

The temperature dependence of organic matter decomposition: Seasonal temperature variations turn a sharp short-term temperature response into a more moderate annually-averaged response.

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Abstract

The temperature dependence of organic matter decomposition is a critically important determinant of any long-term changes of soil-carbon stocks in response to global warming. Due to practical experimental constraints, most knowledge of this temperature dependence is based on short-term studies. These studies generally show a strong temperature dependence of organic matter decomposition. At the same time, many modelling studies, especially global studies, or studies that investigate the effects of climate change, use longer time steps, such as annual. It is investigated here to what extent the use of short-term temperature dependencies are appropriate, or how they may need to be modified, for application over longer time steps.

The work indicated that for global applications, it is critically important to explicitly consider seasonal temperature variations. Across the globe, observed annual mean temperature and the annual temperature range are negatively correlated. Inclusion of this correlation means that the strong short-term temperature dependence becomes much weaker when data are expressed as annual averages for the temperatures experienced across the globe. For short-term responses, the temperature dependence of organic matter decomposition is greater at low than high temperature and deviates strongly from an assumption of a constant Q_{10} across temperature. For annually-averaged values, this pattern also weakens, and temperature dependencies change only slightly with temperature. Using short time steps for simulations leads to the expectation of more positive changes (sequestration) in soil carbon especially for cold regions of the globe than would be predicted for simulations at annual time steps without explicit consideration of seasonal temperature variations. These considerations help to reconcile some of the apparent differences in temperature dependencies obtained by different workers using different approaches.

Introduction

The world's soils contain about 1500 Gt of organic carbon to a depth of 1 metres and 2400 Gt to a depth of 2 metres (Batjes, 1996). Any change by even a fractionally small amount could therefore significantly add to or subtract from net anthropogenic CO₂ emissions. Feedbacks from soil organic matter, or the terrestrial biosphere in general, thus constitute a critically important feedback effect for future atmospheric CO₂ concentrations.

Various global models have been used to study the extent of this potential feedback (Cox *et al.*, 2000; Friedlingstein *et al.*, 2003, 2006; Jones *et al.*, 2005; Sitch *et al.*, 2008). Models generally agree that warming is expected to lead to a loss of soil organic carbon while increasing CO₂ is expected to stimulate plant net primary productivity and increase carbon stocks (Thornley *et al.*, 1991; Kirschbaum, 1993; Lenton & Huntingford, 2003). However, the extent, or even the direction, of the combined effect of both increased CO₂ and climate change still varies greatly between models (e.g. Friedlingstein *et al.*, 2006; Sitch *et al.*, 2008). One of the key parameters in these models is the temperature dependence of organic matter decomposition (e.g. Lenton & Huntingford, 2003), which constitutes one of the central links between climate change and the global carbon cycle.

Many studies have tried to quantify that dependence through the study of specific systems. Much of that work has been summarised in reviews of the responses obtained in different individual studies (Lloyd & Taylor, 1994; Kirschbaum, 1995, 2000; Kätterer *et al.*, 1998; Giardina & Ryan, 2000; Lenton & Huntingford, 2003; Davidson & Janssens, 2006), and additional multi-site comparisons continue to be added to the global data base (Fierer *et al.*, 2006; Kurz-Besson *et al.*, 2006). However, despite that wealth of observations, there is still no global consensus on the quantification of this critically important temperature dependence (Kirschbaum, 2006).

Lloyd & Taylor (1994) had summarised data obtained from field studies, but these observations are likely to be confounded with seasonally changing substrate availability. When conditions are favourable for rapid decomposer activity, it also reduces the availability of the labile substrate necessary for further decomposer activity (Kirschbaum, 2006). This negative feedback between decomposer activity and the availability of labile substrate makes it difficult to confidently infer the underlying intrinsic temperature sensitivity. Kirschbaum (1995, 2000), on the other hand, summarised the findings from short-term laboratory incubations where substrate feed-backs play a lesser role so that the analyses should more directly show the intrinsic temperature sensitivity of organic matter decomposition. Laboratory incubations are, however, conducted under highly artificial conditions and exclude important functional groups such as mycorrhizal fungi and soil fauna.

Both the relationships obtained by Lloyd & Taylor (1994) and Kirschbaum (1995, 2000) indicated a much higher temperature sensitivity (i.e. a greater proportional change in activity for the same change in temperature) at low than at high temperature. This contrasts with a “constant Q₁₀” relationship (which implies the same proportional change in activity per degree increase in temperature) as is often used in global modelling work (e.g. Lenton & Huntingford, 2003; Jones *et al.*, 2005).

If the temperature sensitivity is as strong as that obtained in the reviews of Lloyd & Taylor (1994) and Kirschbaum (1995, 2000), there is greater potential for possible feed-back amplification of climate change than would be the case if the temperature sensitivity were more modest. Jenkinson *et al.* (1991), Kirschbaum (1993, 1995) and others have used the temperature dependence of short-term incubations to predict the effect of climate change on

changes in long-term global carbon stocks and thus assess the potential for positive feedbacks on atmospheric CO₂ concentrations. Others have used simple Q₁₀ functions (e.g. Cox *et al.*, 2000), or the correlation between currently observed short-term fluctuations in CO₂ and temperature, to calibrate appropriate global temperature-response functions of organic matter decomposition (e.g. Jones *et al.*, 2003). Despite the important role of the temperature dependence of organic matter decomposition for future soil carbon stocks, this key process still remains incompletely quantified and thus poorly constrained in global modelling studies.

The question is addressed here whether short-term temperature response function can be used for long-term and global applications, or to what extent they need to be modified to become applicable at different spatial and temporal scales. It specifically assesses how predictions of changes in soil carbon stocks with climate change are affected by the inclusion or omission of inter-annual temperature variations.

Modelling

Annual cumulative organic matter decomposition, d , was calculated as:

$$d = \sum d(T_m) \quad (1)$$

where T_m is monthly mean air temperature (in °C) and $d(T)$ is one of three temperature response functions of organic matter decomposition given below. The interaction between decomposition activity and temperature variations has previously been explored by Ågren & Axelsson (1980) who developed generalised analytical equations that provide a means to analyse the effect of seasonal temperature variations. Using monthly mean air temperatures as the environmental driver was considered to be a reasonable compromise between capturing the range of annual variability experienced by soils while also capturing some of the damping effect of soils that prevent soils from experiencing the extremes of high and low air temperatures. The validity of this assumption is further explored below.

