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Does declining carbon-use efficiency explain thermal acclimation of soil respiration with warming?

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Abstract

Enhanced soil respiration in response to global warming may substantially increase atmospheric CO_2 concentrations above the anthropogenic contribution, depending on the mechanisms underlying the temperature sensitivity of soil respiration. Here, we compared short-term and seasonal responses of soil respiration to a shifting thermal environment and variable substrate availability via laboratory incubations. To analyze the data from incubations, we implemented a novel process-based model of soil respiration in a hierarchical Bayesian framework. Our process model combined a Michaelis–Menten-type equation of substrate availability and microbial biomass with an Arrhenius-type nonlinear temperature response function. We tested the competing hypotheses that apparent thermal acclimation of soil respiration can be explained by depletion of labile substrates in warmed soils, or that physiological acclimation reduces respiration rates. We demonstrated that short-term apparent acclimation can be induced by substrate depletion, but that decreasing microbial biomass carbon (MBC) is also important, and lower MBC at warmer temperatures is likely due to decreased carbon-use efficiency (CUE). Observed seasonal acclimation of soil respiration was associated with higher CUE and lower basal respiration for summer- vs. winter-collected soils. Whether the observed short-term decrease in CUE or the seasonal acclimation of CUE with increased temperatures dominates the response to long-term warming will have important consequences for soil organic carbon storage.

Keywords: *Artemisia tridentata*, carbon-climate feedback, hierarchical Bayesian, Michaelis–Menten, microbial biomass, sagebrush steppe, soil ecology, soil incubation, soil respiration, temperature acclimation

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Introduction

Soil organic matter (SOM) represents a large pool of stored carbon, and the loss of SOM via soil respiration is a major component of global CO_2 fluxes (Raich & Schlesinger, 1992; Couteaux *et al*., 1995; Schlesinger & Andrews, 2000). Soil respiration is positively related to soil temperature (Lloyd & Taylor, 1994), and as global temperatures increase, soil respiration is expected to increase (Cox *et al*., 2000; Jones *et al*., 2005). An amplifying feedback between increased temperatures and heterotrophic soil respiration (outer loop Fig. 1) could contribute approximately 35% more CO_2 to the atmosphere than anthropogenic emissions alone (Cox *et al*., 2000). The magnitude of this feedback, however, is dependent on the temperature sensitivity of soil respiration (Kirschbaum, 1995, 2004).

The positive correlation between soil respiration and temperature has been demonstrated in a wide range of field (Lloyd & Taylor, 1994; Eliasson *et al*., 2005) and laboratory studies (Fang *et al*., 2005; Hartley *et al*., 2007), and is consistent with simple physical and chemical principles related to activation energy and enzyme kinetics (Davidson & Janssens, 2006). In natural systems, however, it is important to recognize that heterotrophic soil respiration is not solely controlled by temperature; it is also affected by substrate bioavailability (both quantity and recalcitrance) (Kirschbaum, 2004; Fierer *et al*., 2005; Hartley & Ineson, 2008), the biotic and abiotic environment (including climatic factors), and intrinsic properties of the soil microbial community (Bradford *et al*., 2008; Lipson *et al*., 2009; Allison *et al*., 2010; Zhou *et al*., 2012). These factors might combine to reduce the temperature sensitivity of soil respiration. In fact, a growing number of studies have documented minimal temperature stimulation of soil respiration (Giardina & Ryan, 2000) or attenuation of the temperature stimulation over time (Luo *et al*., 2001; Melillo *et al*., 2003; Eliasson *et al*., 2005).

This pattern of attenuation has been referred to as thermal 'acclimation' (e.g. Kirschbaum, 2004), 'acclimatization'

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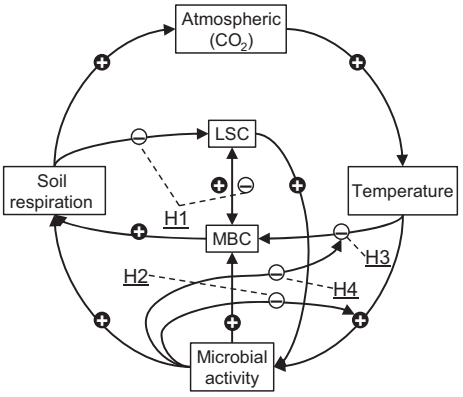

Fig. 1 Conceptual representation of the different mechanisms controlling the response of soil respiration to warming. Arrows represent the direction of the effect, and the plus and minus signs represent positive and negative feedbacks, respectively. The outer loop represents the positive feedback between increased temperature, increased soil respiration, and elevated CO_2 described by Cox *et al.* (2000). Within the outer loop are ecosystem and microbial responses that could amplify or moderate that suggested positive feedback. H1 refers to substrate depletion, H2 refers to physiological acclimation, H3 refers to declining carbon-use efficiency (CUE) with temperature, and H4 refers to CUE acclimating to temperature. LSC and MBC are labile substrate carbon and microbial biomass carbon, respectively.

(e.g. Luo *et al.*, 2001), or 'adaptation' (e.g. Bradford *et al.*, 2008) due to its similarity to the acclimation of plant respiration to different ambient temperatures (Atkin & Tjoelker, 2003). In plants, acclimation refers to a strictly physiological process, while in soils it refers to an ecosystem-level phenomenon potentially driven by multiple mechanisms including substrate depletion, changing microbial community composition (Zhou *et al.*, 2012), and physiological changes. Here, we focus on heterotrophic respiration. We refer to intrinsic physiological changes as thermal acclimation, and contrast this with substrate depletion. We refer to the combined effects of substrate depletion and changes in physiological properties as *apparent* thermal acclimation. Apparent thermal acclimation has been documented for soil respiration as a whole (Giardina & Ryan, 2000; Oechel *et al.*, 2000; Luo *et al.*, 2001; Eliasson *et al.*, 2005; Bradford *et al.*, 2008), and for respiration associated with mycorrhizae (Heinemeyer *et al.*, 2006; Malcolm *et al.*, 2008), soil crust lichens (Lange & Green, 2005), bacteria (Bárcenas-Moreno *et al.*, 2009), roots (Atkin & Tjoelker, 2003), and aquatic bacterioplankton (Hall *et al.*, 2010). Further, it has been demonstrated that the activities of decomposing enzymes acclimate to seasonal temperature changes (Fenner *et al.*, 2005) and that the response of soil respiration to warming varies seasonally (Hartley *et al.*, 2007).

