Biogeochemistry (2013) 112:555–570
DOI 10.1007/s10533-012-9748-6

Soil respiration does not acclimatize to warmer temperatures when modeled over seasonal timescales

A. R. Contosta · S. D. Frey · S. V. Ollinger ·
A. B. Cooper

Received: 30 November 2011 / Accepted: 14 May 2012 / Published online: 6 June 2012

Abstract Soil warming studies have generally demonstrated an ephemeral response of soil respiration to warming suggesting acclimatization to increased temperatures. Many of these studies depict acclimatization as an empirical temperature-respiration model with data collected from late spring through early autumn. We examined the apparent temperature sensitivity of soil respiration in chronically warmed soils over three different timescales: annually, during the growing season, and seasonally during winter, spring, summer, and fall. Temperature sensitivity was evaluated by fitting exponential and flexible temperature functions as mixed effects models. From model coefficients, we estimated annual, growing season, and season-specific Q_{10} values, and assessed the ability of model coefficients to predict daily soil respiration rates over a two-year period. We found that respiration in warmed soils can exhibit characteristics of acclimatized temperature sensitivity depending on the timeframe and the function (exponential or flexible) used. Models using growing season data suggested acclimatization while models using data collected in winter or spring indicated enhanced temperature sensitivity with 5 °C of warming. Differences in temperature sensitivity affected predicted daily soil respiration rates, particularly in winter and spring. Models constructed over longer timescales overestimated daily respiration rates by as much 10–40 % whereas season-specific predictions were generally within 2 % of actual values. Failure to use season-specific models to depict changes in temperature dependence may over- or under-estimate carbon losses due to climate warming, especially during the colder months of the year.

Keywords Temperature sensitivity · Soil respiration · Acclimatization · Season

Introduction

Soils worldwide contain between 2,100 and 2,400 Gt of carbon (Davidson and Janssens 2006). Climate warming could result in a substantial loss of this carbon, but the magnitude of the loss depends, in part, on the temperature sensitivity of soil respiration to elevated temperatures. Coupled climate-carbon cycle models often assume a temperature sensitivity, or Q_{10}, of 2, such that respiration doubles for every 10 °C increase in temperature (e.g. Cox et al. 2000;

A. R. Contosta (✉) · S. D. Frey · S. V. Ollinger
Department of Natural Resources & the Environment, University of New Hampshire, Durham, NH 03824, USA
e-mail: alix.contosta@unh.edu

A. R. Contosta · S. V. Ollinger
Earth Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824, USA

A. B. Cooper
School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada

Friedlingstein et al. 2006). However, soils globally can exhibit Q_{10} values as low as 1.3 and as high as 3.3 (Raich and Schlesinger 1992), and projections for global carbon loss by the year 2100 can vary from 50 to 300 Gt depending on which value of Q_{10} is chosen (Jones et al. 2003).

Many climate-carbon models also assume that Q_{10} remains constant (i.e., remains ~2) even as the climate warms (Friedlingstein et al. 2006). Evidence from numerous soil warming studies contradicts this assumption. Although elevated temperatures can initially stimulate respiration, researchers have reported long-term declines in CO_2 flux in chronically warmed soils (Oechel et al. 2000; Melillo et al. 2002; Strömgren 2001). In some cases, warming has even reduced soil respiration within the first year or two of the study (McHale et al. 1998; Luo et al. 2001; Bronson et al. 2008; Allison and Treseder 2008).

One of the most common hypotheses used to explain decreased soil respiration at chronically warmed sites is that soil organisms acclimatize to the new temperature regime. "Acclimatization" refers to an adjustment of heterotrophic respiration from roots and soil microbes in response to increased temperatures. It does not describe the physiological mechanism for the adjustment, but instead is often applied in field settings when causal variables are unknown (Bradford et al. 2008). Acclimatization can be observed in empirical models of the relationship between temperature and respiration, where lower model slopes (using exponential functions), higher activation energies (using Arrhenius functions), and lower Q_{10} values in heated soils suggest that soil organisms adjust to warmer conditions (McHale et al. 1998; Luo et al. 2001; Melillo et al. 2004; Bronson et al. 2008; Reth et al. 2009).

Depletion of the labile fraction of soil organic carbon (SOC) may also be responsible for depressed CO_2 fluxes in soil warming experiments. Models of SOC dynamics have indicated that warming quickly depletes the fast-cycling, labile pool, leaving behind slow and passive pools (Kirschbaum 2004; Knorr et al. 2005). While the topic is under considerable debate (Kirschbaum 2006; Conant et al. 2011), it is likely that both acclimatization and labile C depletion contribute to the transient response of soil respiration to elevated temperatures. Bradford et al. (2008) reported both lower soil respiration per unit microbial biomass (suggesting acclimatization) and lower labile C availability (suggesting substrate depletion) in heated versus control soils sampled from a 15 year-old warming experiment. In any case, both the acclimatization and substrate depletion theories suggest that climate-carbon cycle feedbacks may not be as positive as they were once believed to be (Luo et al. 2001; Melillo et al. 2002).

A common feature of studies reporting the ephemeral response of soil respiration to elevated temperatures is the timeframe used to conduct the research. In temperate and boreal biomes, field measurements of CO_2 flux are typically made during the growing season (~April to November). These growing-season data are then used to create a single, empirical model of the relationship between temperature and respiration. As a result, the hypothesis that soil respiration acclimatizes to elevated temperatures depends upon observations made during only the warmer half of the year. However, a substantial portion of total annual CO_2 flux can occur in winter (Mo et al. 2005; Contosta et al. 2011) when cold conditions result in high temperature sensitivity of organic matter decomposition. Across a narrow range of temperature, from −5 to 5 °C, Q_{10} values can range from 8 to 1.25×10^6 (Kirschbaum 1995; Janssens and Pilegaard 2003; Monson et al. 2006), implying that small increases in winter soil temperatures could lead to substantially higher rates of soil respiration. Because winter temperatures are expected to increase between 1.1 and 5.4 °C in the Northeastern US by the year 2100 (Hayhoe et al. 2007), it is crucial to develop a more sophisticated understanding of the temperature sensitivity of CO_2 flux in cold soils and how this sensitivity might change with winter warming.

Empirical models constructed only during the growing season may not be able to capture such a change in winter temperature sensitivity. A model constructed over the growing season may be appropriate for predicting fluxes over the same timeframe because the confounding influences of temperature, moisture, and carbon inputs will be similar for both the measured and modeled fluxes. However, this same model may over- or under -estimate soil respiration when making predictions over shorter or longer timescales due to asynchronous changes in temperature, water, and substrate availability (Janssens and Pilegaard 2003; Curiel-Yuste et al. 2004; Mo et al. 2005). To adequately capture the temperature dependence of soil respiration in warmed soils, it may, therefore, be necessary to explicitly measure and model seasonal fluxes, including winter.

Illustrating the temperature sensitivity of CO_2 flux in warmed soils may also be related to the model used to fit the data. Studies showing the transient response of soil respiration to elevated temperatures have typically employed an exponential model structure with a constant Q_{10} (McHale et al. 1998; Luo et al. 2001; Strömgren 2001; Melillo et al. 2004). However, these exponential models tend not to perform as well as more flexible models with variable Q_{10} functions, especially in depicting fluxes in very cold and very warm soils (Lloyd and Taylor 1994). Thus the hypothesis that soil respiration acclimatizes to a warmer temperature regime may be as much a product of model selection as the timeframe used to depict the relationship.

The purpose of this study was to compare the temperature dependence of soil respiration in chronically warmed soils using two different model structures, exponential and flexible, and several different timescales: annually, during the growing season, and seasonally during winter, spring, summer, and fall. An additional objective was to examine how differences in temperature dependence among these timeframes would affect predicted changes in soil respiration with warming. For the purposes of this study, we use "temperature sensitivity" to refer to apparent, not intrinsic, temperature sensitivity (Davidson and Janssens 2006), and soil respiration comprises both autotrophic and heterotrophic fluxes. Using data collected from a soil warming experiment, we tested the hypotheses that (1) 5 °C of soil warming would alter the temperature dependence of soil respiration differently throughout the year, and (2) that exponential and flexible model structures would contrast in their ability to portray this shifting temperature dependence. Regarding our first hypothesis, we predicted that warmed soils during the growing season would show lower temperature dependence consistent with the findings of other researchers. During winter, we expected that warmed soils would show higher temperature sensitivity as has often been demonstrated for cold soils. Over an annual timescale, these shifts in temperature dependence between winter and the growing season would balance one another, resulting in no net change in the temperature sensitivity of heated soils. For our second hypothesis, we anticipated that a flexible model structure with a variable Q_{10} would best represent the effects of increased temperatures on soil respiration, especially in cold conditions.

