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On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}

ERIC A. DAVIDSON*, IVAN A. JANSSENS† and YIQI LUO‡

The Woods Hole Research Center, PO Box 296, Woods Hole, MA 02543, USA, †Department of Biology, University Instelling Antwerp, B-2610 Wilrijk, Belgium, ‡Department of Botany and Microbiology, University of Oklahoma, 770 Van Vleet Oval, Norman, OK 73019, USA

Abstract

Respiration, which is the second most important carbon flux in ecosystems following gross primary productivity, is typically represented in biogeochemical models by simple temperature dependence equations. These equations were established in the 19th century and have been modified very little since then. Recent applications of these equations to data on soil respiration have produced highly variable apparent temperature sensitivities. This paper searches for reasons for this variability, ranging from biochemical reactions to ecosystem-scale substrate supply. For a simple membrane-bound enzymatic system that follows Michaelis–Menten kinetics, the temperature sensitivities of maximum enzyme activity (V_{max}) and the half-saturation constant that reflects the affinity of the enzyme for the substrate (K_m) can cancel each other to produce no net temperature dependence of the enzyme. Alternatively, when diffusion of substrates covaries with temperature, then the combined temperature sensitivity can be higher than that of each individual process. We also present examples to show that soluble carbon substrate supply is likely to be important at scales ranging from transport across membranes, diffusion through soil water films, allocation to aboveground and belowground plant tissues, phenological patterns of carbon allocation and growth, and intersite differences in productivity. Robust models of soil respiration will require that the direct effects of substrate supply, temperature, and desiccation stress be separated from the indirect effects of temperature and soil water content on substrate diffusion and availability. We speculate that apparent Q_{10} values of respiration that are significantly above about 2.5 probably indicate that some unidentified process of substrate supply is confounded with observed temperature variation.

Keywords: Arrhenius function, carbon cycle, CO_2, decomposition, plant respiration, soil carbon, soil respiration

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Introduction

Respiration of terrestrial ecosystems is a major flux in the global carbon cycle and a potentially important mechanism of positive feedback to climate change (Houghton *et al*., 1998; Cox *et al*., 2000; Prentice *et al*., 2001). The temperature dependence of biochemical processes such as respiration has been described mathematically since the late 19th century (Arrhenius, 1889; van 't Hoff, 1898), but a mechanistic understanding of how temperature and other environmental factors affect ecosystem respiration is still lacking. While tremendous advances were made in the 20th century for characterizing the interacting effects of temperature, light, nutrients, and water in conceptual and numerical models of photosynthesis (Farquhar *et al*., 1980), respiration in ecosystems is typically still represented in biogeochemical models by temperature-dependent equations, which have been modified very little from their 19th century origins. Models that are specific to autotrophic respiration at an organismal scale are more advanced, addressing mechanistic relationships among growth, maintenance and wastage (futile) respiration, and the synthesis and translocation of metabolites within plants (Amthor, 2000). Heterotrophic respiration is usually a

Correspondence: Eric A. Davidson, tel. + 1 508 540 9900, email: edavidson@whrc.org

significant fraction of total ecosystem respiration, although measurements of soil respiration and ecosystem respiration cannot clearly distinguish between autotrophic and heterotrophic sources (Hanson *et al*., 2000). Hence, characterization of heterotrophic respiration and its interaction with photosynthesis and autotrophic respiration within an ecosystem context lags behind advances in plant physiology. This entanglement of processes explains why most models of respiration still rely on empirical regressions and have rarely progressed into mechanistic models.

The list of identified problems associated with empirical respiration models is growing. For example, we know that the Arrhenius and van 't Hoff assumption of constant temperature sensitivities of respiratory enzymes at all temperatures is incorrect (Lloyd & Taylor, 1994; Kirschbaum, 2000; Atkin & Tjoelker, 2003). We also know that variation in soil water content affects the diffusion of soluble substrates at low water content and the diffusion of oxygen at high water content, both of which can limit soil microbial respiration (Linn & Doran, 1984; Skopp *et al*., 1990). Furthermore, seasonal variation in soil water content is often confounded with the effects of temperature on soil respiration (Wildung *et al*., 1975; Davidson *et al*., 1998). Rapid changes in substrate availability that accompany wetting of dry soil (Birch, 1958; Bottner, 1985; Kieft *et al*., 1987), girdling of trees (Högberg *et al*., 2001), and shading and clipping of grasses (Craine *et al*., 1999; Wan & Luo, 2003) also clearly affect soil respiration independently of temperature.

Despite our growing appreciation of the inadequacies of empirically derived temperature functions for describing respiration, most attempts to improve models of soil respiration have also used empirical approaches to reveal the influence of precipitation or soil moisture as an additional predictive variable (Schlentner & Van Cleve, 1985; Hanson *et al*., 1993, 2003; Raich & Potter, 1995; Davidson *et al*., 2000b; Reichstein *et al*., 2003). Attempts have been made to find scalars of soil water content that might function consistently across soil types, such as water-filled pore space, soil matric potential, and water content normalized to field capacity, but the utility of most of these empirical functions remains site-specific (but see Reichstein *et al*., 2003, for a recent advance).