The importance of substrate depletion vs. thermal acclimation during SOM decomposition is debated (Kirschbaum, 2004; Hartley *et al.*, 2007; Bradford *et al.*, 2008, 2009; Hartley & Ineson, 2008; Allison *et al.*, 2010). As respiration increases with temperature, substrates are consumed, resulting in decreasing substrate availability. However, SOM is composed of different substrate pools exhibiting different temperature sensitivities (Kirschbaum, 2004; Fierer *et al.*, 2005; Knorr *et al.*, 2005; Hartley & Ineson, 2008; Conant *et al.*, 2011), resulting in complex substrate depletion kinetics. Basic kinetic theory and empirical evidence (Craine *et al.*, 2010) demonstrate that more recalcitrant SOM exhibits higher temperature sensitivity than the more labile substrate carbon (LSC) pool. Given that most (~95%) SOM is recalcitrant (Knorr *et al.*, 2005), depletion of the LSC pool may not lead to long-term loss of carbon stores (Hartley *et al.*, 2008).

In contrast with substrate depletion, which is dependent on pool sizes, thermal acclimation is primarily dependent on the composition and physiology of the microbial community. Here we focus primarily on physiological acclimation, especially with regard to carbon-use efficiency (CUE) and basal respiration (A_b). A_b is mass-specific respiration (R_{mass}) at a reference temperature (here, 10 °C) under substrate saturation. CUE is the ratio of the amount of carbon allocated for growth to total carbon uptake. Empirical work suggests that CUE of soil heterotrophs declines by approximately 0.009 $°C^{-1}$ (Steinweg *et al.*, 2008), likely because of a divergence between the respiration rate and microbial growth at higher temperatures (Joergenson *et al.*, 1990). In a simulation of soil carbon responses to warming, Allison *et al.* (2010) showed that declining and acclimating CUE with increased temperature resulted in both lower respiration rates and substantially higher SOM retention than under constant CUE. This pattern was driven by reduced microbial biomass carbon (MBC) in the declining and acclimating CUE scenarios, which more than compensated for increased R_{mass}. Moreover, Wetterstedt & Ågren (2011) demonstrated that a model allowing CUE to vary with temperature (compared to fixed CUE) resulted in a better fit to soil respiration data.

In this study, we sought to distinguish the roles of LSC depletion and thermal acclimation in high-elevation soils, and we further explored the mechanisms underlying the observed temperature responses. We were particularly interested in comparing short-term acclimation of soils incubated at different temperatures to the seasonal response of soils collected during the winter vs. the summer. We explored the following hypotheses regarding mechanisms involved in thermal acclimation, which are illustrated in Fig. 1:

H1 As microorganisms respire and grow, they deplete the readily available LSC, resulting in reduced respiration (apparent thermal acclimation).

H2 Over time, basal microbial activity decreases with increasing temperatures, resulting in physiological thermal acclimation.

H3 CUE declines, instantaneously, with increasing temperature, resulting in either reduced MBC and therefore reduced respiration, or increased rates of substrate depletion and therefore the process described in (H1).

H4 Over time, CUE acclimates to the ambient temperature, counteracting (H3).

To address these hypotheses, we conducted laboratory incubations with soils collected during winter and summer from a high-elevation sagebrush ecosystem. The incubation data were analyzed via a Bayesian approach that combined a rectangular hyperbola parameterization of the Michaelis–Menten function that incorporates MBC and LSC (Cable *et al.*, 2009) with the Lloyd & Taylor (1994) temperature response function (Davidson *et al.*, 2012). Our data-model integration approach provided a mechanistic framework for separating the influences of MBC and LSC availability from physiological factors related to CUE, A_b, and substrate response rate (A_c).

Materials and methods

Sample collection

Field sampling was conducted on Feb 4, 2011 (winter) and July 1, 2011(summer) at Pole Mountain (41°15′04″N, 105°26′23″W) in southeast Wyoming. The site is dominated by *Artemisia tridentata* (big sagebrush) and *Pinus flexilis* (limber pine) and occurs at 2600 m elevation. The 24-h average soil temperature at 5 cm depth on the day of collection was 0 °C (winter) and 16 °C (summer). Soil temperatures at the site ranged from −0.3 °C to 31.5 °C during 2011. The soil was covered by 30 cm of snow during the winter collection. Eight replicate soil cores were collected from the top 15 cm of the soil profile, within an area of approximately 10 × 10 m. Soil was refrigerated at 1.5 °C for 2 days prior to being passed through a 2 mm diameter sieve to remove rocks, roots, and large litter fragments. We chose to use sieved soil rather than intact cores, partly because we were concerned that variable root respiration and decomposition of fine roots in intact cores would complicate the interpretation of the results with respect to the heterotrophic response. For example, root respiration may continue for days to weeks after severing (e.g. Sun *et al.*, 2012; C. L. Tucker, unpublished results) and would likely vary greatly among cores and decline over the course of the incubations in ways that are difficult to quantify. Thus, all soil samples collected during a particular season were bulked and mixed thoroughly into one large container following established protocols (e.g. Bradford *et al.*, 2010). We recognized that homogenizing soil samples makes it impossible to quantify within-season variability in the response of soils to the applied treatments. However, quantification of such variability was not a goal of this study, and homogenization of soils was necessary to increase the likelihood of detecting physiological responses to the treatments while maintaining manageable samples sizes.

Laboratory incubations

Laboratory incubations were conducted in two phases: an acclimation phase (days 0–28) and a response phase (day 29) (see Fig. 2). During the acclimation phase, a 30 g sample of homogenized soil was incubated at either 1.5 °C, 10 °C, or 22.5 °C, and with dextrose addition or control (no dextrose), for a total of six treatments with 12 replicates each. During the response phase, soils from each acclimation treatment group were subdivided among the six treatment levels (Fig. 2) for a total of 36 treatment levels (6 × 6), with two replicates each. Dextrose was added as 5 mg dextrose g^{-1} soil on days 0 and 29. The dextrose and control treatments received the same amount of DI H_2O: 2 mL for the winter soils and 4 mL for the summer soils to account for differences in initial soil moisture. Soils were watered periodically to prevent drying.

To measure respiration, each 500 mL incubation jar was tightly closed and flushed with CO_2-free air for 3 min. After approximately 1 h, a 15 mL-air sample was taken from each jar and the concentration of CO_2 was determined via the average of three injections into a Licor 820 infrared gas analyzer (Lincoln, NE, USA). Respiration was determined as $R_{obs} = \Delta[CO_2]/\Delta t$,

