Uncertainties related to the temperature sensitivity of soil carbon decomposition

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Abstract

The fate of soil carbon stores in response to global warming is hotly debated as considerable uncertainties remain in forecasts of the temperature sensitivity of soil organic matter decomposition. This is the result of disagreements in the response of heterotrophic respiration and dissolved organic carbon release to temperature. In the case of soil respiration uncertainties are derived from the inclusion of fixed Q_{10} values of 2 and a variable number of carbon pools in the models. For the soluble carbon no consensus has emerged in relation to the causal factors leading to the observed carbon exports from organic soils. In most predictions soil biology is poorly represented despite current knowledge indicating that warming can induce important changes in below-ground invertebrate populations which could have important consequences for organic matter decomposition and nutrient cycling. Furthermore, the evidence that the adaptation of soil invertebrate populations to changing climates will exacerbate decomposition of long-standing soil carbon reservoirs and diminish the predicted respiration acclimation effects is critical to develop more realistic predictions of the fate of our terrestrial sink.

Keywords: soil organic matter, temperature, respiration, dissolved organic carbon, soil biology, Q_{10}, carbon pools.

1. Introduction

Several models predict that soil respiration will increase more than net primary productivity in response to warming leading to the terrestrial sink becoming progressively depleted by the end of this century (*e.g.,* Cox *et al*., 2000; Cramer *et al.*, 2001). In contrast, other studies claim that, in the long-term, carbon storage may increase with increasing temperatures as a result of both greater carbon inputs and soil physico–chemical reactions stabilising soil carbon and protecting it from

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microbial respiration (Thornley and Cannell, 2001). Consequently, an energetic barrier of more recalcitrant C will be buried below the fresh deposits which could reduce or cancel the current assumed responses of decomposition to warming (Fontaine *et al.*, 2004, 2007; Rinnan *et al.*, 2007). However, the decomposition of this deep resistant pool could be activated if, for example, as a result of land management practices, a deeper distribution of fresh C occurs (Fontaine *et al.*, 2007). Furthermore, other experimental data indicate that decomposition could be completely insensitive due to biological adaptation (Luo *et al.*, 2001) or to the influence of other factors such as nutrient availability (Kirschbaum, 2004; Eliasson *et al.*, 2005; Knorr *et al.*, 2005), moisture (Saleska *et al.*, 2003, 2007; Ciais *et al.*, 2005; Davidson and Janssens, 2006) as well as temperature. Each of these assumptions has important repercussions for current predictions of soil carbon turnover and any potential feedbacks from soils to climate.

2. Soils as stores and sources of carbon

Globally, soils contain approximately 1580 Gt of stored carbon, which represents more than twice the stock of carbon held within terrestrial vegetation, and more than twice that presently resident in the atmosphere (Schimel, 1995). A great proportion of the global carbon reservoir is present in organic soils which are estimated to store a third of all terrestrial carbon stocks (Gorham, 1991). In the European Community the quality and quantity of these particular ecosystems has significantly decreased, with surface area losses up to 90% in the majority of the states members. The environmental conditions in these organic rich soils (continuous high precipitation, more than 30 days per annum with risk of frost, frequent cloudiness) have a strong influence on the activities of their communities (plant and animals).

Atmospheric warming is expected to be most pronounced at higher latitudes so that Arctic and upland systems will be particularly influenced by this ecological driver (Sala *et al.*, 2000). Therefore, carbon stores are predicted to respond to climatic change as it has been proven that SOM decomposition rates respond to varying moisture and temperature regimes (Parton *et al.*, 1987; Schimel *et al.*, 1994; Alm *et al.*, 1999). For example, concomitant with a 1°C rise in temperature, soils globally are predicted to release between 10 and 30 Pg of carbon to the atmosphere (Schimel *et al.*, 1994). Furthermore, recent findings suggest that increased temperatures in the UK have been offsetting absorption of carbon by terrestrial sinks and are responsible for carbon losses of 0.6% y^{-1} (relative to the existing soil carbon content) over the past 25 years (Bellamy *et al.*, 2005). This high impact of warming on C fluxes in these particular systems is the result of the stimulation of organic matter mineralisation with associated release of CO_2 to the environment (*e.g.,* Oechel *et al.*, 1993; Lloyd and Taylor, 1994; Trumbore *et al.*, 1996; Grace and Rayment, 2000; Fang and Moncrieff, 2001) and the leaching of nutrients (dissolved organic carbon, DOC) by increasing temperatures (*e.g.,* Ineson *et al.*, 1998; Tipping *et al.*, 1999). Indeed, current concerns have focussed on the potential risk for these systems to become unstable, *i.e.,* changing its role from ‘sinks’ to ‘carbon sources’ in response to changes in climate and land use (*e.g.,* Gill *et al.*, 2002). In relation to this, ‘the coupling between climate and the terrestrial C cycle’ has been included in the Third and Fourth Reports of the Intergovernmental Panel on Climate Change (IPCC, 2001, 2007) to predict the future responses of terrestrial ecosystems to global change. However, our understanding of the biological mechanisms involved in the regulation of soil C remains limited. This information is central to the development of meaningful strategies in the future.