The most important impediment to improving such temperature-moisture empirical models of respiration is that they do not address the underlying physiological processes that temperature and soil water content affect. Just as major advances in the modeling of photosynthesis required mathematical characterizations of how variation in climate and resource availability affects the diffusion of substrates, the harvesting of light, and the maximum enzymatic capacity of photosynthesis, we need to investigate *how* temperature, soil water content, and other climatic and resource variables affect the respiration of aboveground and belowground plant tissues as well as soil microorganisms. Unlike photosynthesis, however, which has evolved conservatively with only a few enzymatic processes across taxa, the vast array of respiratory enzymatic systems across taxa and tissue types renders this task far more challenging for respiration.

The time is ripe for increased research attention to ecosystem respiration and its components. A growing network of eddy covariance studies has demonstrated that intersite and interannual variation in respiration greatly influences variation in net ecosystem productivity and annual terrestrial carbon sequestration (Valentini *et al*., 2000; Barford *et al*., 2001; Janssens *et al*., 2001; Savage & Davidson, 2001; Hui *et al*., 2003; Saleska *et al*., 2003; Hibbard *et al*., 2005). In addition to this seasonal and interannual variability, we also need an improved understanding of the vulnerability of important terrestrial carbon pools to loss or gain over decadal time scales. In particular, we need to address questions regarding the temperature sensitivity of soil carbon pools with decadal turnover times (Giardina & Ryan, 2000; Davidson *et al*., 2000a; Fang *et al*., 2005; Knorr *et al*., 2005), the effects of permafrost melting and altered hydrologic budgets on organic matter decomposition at high latitudes (Goulden *et al*., 1998), and the accumulation and decay rates of coarse woody debris (Saleska *et al*., 2003).

In this paper, we first offer heuristic explanations for why apparent temperature sensitivities of respiration are so highly variable. We then distinguish between the primary effects of temperature and soil water content and their secondary effects due to interactions with substrate availability. We do not consider some extreme or unusual anthropogenic environments, where extremely acid or alkaline conditions or an accumulation of toxins might restrict decomposition of available substrates. A numerical or mathematical model with local or global parameterizations is beyond the scope of this paper. Rather, our objective is to discuss the mechanistic basis upon which such models might be developed.

Why are reported temperature sensitivities of respiration so variable?

Expressions of temperature sensitivities

Numerous equations have been developed to express the temperature sensitivity of respiration (see Kirschbaum, 2000; Janssens *et al*., 2003, for a description of several of these). The most common expressions are the

following:

$$\text{van 't Hoff}: \text{Resp} = \alpha e^{\beta T} \quad (\text{where } Q_{10} = e^{\beta \times 10}), \quad (1)$$

modified van 't Hoff:

$$\text{Resp} = R_{\text{basal}} \times Q_{10}{}^{((T-T_{\text{basal}})/10)} \quad \text{where } Q_{10} = [\text{Resp}_{T_2}/\text{Resp}_{T_1}]^{[10/(T_2-T_1)]}, \quad (2)$$

$$\text{Arrhenius}: \text{Resp} = \alpha e^{-E_a/RT}, \quad (3)$$

$$\text{Lloyd and Taylor}: \text{Resp} = \alpha e^{-E_0/(T-T_0)}, \quad (4)$$

where Resp is respiration, α, β, E_a, E_0, and T_0 are fitted parameters, T, T_1, T_2, and T_{basal} are measured temperatures (in degrees Kelvin for the Arrhenius function), R is the universal gas constant, and Q_{10} is the factor by which respiration is multiplied when temperature increases by 10°. In the following examples, we will only use Q_{10} to express the temperature sensitivity for ranges of 0–10, 10–20, and 20–30 °C, but the results are also valid for other mathematical models.

Canceling effects of V_{max} and K_m temperature sensitivities

In the first example, we consider a single, membrane-bound, plant respiratory enzyme that follows simple Michaelis–Menten (MM) kinetics:

$$R = \frac{V_{\text{max}} \times C}{K_{\text{m}} + C}, \quad (5)$$

where V_{max} is the maximum rate of enzyme activity at a given temperature, K_{m} is the half-saturation constant that reflects the affinity of the enzyme for the substrate at a given temperature, and C is the concentration of the substrate at the active site of the enzyme (Michaelis & Menten, 1913). Both V_{max} and K_{m} are temperature dependent, which can result in the canceling of their respective temperature sensitivities (Berry & Raison, 1981; Atkin & Tjoelker, 2003). As V_{max} increases with increasing temperature, the reaction rate can potentially increase, but as K_{m} also increases with increasing temperature, the affinity for the substrate decreases, so the reaction is slowed. However, K_{m} is an important factor only when the substrate concentration (C) is in the range of the K_{m} value ($C \approx K_{\text{m}}$). When $C \gg K_{\text{m}}$, then K_{m} and its temperature sensitivity become insignificant factors, and the response of respiration to temperature reflects primarily the Q_{10} of V_{max}.