Methods

Site description and experimental design

This research took place at the Soil Warming × Nitrogen Addition Study, located at the Harvard forest long term ecological research (LTER) site in Petersham, Massachusetts (42°50′N, 72°18′W). The experiment was initiated in August, 2006 and has been described in detail by Contosta et al. (2011). The forest in the study area is comprised of even-aged, mixed hardwoods. Soils are of the Gloucester series (fine loamy, mixed, mesic, typic dystrochrepts; Peterjohn et al. 1994). Mean annual air temperature is 7 °C and ranges from a minimum of −25 °C in winter to a maximum of 32 °C in summer. Average total annual precipitation, including water equivalent of snow, is 1,100 mm (Boose et al. 2002). The experimental design consists of 24, 3 × 3 m plots randomly assigned to one of four treatments: control, N addition, warming, and warming × N. Average soil temperature in the heated plots is continuously elevated 5 °C above ambient using heating cables placed at 10 cm depth. Nitrogen fertilization occurs as equal doses of an aqueous solution of NH_4NO_3 applied six times throughout the growing season at a rate of 5 g N m^{-2} $year^{-1}$. Initial data exploration indicated that N additions did not alter the temperature-respiration relationship. Consequently, N addition plots were grouped with controls, and the warming treatment included both warming and warming × N when modeling the relationship between temperature and soil respiration.

Soil respiration

Soil respiration measurements were described in Contosta et al. (2011). Net CO_2 flux was measured bi-monthly from May 2007 to April 2009 using a static chamber technique (Peterjohn et al. 1993) with one chamber per plot. All sampling took place when the average of the diel flux occurs: between 10:00 and 13:00 local time (Davidson et al. 1998). In the summer of 2008, we compared our measurements with fluxes simultaneously made on a dynamic, portable system, and the two techniques were well-correlated ($r^2 = 0.86$, Contosta unpublished data). In addition, measurements made in winter approximated eddy covariance fluxes calculated for the same time of year at the Harvard Forest (Munger et al. 2004). During sampling, soil temperature was measured adjacent to the chamber from the surface to 5 cm depth. Soil volumetric water content was also measured using time domain reflectometry to 20 cm (CS620 Hydro-Sense Water Content Probe, Campbell Scientific, Logan, UT), except during winter when probes could not be inserted into the soil. After collection, gas samples were immediately transported back to the University of New Hampshire and analyzed using a LI-COR LI-6252 infrared gas analyzer (LI-COR Biosciences, Lincoln, Nebraska, USA).

Modeling and statistical analysis

We determined the apparent temperature sensitivity of soil respiration in chronically warmed soils using two different functions, exponential and flexible. The exponential function (EXP), which calculates a constant Q_{10}, is one of the most frequently applied for examining the temperature-respiration relationship:

$$R = \beta \exp^{kT} \quad (1)$$

where β is the model intercept, or flux at 0 °C, in units of mg CO_2-C m^{-2} h^{-1}, k is the model slope, and T is soil temperature (°C) at 5 cm. Since EXP often underestimates flux at low temperatures and overestimates flux at high ones (Lloyd and Taylor 1994), we also applied the flexible temperature function with a variable Q_{10} (Lloyd and Taylor, or LT) designed to overcome this bias:

$$R = A \exp^{(-E_0/(T-T_0))} \quad (2)$$

For Eq. 2, A is a dataset-specific variable in units of mg CO_2-C m^{-2} h^{-1} that accounts for inter-site variation in soil respiration. The E_0 parameter is similar to an activation energy, and represents temperature (K) when $R \to \infty$. The T_0 parameter is temperature (K) when $R \to 0$, and T represents the soil temperature (K) at 5 cm depth.

Using the equations above, we examined the apparent temperature sensitivity of soil respiration in chronically warmed soils at three different time scales: annual, growing season, and season specific. The annual fit included all the months during which we measured soil respiration (May 2007 to April 2009). The growing season fit also contained these months, but included a variable that partitioned the data into measurements taken during winter versus during the growing season. The season-specific fit also contained a variable that separated the data into individual seasons of winter, spring, summer, and fall. Seasons were delineated based on criteria previously defined in Contosta et al. (2011). Winter occurred from December 1 to March 31, spring from April 1 to May 31, summer from June 1 to August 30, and autumn from September 1 to November 30.

Preliminary linear regressions showed that soil respiration did not vary with volumetric water content, even though water content was weakly correlated with soil temperature ($P < 0.0001$, $r^2 = 0.10$). The exception was when water content was lower than the threshold of 0.12 cm^3 cm^{-3} established by Davidson et al. (1998), below which moisture becomes limiting to respiration. This represented ~7 % of the data set, which showed a very weak, positive relationship with water content ($P = 0.01$, $r^2 = 0.07$). Because moisture generally did not affect respiration, but was correlated with temperature, we excluded it from the analysis. This avoided the confounding effects of moisture and soil temperature on soil respiration.

A mixed effect modeling approach was applied when fitting both EXP and LT in each of the three timescales. This allowed for the partitioning of random errors associated with measurement, instrumentation, and site variability not typically addressed in least-square regression models. It also allowed for the specification of temporal autocorrelation between measurements usually ignored in linear and non-linear curve fitting (Hess and Schmidt 1995; Peek et al. 2002).

For the exponential function (EXP, Eq. 1), we used *lme* in R 2.9.2 (Pinheiro et al. 2009; R Development Core Team 2009) to fit three linear mixed effects models: annual, growing season, and season-specific (Table 1). Fluxes were log-transformed to ensure homoscedasticity and normality of residuals. Although log-transformation can cause errors in parameter estimates and predictions when back-transformed to standard units (e.g. Adair et al. 2010), preliminary modeling showed both a log-normal distribution of residuals for all six models and a much closer match between measured and fitted values when

Table 1 Fixed effects model format, residual standard errors (RSE), P-values, r^2 values, and AICc rankings for the exponential (EXP) and flexible (LT) fits of the temperature-respiration relationship during annual, growing season, and season-specific timeframes

Model	Timeframe	Fixed effects model format	RSE	P	r^2	AICc
EXP	Annual[a]	$\ln R \sim \ln\beta + \beta_W * \mathrm{W} + (k + k_W * W) \times T$	0.36	<0.0001	0.82	843.25
	Growing season[b]	$\ln R \sim \ln\beta + \beta_W * \mathrm{W} + \beta_{GS} * \mathrm{GS} + \beta_{W\times \mathrm{GS}} * W * \mathrm{GS} + (k + k_W * \mathrm{W} + k_{\mathrm{GS}} * \mathrm{GS} + k_{W\times \mathrm{GS}} * W * \mathrm{GS}) \times T$	0.35	<0.0001	0.83	826.31
	Season specific[c]	$\ln R \sim \ln\beta + \beta_W * \mathrm{W} + \beta_{\mathrm{SS},i} * \mathrm{SS}_i + \beta_{W\times \mathrm{SS},i} * W * \mathrm{SS}_i + (k + k_W * \mathrm{W} + k_{\mathrm{SS},i} * \mathrm{SS}_i + k_{W\times \mathrm{SS},i} * W * \mathrm{SS}_i) \times T$	0.31	<0.0001	0.87	677.70
LT	Annual[d]	$\ln R \sim \ln A + ((-1 \times \exp(\ln E_0 + E_{0,W} * \mathrm{W}))/(T - (\exp(\ln T_0 + T_{0,W} * \mathrm{W}))))$	0.36	<0.0001	0.82	853.87
	Growing season[e]	$\ln R \sim \ln A + ((-1 \times \exp(\ln E_0 + E_{0,W} * \mathrm{W} + E_{0,GS} * \mathrm{GS} + E_{0,W\times GS} * W * \mathrm{GS}))\ /\ (T - (\exp(\ln T_0 + T_{0,W} * \mathrm{W} + T_{0,GS} * \mathrm{GS} + T_{0,W\times GS} * W * \mathrm{GS}))))$	0.41	<0.0001	0.77	809.61
	Season specific[f]	$\ln R \sim \ln A + ((-1 \times \exp(\ln E_0 + E_{0,W} * \mathrm{W} + E_{0,\mathrm{SS},i} * \mathrm{SS}_i + E_{0,W\times \mathrm{SS},i} * W * \mathrm{SS}_i))\ /\ (T - (\exp(\ln T_0 + T_{0,W} * \mathrm{W} + T_{0,\mathrm{SS},i} * \mathrm{SS}_i + T_{0,W\times \mathrm{SS},i} * W * \mathrm{SS}_i))))$	0.32	<0.0001	0.87	601.19