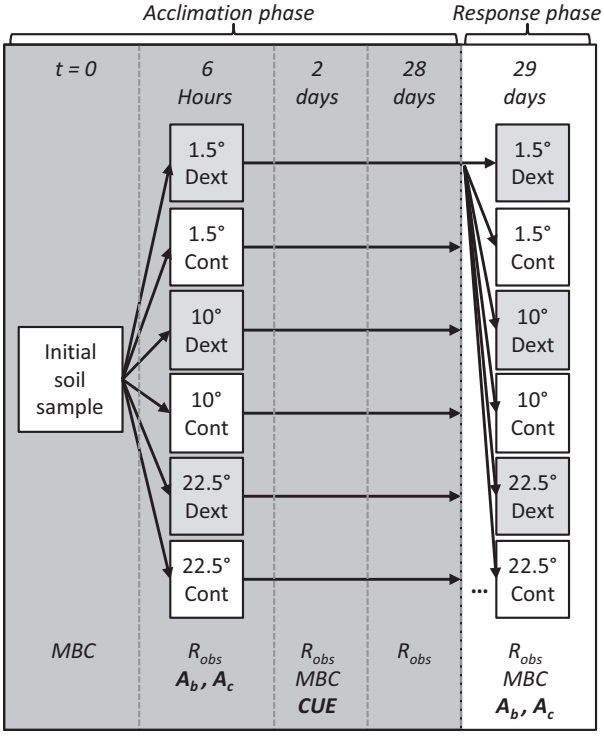

Fig. 2 Incubation experimental design. Soils were split into six treatment groups at $t = 0$, and each group was again split into six groups on day 29. The text at the bottom of the figure records what quantities were measured, and what parameters estimated at each point. The same protocol was followed for summer- and winter-collected soils.

where Δt is the time that the CO_2 was allowed to build-up. Respiration was measured 6 h after substrate addition on day 0, and again on days 2, 28, and 6 h after substrate addition on day 29.

A parallel set of incubations, using the same soil samples and undergoing the same treatments, were conducted concurrently so that the soils could be destructively sampled for total extractable organic carbon (TOC) and MBC using the chloroform fumigation-extraction method (Vance *et al*., 1987). We used extractable TOC as a proxy for LSC in this study. It is important to note that the extractable TOC represents primarily the dissolved organic C pool and is only a small fraction of the total SOC pool. For instance, our TOC pools are only 1–2% of total SOC (wet oxidation) of 19.8 mg C g^{-1} soil measured in a nearby sagebrush ecosystem (Burke, 1989). On day 0 and day 29, in the dextrose treatments, LSC was assumed to be saturating for modeling purposes. TOC and MBC were measured on day 0 (immediately prior to beginning the incubations), day 2, and day 29 (immediately prior to the response phase treatments). Organic carbon was extracted in 0.5 M K_2SO_4 and analyzed on a (Shimadzu TOC-VCSH analyzer, Kyoto, Japan). There were eight replicates for the initial measurement and two (winter) or three (summer) per substrate by temperature level thereafter. Because the experiment was done on a thoroughly homogenized soil sample, it was expected that low within-treatment variation would justify these small sample sizes, and the data would support this assumption.

Data analysis and modeling

We employed a hierarchical Bayesian (HB) approach (Clark *et al*., 2005; Ogle, 2009) to analyze the incubation data, which allowed for comparison of intrinsic physiological factors across seasons and treatments. Our data model describes the likelihood of the observed respiration rates (R_{obs}); for observation i [i = 1, 2, …, 307 (17 observations were missing)], we assume that each $R_{obs(i)}$ comes from a normal distribution with a mean ($\overline{R}$) that depends on the season (D), substrate level (S and SF = acclimation and response phase levels, respectively), and temperature level (T and TF = acclimation and response phase levels, respectively) associated with observation i:

$$R_{\mathrm{obs(i)}} \sim \begin{cases} \mathrm{Normal}(\overline{R}_{D(i),S(i),T(i)}, \sigma^2) & \text{acclimation phase} \\ \mathrm{Normal}(\overline{R}_{D(i),S(i),T(i),SF(i),TF(i)}, \sigma^2) & \text{response phase} \end{cases} \quad (1)$$

We also specified data models for the measured MBC and LSC. For X = MBC or LSC, we assumed the observed data, X_{obs}, come from a normal distribution such that for observation j [j = 1, 2…, 69 (3 observations were missing)]:

$$X_{\mathrm{obs(j)}} \sim \begin{cases} \mathrm{Normal}(\overline{X}_{D(j)}, \sigma_X{}^2) & \mathrm{day} = 0\,(\text{pre-acclimation}) \\ \mathrm{Normal}(\overline{X}_{D(j),S(j),T(j)}, \sigma_X{}^2) & \mathrm{day} = 2\,(\text{acclimation phase}) \\ \mathrm{Normal}(\overline{X}_{D(j),S(j),T(j)}, \sigma_X{}^2) & \mathrm{day} = 29\,(\text{response phase}) \end{cases} \quad (2)$$

Importantly, the predicted respiration ($\overline{R}$) is linked to the predicted MBC and LSC ($\overline{X} = \overline{\mathrm{MBC}}\mathrm{or}\overline{\mathrm{LSC}}$); a more complete description of the data model is given in Supporting information S1.

Following the suggestion of Davidson *et al*. (2006, 2012), $\overline{R}$ is described by combining the Lloyd & Taylor (1994) (LT) temperature response with Michaelis–Menten (MM) kinetics, allowing us to separate the effects of LSC availability, MBC, and intrinsic physiological factors; we refer to the combined model as the MMLT model. The LT function is similar to an Arrhenius-type function, but has been shown to better describe the temperature response of soil respiration (Lloyd & Taylor, 1994). The general model for $\overline{R} = \overline{R}_{D,S,T}\mathrm{or}\overline{R} = \overline{R}_{D,S,T,SF,TF}$ in Eqn (1) is:

$$\overline{R} = R_{\mathrm{base}} \cdot \exp\left[E_{\mathrm{o}}\left(\frac{1}{T_{\mathrm{ref}} - T_{\mathrm{o}}} - \frac{1}{T_{\mathrm{obs}} - T_{\mathrm{o}}}\right)\right] \quad (3)$$

where R_{base} is the base respiration rate at a reference temperature of T_{ref} (here, T_{ref} = 283.15 K), E_o (K) is analogous to activation energy, T_{obs} (K) is the experimentally applied temperature, and T_o (K) is a parameter related to the temperature sensitivity [$0 < T_o <$minimum (T_{obs})]. During the acclimation phase, E_o and T_o vary by season (D); during the response phase they are allowed to vary by season (D) and acclimation temperature level (T). During the acclimation phase ($\overline{R} = \overline{R}_{D,S,T}$), R_{base} varies by season (D) and substrate level (S), and T_{obs} is the actual temperature associated with acclimation temperature level (T). During the response phase ($\overline{R} = \overline{R}_{D,S,T,SF,TF}$), R_{base} varies by D, T, S, and the response phase substrate level (SF), and T_{obs} is the actual temperature associated with the response phase temperature level (TF). For example, we allow for the possibility that respiration during the response phase is affected by the acclimation phase conditions (i.e. T and S), in addition to responding to the response phase conditions (SF, TF); during the acclimation phase, respiration is only affected by the acclimation phase conditions.