These combinations of responses are demonstrated in Fig. 1a, where the MM equation could be expressed using simple Q_{10} functions:

$$R = \frac{V_{\text{max}} \times Q_{10(V_{\text{max}})}^{(T-T_{\text{ref}})/10} \times C}{\left[K_{\text{m}} \times Q_{10(K_{\text{m}})}^{(T-T_{\text{ref}})/10}\right] + C}, \quad (6)$$

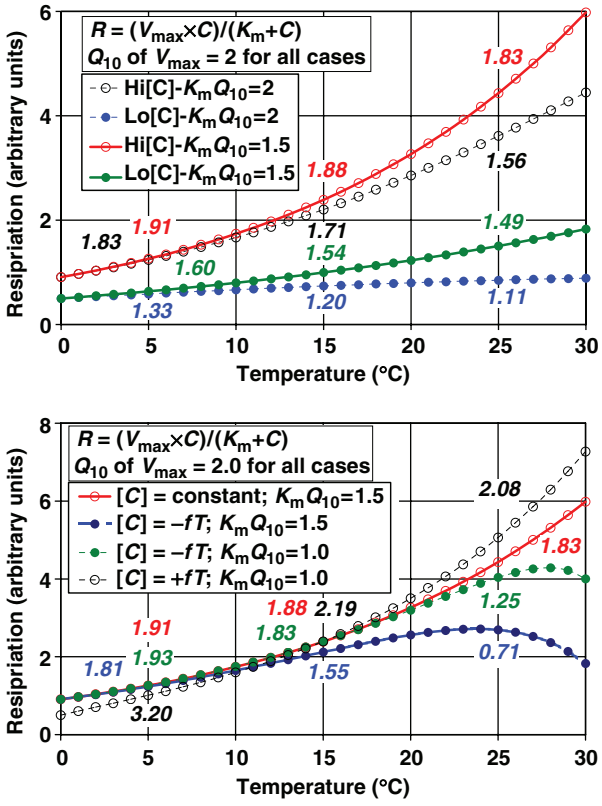

Fig. 1 (a) Upper panel: Heuristic example of a respiratory enzyme that follows Michaelis–Menten kinetics. The temperature sensitivity (Q_{10}) of the maximum enzymatic activity (V_{max}) was assigned a value of 2 in all four scenarios, ranging from a V_{max} of 1 at 0 °C to 8 at 30 °C. All values are in arbitrary units. For the half saturation constant (K_{m}), which is inversely related to the affinity of the enzyme for the substrate, the Q_{10} was assigned a value of 2 (broken black and broken blue lines; K_{m} ranging from 1 to 8) or the Q_{10} was assigned a value of 1.5 (solid red and solid green lines; K_{m} ranging from 1 to 3.4). The concentration of the substrate (C) at the reactive site of the enzyme was assigned either a low value (1; broken blue and solid green lines) or a high value (10; solid red and broken black lines). Above each line, the net temperature sensitivities of the modeled reaction rate is expressed as a Q_{10} for the ranges of 0–10, 10–20, and 20–30 °C. Note that the highest temperature sensitivities occur whenever $C \gg K_{\text{m}}$. (b) Lower panel: Same as upper panel, except that the Q_{10} for K_{m} was either 1.5 (solid red and solid blue lines) or 1.0 (not sensitive to temperature; broken black and broken green lines), and that C was also allowed to vary as a function of temperature, ranging linearly between 0 and 30 °C from 1 to 10 (positive function; broken black line) or from 10 to 1 (negative function; solid blue and broken green lines). All values are in arbitrary units. At the higher end of the temperature range, temperature sensitivity declines and reverses when substrate availability is inversely related to temperature. Conversely, when substrate is positively correlated with temperature, the apparent temperature sensitivity exceeds that of the V_{max} Q_{10} of 2.

where V_{max} and K_m are the values at some reference temperature T_{ref}. When V_{max} and K_m are assigned the same Q_{10} value of 2 and when C is low, then the net effect is almost no temperature sensitivity of the reaction, because the temperature sensitivities of V_{max} and K_m almost completely cancel throughout the temperature range (broken blue line in Fig. 1a). However, when $C \gg K_m$, then the temperature sensitivity of the reaction is very close to the assigned Q_{10} value of 2 for V_{max} (broken black line). A small decrease in the Q_{10} at higher temperature results from the K_m not being entirely insignificant in this example. When the Q_{10}'s for V_{max} and K_m are different (2.0 and 1.5, respectively), then there is some temperature sensitivity regardless of the substrate concentration (solid red and green lines in Fig. 1a). The temperature sensitivity of the reaction is greatest when substrate is least limiting ($C \gg K_m$ and Q_{10} of K_m is low; solid red line in Fig. 1a). The examples in Fig. 1a demonstrate that even a single enzyme can have multiple apparent temperature sensitivities, depending upon the individual temperature sensitivities of maximum enzymatic potential and substrate affinity and also depending upon the substrate concentration.

