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Seasonal variations in the availability of labile substrate confound the temperature dependence of organic matter decomposition

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ABSTRACT

In empirically deriving the temperature dependence of organic matter decomposition, changing substrate availability can confound the derivation of any inferred intrinsic temperature dependence. In essence, when conditions are favourable for rapid decomposition, that fast rate can deplete the pool of available substrate leading to reduced subsequent decomposition rates. This is a potential problem under any experimental or observational setting. Its potential effect for measurements under seasonally varying temperatures is investigated here in a modelling study.

Soil organic matter continuously loses carbon through decomposition which is generally replenished through new litter influx from senescing plant leaves, roots or other carbon sources. The CenW/CENTURY model was used to investigate to what extent inclusion of varying substrate supply within a realistic modelling framework modified the derived temperature dependence of organic matter decomposition. The model was run with different lignin to nitrogen ratios of fresh litter, and with litter either being generated continuously at a constant rate, or with litter fall being restricted to autumn.

In systems with recalcitrant litter, as might be produced by conifers or eucalypts, the confounding effect of changing substrate supply was only slight. In systems with more labile litter, however, such as that produced by nutrient-rich grasslands, the confounding effect of varying substrate availability substantially weakened the derived temperature dependence. This effect was even more pronounced in systems with litter fall restricted to the autumn months. Reported temperature dependencies inferred from measurements with seasonally varying temperatures have shown weaker temperature dependencies than those inferred from laboratory incubation. The direction and magnitude of the confounding effect of changing substrate supply modelled here was consistent with the difference in temperature response observed in these different systems. It thus helps to reconcile these different reported temperature dependencies.

1. Introduction

The world's soils contain an estimated 2400 Gt of organic carbon to a depth of 2 m (Batjes, 1996). This amount is about 300 times as much as annual anthropogenic CO_2 emissions so that even very small fractional changes in this amount could significantly add to or subtract from net anthropogenic CO_2 emissions to the atmosphere. With global warming, it is generally considered that organic matter decomposition would be stimulated more than plant productivity so that greater amounts of organic carbon could be released to the atmosphere and add to global warming (e.g. Jenkinson et al., 1991; Bond-Lamberty and Thomson, 2010).

The importance of that connection depends strongly on the temperature dependence of organic matter decomposition, but despite much research to find appropriate functions, there is still no consensus on the most appropriate function to use (Kirschbaum, 2006). While various studies have attempted to generate generalised temperature response function from the wealth of individual experiments (Lloyd and Taylor, 1994; Kirschbaum, 1995, 2000; Kätterer et al., 1998; Lenton and Huntingford, 2003; Chen and Tian, 2005; von Lützow and Kögel-Knabner, 2009; Yvon-Durocher et al., 2012), they have generated contrasting response functions.

One of the factors contributing to these differences was highlighted by Davidson and Janssens (2006) who drew an important distinction between intrinsic and apparent temperature dependencies. With an intrinsic dependency, they referred to the temperature dependence that would be observed if all other relevant factors remained constant. The intrinsic temperature dependence is an intrinsic property of a system of interest and remains the same even if important aspects of the system change (Perkins et al., 2012). In contrast, the apparent temperature dependence is

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the observable relationship that results when other important drivers of actual organic matter decomposition, such as moisture status or the availability of labile substrate, co-vary with temperature in some form.

Only the intrinsic temperature dependence provides a truly general and constant relationship. The apparent relationship, on the other hand, reflects the peculiarities of an experimental set-up or a natural system under observation. The apparent temperature dependence might be useful as a description of a system under study, but remains valid and meaningful for only as long as the set of co-varying factors remains the same. Apparent temperature dependencies are, therefore, not generally transportable to other systems that may have different sets of co-varying factors.

Measurements can only observe the apparent temperature dependence, and additional steps are needed to derive the underlying intrinsic temperature dependence. In principle, this can be done either by ensuring that any possibly co-varying factors are held constant, or by explicitly including their own variations. However, this additional step is often not taken, either because of the mostly unstated assumption that other factors would remain constant, or maybe simply because the important difference between apparent and intrinsic temperature dependencies is not adequately considered and appreciated.

It can also be very difficult to account explicitly for important co-varying factors as they may not be easily measurable, or, even if they can be measured, it may be more challenging to develop relationships to transform observable values, such as soil moisture content, into an index as a driver of system function (Paul et al., 2003; Dessureault-Rompre et al., 2011; Moyano et al., 2012). These difficulties do not obviate the need, however, to explicitly consider the effect of co-varying factors as long as the ultimate aim of a study is the derivation of the intrinsic temperature dependence of a process.