"W," "GS" and "SS" indicate warming, growing season, and season-specific covariates, respectively. All models included plot as a random intercept and fit log-transformed fluxes. Residual standard error (SE), P, and r^2 values were obtained by regressing fitted values against observed CO_2 fluxes

[a] Where $W = 1$ if warmed, zero otherwise and β_W and k_W represent the effect of warming on the intercept and slope, respectively

[b] Where W is defined as above; $\mathrm{GS} = 1$ if growing season, zero otherwise; and β_W and k_W represent the main effect of warming on the intercept and slope, respectively; β_{GS} and k_{GS} represent the main effect of growing season on the intercept and slope, respectively; and the parameters $\beta_{W\times \mathrm{GS}}$ and $k_{W\times \mathrm{GS}}$ allow the effect of warming on the intercept and slope to differ by growing season and the effect of growing season to differ by warming treatment

[c] Where W is defined as above; SS_i is a dummy variable for spring, summer, fall, or winter (with spring being the baseline); and β_W and k_W are defined as above; $\beta_{\mathrm{SS},i}$ and $k_{\mathrm{SS},i}$ represent the main effect of season i on the intercept and slope, respectively; and the parameters $\beta_{W\times \mathrm{SS},i}$ and $k_{W\times \mathrm{SS},i}$ allow the effect of warming on the intercept and slope to differ for each season and the effect of each season to differ by warming treatment

[d] Where W is defined as above; $E_{0,W}$ represents the effect of warming on E_0, and $T_{0,W}$ represents the effect of warming on T_0

[e] Where W and GS are defined as above; $E_{0,W}$ and $T_{0,W}$ represent the main effects of warming on E_0 and T_0; $E_{0,\mathrm{GS}}$ and $T_{0,\mathrm{GS}}$ represent the main effects of growing season on E_0 and T_0; and $E_{0,W\times \mathrm{GS}}$ and $T_{0,W\times \mathrm{GS}}$ allow the effects of warming to differ by growing season and the effect of growing season to differ by warming

[f] Where W and SS_i are defined as above; $E_{0,W}$ and $T_{0,W}$ represent the main effects of warming on E_0 and T_0; $E_{0,\mathrm{SS},i}$ and $T_{0,\mathrm{SS},i}$ represent the main effects of season i on E_0 and T_0; and $E_{0,W\times \mathrm{SS},i}$ and $T_{0,W\times \mathrm{SS},i}$ allow the effects of warming to differ in each season and the effect of each season to differ by warming

calculated from log-transformed parameters. All three models included plot as a random intercept. Fixed effects included the EXP parameters β (intercept) and k (slope with respect to changes in T), as well as parameters representing changes in model intercepts and slopes seasonally and/or with warming (see Table 1 for full model descriptions). Warming was included as a covariate for all three models. Dummy variables specifying categories of winter/growing season or winter/spring/summer/fall were included in the growing season and season-specific models, respectively. These dummy variables were crossed with warming to create warming × timeframe interactions in the growing season and season specific fits which allow the effect of warming to change by season. Differences in temperature sensitivity, seasonally and/or with warming, were assessed by the marginal significance of each fixed effect and interaction in the fitted model when all other fixed effects were present. F-statistics and P-values were obtained using the *anova* command, with $\alpha = 0.05$. Pairwise comparisons of model slopes and intercepts were assessed by examining mean and 95 % confidence intervals (CIs) of estimated model coefficients, which were calculated using the method outlined below.

For the flexible temperature model structure (LT, Eq. 2), we wrote a self-starting, nonlinear function following the protocol in Pinhiero and Bates (2000), and then used *nlme* in R (Pinheiro et al. 2009) to fit the function with warming and timeframe covariates (Table 1). Plot was included as a random intercept for both E_0 and T_0, and both of these parameters were specified as fixed effects. As with EXP, fixed effects also included the effects of warming and timeframe on E_0 and T_0 (see Table 1). Parameters E_0 and T_0 were fit in log-space to ensure that parameter estimates would always be positive when back-transformed to their natural scale. The site-specific constant, *A*, was calculated by averaging flux for the entire data set, multiplying it by 1,000 (Savage and Davidson 2001), and taking the natural log of the result. For the annual, growing season, and season-specific LT fits, treatment and timeframe covariates were the same as for the EXP function. Significant differences in temperature sensitivity with warming and/or season was determined in the same way as for EXP models.

After fitting EXP and LT models, means and 95 % CIs of model coefficients were estimated using the *mvrnrom* function in the MASS package of R (Venables and Ripley 2002). The *mvrorm* function generates random numbers from a specified multivariate normal distribution which in this case was the variance–covariance matrix of the model. For each EXP and LT fit (annual, growing season, and season-specific), *mvrorm* produced 1,000 new estimates of the coefficients. For EXP the coefficients were β and k as well as the effects of warming and/or timeframe on β and k. For LT, coefficients were E_0 and T_0 and the effects of warming and/or timeframe on E_0 and T_0. Mean β, k, E_0 and T_0 and the effects of warming and/or timeframe on each were calculated as the average of 1,000 estimated values for each coefficient, and 95 % CIs represented upper and lower bounds, or 2.5th and 97.5th percentiles, assuming a normal distribution. Because the EXP and LT models produced log-transformed estimates for β, E_0 and T_0, these estimates were exponentiated before calculating means and percentiles in order to obtain values more commonly reported in the literature.

Estimated model coefficients were also used to calculate mean Q_{10} values plus 95 % CIs. We defined Q_{10} as:

$$Q_{10} = R_{\mathrm{ref}} / R_{\mathrm{ref}+10} \tag{3}$$

where R_{ref} and $R_{\mathrm{ref}+10}$ indicates soil respiration at seasonally appropriate range of soil temperatures. For annual and growing season models, R_{ref} was 10 °C (EXP) or 283 K (LT) and $R_{\mathrm{ref}+10}$ was 20 °C or 293 K. For season-specific models, R_{ref} was 0, 5, 10, or 15 °C (273, 278, 283, or 288 K) for winter, spring, summer, and autumn, respectively. $R_{\mathrm{ref}+10}$ was 10, 15, 20, or 25 °C (283, 288, 293, or 298 K) for winter, spring, summer, and autumn. Calculating Q_{10} with season-specific temperatures made no difference to EXP estimates since Q_{10} values generated from the EXP model are constant across all temperatures. By contrast, the LT model describes a variable Q_{10} that changes from a low to high temperature range. Q_{10} values were determined for all timeframe and treatment combinations using coefficients obtained from the *mvrnrom* function to estimate respiration at R_{ref} and $R_{\mathrm{ref}+10}$ temperatures. This provided 1,000 estimated Q_{10} values, from which means and percentile-based 95 % CIs were calculated.

For all of the EXP and LT fits, model verification consisted of visually inspecting residuals for normality and homoscedasticity. Because *lme* and *nlme* approaches employed likelihood-based instead of least-squares estimation, the residual standard errors (RSE), model-level *P*-values, and r^2 values typically reported for regressions were not available to describe goodness-of-fit. Instead, these statistics were estimated by regressing fitted against observed soil CO_2 fluxes. Models were also assessed for their ability to fit the data with an information-theoretic approach. Higher r^2 values are expected from models that contain greater numbers of parameters. By contrast, an information-theoretic method, such as the Akaike's Information Criteria (AIC), both rewards goodness-of-fit while it penalizes greater numbers of parameters (Burnham and Anderson 2002). We used the AIC modified for small sample sizes (AICc) to rank the EXP and LT models (Burnham and Anderson 2002). Finally, model performance was determined by comparing predicted daily fluxes to actual respiration rates. Predicted fluxes were generated using model coefficients derived from the *mvnorm* function and daily average soil temperatures from May 2007 through April 2009. These predictions were compared to measurements across the entire study period (converted from hourly to daily rates) to highlight periods of agreement or disagreement between measured and modeled respiration fluxes.

Results

Both the exponential (EXP) and Lloyd and Taylor (LT) fits indicated that the temperature sensitivity of soil respiration significantly differed between warmed and unwarmed soils. This difference shifted with the timeframe used to fit the data: annual (January through December), winter versus growing season (December through March versus April through November), or season specific (winter, spring, summer, or fall). Estimated residual standard errors, r^2 values, and AICc rankings suggested that season-specific EXP and LT models explained the data better than annual or growing season fits. In addition, predicted fluxes from season-specific timeframes better matched actual fluxes measured in the field.