3. Soils as the most diverse habitats on earth

Environmental change scenarios suggest that the sensitivity of biomes to climate variations is a product of their diversity (Sala *et al.*, 2000). Soil is one of the most diverse habitats on earth and contains one of the most diverse assemblages of living organisms (Giller *et al.*, 1997; Hågvar, 1998). For example, a single gram of soil may contain millions of individuals and several thousand species of bacteria (Torsvik *et al.*, 1994). This is a consequence of the complex physical and chemical nature of the soil. Its porous structure, immense surface area, and extremely variable supply of organic materials, food, water and chemicals mean that various animal, plant and microbial worlds can co-exist simultaneously and find appropriate niches for their development.

Soil communities are so diverse in both size and numbers of species, yet they are still extremely poorly understood and in dire need of further assessment. The easiest and most widely used system for classifying soil organisms is by using body size (length or width) and dividing them into three main groups: macro-fauna meso-fauna and micro-biota (Wallwork, 1970; Swift *et al.*, 1979). Unfortunately, the ranges that determine each size group are not exact for all members of each group, often leading to considerable confusion as to whether a particular organism should be considered macro or meso, and so on. More recently, ‘functional classifications’ have been launched for certain groups. They are based on the fact that soil biota are responsible, to a varying degree (depending on the system), for performing vital functions in the soil ecosystem. These functions, performed and often controlled by the myriad of organisms in soils, range from physical effects such as the regulation of soil structure and edaphic water regimes, to chemical and biological processes such as degradation of pollutants, decomposition, nutrient cycling, greenhouse gas emission, carbon sequestration, plant protection and growth enhancement or suppression. The division of soil biota into roots, ecosystem engineers, litter transformers, phytophages and parasites, micro-predators and micro-flora (Figure 1) is a good example (see Lavelle, 1996), because it also takes into account the potential top-down regulatory controls of larger organisms (*e.g.,* the ecosystem engineers) over smaller ones.

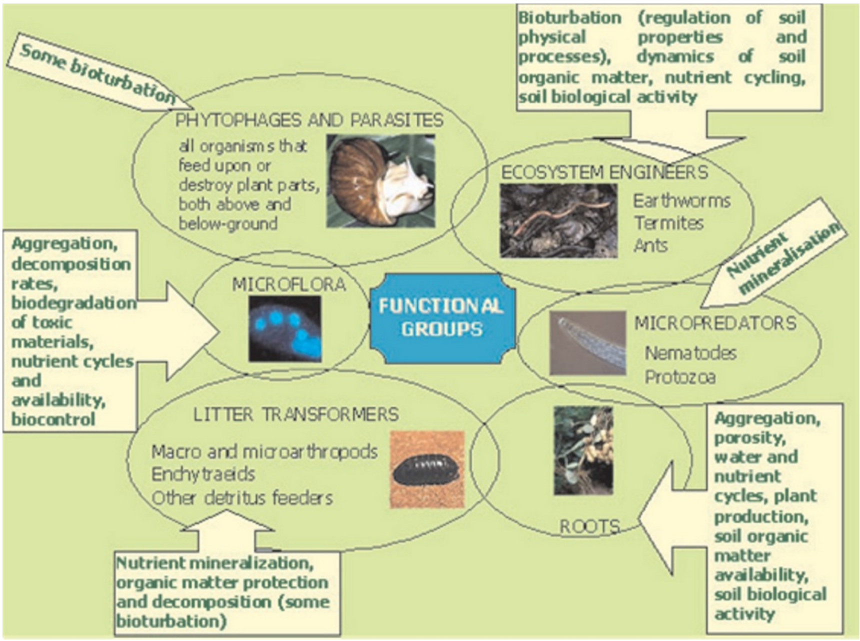

Fig. 1. Functional classification of soil fauna (drawn using information given by Lavelle 1996).