The MM function describes a system where two pools (MBC and LSC) limit the reaction rate, and we employ the rectangular hyperbola form of this function to describe the base rate:

$$R_{base} = \begin{cases} \dfrac{A_b \cdot \overline{MBC} \cdot A_c \cdot \overline{LSC}}{A_b \cdot \overline{MBC} + A_c \cdot \overline{LSC}} & \overline{LSC} < LSC_{saturating} \\ A_b \cdot \overline{MBC} & \overline{LSC} \geq LSC_{saturating} \end{cases} \quad (4)$$

A_b, A_c, MBC, and LSC vary by D on day 0, while on days 2 and 29, those parameters vary by D, T, and S. A_b (basal respiration, mg CO_2-C g^{-1} MBC h^{-1}) describes the biomass-specific respiration rate at T_{ref}, in the absence of substrate limitation. The product of A_b and $\overline{\mathrm{MBC}}$ (mg C g^{-1} soil) is the upper limit of respiration at T_{ref}; that is, when $\overline{\mathrm{LSC}}$ (mg C g^{-1} soil) is saturating ($\overline{\mathrm{LSC}} \geq \mathrm{LSC}_{\mathrm{saturating}}$; effectively, infinite LSC), R_{base} is proportional to $\overline{\mathrm{MBC}}$ and A_b is the proportionality constant. A_c (maximum substrate response, mg CO_2-C g^{-1} LSC h^{-1}) is the maximum rate of increase of respiration with increasing substrate when LSC concentrations are low and at T_{ref}. On day 0 and day 29, the dextrose addition imposes the condition of $\overline{\mathrm{LSC}}$ saturation, such that we can independently quantify A_b and A_c.

After estimating the MMLT parameters (E_o, T_o, A_b, A_c), respiration rates were predicted at normalized values of MBC (set to overall average of summer and winter MBC, $\overline{\mathrm{MBC}}$, on day = 0) and LSC (set to the overall average of summer and winter field LSC, $\overline{\mathrm{LSC}}$). This analysis was used to determine if apparent thermal acclimation was driven by the underlying

factors described by the MMLT parameters, rather than by a change in MBC or LSC availability.

Incubation data collected over the first 2 days (day = 0 and 2) of the acclimation phase were used to compare the CUE of summer- and winter-collected soils at the three incubation temperatures as follows (Lipson *et al*., 2009):

$$\mathrm{CUE} = \frac{\overline{\mathrm{MBC}}_{\mathrm{day}=2} - \overline{\mathrm{MBC}}_{\mathrm{day}=0}}{\overline{\mathrm{MBC}}_{\mathrm{day}=2} - \overline{\mathrm{MBC}}_{\mathrm{day}=0} + 48h \cdot \left(\frac{\overline{R}_{\mathrm{day}=2} + \overline{R}_{\mathrm{day}=0}}{2}\right)} \quad (5)$$

Recall from Eqns (1) and (2) that $\overline{\mathrm{MBC}}_{\mathrm{day}=0}$ varies by D whereas $\overline{R}$ and $\overline{\mathrm{MBC}}_{\mathrm{day}=2}$ vary by D, T, S. In Eqn (5), CUE is the ratio of C converted into MBC to total C used, which is the sum of the increase in MBC plus the C lost through respiration. $\overline{R}$ has units of mg C g^{-1} soil h^{-1}, and we averaged $\overline{R}$ on days 0 and 2 and multiplied the average rate by 48 h to estimate total respired C during the first 2 days. We restricted the CUE analysis to samples that received dextrose because the analysis requires the soil microbial community to be undergoing exponential growth; thus, CUE only varies by D and T. This approach is likely to underestimate instantaneous CUE because it ignores the turnover (death) of microbial biomass, and because we added very high levels of dextrose, the calculated CUE is likely not representative of use of recalcitrant or limiting substrates. As such, it is better employed as a comparative index across the different dates and temperatures than as a measure of the CUE of microbes in natural settings. In Supporting information S3, we present an alternate method for calculating CUE based on the exponential growth rate and biomass-specific respiration rate (e.g. Keiblinger *et al*., 2010). The results from this model are not significantly different from the mass-balance model in Eqn (5), but the CUE estimates obtained from the exponential model are more uncertain due to the greater number of parameters.

The HB data model was implemented in OpenBUGS (Lunn *et al*., 2009), which employs Markov chain Monte Carlo (MCMC) sampling methods to obtain the posterior distribution of all model parameters; the posterior distribution is proportional to the likelihood of the incubation data [derived from Eqns (1) and (2)] times the prior probability distribution of each parameter. The parameters in the MM model (A_b, A_c; Eqn (4)) were given hierarchical normal priors; the overall means (i.e. $\overline{A}_b$ and $\overline{A}_c$) and variances were assigned non-informative priors. The LT model parameters [E_o, T_o; Eqn (3)] were assigned semi-informative priors based on Lloyd & Taylor (1994) and following Cable *et al*. (2009). Using the MCMC samples, we computed the posterior mean and 95% credible interval (CI) for each parameter; the 95% CIs are defined by the 2.5th and 97.5th percentiles, and there is a 95% chance that each 95% CI contains the 'true' parameter value. More detailed information on the model structure is given in Supporting information S1 and model code is presented in Supporting information S2.

Results

Soil respiration responses to incubation treatments

During the acclimation phase, soil respiration increased with both increasing temperature and dextrose addition on day 0 and day 2 (Fig. 3). The effect of dextrose addition increased between day 0 (Fig. 3a) and day 2 (Fig. 3b) for the winter soils, but not for the summer soils. By day 28, respiration under dextrose addition had tapered off substantially, but was still significantly higher than the control within a given temperature level (Fig. 3c), and respiration was still significantly higher under warmer acclimation temperatures.

During the response phase (day 29), soil respiration increased with response temperature for all treatments (Fig. 4). In the soils assigned to the 'control' substrate level during both the acclimation and response phases (control.control) (Fig. 4a and e), winter soils had higher respiration rates when acclimated at 1.5 °C than at 22.5 °C, although the 10 °C acclimated soils were not different from either. There were no significant differences in respiration among acclimation temperatures in the summer soil control.control group. Similarly, in the control soils that received dextrose on day 29 (control.dextrose), winter soils had higher respiration rates when acclimated at 1.5 °C and 10 °C than at 22.5 °C (Fig. 4b), but there were no significant differences in respiration among acclimation temperatures in the summer soils (Fig. 4f). In the soils that initially received dextrose, but that were assigned to the control group on day 29 (dextrose.control), there is a clear effect of acclimation temperature in both winter and summer soils such that response phase respiration rates were negatively correlated with acclimation temperature (Fig. 4c and g). Likewise, in soils that received dextrose on day 0 and day 29 (dextrose.dextrose), the 1.5 °C acclimated soils had higher respiration rates across all response phase temperatures than the warm-acclimated soils, but the respiration rates were indistinguishable between the 10 °C and 22.5 °C acclimated soils (Fig. 4d and h). Across substrate treatments, the dextrose.control treatments exhibited the strongest apparent thermal acclimation, followed in decreasing order by the dextrose.dextrose, control.dextrose, and control.control (Fig. 4).