For the annual timeframe, temperature sensitivity was either higher or similar in warmed soils depending on whether the EXP or LT function was used (Fig. 1; Tables 2, 3, 4). Figure 1 shows the relationship between temperature and respiration modeled at the annual timescale. The lines depict respiration as a function of temperature based on estimated model coefficients (EXP and LT) for each treatment. The slight rightward shift of the line fit for warmed plots using the EXP function (Fig. 1A) typically indicates declining temperature dependence, or acclimatization to warmer temperatures. However, neither model slopes (k) nor estimated Q_{10} values differed between warmed and unwarmed plots ($P = 0.3727$ for the $k \times$ warming interaction). As a result, this rightward shift was not significant, and temperature sensitivity was similar between treatments. By contrast, the temperature dependence of soil respiration was enhanced in warmed plots over an annual timescale when modeled with the LT function. The lines fit for both treatments converged at the extremes of the temperature range, with a rightward shift of the line for the warmed plots between 273 and 293 K (Fig. 1B). In order for the warmed line to rejoin the unwarmed one at 300 K, temperature sensitivity would have to have been higher in warmed soils at the higher end of the temperature range. Model results indicated that T_0 was higher in warmed plots as compared to unarmed ones ($P = 0.001$). In addition, comparison of means and percentile based 95 % CIs showed that Q_{10}s were also substantially higher in warmed plots ($Q_{10} = 2.75$) as compared to the unwarmed treatment ($Q_{10} = 2.36$).

Allowing temperature dependence to vary between winter and the growing season generally resulted in enhanced sensitivity in warmed plots in winter and reduced sensitivity in warmed soils during the growing season, though again this varied between EXP and LT (Fig. 2; Tables 2, 3, 4). Figure 2 shows the relationship between temperature and respiration only during the growing season. As with the annual timeframe, the line fit from estimated EXP model coefficients for warmed soils shifted to the right of the line fit for the

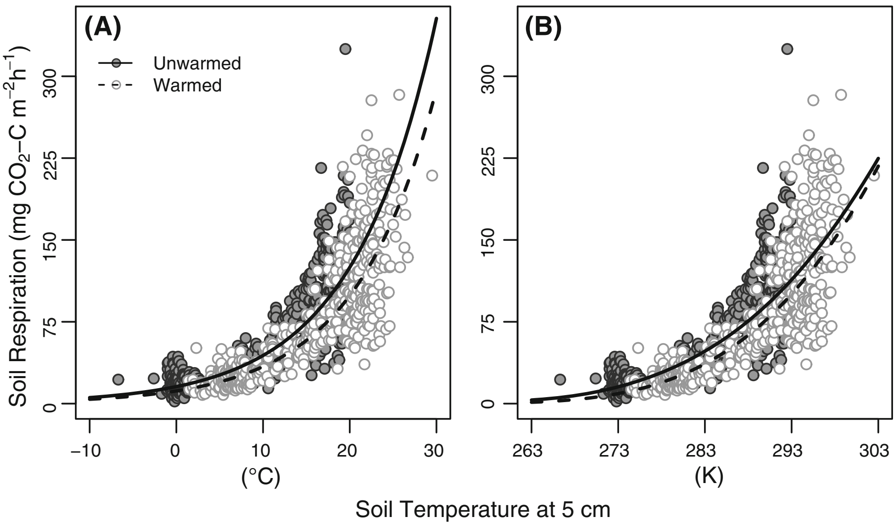

Fig. 1 Relationship between temperature and respiration in warmed and unwarmed soils over an annual timescale for **A** exponential (EXP) and **B** flexible (LT) models. Each *circle* represents an hourly flux. The *solid line* and the *solid circles* depict unwarmed plots, while the *dashed line* and *open circles* show warmed plots

Table 2 *F*-statistics, denominator degrees of freedom (DF), and *P*-values of fixed effects for exponential (EXP) and flexible (LT) models during annual, growing season, and season specific timeframes

Timeframe	EXP				LT			
	Fixed effect	DF	*F*	*P*	Fixed effect	DF	*F*	*P*
Annual	$\text{Ln}\beta$	888	13789.80	*<0.0001*	$\ln E_0$	887	38271.38	*<0.0001*
	$\ln\beta + \beta_W * \text{W}$	22	13.94	*0.0015*	$\ln E_0 + E_{0,W} * \text{W}$	887	4.97	*0.0261*
	k	888	3878.27	*<0.0001*	$\ln T_0$	887	281603.34	*<0.0001*
	$k + k_W * W$	888	0.80	0.3727	$\ln T_0 + T_{0,W} * \text{W}$	887	10.64	*0.0011*
GS	$\text{Ln}\beta$	884	931.71	*<0.0001*	$\ln E_0$	883	15039.23	*<0.0001*
	$\ln\beta + \beta_W * \text{W}$	22	0.20	0.6589	$\ln E_0 + E_{0,W} * \text{W}$	883	0.1	0.7485
	$\ln\beta + \beta_{GS} * \text{GS}$	884	8.80	*0.0031*	$\ln E_0 + E_{0,GS} * \text{GS}$	883	2.72	0.0998
	$\ln\beta + \beta_{W\times GS} * W * \text{GS}$	884	2.45	0.1180	$\ln E_0 + E_{0,W\times GS} * W * \text{GS}$	883	0.48	0.4876
	k	884	560.70	*<0.0001*	$\ln T_0$	883	142710.5	*<0.0001*
	$k + k_W * \text{W}$	884	6.13	*0.0135*	$\ln T_0 + T_{0,W}* \text{W}$	883	0.05	0.8149
	$k + k_{GS} * \text{GS}$	884	32.46	*<0.0001*	$\ln T_0 + T_{0,GS} * \text{GS}$	883	1.71	0.1915
	$k + k_{W\times GS} * W * \text{GS}$	884	13.49	*0.0003*	$\ln T_0 + T_{0,W\times GS} * W * \text{GS}$	883	0.29	0.591
SS	$\text{Ln}\beta$	876	597.76	*<0.0001*	$\ln E_0$	875	3575.76	*<0.0001*
	$\ln\beta + \beta_W * \text{W}$	22	1.30	0.2658	$\ln E_0 + E_{0,W} * \text{W}$	875	5.00	*0.0257*
	$\ln\beta + \beta_{SS,\ i} * \text{SS}_i$	876	9.15	*<0.0001*	$\ln E_0 + E_{0,SS,i} * \text{SS}_i$	875	7.91	*<0.0001*
	$\ln\beta + \beta_{W\times SS,i} * W * \text{SS}_i$	876	0.53	0.6645	$\ln E_0 + E_{0,W\times SS,i} * W * \text{SS}_i$	875	2.48	0.0600
	k	876	45.62	*<0.0001*	$\ln T_0$	875	4581.31	*<0.0001*
	$k + k_W * \text{W}$	876	4.61	*0.0320*	$\ln T_0 + T_{0,W} * \text{W}$	875	3.62	0.0573
	$k + k_{SS,i}* \text{SS}_i$	876	5.06	*0.0018*	$\ln T_0 + T_{0,SS,i} * \text{SS}_i$	875	2.79	*0.0397*
	$k + k_{W\times SS,}* W * \text{SS}_i$	876	4.08	*0.0069*	$\ln T_0 + T_{0,W\times SS,i} * W * \text{SS}_i$	875	1.19	0.3113

Values in italics indicate significant differences at $\alpha = 0.05$

Note: "W," "GS" and "SS" are as in Table 1. *P*-values represent marginal significance of each fixed effect in the fitted model when all other fixed effects are present

unwarmed plots (Fig. 2A). In this case, model coefficients and Q_{10} values indicated that the rightward shift is the result of acclimatization to warmer temperatures. Model slope, or *k*, was higher ($P = 0.0135$) in unwarmed plots during the growing season as compared to warmed ones. Mean Q_{10} was 3.14 in unwarmed plots, and was only 2.66 in the warming treatment. During winter, the difference in temperature dependence between treatments was reversed, with enhanced temperature sensitivity in warmed plots as compared to unwarmed ones. The significant difference in model slopes between treatments and timeframes ($P = 0.0003$ for the $k \times$ warming × growing season interaction) illustrated this change in temperature dependence in warmed soils between the winter and growing season. Higher model slopes and Q_{10} values during winter in warmed plots, as estimated by mean and percentile based 95 % CIs, further indicated stronger temperature dependence of soil respiration during this season, with mean Q_{10}s at 0.92 and 2.07 for unwarmed and warmed soils, respectively.