Effects of temperature and water content on substrate diffusion

In the examples in Fig. 1a, we assumed that the substrate concentration (C) was constant throughout the temperature range for each scenario. However, it is also possible, and, indeed, likely, that substrate concentrations also covary with temperature. Diffusion of both gases and solutes increases with increasing temperature. On the other hand, soils often also become drier as they become warmer, causing a decrease in the rate of diffusion of soluble substrates as soil water films become thinner. The diffusion of extracellular enzymes produced by microbes for breaking down organic matter and the diffusion of soluble C substrates that can be assimilated by microbial cells must occur within the liquid phase of the soil. Hence, microbial respiration can be limited by access to carbon substrates because of low water content and the resulting decrease in diffusion of carbon substrates, extracellular enzymes, and microbial mobility (Grant & Rochette, 1994). A common, simple expression for the effect of soil water content on diffusion of soluble substrates to the surface of a soil bacterial cell was given by Papendick & Campbell (1981):

$$J = \frac{(c_o - c_b) D_o k \theta^3}{s}, \qquad (7)$$

where J is flux, c_o is the solute concentration at a cell surface, c_b is the solute concentration in bulk soil, D_o is diffusivity, k is a constant, θ is the volumetric water content, and s is the diameter of a bacterial cell. Note that the flux is proportional to the volumetric water content raised to the third power, indicating a very strong sensitivity to dry soil conditions.

It is well known that soil water content and soil temperature are inversely correlated in many ecosystems with Mediterranean climates and in desert ecosystems (Wildung *et al*., 1975; Xu & Qi, 2001; Rey *et al*., 2002). Even temperate forests in relatively mesic climates experience decreases in soil water content when summertime evapotranspiration exceeds precipitation, sometimes resulting in severe summer drought (Davidson *et al*., 1998; Epron *et al*., 1999a; Savage & Davidson, 2001; Curiel Yuste *et al*., 2003; Hanson *et al*., 2003). The lower temperature sensitivities of soil respiration (Rey *et al*., 2002; Janssens & Pilegaard, 2003; Curiel Yuste *et al*., 2004) and total ecosystem respiration (Reichstein *et al*., 2002) observed during dry periods may largely be a result of substrate limitation caused by limited diffusion of solutes in thin soil water films.

This interaction of temperature sensitivity with substrate variability is demonstrated in the examples shown in Fig. 1b. The solid red line is the same in Fig. 1a and b. In the other examples of Fig. 1b, substrate availability is allowed to vary as a simple linear function of temperature. When substrate availability decreases because of decreasing rates of solute diffusion as soils become warmer and drier, substrate becomes strongly limiting at high temperatures. Indeed, the response of respiration to temperature can even become negative as substrate limitation becomes increasingly important ($Q_{10} < 1$ at $T > 20\,^{\circ}C$; broken green and solid blue lines in Fig. 1b).

Conversely, substrate availability could also increase with temperature, such as when the associated decrease in soil moisture has a larger effect on redox conditions than on solute diffusion. In wetlands, for example, oxygen rather than organic solutes may be the limiting substrate for aerobic respiration. Summer drought may not dry out the wetland enough to limit significantly the diffusion of soluble substrates, but some drying may favor diffusion of oxygen into the organic layer, thus increasing aerobic respiration. This example is illustrated by the broken black line in Fig. 1b, where the resulting apparent Q_{10} for respiration exceeds the preassigned value of 2 for V_{max}.

The examples in Fig. 1b are not meant as viable mathematical models of the effects of temperature on diffusion of respiratory substrates. Rather, they are presented to illustrate how these processes are likely to be important and that their effects can be both positive and negative. More realistic models of diffusion of gases and solutes and other factors that affect their availability (e.g. consumption rates and other

competing reactions) may need to be incorporated into models of respiration.

Models based only on temperature are likely to reveal widely ranging temperature sensitivities, depending on the relative importance of the processes affecting substrate availability that are demonstrated in Fig. 1. Hence, one explanation for variable Q_{10}'s across the temperature spectrum is that substrate availability can become limiting at high temperatures, either through the temperature sensitivity of the enzyme's K_m (Fig. 1a) or through the effect of temperature and water content on substrate supply (Fig. 1b). These interactions tend to result in higher combined temperature sensitivities at the low end of the temperature spectrum for biological activity (0–10 °C in Fig. 1).

Effects of temperature on substrate supply and tissue growth

In addition to temperature sensitivities of enzymatic affinity for substrate and diffusion of substrate to the enzyme, supply of substrate via active translocation can also covary with temperature and seasonality. Curiel Yuste *et al*. (2004) argued that higher apparent Q_{10} values for soil respiration measured across seasons in a Belgian deciduous hardwood forest compared with an adjacent evergreen conifer forest (both without significant understory vegetation) reflected greater seasonality of belowground *C* allocation in the hardwood stand. When Q_{10}'s were calculated for only 2-month intervals, the hardwood and conifer stands had nearly identical temperature sensitivities, indicating similar responses to diel and synoptic scale variation of temperature. Only when winter, spring, and summer observations were combined, did the hardwood stand appear to have higher temperature sensitivity for soil respiration. The authors argued that this seasonal Q_{10} reflects the greater seasonality of photosynthesis and subsequent supply of substrate belowground in the deciduous hardwood stand compared with the evergreen conifer stand. The larger seasonality, and, hence, the higher seasonal Q_{10} observed in the hardwood forest can be explained partly by phenological responses to seasons rather than higher temperature sensitivity of respiration, *per se*.