Microbial biomass and carbon substrate responses to incubation treatments

MBC was initially (day 0) higher in summer soils [mean = 0.319 mg C g^{-1} soil, 95% CI = (0.244, 0.395)] than in winter soils [mean = 0.215 mg C g^{-1} soil, 95% CI = (0.139, 0.291)] (Fig. 5a). On day 2, after dextrose addition, MBC significantly increased compared to the initial values and the control soils. Moreover, within the dextrose addition treatment, MBC was higher at 1.5 °C than at 10 °C or 22.5 °C (Fig. 5a). By day 29, two interesting patterns emerged: (1) MBC was lower at higher acclimation temperatures for both the dextrose and control treatments, and (2) summer soils always had higher

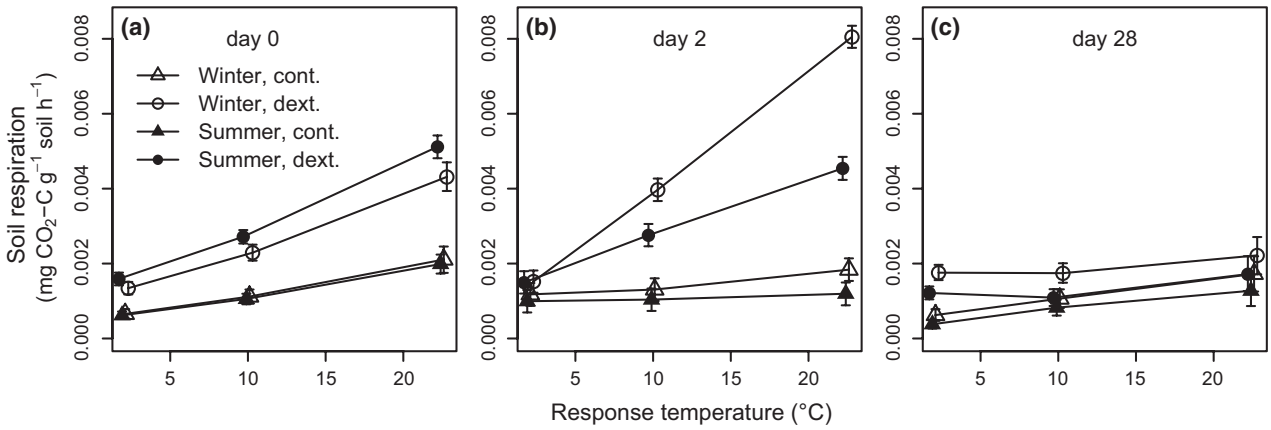

Fig. 3 Mean soil respiration ($\overline{R}$, Eqn 1) during the acclimation phase at the three acclimation temperatures, for both seasons (winter and summer), and for the two substrate levels (cont. = control; dext. = dextrose addition), on (a) day 0, (b) day 2, and (c) day 28. Error bars represent 95% credible intervals. 95% CI's that do not overlap the mean of another sample indicate significant differences.

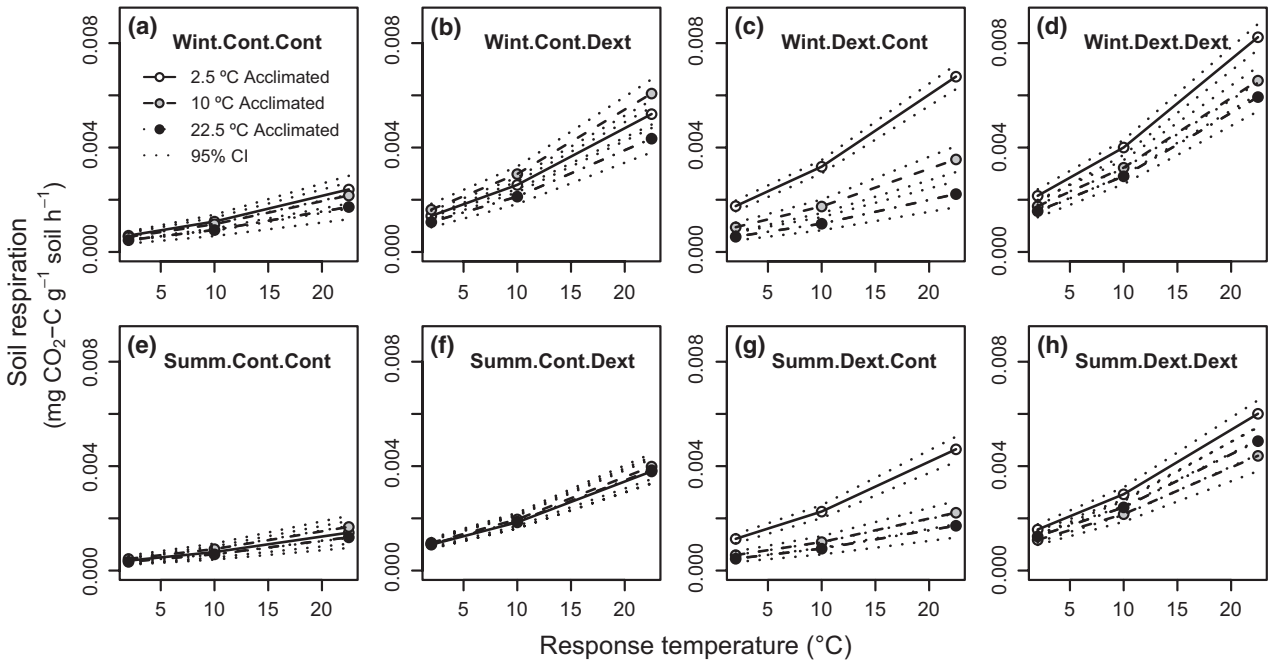

Fig. 4 Mean soil respiration ($\overline{R}$, Eqn 1) during the response phase (day 29), at the response temperatures, of soils acclimated over the previous 4 weeks to the acclimation temperatures (black circle = 22.5 °C, grey circle = 10 °C and white circle = 1.5 °C). The upper row contains the winter-collected soils, and the lower row contains the summer-collected soils. The subtitles show 'Season. Initial substrate. Final substrate'. Dashed lines represent 95% credible intervals.

MBC than winter soils for each substrate-acclimation temperature combination.

In contrast with the MBC pattern, initial (day 0) LSC was higher in the winter soils [mean = 0.210 mg C g^{-1} soil, 95% CI = (0.182, 0.273)] than the summer soils [mean = 0.158 mg C g^{-1} soil, 95% CI = (0.182, 0.237)] (Fig. 5b). The LSC pool remained unchanged for all control soils over the course of the experiment, and dextrose soils incubated at 10 °C and 22.5 °C returned to this baseline LSC value by day 29 (Fig. 5). On day 2, the dextrose soils incubated at 10 °C had significantly higher TOC than the soils incubated at 1.5 °C and 22.5 °C, in both winter and summer (Fig. 5b). The dextrose soils incubated at 1.5 °C maintained high TOC levels for the 29-day incubation period (Fig. 5b).