When depicted with the LT function, the temperature dependence of soil respiration did not differ between treatments or between the winter and growing season timeframes. Lines showing the temperature-respiration relationship for warmed and unwarmed plots overlapped when fit during the growing season (Fig. 2B). Neither E_0 nor T_0 differed between treatments or with the warming × growing season interaction ($P > 0.05$ for all treatment and timeframe combinations). While mean Q_{10} values were higher during winter for both treatments, they were not significantly different from one another or from growing season values (according to pairwise comparisons of 95 % CIs).

Season-specific fits indicated enhanced temperature sensitivity in warmed plots as compared to

Table 3 Estimated β, k, and Q_{10} values (with 95 % CI of the estimates) from exponential (EXP) models of the temperature-respiration relationship during annual, growing season, and season-specific timeframes

Model	Timeframe	Trt	β	k	Q_{10}
Annual	Annual	C	15.59 (13.99, 17.25)	0.104 (0.099, 0.108)	2.83 (2.69, 2.96)
		W	11.64 (10.39, 13.07)	0.107 (0.102, 0.112)	2.92 (2.78, 3.06)
Growing season	Growing Season	C	13.44 (11.31, 16.13)	0.114 (0.105, 0.124)	3.14 (2.87, 3.45)
		W	14.21 (11.58, 17.15)	0.098 (0.089, 0.107)	2.66 (2.44, 2.90)
	Winter	C	17.01 (15.23, 19.01)	−0.011 (−0.051, 0.030)	0.92 (0.60, 1.35)
		W	14.02 (11.14, 17.15)	0.071 (0.042, 0.102)	2.07 (1.52, 2.76)
Season-specific	Spring	C	16.27 (12.88, 20.20)	0.064 (0.046, 0.082)	1.90 (1.59, 2.27)
		W	13.29 (9.86, 17.32)	0.091 (0.075, 0.109)	2.50 (2.11, 2.96)
	Summer	C	56.18 (30.10, 95.48)	0.041 (0.010, 0.072)	1.52 (1.10, 2.06)
		W	58.61 (28.08, 107.46)	0.041 (0.011, 0.070)	1.52 (1.12, 2.01)
	Fall	C	26.92 (20.74, 34.45)	0.067 (0.048, 0.086)	1.97 (1.62, 2.37)
		W	29.81 (21.26, 41.18)	0.058 (0.041, 0.077)	1.80 (1.51, 2.15)
	Winter	C	17.00 (15.29, 18.78)	−0.011 (−0.049, 0.026)	0.91 (0.61, 1.29)
		W	14.48 (11.64, 17.43)	0.068 (0.042, 0.095)	2.00 (1.53, 2.57)

Note: Values for β were obtained by exponentiating the lnβ estimates generated by the model

Table 4 Estimated E_0, T_0, and Q_{10} values (with 95 % CI of the estimates), from flexible (LT) models of the temperature-respiration relationship during annual, growing season, and season-specific timeframes

Model	Timeframe	Trt	E_0	T_0	Q_{10}
Annual	Annual	C	546.9 (512.7, 581.2)	208.3 (204.4, 212.6)	2.36 (2.30, 2.48)
		W	493.6 (463.4, 525.3)	218.0 (213.9, 221.9)	2.75 (2.61, 2.92)
Growing season	Growing Season	C	448.9 (407.7, 495.1)	221.5 (215.2, 227.4)	2.78 (2.55, 3.08)
		W	460.7 (416.7, 510.0)	220.2 (213.3, 227.2)	2.75 (2.50, 3.09)
	Winter	C	574.8 (430.5, 755.3)	209.1 (191.5, 227.6)	3.54 (2.74, 5.89)
		W	516.3 (404.8, 647.9)	214.3 (199.4, 230.4)	3.78 (2.86, 5.87)
Season-specific	Spring	C	882.0 (700.5, 1112.6)	170.7 (145.3, 197.2)	2.04 (1.80, 2.58)
		W	647.6 (544.2, 755.5)	198.9 (185.5, 214.4)	2.53 (2.19, 3.14)
	Summer	C	568.3 (429.8, 739.3)	204.00 (181.5, 228.3)	2.09 (1.80, 2.84)
		W	544.7 (425.3, 688.8)	209.5 (189.2, 230.9)	2.25 (1.88, 3.02)
	Fall	C	751.4 (599.1, 932.9)	180.0 (157.8, 204.5)	1.92 (1.27, 2.32)
		W	697.2 (566.8, 844.0)	188.6 (169.1, 209.7)	2.05 (1.81, 2.57)
	Winter	C	1796.0 (1127.0, 2739.2)	85.1 (14.0, 289.1)	1.70 (1.42, 4.04)
		W	858.1 (684.3, 1064.3)	174.3 (151.5, 199.2)	2.24 (1.96, 2.85)

Note: Values for E_0 and T_0 were obtained by exponentiating lnE_0 and lnT_0 estimates obtained from the model

unwarmed ones during winter and spring and no difference between treatments in summer and fall (Fig. 3; Tables 2, 3, 4). In warmed plots in winter and spring, the leftward shift of lines depicting the temperature-respiration relationship suggested higher temperature sensitivity during these periods (Fig. 3A, D, E, H). By contrast, the overlap of the temperature-respiration lines for warmed and unwarmed plots during summer and fall indicated no difference between treatments (Fig. 3B, C, F, G). Output from both the EXP and LT models also point to shifting temperature dependence seasonally and with warming, though these shifts were more clearly defined when depicted with EXP than with LT. For the season-specific, EXP fit, model slopes (k) differed with warming ($P = 0.0320$) and warming × season

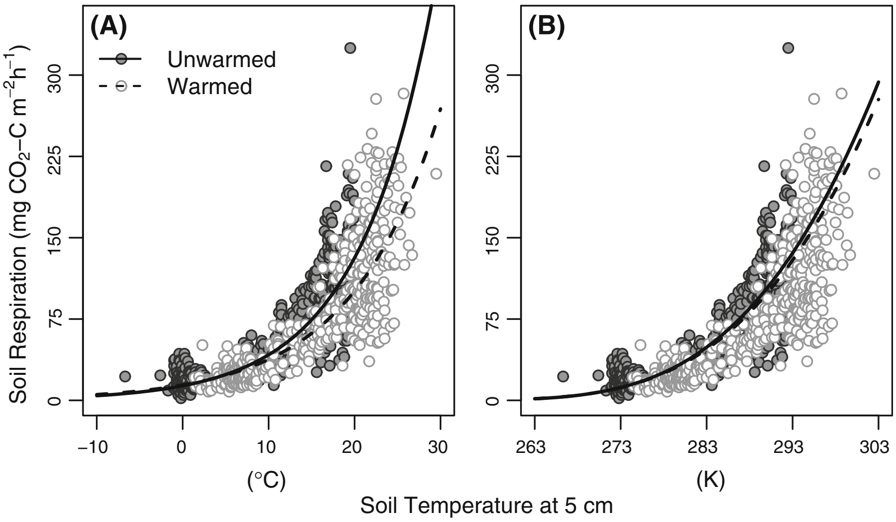

Fig. 2 Relationship between temperature and respiration in warmed and unwarmed soils over during the growing season for **A** exponential (EXP) and **B** flexible (LT) models. *Symbols* are as in Fig. 1

($P = 0.0069$). Pairwise comparisons of the 95 % CIs indicated that slopes were higher in winter and spring in warmed plots but did not vary between treatments during summer and fall. For the season-specific LT fit, E_0 varied significantly with warming ($P = 0.0257$) but only marginally with warming × season ($P = 0.0600$). Likewise, there was only a marginal change in T_0 in the warmed plots ($P = 0.0573$) but not in the warming × season interaction ($P = 0.3113$). Pairwise comparisons indicated that while E_0 was lower in warmed plots in winter, both the E_0 and T_0 model coefficients only marginally differed between treatments during spring and did not differ in summer and fall. Estimated mean Q_{10}s and 95 % CIs followed patterns in EXP and LT model output, with clearer changes in Q_{10} portrayed when calculated with the EXP function than with LT. For the EXP fit, Q_{10}s were higher during winter and spring for warmed plots as compared to unwarmed ones but were similar during summer and fall. When generated with LT model coefficients, mean Q_{10}s were higher for warmed plots in all four seasons, but overlap in 95 % CIs indicated no significant difference between treatments.