The most important problems in deriving the intrinsic temperature dependence arise when key drivers of organic matter decomposition systematically co-vary with temperature. They will then provide systematically biased apparent temperature dependencies that reflect the peculiarities of the system from which they are derived and are therefore not truly transportable to other systems. Two particularly important co-varying factors are the degree of water limitation (Paul et al., 2003; Dessureault-Rompre et al., 2011; Moyano et al., 2012) and the availability of labile substrate (Gu et al., 2004; Kirschbaum, 2004, 2006; Gershenson et al., 2009). The present study addresses the issue of substrate availability.

In essence, when conditions are favourable for fast organic matter decomposition, the fast decomposition rate also depletes the pool of labile substrate, thus reducing the subsequent rate of organic matter decomposition that can be sustained under these favourable conditions (Gu et al., 2004; Kirschbaum, 2006). This can be a very serious problem in soil warming experiments (Kirschbaum, 2004; Eliasson et al., 2005) where it can limit the stimulatory effect of soil warming after a number of years of experimental treatment (e.g. Strömgren, 2001; Luo et al., 2001). It can be a problem even under laboratory conditions (Koepf, 1953; Nicolardot et al., 1994; Kirschbaum, 2006) although its extent and importance as a confounding factor can be minimised under those conditions.

Three of the most widely used temperature response functions are those developed by Lloyd and Taylor (1994), Kirschbaum (1995, 2000) and a simple Q_{10} function (Fig. 1). Lloyd and Taylor (1994) reviewed the temperature dependence of soil respiration observed in field studies under naturally varying temperatures and fitted a general equation to the data they summarised. They were careful to include only studies that they judged not to have been influenced by water limitations and thereby eliminated changing water limitations as a complicating factor. Similar work was repeated by Chen and Tian (2005), based on a wider range of observations; the model they fitted to their widest set of observations was similar to that derived by Lloyd and Taylor (1994).

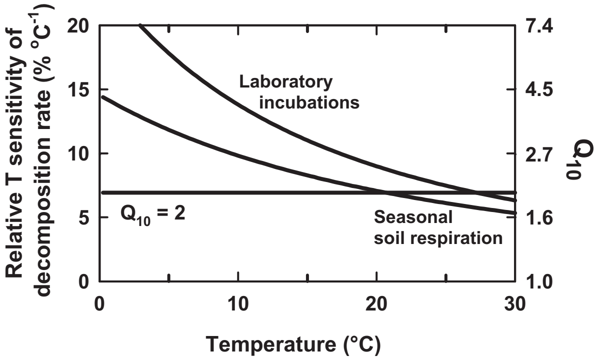

Fig. 1. Relative temperature sensitivity of soil carbon efflux rates estimated based on laboratory incubations (Kirschbaum, 1995, 2000), measurements of soil organic matter decomposition under seasonally varying temperatures (Lloyd and Taylor, 1994), or with a simple Q_{10} function with the often used $Q_{10} = 2$. Data are expressed as relative temperature sensitivity on the left axis and Q_{10} on the right axis. The right-hand axis calculates the proportional increase in decomposition rate for a 10 °C increase in temperature and is thus another measure of its relative temperature sensitivity.

Kirschbaum (1995, 2000) similarly summarised the temperature dependence obtained from laboratory studies under controlled conditions. This generally included controls on moisture levels, and, depending on the nature of respective experiments, changes in substrate supply were no, or only a minor, confounding factor.

Following, Sierra (2012), the term temperature dependence is used here to refer to organic matter decomposition described as a function of temperature, $R = f(T)$. Temperature sensitivity refers to the change in decomposition rate with temperature, $\delta R/\delta T$, and the relative temperature sensitivity is the temperature sensitivity divided by the decomposition rate itself, $(\delta R/\delta T)/T$.

The following also interchangeably refers to either CO_2 efflux or soil respiration rate, as those fluxes are directly measurable, or as organic matter decomposition rate, which is the underlying process that gives rise to soil respiration. As a further complication, soil respiration consists of autotrophic root respiration and heterotrophic respiration from decomposer organisms. The object of the present paper is heterotrophic respiration, but it is recognised that measurements of soil respiration will generally contain a large flux of root respiration that may have a different temperature dependence. This factor is ignored for the purpose of the present paper, but should also be kept in mind in any interpretation of soil respiration measurements.

The relative temperature sensitivity is generally the most useful measure of the system response to temperature changes as it provides the system's relative responses in its current state to a change in its principal external driver. It was found to be strongest for laboratory-based incubations and weaker for observations based on seasonally varying temperatures. Both of these empirically determined relative temperature sensitivities were much greater than that calculated based on a simple Q_{10} function with $Q_{10} = 2$ (Fig. 1). Q_{10} functions appeal because of their attractive simplicity, but they have no underlying theoretical support and are not consistent with empirical observations (Fig. 1).

However, it is not obvious why the two empirically determined compilations show different relative temperature sensitivities. Laboratory incubations are clearly conducted under more artificial conditions than field observations of soil respiration under