The three temperature response functions of organic matter decomposition were:

$$q(T_m) = \alpha_q Q^{\left[\frac{(T_m+10)}{10}\right]} \quad (2)$$

$$l(T_m) = \alpha_L e^{\left[\frac{-308.6}{(T_m+46.05)}\right]} \quad (3)$$

$$k(T_m) = \alpha_K e^{\left[\frac{3.36(T_m-40)}{(T_m+31.79)}\right]} \quad (4)$$

where $q(T_m)$ refers to the temperature dependence according to a Q₁₀ function, $l(T_m)$ is the relationship given by Lloyd & Taylor (1994) and $k(T_m)$ is the relationship given by Kirschbaum (2000). In these equations, the α -terms determine the absolute magnitude of organic matter decomposition, which is not relevant for the present work as it only considered relative temperature responses. The parameter Q is the Q₁₀ value and was taken as 2 in the following. The other parameters in the equations are the parameters fitted by the respective authors.

For each land location (at ½ degree intervals) across the globe, 12 monthly mean air temperatures were obtained from the data base of Leemans & Cramer (1990), and the annual mean temperature and a temperature range $T_r = T_{m,x} - T_{m,n}$ were calculated where $T_{m,x}$ and $T_{m,n}$ are the monthly mean temperatures in the warmest and coldest months, respectively. Locations with annual mean temperatures below -5°C were excluded because those

locations are subject to permafrost, and it is not expected that the physiological determinants of soil organic matter dynamics can be extrapolated to permafrost systems.

Soil carbon stocks and their changes were calculated with an implementation of the CENTURY model (Parton *et al.* 1987) as described in Kirschbaum (1993). The key response variables were the temperature dependence of net primary production (NPP), $p(T)$, the corresponding CO₂ dependence, $f(C)$, and the temperature dependence of organic matter decomposition, $d(T)$, that has been given in eqn. 4 above. The rate constant modifier $d(T)$ was applied equally to all organic matter transformations in the model. It thus assumed that the decomposition of organic matter fractions with different recalcitrance was equally responsive to temperature.

The model was run at a monthly time step. For assessing the effect of explicitly using seasonal temperature variations, monthly temperatures were set either to their respective monthly values or annual averages were used for every month of the year. Organic matter pools were initialised by running it under pre-industrial conditions ($c_a = 280$ ppmv and the defined temperature as given below) until all organic matter pools had reached steady equilibrium values. The model was then run from 1800 with gradually increasing CO₂ concentration and temperature changes from 1860 as observed to the present and projected to 2100 under the SRES A1 scenario (IPCC, 2000). The proportional differences in organic matter (summed over all pools) between these runs and the 1860 values are shown below.

The temperature dependence of NPP, $p(T)$, was calculated as:

$$p(T) = \frac{P_{max} f(c, T)}{1 + e^{[1.693 - 0.1047T_a]}} \quad (5)$$

where P_{max} is maximum NPP at non-limiting CO₂ and temperature, $f(c, T)$ is the response to CO₂ concentration and T_a is annual mean temperature. This equation is based on Lieth (1973) but with slightly modified parameters (Kirschbaum, 1993). This had been done so that the equation with inclusion of the response to CO₂ concentration responded to temperature in a fashion similar to the original formulation of Lieth (1973) that had not explicitly considered the interaction between temperature and CO₂ concentration. While this equation explicitly includes only temperature as a driver, it implicitly also includes the dependence on other systematically varying drivers, most importantly, solar radiation. For the work reported here, the numeric value of P_{max} did not need to be specified.

The CO₂ response of net primary production, $f(c, T)$, was described following Farquhar & von Caemmerer (1982) as:

$$f(c, T) = \frac{c_i - \Gamma_*}{c_i + 2\Gamma_*} \quad (6)$$

where $f(c, T)$ is the CO₂ response function at a particular CO₂ concentration and temperature, c_i is the intercellular CO₂ concentration and Γ_* is the CO₂ compensation point without non-photorespiratory respiration. The intercellular CO₂ concentration was taken here as being a constant 2/3 of the ambient CO₂ concentration.

Γ_* was calculated following Bernacchi *et al.* (2001) as:

$$\Gamma_* = 42.75e^{\left[\frac{15.26(T_d - 25)}{(T_d + 273.15)} \right]} \quad (7)$$

where T_d is mean daytime temperature.

Different workers have described the time course of temperature throughout the day (e.g. McMurtrie *et al.*, 1990; Goudriaan & van Laar, 1994) from which simplified equations could be developed (e.g. Running *et al.*, 1987; Goudriaan & van Laar, 1994). After comparing diurnal time courses under a range of assumptions, the equation of Goudriaan & van Laar (1994) was used to calculate daytime temperature for the present work as:

$$T_d = 0.71 T_{max} + 0.29 T_{min} \quad (8)$$

where T_{max} and T_{min} are daily maximum and minimum temperatures. With diurnal temperature ranges across the globe typically being around 10°C (Durre & Wallace, 2001; Makowski *et al.*, 2008), and applying eqn. 8, T_d was set at 2°C above T_m .

In addition, the CO₂ sensitivity was weighted towards the months of the year with moderate temperatures, using a hump function so that

$$P_t = 0 \quad \text{if } T_m \leq 0^\circ\text{C} \quad (9a)$$

$$P_t = T_m / 20 \quad \text{if } 0^\circ\text{C} < T_m < 20^\circ\text{C} \quad (9b)$$

$$P_t = 1 \quad \text{if } 20^\circ\text{C} \leq T_m \leq 30^\circ\text{C} \quad (9c)$$

$$P_t = (40 - T_m) / 10 \quad \text{if } 30^\circ\text{C} < T_m < 40^\circ\text{C} \quad (9d)$$

$$P_t = 0 \quad \text{if } T_m \geq 40^\circ\text{C} \quad (9e)$$

where P_t is the photosynthetic contribution in a particular month. A combined annual CO₂ response function was then calculated as:

$$f(C) = \frac{\sum_{m=1}^{12} P_t f(c, T_m)}{\sum_{m=1}^{12} P_t} \quad (10)$$

The model was run here with and without nitrogen feed-back limitations. For runs without nitrogen limitation, nitrogen inputs were simply set to high values so that nitrogen dynamics did not become limiting.