The six EXP and LT models fit in this study varied their ability to explain the data. There were some visual differences in the temperature sensitivity of soil respiration when modeled with EXP compared to LT parameters, with regression lines showing respiration as a function of temperature steeper when drawn from EXP coefficients than they were with LT (Figs. 1, 2). Estimated Q_{10}s from annual and growing season models supported this observation, with mean Q_{10}s generally higher when calculated with EXP than they were when determined with LT (Tables 2, 3). However, these differences between functions were not as apparent on a season-specific timescale, nor did estimated r^2 values and AICc statistics suggest much difference between the two model structures within a given timeframe. More striking were differences in model fits among annual, growing season, and season-specific time scales. Estimated r^2 values indicated that season-specific fits were able to explain 87 % of the variation in the data, as compared to 82 % in models fit over an annual timeframe and 77 % of the variation explained by the LT model that including growing season as a covariate. The multi-model comparison corroborated this finding, with both the season-specific EXP and LT fits showing substantially lower AICc values than the annual or growing season models.

The superior data-model fit obtained with season-specific models was also evident when coefficients were used to predict daily soil CO_2 efflux over the May 2007 through April 2009 study period. Figure 4 compares measured soil respiration rates to predictions made from model coefficients and a continuous record of daily soil temperatures. The most obvious discrepancy between measured and predicted values resulted from growing season, LT predictions of fluxes

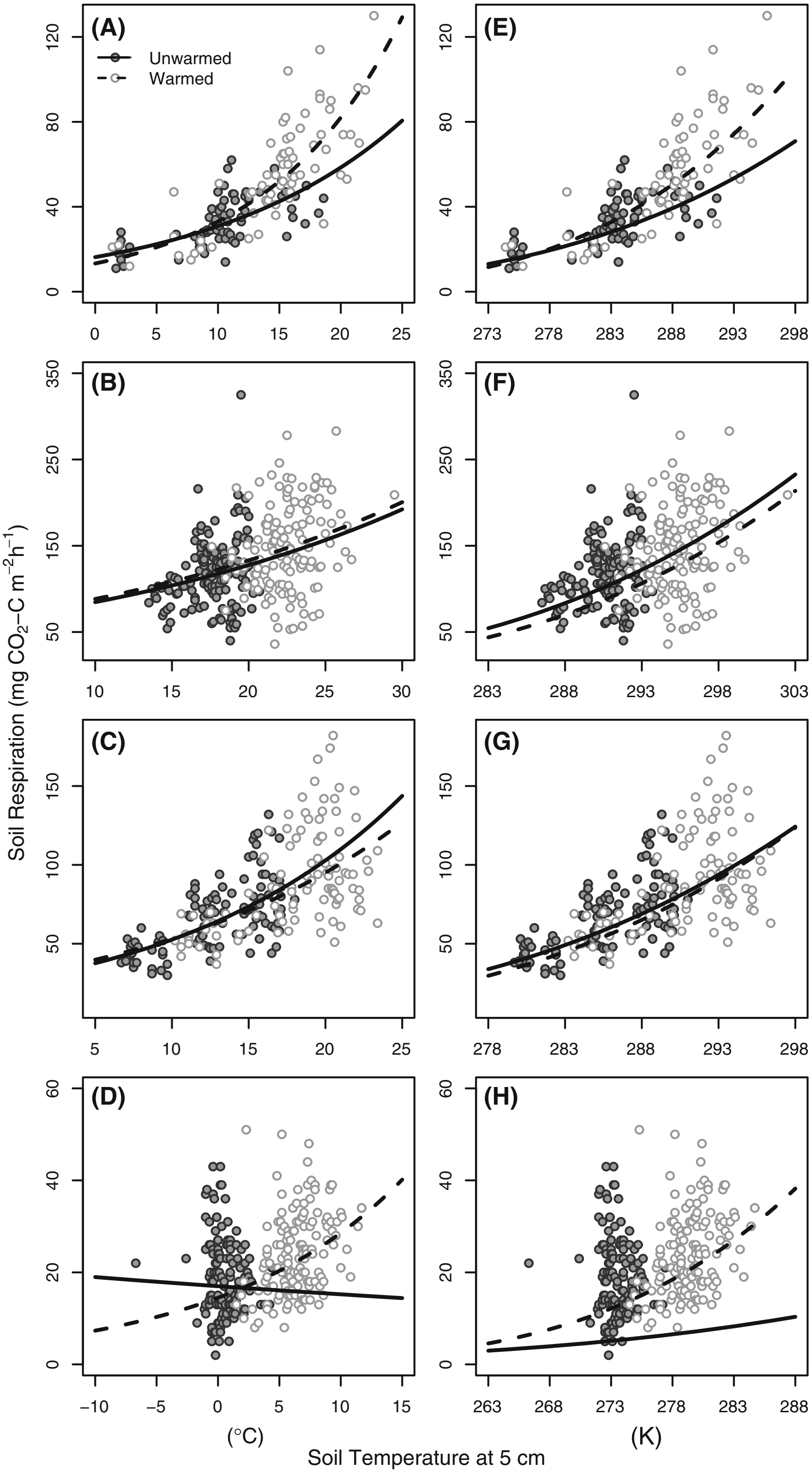

Fig. 3 Relationship between temperature and respiration in warmed and unwarmed soils over seasonal timescales for exponential (*EXP*) and flexible models (*LT*). **A** EXP spring, **B** EXP summer, **C** EXP fall, **D** EXP winter, **E** LT spring, **F** LT summer, **G** LT fall, and **H** LT winter. *Symbols* are as in Fig. 1

from warmed soils (Fig. 4B). In this case, predicted fluxes were an average 40 % higher than actual values over the duration of the study period. More subtle deviations between measured and modeled fluxes resulted from annual and growing season EXP and LT predictions during winter and spring. At these times of year, estimated fluxes from annual and growing season EXP and LT models were 20–60 % higher than actual values. By contrast, CO_2 fluxes predicted from season-specific models generally varied less than 2 % from actual measurements. The exceptions were in winter, when the season-specific EXP and LT models underestimated fluxes by ~30 %.

Discussion

Seasonal shifts in the temperature dependence of soil respiration with warming

We compared the temperature sensitivity of soil respiration in chronically warmed soils at annual, growing season, and season-specific timescales. Our results indicate that soil respiration can show characteristics of acclimatized, enhanced, or constant temperature dependence depending on the timeframe and the function (EXP or LT) used to fit the data.

While the EXP and LT functions depicted temperature sensitivity differently, both models showed an overall trend toward lower temperature dependence, or acclimatization, with 5 °C of warming when using a growing season instead of an annual timeframe. We hypothesized that enhanced temperature sensitivity in warmed plots during winter would counterbalance acclimatized temperature dependence in warmed soils during the growing season, resulting in constant temperature sensitivity over an annual timescale. This was partly true: warmed soils generally had enhanced temperature dependence in winter as compared to unwarmed ones. However, enhanced temperature sensitivity in warmed plots during winter probably did not compensate for the acclimatization observed during the growing season. Neither model coefficients nor Q_{10} values differed among annual, winter, and growing season timeframes within the warming treatment (Tables 3, 4), suggesting that including winter values in a temperature-respiration model would not alter the outcome for warmed soils. By contrast, the temperature-respiration relationship during winter in unheated plots was significantly weaker than it was during the growing season, suggesting that it played a more important role in shifting temperature dependence between treatments over annual and growing season time scales.

Lower temperature sensitivity in unwarmed winter soils may have resulted from the temperature range over which fluxes were measured. In the unwarmed plots, soil temperatures from the surface to 5 cm depth were relatively constant, and measured ~0 °C until late February–March of both years. At the same time, soil respiration rates were quite variable, ranging from 2 to 43 mg CO_2-C m^{-2} h^{-1}. In a report of continuous measurements of winter soil CO_2 flux from a temperate peatland, Bubier et al. (2002) also showed that the highest and most variable respiration rates occurred when temperatures hovered around 0 °C. The largest pulses of CO_2 were released as soon as soil temperatures climbed above freezing, leading Bubier et al. (2002) to infer a release of stored CO_2 or stimulated microbial activity during thaw events. Here, we lack the high frequency measurements of soil respiration, temperature, and moisture that would be necessary to develop a mechanistic understanding of controls on soil respiration at cold temperatures. However, our results illustrate the failure of temperature-respiration models to portray soil CO_2 flux in the cold conditions that predominated in the unwarmed plots. Because winter fluxes can amount to 14 % of the total annual amount in this system (Contosta et al. 2011), it is critical that we develop a better understanding of the dynamics that affect soil respiration at near-zero temperatures and how to model these dynamics.