Functional classifications are important because it is the only way to understand the effects of global change on ecosystem functioning. And thus, acting through the diversity of soil organisms, the various climate and land use factors influence 5 main ecosystem functions (decomposition, trace gas flux, nutrient dynamics, soil physical structure, trophic structure). These in turn have both actual and potential feedback effects, through the vegetation and the above ground fauna, and through climate and land use (Heal, 1997).

4. Enchytraeid worms: key stone group in organic soils

Enchytraeid worms (Figure 2) are frequently the most abundant oligochaete invertebrates in carbon rich soils of peatlands and pastures. This group of invertebrates (individual 1–4 mm length) can comprise over 70% of the belowground faunal biomass and have a larger mass (on a live weight basis) than the sheep on a unit area (Coulson and Whittaker, 1978). In spite of the numerical abundance of Nematodes, Acarina and Collembola they never contributed more that 3% of the total biomass (Table 1).

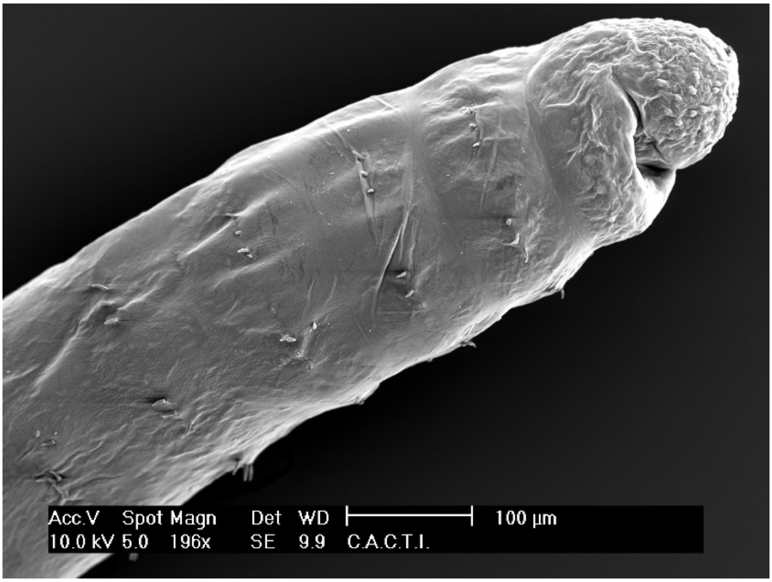

Fig. 2. Scanning electron micrograph (SEM) of *Cognettia sphagnetorum*, a dominant enchytraeid worm in carbon rich soils where it may constitute up to 95% of the total enchytraeid biomass.

Table 1. Population densities (numbers m^{-2} in summer) and biomass of animals on shallow peat soils at Moor House (*Juncus grasslands*) (from Coulson and Whittaker, 1978).

	Density (Numbers m^{-2})	**Biomass (g m^{-2})**
Enchytraeids	200,000	4.6
Tipulids	2,500	1.96
Nematodes	3,900,000	0.18
Collembola	23,000	0.05
Acari	45,000	0.32
Sheep	0.00013	3.2

These soil animals are distributed worldwide although a recent review study (Briones *et al.*, 2007a) showed that the greatest numbers of these organisms are found in moorlands and associated to pH values between 4 and 5 (Table 2). This comprehensive study also evidenced the strong relationship between climate and their population numbers, with temperature being the most critical factor controlling their geographical distribution. Indeed, enchytraeids have been found at sites with mean annual temperatures (MAT) in excess of 25°C but some genera (*e.g., Bryodrilus, Mesenchytraeus, Cernosvitoviella, Stercutus*) and the species *Buchholzia fallax* have never been recorded at MAT > 12.5°C. Crucially, the usual dominant species in moorland systems (*Cognettia sphagnetorum*) has never been reported at MAT > 16°C and it is not present in sites with hot dry summers.

Table 2. Results from meta-analysis and non-parametric ANOVA for enchytraeid abundance data of 44 published papers (from Briones *et al.* 2007a).