Seasonal variation in *C* allocation can affect both maintenance respiration and growth of roots, mycorrhizae, and rhizosphere microorganisms. If a pulse of root growth occurs in the spring, then the amount of respiring tissue increases at the same time as specific root respiration (i.e. CO_2 production per gram of tissue or per unit of enzyme capacity) also increases in response to temperature. In this case, the apparent Q_{10} of soil respiration may be the sum or the product of these two responses to increasing temperature. Hanson *et al*. (2003) reported a Q_{10} of 2.5 for soil respiration in an oak forest in Tennessee, USA, when dates associated with root growth observed in minirhizotrons were excluded. These authors noted that apparent temperature sensitivities would be inflated if data from springtime root growing periods were included.

Similarly, in trenched plots without roots and control plots with roots in temperate forests, Boone *et al*. (1998) reported Q_{10}'s of 2.5 and 3.5, respectively, and Epron *et al*. (1999b) reported 2.3 and 3.9, respectively. Boone *et al*. (1998) calculated a Q_{10} of 4.6 for the root respiration inferred from the difference between the control and trenched plots. However, as Boone *et al*. (1998) point out, this root respiration Q_{10} includes the effects of both seasonal changes in root biomass (i.e. root growth) and direct responses of existing root biomass to changing temperature. Total root respiration may therefore be more responsive to temperature than microbial respiration, but this is not necessarily the case for specific root respiration. Bååth & Wallander (2003) grew pine seedling roots, mycorrhizae, and soil microorganisms in separate experimental compartments of growth chambers that were exposed to the same varying temperature regimes over time periods sufficiently short to preclude significant tissue growth. The results demonstrated that all organisms exhibited similar temperature sensitivities of respiration, with Q_{10}'s of about 2.3. Thus, in addition to understanding the temperature and moisture responses of the enzymes, it is also important to understand the temporal changes in the abundance of reactive enzymes and tissues.

Root growth is not always a spring phenomenon, however, as it commonly occurs with the onset of autumn rains in Mediterranean climates (Rey *et al*., 2002). This creates an interesting possible combination of increasing root biomass as temperatures decline.

When Q_{10} values vary temporally or across sites, these data are likely to be indicative that some factor other than temperature is also varying, thus causing the inflated or suppressed apparent Q_{10}. Seasonal hysteresis of Q_{10}'s for total ecosystem respiration and soil respiration at the Howland forest of Maine, USA, provides an example. Soil respiration always exhibited a higher Q_{10} in the spring than in the autumn (Table 1), perhaps because of springtime root growth, as discussed above. Soils warm from the top downward in the spring, and they cool from the top downward in the autumn, so hysteresis based on temperature measured at a fixed depth could be influenced by varying soil depths of CO_2 production. Springtime Q_{10} of soil respiration was always higher than springtime Q_{10} of total ecosystem respiration, but the reverse was observed in the autumn (Table 1). These seasonal differences in apparent temperature sensitivities of soil

Table 1 Hysteresis of Q_{10} values (respiration at 15 °C/respiration at 5 °C) for soil respiration and total ecosystem respiration at the Howland Forest, Maine, USA

Pairwise comparison	1997	1998	1999	2000	2001	2002	All years
Spring							
Ecosystem R	2.8	2.7	3.2	3.9	3.5	2.9	3.1
Soil R	4.5	3.0	3.3	5.0	3.9	3.2	3.5
Fall							
Ecosystem R	4.1	3.5	3.2	4.1	3.1	3.1	3.4
Soil R	2.8	2.6	3.2	3.0	2.3	1.9	2.5
Soil R							
Spring	4.5	3.0	3.3	5.0	3.9	3.2	3.5
Fall	2.8	2.6	3.2	3.0	2.3	1.9	2.5

Soil respiration Q_{10}'s were derived from data in Savage & Davidson (2001) and Davidson *et al*. (2005). Total ecosystem respiration Q_{10}'s were derived from nighttime eddy covariance measurements reported by Hollinger *et al*. (1999, 2004). Pairwise *t*-tests for each comparison across years indicate that the differences are statistically significant at $P < 0.05$.

respiration and total ecosystem respiration could result from different patterns of changing air and soil temperature, different phenologies of aboveground and belowground process, and different temperature sensitivities of these processes.

Unlike the pine forests of the more moderate temperate climate of Belgium (Curiel Yuste *et al*., 2004), the spruce forest of Maine (Hollinger *et al*., 1999, 2004) appears to be highly seasonal, and this phenology is reflected in its relatively high seasonal Q_{10} values (Table 1). This difference in seasonality may help explain why ecosystems with low mean annual temperature but a large annual amplitude of temperature often have a higher interseasonal Q_{10} of soil respiration than do warmer ecosystems with lower annual amplitudes of temperature variation (Schleser, 1982; Kirschbaum, 1995).