The enhanced temperature sensitivity that the heated plots displayed in spring was also contrary to expectations, since we predicted that heated soils throughout the growing season would show symptoms of acclimatization to warmer temperatures. Overall, a strong relationship between temperature and respiration is to be expected in spring, when roots show higher temperature sensitivity than during other times of the year (Mo et al. 2005). In addition, lower labile C availability in spring (Bradford et al. 2008) may cause higher temperature dependence of microbial respiration at the same time as a greater volume of soil becomes active for both root and microbial activity (Rayment and Jarvis 2000). In warmed plots, higher apparent temperature dependence during spring could have resulted from all three of these mechanisms:

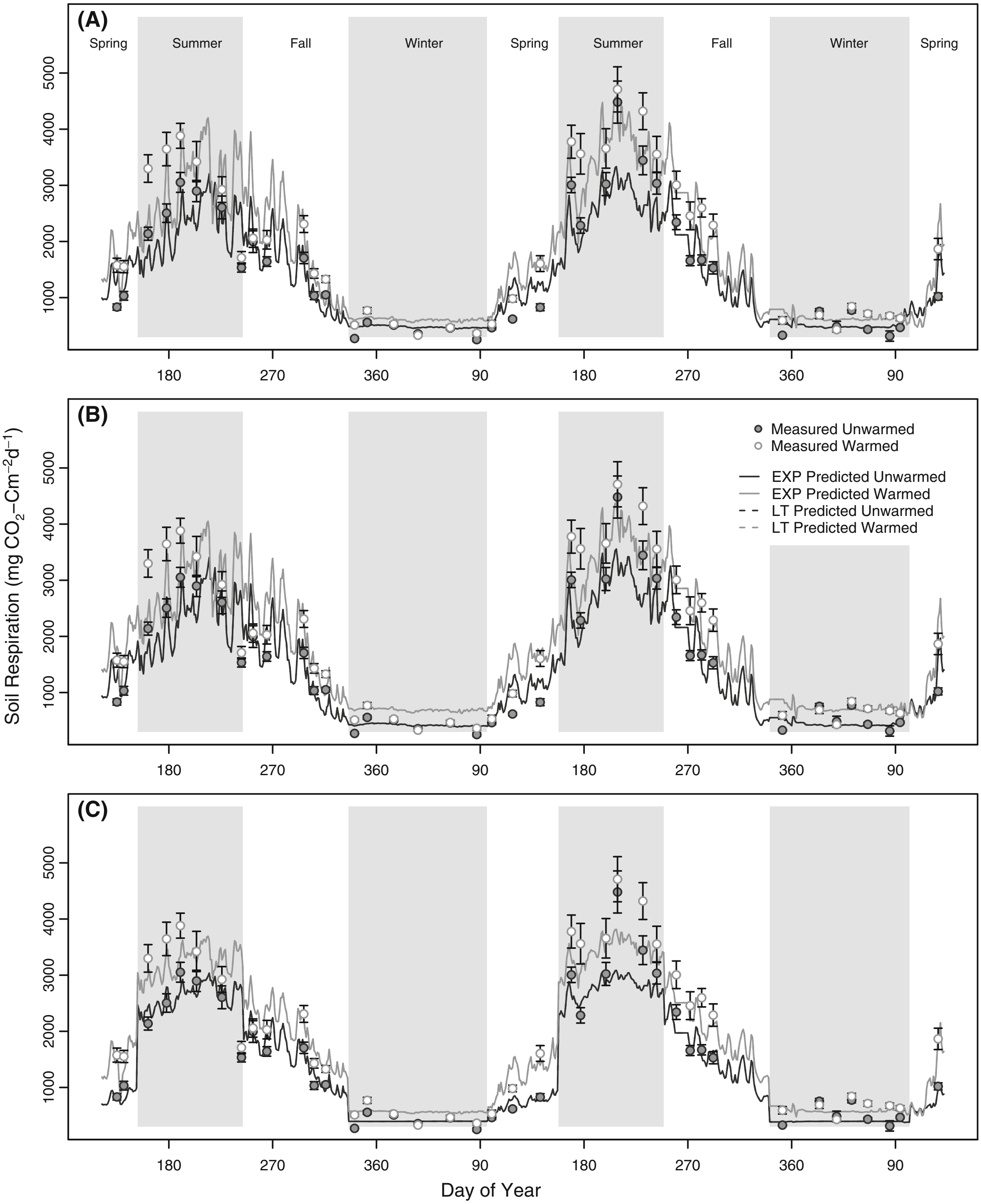

Fig. 4 Average predicted daily soil respiration rates in warmed and unwarmed soils from May 2007 to April 2009 estimated from **A** annual, **B** growing season, and **C** season specific model coefficients generated from exponential (EXP) and flexible (LT) models. The *solid circles* depict measured respiration rates from unwarmed plots, while the *open circles* indicate respiration from warmed plots. *Error bars* represent 95 % CIs. The solid lines show continuous predictions of CO_2 flux calculated from EXP model coefficients, and the *dashed lines* depict predictions from LT model parameters

earlier root growth and activity, earlier microbial activity, and/or deepening of the active layer responsible for soil respiration. However, declines in root biomass and mass specific root respiration reported for this and other soil warming experiments at the Harvard Forest (Burton et al. 2009; Zhou et al. 2011) suggest that accelerated root growth is not responsible. Reductions in microbial respiration and biomass in April at an adjacent soil warming experiment (Bradford et al. 2008) also suggest that enhanced microbial activity in heated soils during spring did not drive higher temperature dependence during this season. A deeper active layer in warmed plots during spring would increase the volume of soil available for respiration, possibly making CO_2 flux higher at a given temperature. Soil temperatures measured from the surface through 10 cm depths (data not shown) showed a much weaker gradient in the warming treatment during spring, suggesting that warmed soils had heated up more quickly than unwarmed ones. No matter what the cause, accelerated temperature dependence in warmed soils during spring is of concern given that springtime respiration already comprises ~15 % of the total annual amount (Contosta et al. 2011), and climate warming is expected to extend spring several weeks into what was historically the winter season (Hayhoe et al. 2007).

The nearly identical temperature-respiration relationship observed for warmed and unwarmed plots during summer and fall also did not agree with our hypothesis that warmed soils would acclimatize to higher temperatures during the growing season. Bradford et al. (2008) reported strong seasonal trends in thermal adaptation to soil temperature, with the lowest rates of microbial respiration (corrected for differences in microbial biomass) taking place in summer and fall following 2.5 months of warm soil temperatures. However, incubation studies such as Bradford et al. (2008) hold moisture constant in order to isolate the effects of changing microbial biomass and C substrates on soil respiration, and moisture conditions in situ may play a much stronger role in driving the apparent temperature dependence of CO_2 flux. Moisture was not explicitly included in our modeling because it rarely fell below the 0.12 $m^3\ m^{-3}$ empirical threshold where it becomes limiting to respiration (Davidson et al. 1998). However, the 7 % of the measurements that fell below this threshold all occurred in summer and fall and may have contributed to the low apparent temperature-respiration relationship in both treatments during these seasons.

Exponential versus flexible models of soil respiration and multi-model inference

One of the goals of this study was to compare the ability of exponential (EXP) and flexible (LT) functions to model the temperature sensitivity of soil respiration seasonally and with warming.

Despite some visual differences in the depiction of respiration as a function of temperature, there was little conclusive evidence that the LT model was preferable to EXP. Within each modeled timeframe, estimated r^2, residual standard errors, and AICc values were similar between the EXP and LT functions, suggesting that they were equally able to capture the temperature-respiration relationship. Other researchers have cited better performance of the LT model across a range of temperatures (e.g., Richardson and Hollinger 2005; Adair et al. 2008), but they did not report the spikes that we observed at ~0 °C in unwarmed winter soils. The wide range in soil respiration rates measured around 0 °C resulted in poor model fit for both the EXP and LT functions and may have downplayed any inherent differences between them.

More striking than differences between the EXP and LT function was the variation among timeframes in modeling the temperature-respiration relationship. Estimated RSE, r^2 values, and AICc rankings of the six models used to examine the temperature sensitivity of soil respiration showed that the season-specific LT and EXP fits explained more of the variation in the data than annual or growing season models. This finding fits with our own observations of changing model coefficients and Q_{10} values among seasons, as well as other reports that the temperature dependence of soil respiration changes seasonally and is not constant throughout the year (Curiel-Yuste et al. 2004; Mo et al. 2005).