	Higher Enchytraeid Densities
Habitat	Mostly moorlands but also grasslands
Soil type	Moder, loamy, brown, calcareous and podzol
Soil pH	4–5
Climate regime	Main association is temperate rainy climates, moist all year with moderate or cold summers (*i.e.,* < 4 months with means >10°C)
Mean annual temperature (MAT)	0–16°C
Mean monthly rainfall (MMR)	No apparent relationship

Enchytraeids also exhibit an aggregated horizontal distribution, giving rise to a high spatial and temporal heterogeneity (Didden, 1993). It also seems to be a common feature that populations are concentrated in the top soil layers with significantly higher numbers being found in the first 4 cm of the soil profile and gradually decreasing with depth (Briones *et al.*, 2007a). Living in the surface horizons in this way makes the population vulnerable to the regnant conditions, and consequently, these key species could be lost if atmospheric temperatures increase, particularly at sites where the mean annual temperature crosses the temperature boundaries identified above, with important implications for those systems where these species are dominant (*e.g.,* moorlands and tundra biomes) (Briones *et al.*, 2007a).

In addition, field and controlled laboratory experiments showed that the potential effects of climate change on these organisms is highly specific, with warmer temperatures having a positive effect on the reproduction rates of the more tolerant species and a detrimental effect on the less resilient ones (Briones *et al.*, 1997). For certain species survival is attained by vertical migration (Springett *et al.*, 1970; Briones *et al.*, 1997), however readily available organic matter is concentrated in the first top 10 cm and could limits the extent to which downward faunal movements occur. Furthermore, migration to the deeper layers can also become an unsuitable strategy if the new conditions persist.

5. The link between climate, soil biology and the carbon cycle. Implications for climate change modeling

It is now accepted that the diversity, abundance and activity of soil organisms (bacteria, fungi, mesofauna and macrofauna) will be central to the capacity of soils to both sequester and respire carbon inputs derived from net primary producers

(Bradford *et al.*, 2002). However, they are often underestimated in carbon turnover predictions and uncertainties will remain until the interaction between soil animals and soil carbon stocks is better represented in soil carbon models. Some examples of how soil biology could challenge previous assumptions of the temperature responses of SOM decomposition are given below.

5.1. Dissolved organic carbon (DOC) release from soils

The observed rapid increase in the DOC concentrations in the rivers draining from peatland systems has drawn scientific attention as it is considered as an unequivocally sign of destabilization (Freeman *et al.*, 2001a; Tranvik and Jansson, 2002), with important implications for water quality (Worrall *et al.*, 2003). Nonetheless, the causes for the losses of this globally important source of carbon remain uncertain.

Field studies have shown that increasing temperatures have a major effect on DOC release, with maximum concentrations occurring during the summer (Tipping *et al.*, 1999). Furthermore, the reported increase in DOC concentrations in 11 English lakes during 1988–2000 and the parallel increment of phenolic compounds in peat soils in response to rising temperatures led Freeman *et al.* (2001a) to conclude that warmer conditions are responsible for the export of peatland carbon to the oceans. Additionally, the fact that the observed seasonal increases in DOC production mimic the peaks of solar radiation (Harrison *et al.*, 2008) confirms previous assumptions that DOC release is linked to primary production (Fitter *et al.*, 1999).

However, these increases are not fully explained by the direct effect of increasing temperatures alone (Pastor *et al.*, 2003). And for example, the observed reductions in sulphur emissions during the last 20 years in the UK has been identified as a key cause of rising DOC in north America and northern Europe (Evans *et al.*, 2006; Monteith *et al.*, 2007) due to decreased soil water acidity. Hydrology has been considered to be another contributing factor to increasing DOC concentrations and thus, the observed increases in the discharge capacity of the rivers (Forsberg, 1992) could be related to DOC release, although this relationship between DOC concentrations and discharge volume has not always been recorded (Evans *et al.*, 2002; Worrall *et al.*, 2003).

Other possible explanations for carbon losses in the soil solution are related to the iron mobility (Lundström, 1993), possibly as result of its role in the formation of organic matter complexes. Alternatively, the increase in the concentrations of greenhouse gasses, such as CO_2, in the atmosphere and their effects on plant structure (increasing dominance of vascular plants in detriment of mosses) and root exudation could also be responsible for these carbon exportations (Freeman *et al.*, 2004).

