes in temperature sensitivity of soil metabolic activity (Q_{10}) during repeated DW cycles of soils with varying substrate availability and quality. (1) What is the temperature sensitivity of soil CO_2 efflux following wetting of previously dry soils? (2) How does the temperature sensitivity change through repeated DW cycles? (3) How does the temperature sensitivity through repeated DW cycles vary spatially at landscape scales of an elevation gradient and local scales of microenvironment?

2. Materials and methods

2.1. Site description

We selected three sites approximately 1000 m apart on a 2800 m topographic gradient on Santa Rosa Mountain near Palm Springs, CA, USA

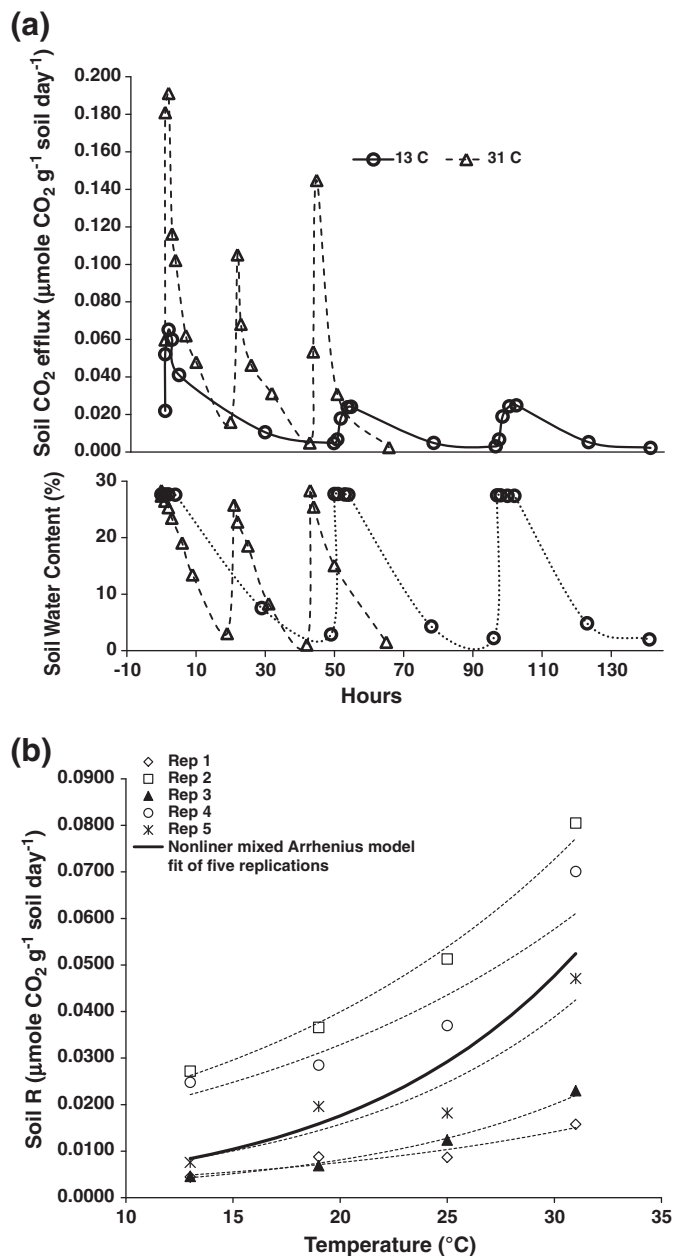


Fig. 1. (a) Changes in soil CO_2 efflux ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ soil day}^{-1}$) and soil water content over time (hours) at 13 and 31 °C incubation temperatures at three drying rewetting events and (b) nonlinear mixed Arrhenius model fit of five field replicated soil CO_2 flux data of base-canopy soils within the 1st DW cycle according to Arrhenius equation.

(33°49'26"N 116°31'49"W) (Table 1). These three sites include the major transitions in plant communities along a transect from desert scrub at the base (289 m) to chaparral in the mid (1592 m) and then

Table 1

Site locations, water holding capacity and organic matter content within canopy and interspace along the elevation gradient.

Site code	Space	Location	Elevation (m)	MAT (°C)	MAP (cm)	Dominant vegetation	Soil type	WHC ($\text{g H}_2\text{O g}^{-1} \text{ soil}$)	Soil OM%
Base	Canopy	33°34'55" N	289	24	15	Desert scrub (<i>Larrea tridentata</i>)	Carrizo stony sand, sandy-skeletal, mixed, hyperthermic Torriorthents	0.43 (0.03)	1.92 (0.16)
	Interspace	116°22'16"W						0.41 (0.02)	1.47 (0.12)
Mid	Canopy	33°32'51.9"N	1592	21	84	Evergreen shrub (<i>Quercus cornelius-mulleri</i>)	Osito–Modesto families, loamy, mixed, thermic, shallow Xerochrepts sandy loam	0.52 (0.03)	3.38 (0.19)
	Interspace	116°30'17.8"W						0.45 (0.03)	2.90 (0.13)
Summit	Canopy	33°31'16.4"N	2489	15	132	Evergreen needle-leaf tree (<i>Pinus jeffreyi</i>)	Crouch rocky coarse-loamy, mixed, mesic Ultic Haploxerolls	0.64 (0.02)	7.41 (1.42)
	Interspace	116°25'11.1"W						0.64 (0.06)	7.30 (0.81)

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