Biogeochemistry **48:** 21–51, 2000.

Will changes in soil organic carbon act as a positive or negative feedback on global warming?

MIKO U.F. KIRSCHBAUM
CSIRO Forestry and Forest Products, PO Box E4008, Kingston ACT 2604, Australia (Phone: +61 2 6281 8252; Fax: +61 2 6281 8312; e-mail: Miko.Kirschbaum@ffp.csiro.au)

Received 4 March 1999; accepted 16 April 1999

Key words: carbon cycle, decomposition, global change, soil organic matter, temperature

Abstract. The world's soils contain about 1500 Gt of organic carbon to a depth of 1m and a further 900 Gt from 1–2m. A change of total soil organic carbon by just 10% would thus be equivalent to all the anthropogenic CO_2 emitted over 30 years. Warming is likely to increase both the rate of decomposition and net primary production (NPP), with a fraction of NPP forming new organic carbon. Evidence from various sources can be used to assess whether NPP or the rate of decomposition has the greater temperature sensitivity, and, hence, whether warming is likely to lead to an increase or decrease in soil organic carbon.

Evidence is reviewed from laboratory-based incubations, field measurements of organic carbon storage, carbon isotope ratios and soil respiration with either naturally varying temperatures or after experimentally increasing soil temperatures. Estimates of terrestrial carbon stored at the Last Glacial Maximum are also reviewed. The review concludes that the temperature dependence of organic matter decomposition can be best described as: $d(T) = \exp[3.36\,(T - 40)/(T + 31.79)]$ where d(T) is the normalised decomposition rate at temperature T (in °C). In this equation, decomposition rate is normalised to '1' at 40 °C.

The review concludes by simulating the likely changes in soil organic carbon with warming. In summary, it appears likely that warming will have the effect of reducing soil organic carbon by stimulating decomposition rates more than NPP. However, increasing CO_2 is likely to simultaneously have the effect of increasing soil organic carbon through increases in NPP. Any changes are also likely to be very slow. The net effect of changes in soil organic carbon on atmospheric CO_2 loading over the next decades to centuries is, therefore, likely to be small.

Introduction

Estimates of total global soil organic carbon are converging on about 1500 Gt C in the top one metre (Adams et al. 1990; Anderson 1992; Eswaran et al. 1993; Batjes 1996), with possibly as much as another 900 Gt at a depth of 1–2 metres (Batjes 1996). These estimates include a large amount of charcoal, especially in areas where vegetation is subject to frequent burning (e.g. Kuhlbusch & Crutzen 1995; Skjemstad et al. 1996). There are also 700–800 Gt carbonate carbon in the top one metre (Schlesinger 1982; Batjes 1996).

Because of the large amounts of carbon involved, if Greenhouse-gas induced climate change were to cause even small relative changes in organic carbon, it could constitute a significant feed-back effect on Greenhouse gases in the atmosphere. A change by just 10% in soil organic carbon would be equivalent to all the anthropogenic CO_2 emitted over 30 years.

Changes in stored charcoal are unlikely to be important in terms of feed-back effects with the atmosphere as charcoal is extremely inert and could not be lost at significant rates, although changes in burning regime could alter the formation rate of new charcoal. Carbonates, which are mainly found in desert soils, originate from the weathering of parent material and remain *in situ* in arid environments with low acidity, and where Ca^{++} or Mg^{++} are not removed through leaching.

Carbonates might be lost with climate change if currently dry environments were to become wetter, with cations leached from the soil and CO_2 being released to the atmosphere. Any build-up of carbonates in currently moist regions that may become drier, however, is likely to be less important as its rate of build-up would be very slow and is essentially determined by the rate of rock weathering.

The question that is addressed here is whether decomposition rate or net primary production (NPP) are more responsive to increasing temperature, and whether changes in soil organic carbon would consequently act as positive or negative feedbacks on climate change. If soil organic carbon were to increase with warming it would constitute a negative feed-back. It would lower the build-up of CO_2 in the atmosphere and reduce further warming. A loss of organic carbon with warming, on the other hand, would constitute a positive feed-back by further adding to the build-up of CO_2 in the atmosphere.