For runs with nitrogen limitation, the key processes were:

- 1) It was assumed that 5% of mineralised nitrogen was lost during nitrogen turn-over (Parton *et al.*, 1987; Kirschbaum, 1993).
- 2) Nitrogen input into the system was linked to carbon fixation and set to 0.2% of carbon fixation. That ensured that the processes that stimulated carbon fixation, such as increased temperature and elevated CO₂ concentration, also stimulated nitrogen input into the system (Kirschbaum, 1993).

For testing the effect of using daily, weekly, monthly or annual temperatures on calculating total annual decomposition activity, daily soil and air temperatures observed at a site in Australia were used (Leuning *et al.*, 2005) in order to obtain a realistic sequence of day to day variability. In this data set, annual mean soil temperature was about 0.4 °C higher than annual mean air temperature. Synthetic sequences were then generated from these data by varying either mean or interannual variability by calculating synthetic data as:

$$T_{s, i} = T_d + T_{mean} + v (T_{o, i} - T_{mean}) \quad (11)$$

where $T_{s, i}$ is the synthetic temperature generated for day i , based on $T_{o, i}$, the observed temperature for that day, T_{mean} is the observed overall mean temperature, T_d is an applied temperature offset and v is a parameter that determines the interannual variance in the

synthetic data. So, for $T_d = 0$, $\nu = 1$, the derived synthetic data would be identical to the observed data, and for $T_d = 0$, $\nu = 0$, the derived synthetic data would have no interannual variance.

These derived synthetic soil and air temperatures were then either taken as daily values, or averaged weekly, monthly or annually, and those temperatures were used with eqn. 4 to generate respective annual decomposition rates. Rates calculated from daily soil temperatures were taken as the correct reference values, and rates calculated based on any of the other derived temperatures were compared against these reference values.

Results

Seasonal temperature variation

Soil temperature typically lags behind air temperature because of the inertia of buffering by the large soil mass. Soil therefore typically do not experience the same extremes of high and low temperatures that may be evident in air temperature. The use of monthly data is useful in that it similarly excludes extremes of high and low data while capturing a large part of annual temperature variations.

This was tested for a site in eastern Australia for which detailed air and soil-temperature measurements were available over a period of 3 years (Leuning *et al.*, 2005). This allowed exploration of the effect of using daily data (Fig. 1b) or averaging them over a month (Fig. 1c).

Daily soil temperatures did not correlate very well with daily air temperatures ($r^2 = 0.888$) because of the buffering effect of the soil. Not only was there much random variation, but the slope of the relationship was also only 0.81 as the extreme highs and lows of air temperature were not reflected in similar variations in soil temperature (Fig. 1b). In contrast, when monthly averages were used, air temperature and soil temperature correlated much more strongly ($r^2 = 0.974$) and the slope of the relationship was closer to 1 (Fig. 1c).

Figure 1: Observed soil temperature (a), and soil temperature plotted against air temperature using either daily (b) or averaged monthly (c) values. Data from Leuning *et al.* (2005).

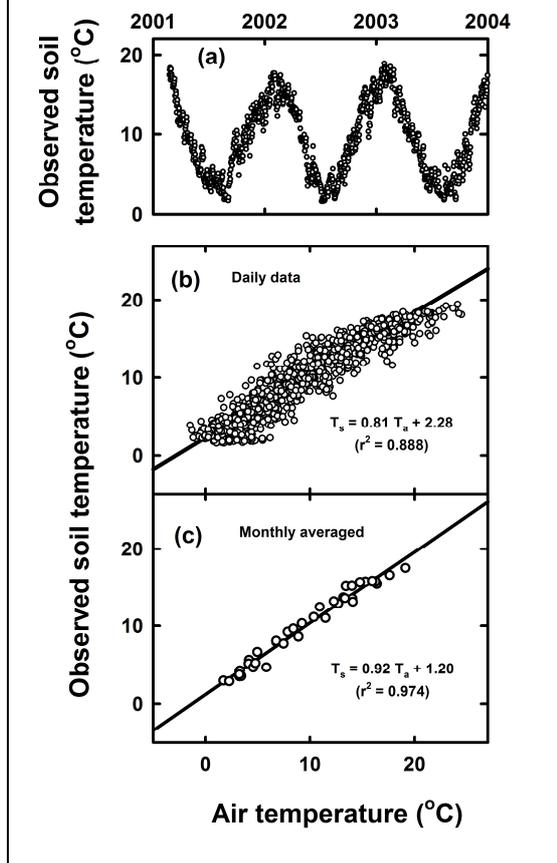
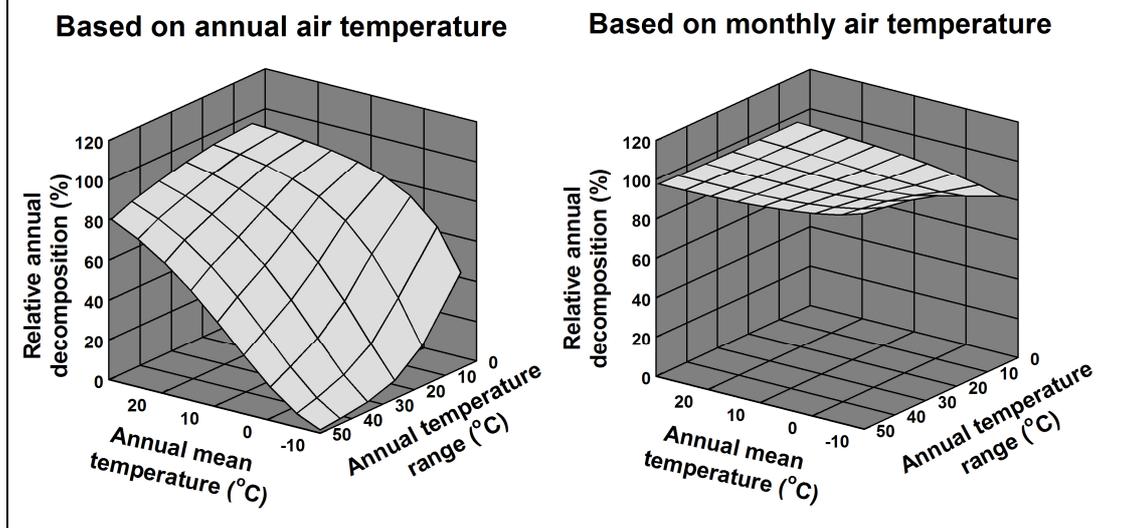


Table 1: Comparison of annual decomposition activity calculated based on daily, weekly, monthly or annually averaged soil or air temperatures. All results are expressed relative to the activity calculated based on daily soil temperatures. These calculations are based on the temperatures shown in Figure 1.