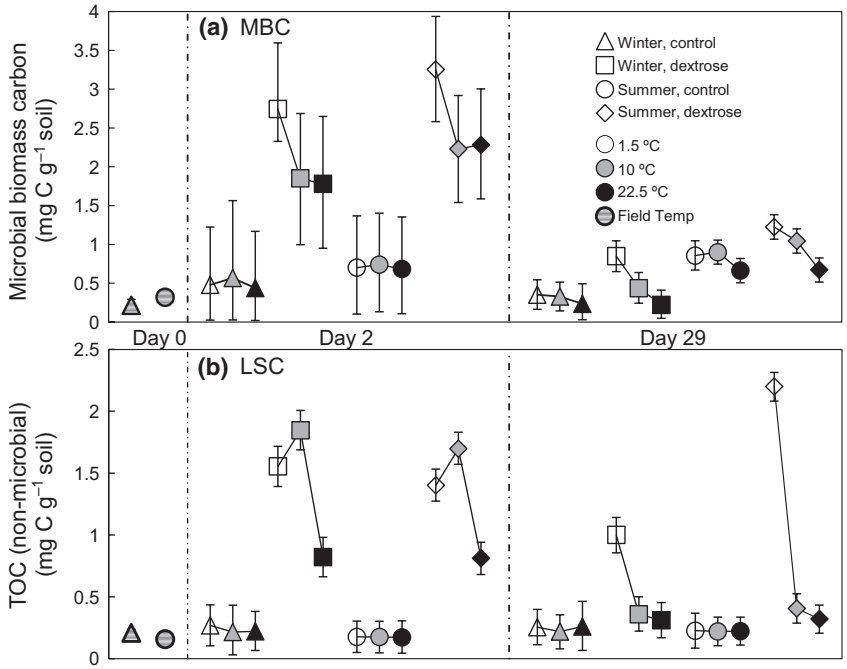

Fig. 5 (a) Microbial biomass carbon (MBC) and (b) labile substrate carbon (LSC) as estimated from extractable total organic carbon (TOC) on days 0, 2, and 29. The different shapes represent different season by substrate combinations, and the different shades represent the different temperatures. Three points connected by a line represent samples from the same season, on the same day, subjected to the same substrate treatment, at three different temperatures. On day 0 and day 29, LSC is presented prior to dextrose addition. Error bars represent 95% credible intervals.

Respiration response (MMLT model) parameters

The MMLT model fit the incubation data well (r^2 = 0.91 for observed vs. predicted respiration; Fig. 6). The value E_o was invariant [mean = 308 K, 95% CI = (302, 314)] across seasons and acclimation temperatures, and was not different than the informative prior derived from the Lloyd & Taylor (1994) meta-analysis (see Supporting material S4). T_o was slightly lower during the acclimation phase for summer soils [mean = 212.3 K, 95% CI = (208.3, 216.3)] than for winter soils [mean = 219.4 K, 95% CI = (214.9, 224)], but during the response phase T_o did not differ between seasons and was equal to the winter soil acclimation phase value (see Supporting material S4). On day 0, neither A_b (basal respiration) nor A_c (maximum substrate response) differed significantly between the winter and summer soils (Fig. 7). During the response phase, A_b exhibited two interesting patterns (Fig. 7b). First, the summer soils had significantly lower A_b than the winter soils, across all three acclimation temperature levels. Second, higher acclimation temperatures resulted in higher A_b. A potential negative correlation emerged between A_b and A_c after 29 days of acclimation (Fig. 6a vs. 6b). For winter soils, A_c declined significantly with increasing acclimation temperature, while there was no significant difference in A_c among the acclimation temperature levels for summer soils (Fig. 7a).

Carbon-use efficiency under different temperature acclimation scenarios

CUE in both seasons decreased with increasing acclimation temperature (Fig. 8). The decrease across the entire temperature range (1.5–22.5 °C) was approximately 0.011 °C^{-1} (summer) and 0.017 °C^{-1} (winter), which is consistent with the estimate of 0.009 °C^{-1} derived by Steinweg *et al.* (2008) using a different method in a different ecosystem. A better comparison with the Steinweg *et al.* (2008) results is limited in the range from 10 °C to 22.5 °C, over which CUE decreased by 0.009 °C^{-1} (summer) and 0.014 °C^{-1} (winter). Comparing between seasons, CUE was similar at 1.5 °C for summer and winter soils, but CUE diverged between seasons as the acclimation temperature increased, resulting in significantly higher CUE for summer than for winter soils at 22.5 °C.

Predicted respiration at normalized MBC and LSC

At normalized MBC and LSC, set to the overall average MBC and LSC values across seasons on day 0, the

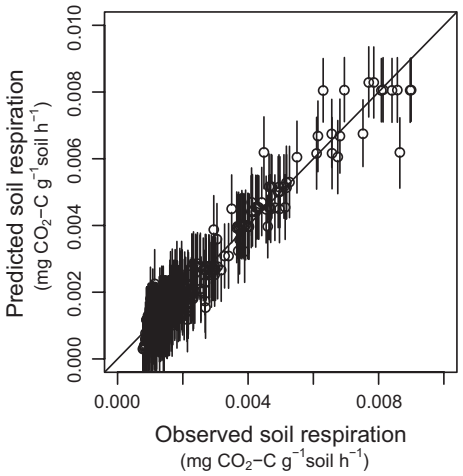

Fig. 6 Observed vs. predicted respiration from the MMLT model, where the predicted values are the posterior means (symbols) and 95% credible intervals of the 'replicated' or predicted soil respiration data (Gelman *et al.*, 2004). Values shown are for all temperature and substrate treatments on days 0, 2, and 29. The solid line is the one-to-one line.

model predicted that summer soils had lower respiration rates across all acclimation temperatures winter soils (Fig. 9). For soils collected within a season, there were no significant differences in the predicted respiration rates across the different acclimation temperatures. At normalized MBC and LSC, the predicted respiration rates fall approximately within the zone of 'full seasonal acclimation' wherein winter soil respiration rates at the average winter field temperature (0 °C) are equal to summer soil respiration rates at the average summer field temperature (16 °C) (Fig. 9).

Discussion

A major challenge addressed by this study was to separate the effects, on soil respiration, of changes in MBC and LSC availability from changes in underlying physiological parameters, when all of these factors are related and may change in tandem. Both seasonally (between winter- and summer-collected soils) and during short-term incubations, we observed a pattern of apparent thermal acclimation of soil respiration, but the underlying mechanisms differed between the two time-scales. Seasonal thermal acclimation appeared to be driven by acclimation of CUE (supporting H4) and basal respiration (A_b) (supporting H2). Short-term apparent thermal acclimation, however, was attributed to depletion of LSC (supporting H1) and to declining CUE with increasing temperature, as evidenced by lower MBC after acclimation at higher temperatures (supporting H3). CUE did not appear to acclimate to the short-term incubation temperature, but we cannot entirely eliminate this possibility, and in the short-term, A_b appeared to actually be stimulated by increasing temperatures (contradicting H2). Below we elaborate on the potential mechanisms underlying the seasonal and short-term acclimation responses.