It is also possible that increased aerobic conditions during the summer months, as a result of lower water levels (Wetherald and Manabe, 1999), could remove the enzymatic constrains causing the accumulation of phenolic compounds in wetlands

Fig. 3. Dissolved organic carbon (DOC) release from microcosms containing soil from the 0–3 cm, 3–6 cm and 6–9 cm layers in the absence and presence of enchytraeids.

and peatlands (Freeman *et al.*, 2001b) and thus, promoting decomposition and the subsequent release of DOC. In relation to this, other biological changes such as the temperature induced increases of enchytraeid numbers in C rich soils have also been correlated with leaching of DOC (Figure 3), suggesting that warmer temperatures will result in an increase in the turnover of soil carbon and other nutrients (Briones *et al.*, 1998a,b; Cole *et al.*, 2000, 2002a,b). Therefore, a better understanding of the biological mechanisms responsible for the mobilization of this long-standing carbon is essential to develop more realistic predictions of the future carbon export rates from peatlands.

5.2. Carbon dioxide (CO_2) emissions from soils

Soil respiration is the second largest pathway in the global carbon cycle, producing an annual global flux of 68–100 × 10^5g C y^{-1} (Musselman and Fox, 1991; Raich and Schlesinger, 1992). With such a significant flux, even small changes could be significant on global scale. Due to a large increase in anthropogenic CO_2 emissions into the carbon cycle, global surface temperature has been seen to increase in 0.74 ± 0.18 ºC over the period 1906–2005 (IPCC, 2007).

However, despite the importance of soil global carbon cycles, little is known about the way soil will respond to future climate predictions. Some studies suggest the terrestrial biosphere is gaining carbon at a rate of 2 ± 1 Gt C y^{-1} (Steffen *et al.*, 1998; Royal Society, 2001), but concerns also exist that, due to increases of heterotrophic respiration in a warming climate, soil will convert to a carbon source (positive feedback) accentuating the problem (Woodwell *et al.*, 1998; Cox *et al.*, 2000; Lenton, 2000; Sarmiento, 2000; Cramer *et al.*, 2001; Powlson, 2005; Heimann and Reichstein, 2008).

Cox *et al.*'s (2000) model incorporating the response of biota to warmer climates to predict future climate, contains large uncertainties with regard the respiration of organic matter in soils. In particular, the temperature sensitivity of soil carbon decomposition is identified as an important determinant of carbon driven climate change in the future (Trumbore *et al.*, 1996; Kätterer *et al.*, 1998; Grace and Rayment, 2000; Holland *et al.*, 2000; Fang and Moncrieff, 2001; Thornley and Cannell, 2001; Sanderman *et al.*, 2003). However, this response of SOM decomposition to temperature is hotly debated and several answers to this question have been published in the recent literature:

(i) Rising temperatures will result in a faster decomposition rate of SOM, releasing additional amounts of CO_2 and accelerating climate change. This will be the consequence of the positive influence of temperature on microbial activities (*e.g.,* Knorr *et al.*, 2005).

A conventional way to express the response of soil heterotrophic respiration to temperature increases is the soil respiratory quotient Q_{10} which has been widely used in several climate models (*e.g.,* HadCM3LC). Within this framework it has been estimated that soil heterotrophic respiration and CO_2 production doubles with every 10°C increase in atmospheric temperature, *i.e.,* $Q_{10} = 2$ (Sarmiento, 2000). However, this simple exponential function is only true under specific conditions, *i.e.,* providing that soil substrate availability does not become limiting (Knorr *et al.*, 2005), and for reactants with an activation energy around 50 kJ mol^{-1} incubated at temperatures between 273 K and 303 K (Davidson and Janssens, 2006). Other difficulties in their application derive from mathematical restrictions in its calculation (Tuomi *et al.*, 2008) and its natural variation with soil depth (Graf *et al.*, 2008).

Furthermore, when soil biology is taken into account significant increases in the Q_{10} value are observed. For example, under warmer conditions (>10°C) the interactions between mesofauna and microorganisms could increase the respiratory quotient over 3.4 (Briones *et al.*, 2004). This higher Q_{10} is closer to the upper limit forecast by previous models ($Q_{10} = 3.63$) (Lenton and Huntingford, 2003), and confirms stronger sensitivity of soil respiration to temperature in the presence of invertebrates. This has important implications for future climate predictions, and concomitant with temperature increases we will see an increase in the biomass of these soil invertebrates. Such animal increases have been observed in the field (Briones *et al.*, 1997; Cole *et al.*, 2002b) and have the potential to increase soil CO_2 production that could, in turn, contribute further to climate forcing. Indeed the results of a simple regression model between atmospheric temperature, enchytraeid biomass and total soil CO_2 for two organic soils suggest that soil warming could produce important increases in soil CO_2 release (Table 3). This model assumes that the role of enchytraeids in this process is biomass dependent and that soil temperature and moisture levels are maintained within a range suitable for the survival and reproduction of these organisms.