	Daily	Weekly	Monthly	Annual
Soil temp	100%	99.4%	98.6%	87.2%
Air temp	99.4%	96.9%	95.0%	82.0%

The use of temperature averaging was further tested by calculating annual decomposition activity with eqn. 4 with either daily air or soil temperatures, or values that were averaged weekly, monthly or annually (Table 1). The activity based on daily soil temperatures was taken as the truest indication of the total decomposition activity that would have been expected in this soil. Very little bias would be introduced if weekly or monthly averaged soil temperatures were used instead, but with annually-averaged values total activity would be underestimated by 13%. If air temperatures were used instead, virtually no bias would be introduced if daily values were used but calculated values would be underestimated by 3.1%, 5.0% and 18% for temperatures averaged weekly, monthly or annually, respectively.

Figure 2: The effect of using annual mean air temperature or monthly mean air temperature for estimating annual decomposition activity. All data are expressed as a percentage of the decomposition activity calculated from daily soil temperatures.



It is noteworthy that decomposition activity based on daily air temperatures was nearly identical to activity based on daily soil temperatures despite the poor correlation between them (Fig. 1b). Soil temperatures also did not reach the same high temperatures as air temperature which means that activity calculated from air temperatures should have been higher. However, measured soil temperatures in this system were on average 0.4°C warmer than air temperatures. This warmer average temperature in the soil compensated for the absence of the high-temperature peaks seen in air temperature, with the result that total calculated decomposition activity was nearly identical (Table 1).

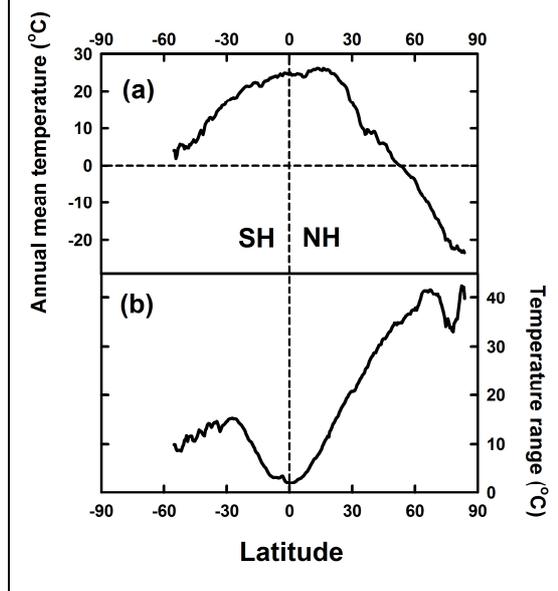
In the observed data set, the effect of different averaging periods was only moderate because the site's mean temperature was reasonably high and its annual temperature range moderate (Fig. 1). For sites with lower annual mean temperatures, or a wider seasonal temperature range, the effect of different averaging periods is likely to be much more important (Fig. 2). When annual air temperature averages are used as the basis for calculation, it introduces massive errors for sites where annual mean temperatures are low and the annual temperature range is large. When calculations for such sites are based on the annual mean temperature it would suggest that there should be almost no decomposition activity at all, whereas in reality, substantial activity is possible over the warmer summer months.

In contrast, calculations based on monthly averages remove most biases over the whole range of mean temperatures and annual temperature ranges. Errors introduced by basing calculations on monthly averages remain within a range of +/- 10% even under the most extreme temperature conditions (Fig. 2). This comparison provides good support for the use of monthly-averaged air temperatures as a means to provide an approach with little bias for assessing the effect of seasonal temperature variations on organic matter decomposition.

The observed patterns of annual mean temperature and annual temperature range are shown as functions of latitude in Figure 3. Annual mean temperature is highest about 15° north of the equator, and then falls steadily towards high northern latitudes (Fig. 3a). The annual mean temperature also falls as one moves south, but the fall-off is less steep than in the northern hemisphere, and there are no significant land masses beyond about 55° S.

The annual temperature range is smallest near the equator and increases towards much larger values in the northern hemisphere before the pattern becomes somewhat irregular beyond 60° N (Fig. 3b). This increase in temperature amplitude towards high northern latitudes is driven by the large effect of seasonally changing solar radiation which leads to strong temperature fluctuations on the massive land masses of Eurasia and North America.

Figure 3: Global annual mean air temperature (a) and annual temperature range (b) as a function of latitude for land-based locations. Temperature range is the temperature difference between air temperature in the warmest and coldest months. Data are expressed as latitudinal means in ½ degree bands. Data after Leemans & Cramer (1990).



The pattern on the southern hemisphere mirrors that on the northern hemisphere only up to about 30° S, but further south, the temperature amplitude diminishes again because the existing land areas tend to be close to oceans or even just small islands so that a moderating maritime influence largely negates the effect of seasonal variations in solar radiation and leads to a flat or even reducing temperature amplitude as one moves further south beyond 30° S (Fig. 3b).

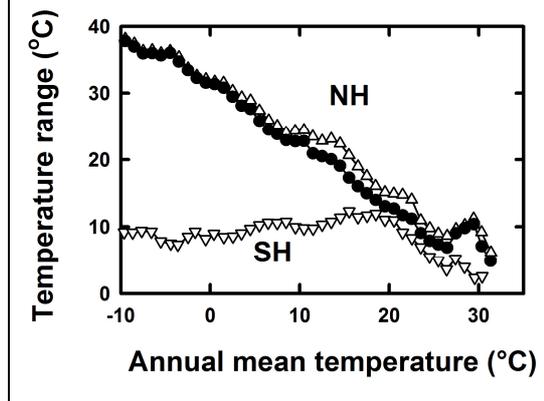
The annual temperature range expressed as a function of annual mean temperature, consequently shows distinctly different patterns for the southern and northern hemispheres (Fig. 4). While the annual variations in solar radiation is very similar for the southern and northern hemispheres, the moderating oceanic influence is much more pronounced for the southern than the northern hemisphere.

The land-area-weighted global relationship between annual temperature range and annual mean temperature is dominated by the pattern found in the northern hemisphere at temperatures below about 15°C because a vastly greater land area in the northern hemisphere experiences these cooler annual mean temperatures than in the southern hemisphere. The global pattern is shared between the two hemispheres only at temperatures higher than about 15-20°C where the patterns also becomes more similar for the two hemispheres (Fig. 4).