Mathematical interdependence of temperature sensitivity and basal respiration

For all the temperature response functions, the parameter for temperature sensitivity (Q_{10}, β, E_a or E_0 in Eqns (1)–(4)) is frequently dependent on the basal respiration rate (i.e. the respiration rate at an arbitrarily defined temperature such as 10 °C; R_{basal} or α in Eqns (1)–(4)). Our third heuristic example demonstrates why this interdependence of basal respiration rate and temperature sensitivity makes intercomparisons of Q_{10}'s from different sites difficult. The seasonal soil respiratory patterns are plotted for adjacent stands of oak with evergreen rhododendron understory and pine with grass understory, which experience similar seasonal changes in temperature and precipitation (Curiel Yuste *et al*., 2004). The oak/rhododendron site had a 50% larger seasonal change in leaf area, generally higher soil respiration rates, and a 60% larger seasonal amplitude in soil respiration compared with the pine/grass site (Fig. 2a). Given the similar seasonal amplitudes in temperature in both sites, one might intuitively conclude that the larger seasonal amplitude in soil respiration at the oak/rhododendron site would translate into a higher Q_{10} value. This is not the case (Fig. 2b), however, because the Q_{10} (or any of the other parameters of temperature sensitivity) acts as a multiplier of the basal respiration rate (R_{basal} in Eqn (2); R_{10} in Fig. 2b) and is thus not independent of the basal rate of respiration. The higher R_{10} at the oak/rhododendron site results in a smaller Q_{10} ratio than might be expected based on casual inspection of the relatively large seasonal amplitude. Therefore, comparing Q_{10} values among sites can be misleading unless differences in basal respiration rates are also considered.

Climate change could affect either basal respiration or temperature sensitivity or both. If one of the effects of longer growing seasons because of climatic change is to increase GPP and, hence, substrate supply for respiration, then the basal rate of respiration could increase at the same time that temperature increases. Furthermore, if the relative stimulation of wintertime fluxes exceeds that of summertime fluxes, then the increase in basal respiration would be accompanied by a decrease in interseasonal Q_{10}. Models that use fixed Q_{10} and/or fixed basal respiration rates to simulate change in respiration are unlikely to accurately simulate these responses.

Primary effects of temperature, water content, and substrate supply on respiration

Temperature

Low temperatures can limit the capacity of both soluble and membrane-bound enzymes, although the transition from a gel-like state to a fluid state in plant membranes may be particularly important (Atkin & Tjoelker, 2003).

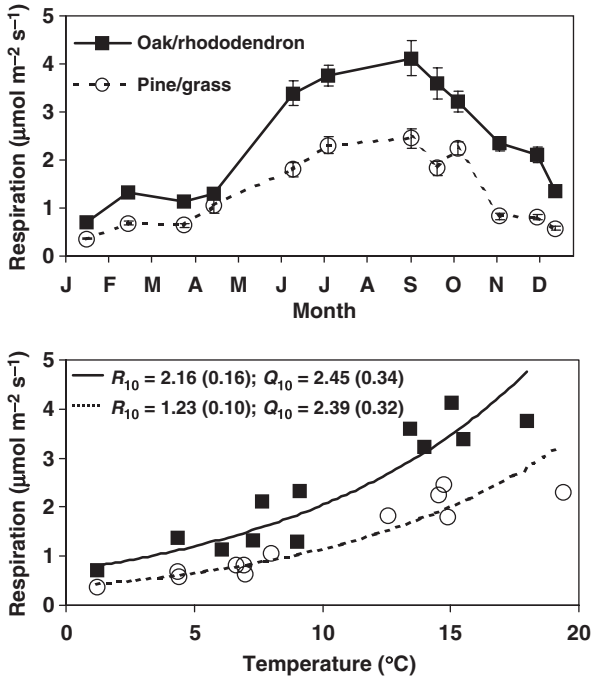

Fig. 2 Example of the dependence of Q_{10} values on basal soil respiration rates in two adjacent forest sites: one pine-dominated with grass understory and one oak-dominated with rhododendron understory (Curiel Yuste *et al.*, 2004). Both sites experience a similar temperature regime. Upper panel: Soil respiration (means plotted with standard errors for each date) in the oak/rhododendron stand has a larger seasonal amplitude (3.4 μ mol $m^{-2} s^{-1}$) than does the pine/grass stand (2.1 μmol $m^{-2} s^{-1}$). Lower panel: Soil respiration from upper panel expressed as a Q_{10} temperature function of a basal respiration rate (R_{10}) at 10 °C: Respiration = R_{10} * Q_{10} $^{[T/10]}$; (95% confidence intervals of fitted parameters in parentheses). The R^2 for both regression equations is 0.84 and the regressions are significant at $P < 0.0001$. Because the oak/rhododendron site has a higher basal respiration rate (R_{10}), its Q_{10} value is nearly the same as the Q_{10} for the pine/grass site, despite a larger seasonal amplitude.

As already discussed in our first heuristic example, temperature can also affect the affinity of the enzyme for the substrate. Concentration gradients across membranes are also affected by intracellular supply and demand of substrates and adenylates and by membrane properties, which can be temperature dependent (Atkin & Tjoelker, 2003). Much less is known about cellular regulation of respiration by soil microorganisms. From an ecosystem perspective, we consider these cellular and organismal biochemical controls on respiration to be the principal primary effects of temperature on respiration.