Seasonal acclimation and carbon-use efficiency

After 29 days of incubation, we expected that soils incubated at the same temperature would have similar predicted respiration rates, whether they were collected in winter or summer. We also expected that cold-incubated soils would have higher predicted respiration rates at a

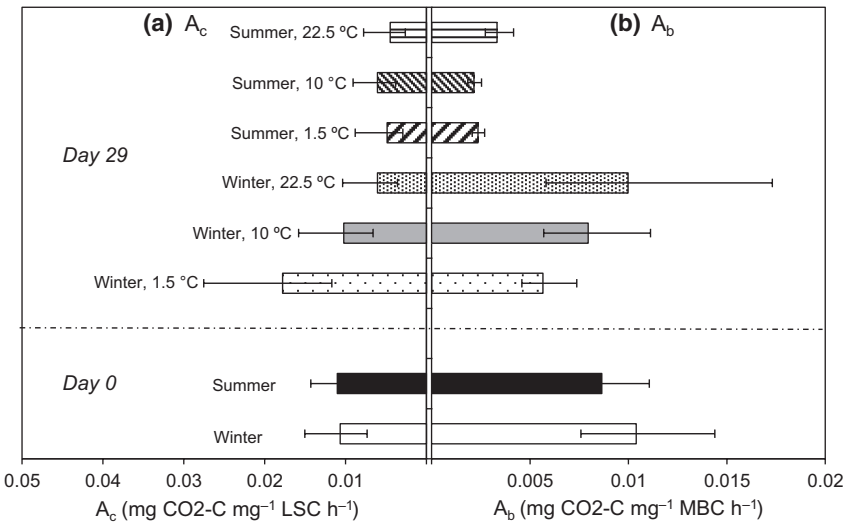

Fig. 7 (a) Substrate response rate (A_c) and (b) labile substrate carbon-saturated microbial biomass carbon-specific respiration at 10 °C (A_b), on day 0 and 29. On day 0, parameter estimates are given for each season, while on day 29, after the thermal acclimation test, estimates are given for each season and acclimation temperature.

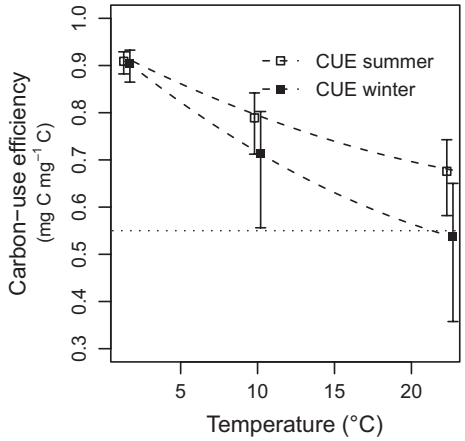

Fig. 8 Carbon-use efficiency (CUE) over the first 2 days of incubation at the three acclimation temperatures (1.5 °C, 10 °C, and 22.5 °C), for winter-collected and summer-collected soils. The horizontal dashed line represents the CUE value used across all sites, temperatures and seasons in the CENTURY model (Parton *et al.*, 1987). Error bars represent 95% credible intervals.

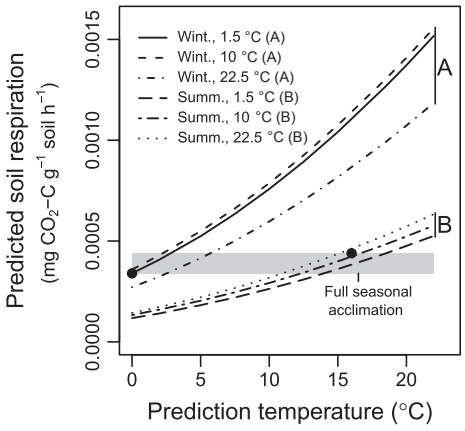

Fig. 9 Predicted soil respiration between 0 °C and 22.5 °C, under common microbial biomass (MBC) and labile substrate carbon (LSC) for soils acclimated for 29 days at 1.5 °C, 10 °C, and 22.5 °C, collected during the winter and summer. Respiration rates were estimated at average field LSC and MBC based on parameter estimates produced by the HB analysis. The gray zone of full seasonal acclimation was estimated by connecting the mean respiration rates of summer soils at summer field temperature with those of winter soils at winter field temperature (black circles). For clarity of presentation, the 95% Bayesian credible intervals (CIs) are not shown, but letters (A and B) beside the lines represent nonoverlapping 95% CIs, indicating significant differences.

common temperature than warm-incubated soils. Instead, after normalizing for differences in LSC and MBC, winter-collected soils had higher predicted respiration rates than summer-collected soils, but predicted respiration was not different across acclimation temperatures (Fig. 9). Furthermore, the predicted respiration rate of winter soils at 0 °C was comparable to the predicted respiration rate of summer soils at 16 °C (Fig. 9). Following the definition of 'full' acclimation given by Luo *et al.* (2001), this suggests that the full thermal acclimation of soil respiration occurred between seasons. Full acclimation occurs when soil respiration values tend toward the same 'optimal' value under different environmental conditions. While Luo *et al.* (2001) demonstrated full acclimation to a 2–2.6 °C warming, we find it surprising that soil respiration exhibited full acclimation over the greater range of temperature and field conditions that occur between winter and summer at this site. Moreover, Luo *et al.* (2001) measured total soil respiration in the field (heterotrophic and autotrophic), while we measured only the heterotrophic component in laboratory incubations. Further, in our study, 'full' acclimation between seasons was not initially apparent, but manifested after 4 weeks, possibly because of transitory effects related to soil sieving (Hartley *et al.*, 2007). In addition, what we are calling 'full' acclimation, is in fact only physiological acclimation, because we removed the effects of variable MBC and LSC through the normalization process. This result therefore provides an unambiguous demonstration of thermal acclimation separate from depletion of LSC.

Higher CUE at a given temperature in summer than in winter soils (Fig. 8) provides one mechanism for the observed seasonal thermal acclimation. Linked to higher CUE during the summer, summer soils had lower basal respiration (A_b) than winter soils (Fig. 7). Previous work has demonstrated that the trade-off between growth rate and CUE favors higher intrinsic growth and respiration rates at colder temperatures, and higher CUE at warmer temperatures (Lipson *et al.*, 2009). This trade-off represents an adaptation to the increased rate of substrate depletion that occurs at warmer temperatures. Alternatively, the much reduced CUE of winter soils incubated at high temperatures may reflect a shift from growth respiration to maintenance and survival respiration by organisms far outside their natural thermal environment (Schimel *et al.*, 2007).