Temperature Dependence of Organic Matter Decomposition

When sites with low annual mean temperature have a large annual temperature range, even these sites can experience some months with favourable temperatures. Those favourable temperatures then enable greater organic matter decomposition than would be possible if soils at these sites would be experiencing their mean temperature throughout the year (Fig. 5). This has little effect at warm sites but is critically important for soils with low annual mean temperature. Actual organic matter decomposition in cold soils can therefore be much greater than would be predicted from calculations based solely on a site's annual mean temperature (Fig. 2).

Figure 4: Annual temperature range plotted against annual mean temperature with each point representing the mean of all values in a one-degree band of annual mean temperature. Data for the northern hemisphere (Δ), southern hemisphere (∇) and (\bullet) the area-weighted mean of both hemispheres. The relationship between global area-averaged annual mean temperature and temperature range can be approximated by: $T_r = 31 - 0.85 T_a$. Data after Leemans & Cramer (1990).



The greater the annual temperature range the greater is the deviation from the response predicted based on annual mean temperature alone. This is further illustrated in Figure 6 which shows relative annual decomposition activity as a function of temperature. The graph illustrates several key aspects. For the same annual mean temperature, total decomposition activity increases with the magnitude of the annual temperature range. It simply indicates that soils with low annual mean temperature, but a wide temperature range experience a larger part of the year at a high temperature than a soil with the same mean temperature but a lesser temperature range.

The graph also shows that the proportion of site with a high temperature range decreases as annual mean temperature increases. Hence, at -5°C, about ¼ of sites experience an annual temperature range of more than 40°C, whereas no site with annual mean temperature above 6°C, experiences such a wide temperature range. Conversely, below 0°C, there are few sites with temperature range of less than 20°C, but above 10°C, more than a ⅓ of sites have such a narrow annual temperature range.

Figure 5: Relative annual decomposition activity (relative to rates at optimal temperature) as a function of annual mean temperature. Data points show individual locations where calculations were based on the specific annual mean temperatures and temperature ranges at those locations. The solid line gives an equation fitted through those points and the dashed lines gives the relationship that would have been expected if the temperature were constant throughout the year. For clarity, only 2% of randomly selected sites are shown.

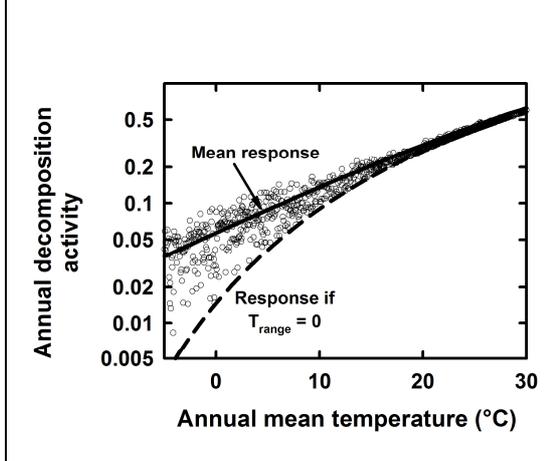
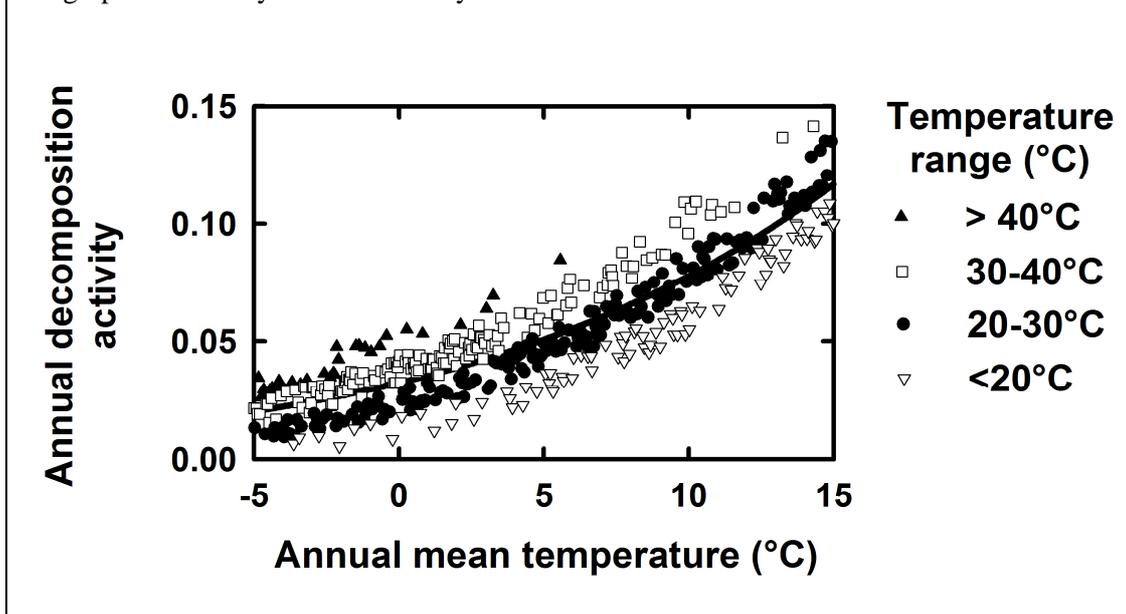


Figure 6: Calculated annual decomposition activity (relative to the rate at optimum temperature) as a function of annual mean temperature. Each data point refers to a different location, and different symbols refer to the annual temperature range of respective locations. The solid line drawn through the points give a line of best fit fitted to all the data. For clarity, this graph shows only 2% of randomly selected locations out of the whole data set.



Explicit inclusion of the annual temperature range has the consequence that the differences between temperature response functions greatly diminishes (Fig. 7). The function developed by Kirschbaum (2000) shows a very strong temperature dependence at low temperatures, with a Q_{10} exceeding 6 at temperatures below 6 °C (Fig. 7a). But averaged over a whole year, with inclusion of the correlation between annual temperature and the annual temperature range, this very steep temperature sensitivity flattens to a much more moderate temperature sensitivity with a Q_{10} of only 2.6 at 0°C.