Water content

Although the water content of soil and plant tissue has numerous physiological and physical effects, the principal primary effect is desiccation stress. Loss of tissue turgor, stomatal closure, and leaf shedding in plants (Aber & Melillo, 1991), and dormancy or spore formation in soil microorganisms (Harris, 1981) are adaptations to low water potential in plant and microbial tissues that can result in substantial reductions in respiration per unit biomass or reductions in total respiratory biomass.

Substrate availability

Substrate availability has received the least attention as a controller of respiration in ecosystems, probably because it is so difficult to measure compared with temperature and water content. Intercellular and intracellular concentrations of sugars, starches, and other carbohydrates can also be extremely dynamic. In the case of soils and soil microorganisms, substrates that might be measured range from simple sugars to complex humic acids and lignins. Only relatively simple and small compounds, such as sugars and amino acids, pass readily through cell membranes, so many of the organic matter substrates in soils must first be degraded by microbial extracellular enzymes.

Despite this complexity, it is becoming increasingly apparent that temporal and spatial variation in substrate availability may explain a large fraction of observed variation in respiration. A tree girdling experiment demonstrated a rapid decline in soil respiration because of an abrupt decrease in belowground allocation of carbon (Högberg *et al.*, 2001), indicating that respiration of roots and perhaps mycorrhizae and rhizosphere microorganisms utilizing substrates translocated or exuded from roots was strongly substrate-limited. Clipping and shading experiments in grasslands have also demonstrated rapid changes in soil respiration in response to experimental manipulation of photosynthesis (Craine *et al.*, 1999; Wan & Luo, 2003), which also indicates a direct and dynamic link between allocation of carbon substrates and soil respiration.

At coarse spatial and temporal scales, it may be possible to find more easily measured surrogates for variation of substrate production and subsequent availability for respiration. Reichstein *et al.* (2003) found that using leaf-area index (LAI) as a surrogate for site productivity across a range of temperate forests could help explain differences in annual respiration: the larger the site LAI, the more substrates are presumably produced for respiration. The temporal pattern of respiration was modeled as functions of temperature and soil water content, while the intersite differences in respiration rates at reference temperatures and water contents were attributed primarily to photosynthetic capacity as indicated by LAI. Climate variables alone cannot

always predict site productivity because productivity is also affected by nutrient availability and site history.

That availability of substrate can affect soil respiration independently of temperature and water content was demonstrated by a mesocosm experiment of a model grassland ecosystem (Verburg *et al*., 2004). The study covered two cropping cycles of cheat grass (*Bromus tectorum* L.), with constant day and nighttime temperatures, (28 and 22 °C, respectively) and relatively constant soil water content. Measured soil respiration rates increased from near zero without plants, to 4 μmol $m^{-2} s^{-1}$ in 1999 with crop development, and to 7 μmol $m^{-2} s^{-1}$ in 2000 with crop development fertilized by N. These results demonstrate that significant seasonal variation in root respiration and in microbial respiration supported by recent rhizodeposition can result from changes in only substrate supply, while temperature and water content regimes are held constant in an experimental mesocosm design.

Where temperature and substrate supply positively covary naturally, the apparent Q_{10} is likely to be elevated, reflecting both the true temperature sensitivity of respiration and the seasonality of substrate supply. Gu *et al*. (2004) demonstrated this concept using a multi-pool soil C modeling framework. They showed how temperature sensitivity of bulk soil respiration can be overestimated or underestimated depending on whether variation in temperature is in phase or out of phase with variations in the labile C pool.

Secondary effects of temperature and water content via substrate supply

We have already discussed how temperature and water content are often inversely correlated and how substrate diffusion can be strongly affected by water content. In this sense, variations of temperature and soil water content indirectly affect respiration via their effects on substrate availability. Although this may appear to be a simple semantic distinction between primary and secondary (or proximal and distal) effects, we think it is important to recognize that empirical functions relating water content to soil respiration are mostly representing constraints on substrate supply. Only at extremely low water contents is desiccation stress important, so that most of the range of responses to varying soil water content reflects the importance of diffusion of solutes and gases (Linn & Doran, 1984; Skopp *et al*., 1990; Grant & Rochette, 1994). Little is known about the effects of plant water stress on allocation of carbon to roots, and responses are likely to vary among species. The critical soil water content for desiccation stress varies among taxa of soil microorganisms, with actinomycetes, free-living fungal hyphae, and mycorrhizae probably more tolerant of extremely dry conditions (Swift *et al*., 1979). In general, however, at water contents between desiccation stress (usually < -1.5 MPa matric potential) and field capacity (about -0.1 MPa matric potential), variation in soil water content is thought to affect microbial respiration primarily through its effect on diffusion of organic solutes (Linn & Doran, 1984; Skopp *et al*., 1990; Grant & Rochette, 1994). Extracellular enzymes exuded by microbes also depend upon diffusion in soil water films to come into contact with substrates.