However, this observed soil respiration enhancement in response to warming could be a transient response and therefore, heterotrophic 'acclimatization' could be an important factor in reducing soil CO_2 release in the longer term (Luo *et al.*, 2001). From this study it is also anticipated that this process would be less important in ecosystems with high carbon content than in those with low carbon storage. However, evidence suggests that there is not thermal adaptation of microbial communities and consequently, the temperature sensitivity of the C mineralisation rate is not affected by the microflora structure (Vanhala *et al.*, 2008). Furthermore,

Table 3. Potential soil CO_2 production at current and elevated mean annual atmospheric temperatures at 60% soil moisture for Sourhope and Great Dun Fell soils. Sourhope mean annual temperature (1993–2003) was 7.38 ± 0.15°C and Great Dun Fell mean annual temperature (1993–2003) was 5.97 ± 0.12°C. Actual biomass is that measured from soil cores (0–10 cm) obtained from field sites. Calculations were performed based on results obtained in a previous microcosm experiment (Briones *et al.* 2004): Predicted biomass represents biomass calculated as a function of temperature, *i.e.,* (biomass = 0.05 × temperature) – 0.0591; $R = 0.78$, $p < 0.04$, $n = 12$. Total respiration was calculated as a function of biomass *i.e.,* 1 mg biomass = 77.0 ± 6.05 CO_2-C μg mg enchytraeid tissue^{-1} day^{-1}. Total respiration = (62.802 × biomass) + 3.6508; $R = 0.65$, $p < 0.05$, $n = 8$. Estimates of potential soil respiration annotated with different letters were significantly different (ANOVA; $p < 0.01$).

Site	**Temperature °C**	**Enchytraeid Biomass (g m^2)**	**Potential Soil Respiration CO_2-C (mg m^2 day^{-1})**
Sourhope grassland			
Actual biomass	Ambient	0.30 ± 0.04^a	18.60 ± 2.39^a
Predicted biomass	+2.6	0.39 ± 0.05^{ab}	29.88 ± 3.83^b
Predicted biomass	+5.0	0.46 ± 0.06^b	35.57 ± 4.56^c
Great Dun Fell moor			
Actual biomass	Ambient	5.17 ± 0.45^c	324.81 ± 28.31^d
*Actual biomass**	+2.6	5.28 ± 0.99^{cd}	331.90 ± 61.90^d
Predicted biomass	+2.6	6.73 ± 0.59^{de}	422.25 ± 36.79^d
Predicted biomass	+5.0	8.07 ± 1.54^e	621.25 ± 118.35^e

Actual biomass* at ambient and +2.6°C in the Great Dun Fell moor soil were taken from Briones *et al.* (1997, 1998a). Actual biomass at ambient in the Sourhope grassland was taken from Briones *et al.* (2004).

our results in organic soils indicate that the impacts of soil warming on frequently large enchytraeid populations and their interactions with microbial activities will be determinant to the C sink/source function of these ecosystems and that the net effect of increasing atmospheric temperatures on soil carbon stocks will be determined by the interaction between short-term ‘ecological adaptation’ and longer term ‘acclimatization’ of soil respiration (Oechel *et al.*, 2000, Luo *et al.*, 2001).

(ii) Temperature does not dominate the carbon balance. After compiling decomposition data from 82 sites on five continents Giardina and Ryan (2000) found that decomposition rates are not controlled by temperature limitations to microbial activities and consequently, global warming will not result in a positive feedback from soil to climate.

However, other studies assume that although biological processes respond to temperature in an exponential way they are not affected by the atmospheric CO_2 concentrations (Kirschbaum, 2006; Davidson and Janssens, 2006) and consequently, led to the erroneous conclusion that positive feedbacks will not be observed until the temperature stimulating effect on soil respiration exceeds that of CO_2 fertilisation (Heimann and Reichstein, 2008).

There are other factors besides temperature which could alter SOM decomposition rates in response to climate change. Among them, nitrogen limitation can alter plant productivity (and hence the rate of uptake of CO_2 from the atmosphere), plant C allocation and enhance decomposition of lignin by fungi (Heimann and Reichstein, 2008). This has led to claim for the need of an Earth-system perspective of the nitrogen–carbon–climate interactions to reduce uncertainties in the climate change projections (Gruber and Galloway, 2008).

