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News and Views

On the 'temperature sensitivity' of soil respiration: Can we use the immeasurable to predict the unknown?

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ABSTRACT

The temperature dependence of soil respiration (R_S) is widely used as a key characteristic of soils or organic matter fractions within soils, and in the context of global climatic change is often applied to infer likely responses of R_S to warmer future conditions. However, the way in which these temperature dependencies are calculated, interpreted and implemented in ecosystem models requires careful consideration of possible artefacts and assumptions. We argue that more conceptual clarity in the reported relationships is needed to obtain meaningful meta-analyses and better constrained parameters informing ecosystem models. Our critical assessment of common methodologies shows that it is impossible to measure *actual* temperature response of R_S, and that a range of confounding effects creates the observed *apparent* temperature relations reported in the literature. Thus, any measureable temperature response function will likely fail to predict effects of climate change on R_S. For improving our understanding of R_S in changing environments we need a better integration of the relationships between substrate supply and the soil biota, and of their long-term responses to changes in abiotic soil conditions. This is best achieved by experiments combining isotopic techniques and ecosystem manipulations, which allow a disentangling of abiotic and biotic factors underlying the temperature response of soil CO_2 efflux.

1. Background

Soil CO_2 efflux (or soil respiration, R_S) is considered the largest source of CO_2 from terrestrial ecosystems. Recent estimates indicate global soil CO_2 emissions in the range of 98 ± 12 Pg y^{-1}, with annual increases of 0.1 Pg that have been suggested to be temperature-associated (Bond-Lamberty and Thomson, 2010). At a global, regional and local scale, soil temperature (T_S) and soil moisture have been considered the most important abiotic parameters determining R_S and its underlying processes (Kutsch et al., 2009). Empirical response functions are commonly used to derive annual estimates of R_S based on sporadic field measurements (e.g. Savage et al., 2008), whilst short-term (i.e. diurnal) deviations from an average abiotic response of R_S have been interpreted as effects of photosynthesis on R_S (Tang et al., 2005). Although temperature is undoubtedly one of the most important environmental factors

affecting respiratory processes on a physiological scale, we argue that its *direct* influence on soil CO_2 efflux can at best be approximated, which calls for more care in the interpretation and extrapolation of what is often assumed to be a T_S–R_S relationship. The response of R_S to climate change is a critical component in predicting possible feedbacks between the global carbon cycle and the climate system, and simplistic temperature-based extrapolations will not advance our ability to forecast these changes (Davidson et al., 2006). In the following we demonstrate that several of the assumptions, on which the T_S–R_S relationship and its interpretation have often been based, are somewhat arbitrary and deserve careful reconsideration.

2. Incubation experiments – effects of substrate supply and depletion on the apparent temperature sensitivity of soil C turnover

Lab incubations of soil samples indicate generally consistent temperature response functions, illustrating the fact that in principle the decomposition process in homogeneous soils can be well described using soil temperature (e.g. Reichstein et al., 2005). Experimental warming of incubated soils has been found to lead

only to a transient increase in soil CO_2 production, with an apparent compensation for the increase in temperature by a reduction of temperature sensitivity (commonly expressed as Q_{10}, representing the respiration rate change over a temperature shift by 10 °C). However, there is good evidence that such apparent thermal acclimation is caused by the depletion of substrate pools in the soil rather than an intrinsic ability of soils to "adapt" to changes in temperature conditions (Hartley and Ineson, 2008; Kirschbaum, 2004). The apparent acclimation does not however indicate *per se* that an intrinsic temperature sensitivity of R_S is altered, as a range of environmental constraints to decomposition are temperature dependent in themselves and physico-chemical mechanisms of SOM stabilization and destabilization are confounded with the kinetic properties of substrates and enzymes (Davidson and Janssens, 2006). Furthermore, decomposition of more recalcitrant soil organic matter (SOM), whilst being of lower magnitude, may display a higher Q_{10} (Conant et al., 2008). It is therefore necessary to express soil CO_2 efflux rates in warming experiments or lab incubation studies in relation to pool sizes of different substrate qualities. Furthermore, soil incubation experiments generally do not account for the fact that belowground carbon allocation (Litton et al., 2007) and its effects on root and rhizosphere respiration (Curiel Yuste et al., 2004) as well as priming of SOM decomposition (Fontaine et al., 2004; Kuzyakov, 2002) may alter soil C turnover and CO_2 emissions at any given temperature.

3. Inherent problems related to *in situ* testing of temperature dependent and − independent effects on soil CO_2 efflux

Whilst R_S measurements in the field have the advantage of including all CO_2 sources of intact soils (i.e. SOM decomposition as well as root and rhizospheric CO_2 flux), the interpretation of annual or seasonal temperature relations requires some caution. Belowground C allocation in plants, which contributes around 40−60% of R_S seasonally in most biomes (Subke et al., 2006), shows immense seasonal variation in the majority of ecosystems. Fig. 1 illustrates how the coincidence of peak rhizospheric CO_2 flux with seasonal maxima in T_S results in an apparently high T_S−R_S response, owing to increased plant C supply to the soil during summer (Fig. 1; see also Davidson et al., 2006; Reichstein and Beer, 2008).