For transpiring plants, the water, itself, is a much-needed resource, along with its dissolved inorganic minerals. Aboveground respiration could be affected by varying soil water content if conditions are sufficiently droughty to cause foliar water stress. However, roots obtain substrate for respiration from within the plant, and it is unclear to what extent root respiration declines as a function of declining soil water content before root desiccation stress becomes important. Recent radiocarbon data suggest that respiration of young carbon substrates, such as those respired by live roots, is less affected by drought in forest ecosystems than is microbial decomposition of older substrates in the litter layer (Borken *et al*., 2005). If this is true, then variation of soil water content within an intermediate range may affect soil respiration primarily through its effect on diffusion of solutes to soil microorganisms.

At soil water contents above field capacity, variation in water content determines the fraction of macropore spaces that are air filled, thus strongly affecting the rate of gaseous diffusion (Skopp *et al*., 1990; Rolston & Moldrup, 2002). Because oxygen is a substrate for respiration for both soil microbes and roots, this can be a limiting factor to total soil aerobic respiration. For this reason, most moisture response functions that are meant to cover the full range of soil water contents employ parabolic-like functions (e.g. Schlentner & Van Cleve, 1985; Raich & Potter, 1995; Janssens *et al*., 1999; Pumpanen *et al*., 2003; Reichstein *et al*., 2003).

An example of both positive and negative correlations of water content with soil respiration can be found in adjacent areas within the New England forested landscapes of Massachusetts and Maine. Savage & Davidson (2001) demonstrated that summer drought induced decreases in soil respiration on well-drained mineral soils, where solute diffusion was presumably limiting, and increased soil respiration in adjacent wetlands, were oxygen diffusion was presumably limiting (Savage & Davidson, 2001). In all cases, however, it was probably substrate availability that was the direct cause of changes in respiration, resulting from the secondary effect of varying soil water content.

Pulses of CO_2 production following wetting of dry soils have been recognized for many years and have

been attributed largely to death of microbial cells during drought and/or release of organic solutes from live and dead cells following wetting (Birch, 1958; Bottner, 1985; Kieft *et al.*, 1987). The remaining viable microbial biomass is able to respond almost instantaneously to this sudden burst of availability of substrates. Additions of as little as 0.5 mm precipitation can cause a significant increase in soil respiration of dry soil (Liu *et al.*, 2002; Borken *et al.*, 2003; Savage & Davidson, 2003). Borken *et al.* (2002) correlated the change in soil matric potential since the last respiration measurement with the residuals of a temperature model of soil respiration in three European forests. The change in matric potential gave a better fit than did the absolute values of matric potential. Larger than expected fluxes based on the temperature function tended to occur when the soil had recently experienced wetting. Hanson *et al.* (2003) developed a model of soil respiration that included separate, empirically derived water potential functions for litter and mineral soil, which reproduced increased respiration following even small wetting events that wetted only the litter layer. Such empirical functions may yield improvements for modeling soil respiration at hourly to weekly time scales, but it should be kept in mind that the abrupt, and sometimes small changes in water content are actually reflecting an abrupt change in substrate availability. A mechanistic representation of this effect would explicitly include rapid changes in readily available carbon substrates following wetting events.

Summary

Several temperature-sensitive processes, including enzyme activity, diffusion of O_2 and soluble carbon substrates through soil air and water and across cellular membranes, and growth of microbial populations and root tissues, can have multiplicative effects, yielding unusually high or unusually low Q_{10} characterizations of their net effect on respiration. Improved understanding of variability in temperature sensitivities of respiration will require separation of these processes in conceptual, empirical, and numerical models. For example, the confounding effects of soil temperature and water content on respiration may be disentangled more easily if substrate supply is recognized explicitly as a major controlling factor:

Soil respiration = f(Root and microbial biomass, Substrate supply, Temperature, Desiccation stress)

Substrate supply is, in turn, affected by the phenology of inputs of carbon substrates and diffusion of substrates through soil air and water:

Substrate supply = f(Phenology of C inputs, Solute diffusion, Oxygen diffusion)

Temperature and soil water content directly affect respiratory enzymatic activity and also indirectly affect respiration via their effects on substrate supply. Mathematical expressions of these functions and the observations and experiments needed to parameterize them may vary with temporal and spatial scales. Hence, our purpose is not to be prescriptive for specific functions, but rather to emphasize that robust mechanistic models of soil respiration will need to address these processes separately. Substrate supply is important at scales ranging from transport across membranes, diffusion through and across soil water films, allocation to aboveground and belowground plant tissues, phenological patterns of carbon allocation and growth, and intersite differences in productivity.

We have focussed here primarily on short-term (minutes to years) responses of respiration to climate and substrates. Decadal-scale responses of soil organic matter and peat to changing temperature are equally or more important with regards to climatic feedbacks. Even at these longer time scales, however, the effects of temperature must interact with diffusion of oxygen and extracellular enzymes to the locales where carbon is temporarily sequestered in flooded peatlands, in frozen soils, or in the interior of soil aggregates. The best ways to model interactions among temperature, water content, and substrate availability will depend upon the temporal and spatial scales of interest.

We speculate that one indicator that such models properly include the most important interactions will be relatively consistent parameterizations of the temperature sensitivities of the primary effects of temperature. Our understanding of soil respiration will have moved beyond Q_{10}'s when variations in apparent Q_{10} functions become uninteresting because they are readily explained by the effects of desiccation stress, substrate diffusion, substrate production and allocation, and phenology.

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