The equation of Lloyd & Taylor (1994) also increases to reasonably steep values of a Q_{10} of about 4.5 at 0°C, but flattens to a Q_{10} of 2.3 at 0°C for calculations based on annual values. Both equations retain their property of an increase in temperature sensitivity at lower temperature when integrated over a whole year, but that pattern is much less pronounced than for short-term responses.

The strong temperature sensitivity is largely lost over annual time steps because the steeper the temperature response, the less important the contribution during the colder months becomes (Ågren & Axelsson, 1980). In addition, as the temperature range decreases with increasing temperature, it means that temperatures in the warmest months of the year are much more similar across the globe than annual mean temperatures. Since annual organic matter decomposition is dominated by the activity during the warmest months of the year, the differences between sites with different temperatures are therefore greatly reduced, and the temperature response functions become more similar.

This indicates that temperature response functions are context specific. Temperature response functions based on observations at one temporal scale can only be applied at a different temporal scale if the variability within the longer time scale is explicitly considered and included to derive a different response function at the longer time scale.

Changes in Soil Carbon Stocks

These considerations are then applied to an assessment of likely trends in soil organic carbon stocks and the potential for any positive or negative feedbacks between climate change and soil organic carbon stocks based on calculations with the CENTURY model (Parton *et al.*, 1987; Kirschbaum, 1993).

Figure 7: Relative temperature dependence of decomposition activity for short-term (a) or annually averaged values based on the empirically observed natural temperature patterns across the world (b). Three equations are displayed, those developed by Lloyd & Taylor (1994), Kirschbaum (2000) and a simple $Q_{10} = 2$ relationship.

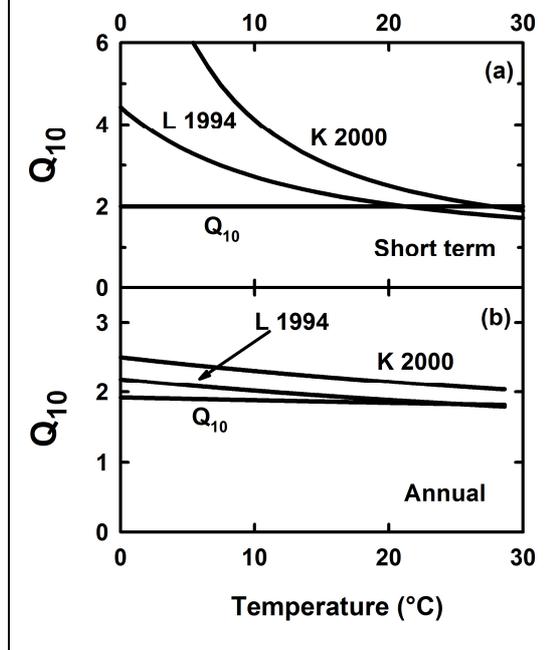


Figure 8: Change in soil organic carbon stocks (a, c, e) and net primary production (b, d, f) at different temperature anomalies (g) and CO₂ concentration (h) as observed since 1860, and as anticipated to the end of the 21st century based on the SRES A1 (IPCC, 2000) scenario. These calculations are done for three base temperatures as given in the Figure, with global temperature anomalies added to those base temperatures. Calculations are done at annual time steps (a, b), with inclusion of the seasonal but not the nitrogen cycle (c, d), and with inclusion of both seasonal and nitrogen cycles (e, f).

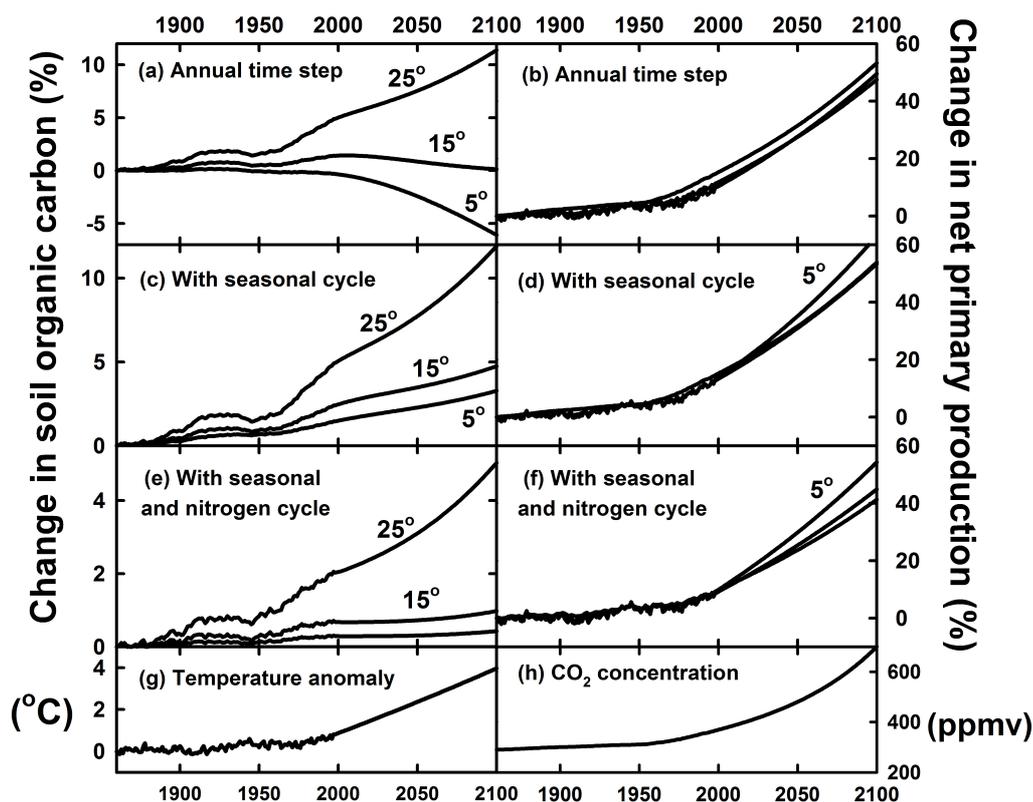


Figure 8a shows that for calculations at an annual time step, the effect of increasing CO₂ concentration dominates for warm soils (at 25°C), leading to increasing carbon stocks over the past 150 years and anticipated further increases over the 21st century (Fig. 8a). In contrast, for cool soils, the effect of warming would have a greater effect than increasing CO₂ concentration, with the consequence of carbon losses, especially over the 21st century.