A further problem for identifying temperature-related and temperature-independent effects on R_S *in situ* relates to the fact that in ecosystems T_S is rarely constant across the soil profile (Fig. 2), and its change with depth may vary from diel to seasonal timescales. Accordingly, the choice of the soil depth used for inferring the temperature sensitivity of R_S may strongly influence the shape of the temperature response curve, and thus Q_{10} (Fig. 3; Pavelka et al., 2007; Reichstein and Beer, 2008). It has been shown that commonly used temperature measurement depths in field experiments are likely to result in an underestimation of temperature sensitivity and that an arbitrary selection of a reference depth can produce an unrealistic range of Q_{10} values (Graf et al., 2008). Even the maximum R^2 depth method, which helps identify a reference depth yielding a minimum bias, can only provide rough approximates, which may change if there are shifts in respiratory activity or diffusivity across the soil profile. Errors in apparent Q_{10} as related to temperature measurement depth are further increased by a pronounced and heterogeneous horizon of respiration activity, a low thermal and CO_2 diffusivity of the soil and a low annual temperature amplitude (Graf et al., 2008).

Also the assessment of 'temperature-independent' effects on a diel timescale from observed hysteresis in the T_S−R_S relationship (Fig. 3B; see also Liu et al., 2006; Tang et al., 2005; Vargas and Allen, 2008) faces the major drawback that it does not consider shifts in
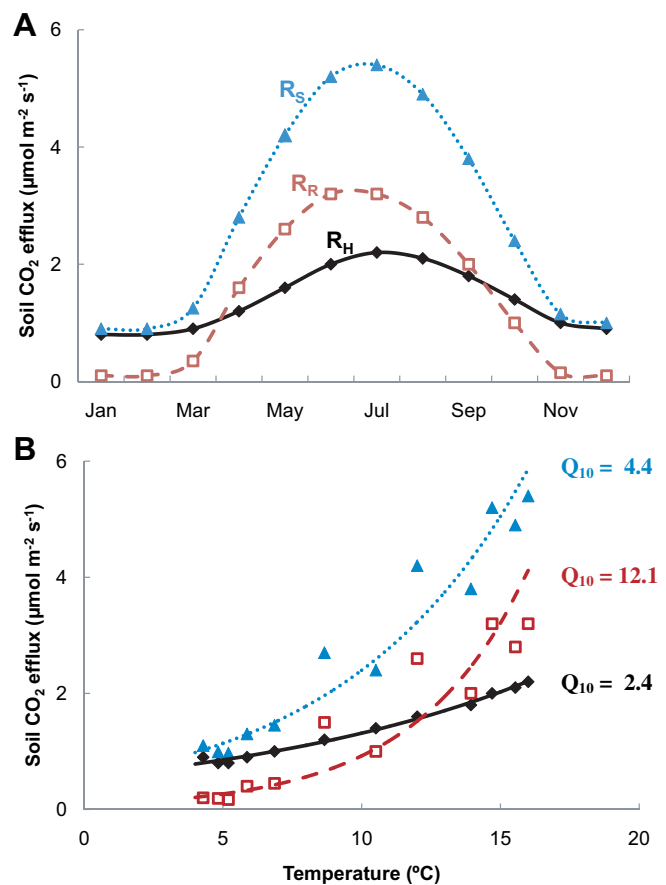
Fig. 1. Heuristic example of seasonal soil CO_2 efflux dynamics, based on simulated data representative of a temperate ecosystem setting with clear seasonality. (A) Seasonal flux contributions from heterotrophic decomposition (R_H; solid black line), root derived CO_2 (roots and rhizosphere; R_R, dashed red line), and resulting total soil CO_2 efflux (R_S; dotted blue line). (B) Same monthly fluxes as in panel A, plotted against typical monthly temperatures, and showing exponential regression fits. R_R flux dynamics are governed by plant productivity changes over the season, and cause a strong apparent temperature "response" of R_S, with an excellent exponential fit ($R^2 = 0.95$), but only a fraction of the flux response is directly influenced by temperature changes. For examples of actual field data, please see partitioning studies (e.g. Gaumont-Guay et al., 2008; Fig. 5 in Moyano et al., 2008) illustrating the same temperature response relations as described here.

phase and amplitude in T_S with soil depth, and may thus be confounded by an arbitrary selection of the soil depth at which temperature is measured and to which CO_2 efflux is related (Bahn et al., 2008; Reichstein et al., 2005). Moreover, besides temperature, a range of further factors may strongly influence an apparent diurnal T_S−R_S relationship, or any deviation from it (compare also Fig. 2): 1) soil moisture and CO_2 diffusivity at a single point in space and time, and their respective diurnal changes; 2) the vertical distribution of roots and microbes, their specific respiration rates and T_S responses; 3) changes in the quality of SOM and its accessibility to microbes and enzymes across the soil profile. 4) Effects of fresh photoassimilates on root and rhizosphere respiration, incl. priming effects (see above), may potentially also cause deviations from a simple diurnal Ts − R_S relationship. However, due to a range of likely confounded effects (see above) it is not possible to consistently infer such 'temperature-independent' effects of photosynthesis on R_S. Conversely, changes in abiotic and biotic conditions across the soil profile may alter both the (immeasurable) actual and the (generally reported) apparent temperature response of soil respiration.