Whether changes in soil organic carbon act as a positive or negative feed-back essentially depends on the relative temperature dependencies of NPP and soil organic carbon decomposition rates (Figure 1). Carbon enters ecosystems through photosynthesis, of which a fraction is lost in autotrophic respiration. The net gain is the net primary production (NPP). In natural systems, this carbon is eventually transferred to the soil in litter fall, root turn-over or death of individual plants, thus providing the substrate for the formation of soil organic carbon.

Carbon is eventually returned to the atmosphere by decomposition of soil organic carbon (heterotrophic soil respiration). The rate of organic carbon decomposition is determined by soil specific factors (texture, pH, etc.), climatic factors and by the amount of soil organic carbon present, which can be expressed either as the total amount of organic carbon (Olson 1963), or as the amount in different fractions with different decomposability as is used in

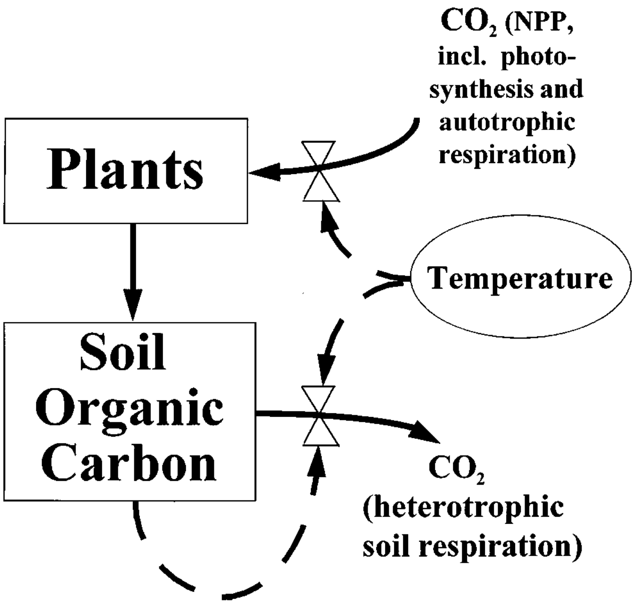

Figure 1. Diagrammatic representation of the basic relationship between carbon gain and carbon loss from whole ecosystems.

most organic carbon simulation models (e.g. Parton et al. 1987; Jenkinson et al. 1991).

In the steady state, carbon gain by the system over a year or more must equal carbon loss so that:

$$p(T)\ f_o\ P = d(T)rO, \qquad (1)$$

where P is NPP at optimal temperature, f_o the fraction of NPP that is added to the pool of soil organic carbon, O the soil organic carbon pool, and r is the fraction of total organic carbon that can decompose at optimal temperature over one year. The functions p(T) and d(T) describe the temperature dependence of NPP and organic carbon decomposition, respectively.

Amounts of organic carbon are not likely to ever be in a true steady state (see 'The Question of Time' below) as they are generally adjusting to past changes in conditions at all time schedules from daily to millennial. However, for the purposes of this discussion, the assumption of steady state is an appropriate place to start.

Eq. 1 can be rearranged and simplified to

$$O/k = p(T)/d(T), \qquad (2)$$

where $k = f_oP/r$ which can be treated as constant for a given set of soil and environmental conditions other than temperature. It may differ, however, if vegetation type were to change as different plant communities may have different NPP, different decomposability or different fractions of NPP that add to soil organic carbon.