However, once seasonal temperature fluctuations are explicitly incorporated, the response to changes in temperature and CO₂ concentration becomes positive for all regions. The positive effect for cold soils is caused by two reasons: Firstly, when the seasonal cycle is included, overall activity starts to be dominated by the activity during warmer months, and for warmer temperatures, the stimulation by further temperature increases is less than for activities at cooler temperatures (Fig. 7a). Secondly, the CO₂ responsiveness of primary production, and thus carbon input for organic matter formation, is much greater at higher than lower

temperature (see Eqns. 8, 9), and with explicit inclusion of the seasonal temperature cycle, carbon gain is concentrated in the warmer months and the stimulatory effect of elevated CO₂ is thus greater than for calculations based on annual mean temperature.

For warm soils, inclusion of the seasonal cycle has little effect on expected organic-matter trends. The magnitude of the response to altered conditions is also still expected to be much larger for warmer than colder soils (Fig. 8c). This difference remains because even with consideration of the seasonal temperature cycle, total annual organic matter decomposition activity in soils from cold regions is still considerably less than that in soils from warmer regions so that these soils are much slower to respond to changes in input and output conditions.

Inclusion of constraints through nitrogen cycling reduces the response to environmental change at all temperatures, but especially for colder soils (Fig. 8e). Inclusion of nitrogen cycling constraints reduces the calculated increase in soil carbon by about half at 25°C and by even more for the cooler soils at 15 and 5°C. When conditions change to favour carbon accumulation, it intensifies existing nutrient limitations and thereby limits the short-term response to the more favourable conditions. This feed-back effect is more pronounced for cooler soils because of the slower carbon turn-over rates in those soils.

Stimulation of net primary production is similar for soils at the different temperatures (Figs. 8b, d, f) although the responsible factors differ. Plants in warm regions benefit primarily from increasing CO₂ concentration, whereas in cooler regions, stimulation by increasing temperature is more important. Inclusion of the seasonal cycle slightly increases the NPP stimulation (Fig. 8d) because plants effectively operate at higher temperatures at which CO₂ sensitivity is greater. NPP stimulation is reduced once nutrient limitations are explicitly included (Fig. 8f) because nutrition provides a negative feedback that limits the NPP responsiveness when conditions favour enhanced productivity.

General Discussion

The temperature dependence of organic matter decomposition is a central link between climate change and its effect on the global carbon cycle. The evidence from detailed site level investigations generally indicates that organic matter decomposition has a strong temperature dependence. This has been concluded from a number of reviews (e.g Lloyd & Taylor, 1994; Kirschbaum, 1995, 2000) and incorporated in the Rothamsted (Jenkinson *et al.*, 1991) and CENTURY (Parton *et al.*, 1987) models, the two most widely used organic-matter turn-over models.

At the same time, global models generally use models with weak temperature responses. Lenton & Huntingford (2003), for example, concluded that the use of a temperature response function with a Q₁₀ greater than 3 would not result in realistic simulations in their global model. However, their model used an annual time step, and the work presented here indicates that a strong short-term temperature response can be consistent with a weak annual temperature response (Fig. 7). Recognition of the time-scale dependence of temperature sensitivity helps reconcile these divergent conclusions from different studies.

Explicit inclusion of the seasonal temperature cycle reduces the earlier concerns of strong positive feed-back between global warming and soil carbon stocks. This concern was strongly expressed through the work of Jenkinson *et al.* (1991), but that concern was already reduced once the positive effect of increasing CO₂ concentration and the dampening effect of nutrient feed-backs had been factored in (Thornley *et al.*, 1991; Kirschbaum, 1993). A shift of analysis from using annual to monthly temperatures (Figs. 8a, 8c) changes even the

direction of expected soil-carbon stock changes for soils in cold regions, with inclusion of monthly temperatures having little effect on the patterns in warmer regions of the world.

Jones *et al.* (2005) showed that predicted response patterns can also differ significantly depending on the details of the organic matter turn-over model that is used. Key elements that determine the strength of that feedback effect are the complexity of the soil organic matter model used and the underlying temperature sensitivity of organic matter decomposition. Jones *et al.* (2005) showed that use of a simpler one-pool organic carbon model leads to significantly greater soil-carbon feed-back than equivalent simulations with the more complex Rothamsted model that subdivides soil-organic matter into a number of pools with different turn-over times. The Rothamsted model showed less feed-back response even though it used a much greater temperature sensitivity than the simple one-pool model for which a constant Q_{10} of 2 was used across the whole temperature range.

Most global models still do not use nutrient-cycle feedback limitations even though it is clear that the inclusion of nutrient cycling would dampen any response to external driving forces (e.g. Thornton *et al.*, 2007; Figs. 8c-8f). While it is thus clear that nutrient cycling is important, it is much less clear how it should be implemented, how strongly nutrition currently limits productivity across the globe, and in what way nutrient inputs and losses are likely to change in response to changing external conditions. Nonetheless, while the functional form of nutrient dynamics might be uncertain, it is clear that many systems are affected by nutrient limitations and that interactions with those limitations will play an important role in any future response to changed environmental conditions (Thornton *et al.*, 2007; Reay *et al.*, 2008).

The work of Sitch *et al.* (2008) conducted a comparison study with five dynamic global vegetation models and showed that all models predicted soil-carbon losses with 21st century (non-CO₂) climatic changes, that they predicted increases in soil carbon in response to elevated CO₂, but that there was a divergence in predicted responses between models when both CO₂ and climatology were changed together. Most of the model predicted increases in carbon that were similar to the simulations shown here (Fig. 8), but there were also exceptions to those predictions.

The models used by Sitch *et al.* (2008) did not exhibit the large losses of terrestrial carbon shown in the Cox *et al.* (2000) and Jones *et al.* (2005) simulations. The extent of divergence between model estimates thus continues to be disconcerting. The urgency of climate change mitigation efforts is strongly affected by the extent of any possible biospheric, or oceanic, feed-back processes that might be expected. It is therefore urgent and warranted to conduct further work on trying to identify the likely causes for model discrepancies and generate the most appropriate formulations for future use to best describe the patterns that actually occur in the biosphere.