(iii) The temperature sensitivity of SOM decomposition varies with the different carbon pools existing in the soil. This conclusion has raised a new debate not only regarding the number of these hypothetical pools to be considered in the models, but also in relation to their dynamic behaviour in response to warming.

First attempts to obtain a more realistic simulation of SOM matter turnover included two pools: (i) a young, rapidly turned over labile pool and (ii) an older, longer lived non labile pool. The investigation of the responses of these two SOM pools to changes in temperature has resulted in opposite conclusions. One current opinion is that the decomposition of soil labile carbon is sensitive to temperature variation whereas resistant components are insensitive (Liski *et al.*, 1999; Giardina and Ryan, 2000; Thornley and Cannell, 2001). This is derived from the idea that most respired carbon dioxide is derived from recently deposited or ‘young’ labile SOM stocks (Trumbore, 2000). Consequently, as labile C pools become depleted, by increasing heterotrophic activity, a decrease in the rate of soil respiration will be observed (Kirschbaum, 2004; Eliasson *et al.*, 2005; Knorr *et al.*, 2005; Hartley *et al.*, 2007).

In contrast, other authors (*e.g.,* Fang *et al.*, 2005; Reichstein *et al.*, 2005; Connen *et al.*, 2006) claimed that both pools show the same temperature sensitivity, and resistant carbon responds equally to temperature variations as labile carbon pools. From this, the observed decline in soil basal respiration with incubation time is the result of the rapid degradation of the more labile substrates so that the resistant C component contributed in a greater proportion to soil respiration.

However, this conclusion was challenged by Knorr *et al.* (2005) who re-examined Giardina and Ryan data and used a model containing three carbon pools, *i.e.,* fast, intermediate and very slow. The outcome of this study shows that increasing temperatures accelerate SOM decomposition rates resulting in an even greater positive feedback to climate than previously thought. This is the consequence of the non-labile soil organic carbon being more sensitive to temperature than labile soil organic carbon. Accordingly, the temperature sensitivity of SOM decomposition increases with substrate recalcitrance and hence determining the magnitude of the feedback response to the climate system (Hartley and Ineson, 2008).

Multipool carbon models such as CENTURY (Parton *et al.*, 1987) and ROTH-C (Jenkinson, 1990) incorporate up to seven conceptual pools, although reliable measures of the decomposability of these various pools has been only partly successful (Davidson and Janssens, 2006). Further research using more powerful techniques to better characterise the diversity of soil substrates found in soils is therefore needed to determine the stability of SOM to future temperature increases.

(iv) The temperature sensitivity of SOM turnover is also determined by the temperature sensitivity of soil biology. It has already been shown that microbial (Fontaine *et al.*, 2004) and certain key soil invertebrates are important regulators of soil carbon storage (Briones *et al.*, 1998b, 2004), with their activities being constrained by prevailing climatic conditions. Yet, despite considerable knowledge of soil invertebrate ecology and their role in nutrient cycling (*e.g.,* Coleman *et al.*, 2004) their contribution to net terrestrial carbon balances has not yet been addressed (Fang *et al.*, 2005; Knorr *et al.*, 2005; Wall *et al.*, 2008). This omission is of particular concern when attempts are made to predict the effects of climate change on the decomposition and respiration of old non-labile carbon from organic soils.

For example, Fontaine *et al.* (2004, 2007) found that the addition of labile materials to the soil could stimulate the decomposition of 'old' carbon. Similarly, although studies indicate that enchytraeid worms assimilate carbon components which are predominantly of material that is ca. 5–10 years old (Briones and Ineson, 2002), recent findings suggest that warming induced changes in belowground invertebrate populations increased the turnover of old non labile soil carbon (Briones *et al.*, 2007b). Therefore, feeding adaptation by soil organisms will increase the temperature sensitivity of non labile soil carbon to offset acclimatization of soil respiration (Oechel *et al.*, 2000; Luo *et al.*, 2001).

Organic soils such as peatlands and upland pastures represent a large global carbon reservoir with decomposition being constrained by low biological activity due to cold temperature regimes (Moorhead and Reynolds, 1993). Furthermore, molecular oxygen limitation on a single enzyme (phenol oxidase) prevents these systems from releasing 455 Gt of stored carbon into the atmosphere (Freeman *et al.*, 2001b). Increased aeration through, for example, enchytraeid burrowing and warmer temperatures would then have the potential to accelerate carbon losses.