Given that seasonal thermal acclimation of A_b and CUE were observed, one would predict lower respiration rates at a given temperature in summer soils than winter soils. This difference was not initially apparent (Fig. 3), however, because initial MBC was higher in the summer than in the winter (Fig. 5), which resulted in a 'cancelling-out' of the effects of the lower A_b. By day 2, there was higher respiration in winter soils (Fig. 3), while MBC was not significantly different (Fig. 5), which supports the hypothesis of seasonal thermal acclimation. This result is inconsistent with the prediction

by Allison *et al.* (2010) that acclimation toward higher CUE would increase total soil respiration by increasing MBC. Because their simulation was done on a longer time scale than our study, it is possible that, rather than representing different underlying dynamics, our result represents a transient phenomenon that would eventually converge to the Allison *et al.* (2010) predictions.

Short-term apparent thermal acclimation and substrate depletion

While predicted respiration rates did not vary by acclimation temperature within a season (i.e. there was no short-term acclimation) (Fig. 9), after 29 days there was clear *apparent* thermal acclimation under several treatments (Fig. 4b, c, d, g, and h), largely supporting the hypothesis (H1) that LSC depletion drives decreasing respiration with warming. Apparent full thermal acclimation was induced via LSC limitation in the dextrose. control treatment (dextrose added on day 0, but not day 29) (Fig. 4c and g) because the initial dextrose had been entirely respired in the warm treatments, but not in the cooler treatments (Fig. 5b). In soils receiving the dextrose.dextrose treatment, the pattern of apparent thermal acclimation (Fig. 4d and f) cannot be explained by LSC depletion because saturating levels of LSC were added just before respiration was measured. Instead, lower MBC at higher temperatures (Fig. 5a) drove the observed difference, consistent with the observed decrease in CUE with temperature. Under stable CUE, along with higher respiration rates, we would expect MBC to be higher in the warmed soils (Allison *et al.*, 2010), which was not the case in our study. The observed pattern is also consistent with acclimating CUE, but we rejected this mechanism because A_b was *stimulated* by higher acclimation temperatures (Fig. 7). Thus, we present the following three possibilities for the relationship between A_b and CUE: (1) A_b increases, but ΔMBC increases more → increased CUE, (2) A_b increases, but ΔMBC increases less → decreased CUE, and (3), A_b increases, and ΔMBC increases directly proportionately → no change in CUE. Based on Lipson *et al.* (2009), who demonstrated a trade-off between growth yield (analogous to CUE) and growth rate (analogous to ΔMBC), and the work of Pfieffer *et al.* (2001), who demonstrated a trade-off between the rate of ATP synthesis and the final quantity of ATP synthesized, we suggest that the first possibility is thermodynamically unlikely. Therefore, an increase in A_b suggests, although does not conclusively prove, that CUE did not increase over the course of the short-term incubations. Acclimating CUE would result in an increase in CUE at higher temperatures over time, so we use this as indirect evidence against short-term acclimation of CUE.

We offer two possible explanations for thermal stimulation of A_b. First, coupling of rates of respiration and gross mineralization of nitrogen or phosphorous would allow construction of more N- or P-rich cellular organelles associated with increased maximum respiration rates (Hall *et al.*, 2010). Second, the observed negative correlation (Fig. 7) of A_b and A_c suggest two ecological strategies: (1) high basal respiration, but a slow response to added substrate, (non-substrate limited), and (2) low basal respiration rate, but a fast response to added substrate (substrate limited). Strategy (1) occurred in warm-acclimated soils, while strategy (2) was more evident in cold-acclimated soils. Rather than absolute substrate limitation, this pattern might be explained by the observation that diffusion of the substrate to the microorganisms should be more limiting at lower temperatures (Davidson *et al.*, 2006). At cold temperatures, low A_b and high A_c would counteract the reduced rate of substrate diffusion. We emphasize that this trade-off is unlikely to be an artifact of model structure. When LSC is saturating, R_{base} simplifies to a function of temperature, A_b and MBC, so that A_b is quantified independently of A_c, and there is little potential for the two parameters to be correlated due to model structure.

In determining the short-term acclimation on day 29 of the study, there were obviously some limitations. Our sampling method was fairly labor- and sample-intensive, and we traded temporal resolution for unambiguous results on day 29. We chose 29 days as a subseasonal timescale, and from previous incubations using dextrose amendments, we noted that the effect of dextrose addition on soil respiration flattened out after approximately 4 weeks. Moreover, this time frame was appropriate for our study as evidenced by the convergence of control and dextrose addition respiration rates after 28 days of incubation. However, it is inevitable that interesting dynamics, particularly with respect to the difference between physiological acclimation of individual organisms, and soil microbial community turnover, were missed.

Implications for soil organic carbon storage

Changes in soil carbon storage depend on which mechanisms drive soil respiration responses to temperature. Apparent acclimation may be driven by depletion of the LSC pool (Hartley *et al.*, 2008; this study), without having much of an effect on total soil carbon storage because LSC is a small fraction of total SOC (Knorr *et al.*, 2005). Further, under conditions of warming and elevated CO_2 that are expected over the coming century (IPCC, 2007), increased plant carbon inputs to the soil may eliminate the potential for substrate depletion.

Conversely, increased rates of LSC depletion may enhance losses of soil carbon pools via the effect of 'priming' (enhanced decomposition of more recalcitrant SOM pools) (Kuzyakov & Bol, 2006).

The effects of declining and acclimating CUE on soil carbon storage can be predicted with more confidence than the effects of LSC depletion (Allison *et al*., 2010). Under conditions of declining CUE (which we see in the short-term), a 5 °C warming should have little impact on soil organic carbon storage over a 30-year timeframe. Acclimating CUE, on the other hand, would increase the amount of MBC the soils can support (relative to declining CUE), thereby increasing the respiration rate and reducing SOC (dependent, of course, on the level of CUE acclimation) (Allison *et al*., 2010). The relative importance of seasonal acclimation of CUE vs. short-term declines in CUE, as seen in our study, to long-term warming responses remains to be determined.

In conclusion, our data-model integration approach allowed us to separate and quantify the mechanisms underlying thermal acclimation of soil respiration. We found that CUE plays an important role in the response of soil respiration to warming. Over the short-term, CUE declines with increasing temperature, resulting in lower microbial biomass and therefore reduced respiration at warmer temperatures. Seasonally, CUE acclimates to the ambient temperature such that biomass-specific microbial respiration rates are reduced. The difference between declining and acclimating CUE has potentially important implications for soil carbon storage in terrestrial ecosystems, and future work should focus on separating these two mechanisms under field conditions, potentially involving field-warming experiments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. The detailed model. This supplement contains details about the levels and replication of each variable, as well as complete mathematical equations for the process model and statistical model.
Data S2. The Open BUGS code. This supplement contains the annotated model code that was run in OpenBUGS version 3.2.1.
Data S3. An alternative method for estimating carbon-use efficiency and the results compared to our original method.
Data S4. Table of parameter estimates for E_0 and T_0 derived from MMLT model.

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