Ise & Moorcroft (2006) used global observations of existing soil carbon stocks to calibrate the temperature sensitivity of organic matter decomposition. They used monthly climatic data and independently assessed the temperature and moisture limitations of each grid point. With their analysis, they derived a very weak temperature dependence of organic matter decomposition. However, in deriving that estimate, they also modified the carbon-input function from the equation originally developed by Lieth (1973) into one with very little temperature dependence across the range of relevant temperatures. If such a flat temperature dependence for carbon input is used, it is perhaps not surprising that a flat temperature response for carbon loss would be required to match the observed patterns of carbon stocks.

In constraining the temperature dependence of organic matter decomposition by observed patterns of carbon stocks, the temperature dependence of carbon input, which can be taken as proportional to net primary production, is a critical additional link. This temperature dependence of NPP was originally estimated by Lieth (1973) which has been used extensively since then, including for the present work. Various workers (e.g. Schuur, 2003; Kerkhoff *et al.*, 2005; Zaks *et al.*, 2007; del Grosso *et al.*, 2008) have recently attempted to provide updated relationships of the temperature dependence of net primary production based on the much larger data base of net primary production across the globe that is available now. However, the equations presented by these different authors still diverge widely. If global patterns of carbon stocks are used as the key constraint, then any uncertainty in the temperature dependence of carbon-input rates leads to a corresponding uncertainty in the temperature dependence of carbon-loss rates. Observed patterns of carbon stocks therefore cannot currently provide a strong constraint on the temperature dependence of organic matter decomposition.

Other key conceptual issues revolve around interactions between temperature dependence of organic matter decomposition and substrate limitations, between temperature and moisture limitations and around the interaction between chemical recalcitrance and the temperature dependence of decomposition. The issue of substrate limitations was highlighted by Gu *et al.* (2004), Nicolardot *et al.* (1994), Kirschbaum (2006) and others. In essence, if favourable temperatures lead to faster substrate depletion it can reduce the apparent effect of temperature on organic matter decomposition and thus lead to an apparent weak temperature dependence. This factor caused Davidson & Janssens (2006) to call for a distinction to be made between intrinsic and apparent temperature dependencies of organic matter decomposition, with intrinsic dependence referring to the temperature response at a biophysical and enzymatic level as it would manifest itself at a given level of substrate availability and specific environmental conditions, whereas the apparent temperature dependence is the actually observable dependence where substrate availability and other environmental variables also change in response to changes in temperature.

The problem of feedback limitations has been clearly highlighted in the case of soil warming experiments. Many soil-warming experiments provide only weak apparent temperature sensitivities of organic matter decomposition, which has been linked to possible acclimation of decomposer organisms (e.g. Luo *et al.*, 2001; Strömberg, 2001). An alternative explanation has implicated changes in the availability of labile substrate to explain these observed results (e.g. Kirschbaum, 2004; Eliasson *et al.*, 2005). Recent work has attempted to distinguish between acclimation and substrate feedbacks through a detailed study of a warmed ecosystems (Bradford *et al.*, 2008). They concluded that both substrate depletion and some degree of thermal acclimation appeared to play a role in explaining reduced CO₂ efflux rates in their warmed plots.

Moisture limitations can also negatively interact with the temperature dependence of organic matter decomposition. It is well-recognised that organic matter decomposition can be limited by moisture conditions in the soil (e.g. Paul *et al.*, 2003). Since moisture limitations tend to become more pronounced with increasing temperature, any intrinsic temperature dependence can be masked in observational data because a positive stimulation by temperature can be negated if moisture limitations become more severe at higher temperature (e.g. see Kirschbaum, 2000). For that reason, Lloyd & Taylor (1994) aimed to restrict their data compilation to sets that were judged to have been unaffected by moisture limitations, but such precautions are not taken by all researchers. It is, therefore, not always clear whether reported apparent temperature dependencies correspond to intrinsic

temperature dependencies or whether confounded changes with other environmental variables have modified any intrinsic temperature dependence.

To date, models generally had to assume that the decomposition of all different organic matter constituents is equally sensitive to temperature. This assumption was also made for the present work. However, the extrapolation from short-term to long-term responses could lead to vastly different outcomes if the temperature sensitivity of organic matter decomposition were very different for labile and more recalcitrant organic matter fractions (e.g. Thornley & Cannell, 2001). It is now generally assumed that if there are differences in temperature sensitivity, the decomposition of more recalcitrant fractions is more likely to be more sensitive to temperature than that of more labile fractions (e.g. Ågren & Wetterstedt, 2007), but experimental support for this notion is still inconsistent (e.g. Reichstein *et al.*, 2005; Conant *et al.*, 2008; Smith *et al.*, 2008). Further work will hopefully further clarify this key interaction, but at the present stage, it is considered to still be most appropriate to assume the same temperature sensitivity for all organic matter fractions.

Despite the remaining uncertainty around some key questions, it is clear, however, that the temperature dependence of organic matter decomposition is of considerable importance for the Earth's response to climate change. If global warming leads to significant losses of soil carbon it will constitute a dangerous feedback that can significantly increase future warming. It will have a strong bearing on the extent of any response of the Earth to the cumulative load of fossil-fuel based CO₂ emissions (Cox *et al.*, 2000; Cramer *et al.*, 2001; Friedlingstein *et al.*, 2003; Jones *et al.*, 2005). On the other hand, if biosphere carbon stocks were to increase in response to the combined effect of changes in the climate and CO₂ concentration (Sitch *et al.*, 2008; Fig. 8), it would provide lesser urgency in anthropogenic emission reductions. It is thus extraordinarily important to better understand the direction and strength of biospheric feedbacks for making rational future climate mitigation policy, and further work in that area is urgently needed.

Conclusions

The work shown here indicates that the temperature dependence of organic matter decomposition cannot be quantified without specifying the spatial and temporal scale over which it is used. Short-term measures of the temperature dependence cannot be applied at different temporal scale without explicitly considering the variability of temperature over the longer temporal scale.

The same issue also affects application at different spatial scale through interaction between annual mean temperature and monthly temperature variation between sites. There is a wealth of observations at small and short scales. Long-term and global responses can be derived from these short-scale observations, but scaling up needs to be done with further analyses to understand and incorporate the factors that operate and interact at these various scales of interest.

Incorporation of these considerations leads to the conclusion of more positive carbon trends in the recent past, and into the future. Nitrogen-cycling constraints add a factor to stabilise existing soil-carbon stocks. The direction and strength of any possible feed-backs from carbon storage in the biosphere has a strong bearing on future expectations of ultimate climate change associated with a given amount of fossil-fuel emissions. Improved understanding of these feed-back processes is thus urgently needed.

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