Taken together it becomes clear that both the 'biological' and 'temperature' sensitivity of SOM decomposition are both critical for modelling changes in soil carbon stocks. It seems that increasing atmospheric temperatures will result in a rapid decomposition of labile SOM and, as the ordinarily exploited sources of food become limited, the 'biological feeding flexibility' of certain soil organisms (*e.g.,* enchytraeids) will lead to increased forage of older organic substrates and hence a progressive respiration of old, previously unused soil carbon to the atomsphere. These findings clearly contradict the opinion that non labile soil carbon is insensitive to temperature increases (Liski *et al.*, 1999; Thornley and Cannell, 2001; Luo *et al.*, 2001*)*, but do confirm that the mechanism for the release of these resistant C pools can be attributed to 'ecological adaptation' of soil biology.

6. Conclusions

The future of our terrestrial sink under warmer scenarios is highly controversial with no clear trends of decreasing soil carbon with increasing temperature regimes at least for certain parts of the world (*e.g.,* Kirschbaum, 2000; Thornley and Cannell, 2001). Part of the problem is the lack of agreement in the direction of these responses, *i.e.,* top-down (*e.g.,* climate variables (temperature, rainfall patterns), CO_2 concentrations in the atmosphere, plant growth, etc.) or bottom-up (*e.g.,* nutrient availability, chemical reactions, substrate complexity and soil biology) regulation. Soils are very heterogeneous systems where a great number of complex interactions occur, not only between below-ground components but also between plants above and organisms and nutrients below and therefore, predicting decomposition rates in a future warmer scenario is not a simple task and requires a multidisciplinary approach.

Another conflicting issue is that temperature dependencies in the carbon models are usually expressed using a fixed Q_{10} value without taking into account the intrinsic characteristics of the soil (*e.g.,* organic matter content, physical protection of soil aggregates, nutrient availability, enzymatic activities and the structure of the soil communities) and ecosystem processes (*e.g.,* changes in net primary production and variations in the potential evapotranspiration:precipitation ratio across different biomes). Obviously, an understanding of soil respiration and its potential responses to climate is critical to predict future changes in the terrestrial carbon pools (van Hees *et al.*, 2005).

Importantly, the temperature sensitivity of different carbon pools has become an important source of uncertainty in current climate driven carbon models. From the published literature it is clear that using multipool soil carbon models provides a more realistic estimate of the fate of global carbon (see also Davidson and Janssens, 2006). And thus, re-examination of previous published data using three different carbon pools instead of one contradicted previous conclusions (Knorr *et al.*, 2005) and led to a greater appreciation of the importance of the different organic fractions in the soil responses to climate change (Powlson, 2005). Similar re-analyses of previous published data have been produced by Smith *et al.* (2007) who concluded that the predicted carbon losses for the England and Wales (Bellamy *et al.*, 2005) are only possible if an unrealistic Q_{10} value of 13 is included in the model and consequently, only 10–20% of the overall losses reported are explained by climate change alone. However, for these calculations a single pool model and a fixed value of Q_{10} of 2 was used which perhaps questions this new re-assessment. More research is needed to identify all the different pools which integrate SOM and to determine the influence of a great number of factors (including chemical protection, the effect of CO_2 fertilisation on primary productivity, N deposition, frequency of droughts, land use, etc.) which may affect the decomposition rates of the different soil C compounds.

Surprisingly, soil biology is usually underestimated in most models despite the fact that some keystone organisms (such as enchytraeids) do have the potential to exert a positive influence on C release from organic soils (*e.g.,* Briones *et al.*, 1998a,b, 2004) and more importantly, to 'unlock' previously unused C sources (Briones *et al.*, 2007b), adding more information to the current debates on the temperature sensitivity of different carbon pools described above. Therefore, they could be used as measurable indices of biological sensitivity to climatic changes which should be monitored at selected 'vulnerable' ecosystems (such as those with the higher carbon densities, *i.e.,* wetlands, peatlands and permafrost soils) to detect any important changes in their carbon storage function.

In summary, to answer the question of how climate change under different changing land scenarios will alter the carbon balance in our terrestrial sink will require of more experimental work at the communities and processes level. Only with this type of information it would be possible to calculate more realistic Q_{10} values and to define more adequately the factors which need to be included in the models.

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