Predictions of daily soil respiration rates reflected our ranking of EXP and LT models and carry important implications for depicting soil carbon cycling in a warmer world. Growing season models typically employed in soil warming studies to demonstrate acclimatization to higher temperatures and/or to estimate annual fluxes (e.g., Luo et al. 2001; Bronson et al. 2008; Mellilo et al. 2011) overestimated daily respiration rates by as much as 40 % over the entire study period. Annual models also over-predicted fluxes by ~10 % from May 2007 through April 2009. The largest periods of disagreement between measured and modeled fluxes occurred in winter and spring—seasons that together comprise ~25 % of the total annual flux in this system (Contosta et al. 2011). By contrast, season-specific models much more closely matched observed values, deviating by ~2 % for most of the study. Consistent with many of our other findings, both the season-specific EXP and LT models poorly predicted winter respiration rates, again highlighting the need to develop a better understanding of drivers of CO_2 flux in cold soils and how these drivers might respond to a changing climate.

Conclusion

The shifting temperature dependence we observed between treatments and across timescales suggest that a 5 °C increase of soil warming does not have a constant effect on soil respiration throughout the year. In winter, warming may keep soils above 0 °C, minimizing CO_2 pulses from freeze–thaw. In summer and fall, warming may introduce moisture limitations that mask differences in the temperature sensitivity of soil respiration. During spring, warming may increase the volume of soil available for root and microbial activity, thereby enhancing soil respiration. Here, we can only speculate that these mechanisms are responsible for the changing temperature dependence we observed in warming × season interactions. However, our results clearly indicate that soil respiration modeled on longer timescales, such as annually or during the growing season, will not portray these short-term influences on soil respiration that may become more prominent as the climate warms. Our multi-model comparison illustrates this point even more clearly: season-specific EXP and LT models showed a superior-data model fit, suggesting that temperature sensitivity is not constant throughout the year. Furthermore, these season-specific models were best able to predict daily soil respiration rates over our 2 year study period. The large uncertainty in predictions of winter respiration rates derived from annual, growing season, and season-specific model coefficients alike highlights the importance of understanding drivers of CO_2 flux in winter soils and how these might change in a warmer world.

Acknowledgments We thank the three anonymous reviewers whose feedback substantially improved this manuscript. This work was supported by the US National Science Foundation (DEB 0447967) and the Northeastern States Research Cooperative Northern Forest Scholars program.

References

Adair EC, Parton WJ, Del Grosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC (2008) Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Glob Change Biol 14:2636–2660

Adair EC, Hobbie SE, Hobbie RK (2010) Single-pool exponential decomposition models: potential pitfalls in their use in ecological studies. Ecology 91:1225–1236

Allison SD, Treseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Glob Change Biol 14:2898–2909

Boose E, Gould E, Hall E (2002) Shaler meteorological station data archive. http://harvardforest.fas.harvard.edu/data/p00/hf000/hf000.html

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11:1316–1327

Bronson DR, Gower ST, Tanner M, Linder S, van Herk I (2008) Response of soil surface CO_2 flux in a boreal forest to ecosystem warming. Glob Change Biol 14:856–867

Bubier J, Crill P, Mosedale A (2002) Net ecosystem CO_2 exchange measured by autochambers during the snow-covered season at a temperate peatland. Hydrol Process 16:3667–3682

Burnham KP, Anderson DR (2002) Model selection and multi-model inference, 2nd edn. Springer, New York

Burton AJ, Melillo JM, Frey SD (2009) Adjustement of forest ecosystem root respiration as temperature warms. J Integr Plant Biol 50:1467–1483

Conant RT, Ryan MG, Ågren GI et al (2011) Temperature and soil organic matter decomposition rates: synthesis of current knowledge and a way forward. Glob Change Biol. doi:10.1111/j.1365-2486.2011.02496.x

Contosta AR, Frey SD, Cooper AB (2011) Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. Ecosphere 2:1–21

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187

Curiel-Yuste J, Janssens IA, Carrara A, Ceulemans R (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Glob Change Biol 10:161–169

Davidson EA, Janssens IA (2006) Temperature sensitivity to soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Davidson EA, Belk E, Boone RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob Change Biol 4:217–227

Friedlingstein P, Cox P, Betts R et al (2006) Climate-carbon cycle feedback analysis: results from the C^4MIP model intercomparison. J Clim 19:3337–3353

Hayhoe K, Wake CP, Huntington TG, Luo L, Schwartz MD, Sheffield J, Wood E, Anderson B, Bradbury J, DeGaetano A, Troy TJ, Wolfe D (2007) Past and future changes in climate and hydrologic indicators in the US Northeast. Clim Dyn 28:381–407

Hess TF, Schmidt SK (1995) Improved procedure for obtaining statistically valid parameter estimates from soil respiration data. Soil Biol Biochem 27:1–7

Janssens IA, Pilegaard K (2003) Large seasonal changes in Q_{10} of soil respiration in a beech forest. Glob Change Biol 9:911–918

Jones CD, Cox P, Huntingford C (2003) Uncertainty in the climate-carbon-cycle projections associated with the sensitivity of soil respiration to temperature. Tellus 55B:642–648

Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of Glob. Warming on soil carbon storage. Soil Biol Biochem 27: 753–760

Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Glob Change Biol 10:1870–1877

Kirschbaum MUF (2006) The temperature dependence of organic matter decomposition—still a topic of debate. Soil Biol Biochem 38:2510–2518

Knorr W, Prentice IC, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. Funct Ecol 8:315–323

Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413:622–625

McHale PJ, Mitchell MJ, Bowles FP (1998) Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition. Can J For Res 28:1365–1372

Melillo JM, Steudler PA, Aber JD et al (2002) Soil warming and carbon-cycle feedbacks to the climate system. Science 298:2173–2175

Melillo JM, Steudler PA, Aber JD et al (2004) Soil warming: a major consequence of global climate change. In: Foster DR, Aber JD (eds) Forests in time: the environmental consequences of 1,000 years of change in New England. Yale University Press, New Haven, pp 280–295

Mellilo JM, Butler S, Johnson J et al (2011) Soil warming, carbon–nitrogen interactions and forest carbon budgets. PNAS 108:9508–9512

Mo W, Lee M-S, Uchida M, Inatomi M, Saigusa N, Mariko S, Koizumi H (2005) Seasonal and annual variations in soil respiration in a cool-temperate deciduous broad-leaved forest in Japan. Agric For Meteorol 134:81–94

Monson RK, Lipson DA, Burns SP, Turnipseed AA, Delany AC, Williams MA, Schmidt SK (2006) Winter forest soil respiration controlled by climate and microbial community composition. Nature 439:711–714

Munger JW, Barford C, Wofsy S (2004) Exchange between the forest and the atmosphere. In: Foster DR, Aber JD (eds) Forests in time: the environmental consequences of 1,000 years of change in New England. Yale University Press, New Haven, pp 202–230

Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal warming. Nature 406:978–981

Peek MA, Russeck-Cohen E, Wait DA, Forseth IN (2002) Physiological response curve analysis using nonlinear mixed models. Oecologia 132:175–180

Peterjohn WT, Melillo JM, Bowles FP, Steudler PA (1993) Soil warming and trace gas fluxes: experimental design and preliminary flux results. Oecologia 93:18–24

Peterjohn WT, Melillo JM, Steudler PA, Newkirk KM (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol Appl 4:617–625

Pinheiro J, Bates D, DebRoy S, Sarkar D, and the R Core team (2009) nlme: linear and nonlinear mixed effects models. R package version 2.9.2

Pinhiero J, Bates D (2000) Mixed effects models in S and S plus. Springer, New York

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relation to vegetation and climate. Tellus 44B:81–99

Rayment MB, Jarvis PG (2000) Temporal and spatial variation of soil CO_2 efflux in a Canadian boreal forest. Soil Biol Biochem 32:35–45

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org

Reth S, Graf W, Reichstein M, Munch JC (2009) Sustained stimulation of soil respiration after 10 years of warming. Environ Res Lett. doi:10.1088/1748-9326/4/2/024005/

Richardson AD, Hollinger DY (2005) Statistical modeling of ecosystem respiration using eddy covariance data: maximum likelihood parameter estimation, and Monte Carlo simulation of model and parameter uncertainty, applied to three simple models. Agric For Meteorol 131:191–208

Savage KE, Davidson EA (2001) Interannual variation in soil respiration in two New England Forests. Glob Biogeochem Cycles 15:337–350

Strömgren M (2001) Soil surface CO_2 flux and growth in a Norway spruce boreal stand: Effects of soil warming and nutrition. Dissertation. Swedish University of Agricultural Sciences, Uppsala

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Zhou Ym Tang J, Melillo JM, Butler S, Mohan JE (2011) Root standing crop and chemistry after six years of soil warming in a temperate forest. Tree Physiol 31:707–717