We can then take the derivative of Eq. 2 with respect to temperature as

$$\frac{d(O/k)}{dT} = \frac{d(T)p'(T) - p(T)d'(T)}{d(T)^2} \tag{3a}$$

or

$$\frac{d(O/k)}{dT} = \frac{p'(T)/p(T) - d'(T)/d(T)}{d(T)/p(T)}, \tag{3b}$$

where $p'(T)$ and $d'(T)$ are the derivatives of $p(T)$ and $d(T)$, respectively. There is positive feed-back in the global carbon cycle if organic carbon decreases with increasing temperature: $d(O/k)/dT < 0$. That is the case if the relative temperature sensitivity of net primary production, $p'(T)/p(T)$ is less than the relative temperature sensitivity of organic carbon decomposition, $d'(T)/d(T)$.

An equation to describe the temperature dependence of NPP and a number of equations commonly used to describe the temperature dependence of organic carbon decomposition are described and discussed in the Appendix.

Various experimental and modelling approaches can be used to identify the functional form of the temperature dependence of organic carbon decomposition, d(T). This can be done through direct approaches or indirectly through the effect on the resultant total soil organic matter under different temperature regimes. In the following Sections, a variety of research approaches are reviewed to try and determine the temperature dependence of organic carbon decomposition.

Estimates of soil organic matter under different climatic regimes

Various studies have estimated the amount of total terrestrial or soil carbon stored during past climatic or anticipated future climatic conditions. One approach is based on modelling the distribution of biomes at the Last Glacial Maximum (about 18,000 years ago) or under $2\times CO_2$ climate scenarios. To get an estimate of total biospheric carbon storage, the carbon stored by each biome was multiplied by the area covered by that biome (Prentice & Fung 1990; King & Neilson 1992; Smith et al. 1992; Friedlingstein et al. 1992; Prentice et al. 1993; van Campo et al. 1993; Cramer & Solomon 1993; Solomon et al. 1993; Neilson 1993; Prentice & Sykes 1995).

A second approach has been used for past climatic conditions by using palaeoecological information rather than climate modelling to infer the distribution of vegetation types (Adams et al. 1990; Crowley 1995). A third approach was based on modelling the response of carbon fixation and decomposition rates to CO_2 concentration and temperature for each biome and then summing this over all different biomes (King et al. 1997). A fourth approach was based on constraining the total carbon budget by the observed changes in carbon isotopes in the oceans and atmosphere (Crowley 1991, 1995; Bird et al. 1994, 1996b).

The different estimates obtained by the different approaches have been summarised in Figure 2. There is a consistent pattern, with virtually all studies estimating a significant increase in terrestrial carbon storage from the Last Glacial Maximum to the present. By far the largest increase was postulated by Adams et al. (1990). They used the most thorough data for estimating changes in vegetation types, but have been criticised for using some extreme carbon densities for some vegetation types.

When the analysis of Adams et al. (1990) was repeated by Crowley (1995), with a careful re-evaluation of the original data and improved palaeovegetation distribution, it resulted in only a slightly lower estimate of the amount of carbon thought to have been gained since the Last Glacial Maximum. Based on the distribution of palaeovegetation, Crowley (1995) still estimated greater carbon gain than that estimated from the carbon isotope record and greater than estimates based on modelling the distribution of biomes.

Soil carbon storage is also thought to have increased (Prentice & Fung 1990; Adams et al. 1990; Friedlingstein et al. 1992; van Campo et al. 1993; Prentice et al. 1993; Solomon et al. 1993; Prentice & Sykes 1995), although inferred changes in soil carbon are based on weaker information. Changes in soil carbon could only be estimated through modelling or inferring the distribution of vegetation classes and assuming that there was no change in soil carbon storage for each biome type.

The total biologically active land area at the Last Glacial Maximum is thought to have been similar to its present area (e.g Adams et al. 1990; Friedlingstein et al. 1992; van Campo et al. 1993; Prentice et al. 1993). While massive ice sheets that covered large areas of land have retreated, that gain has been largely balanced by the inundation of land by rising sea levels. The large increase in carbon storage must, therefore, be due to greater proliferation of vegetation types with high carbon density, especially forests.

Deserts, especially cool deserts, were much more abundant at the Last Glacial Maximum. The estimated effect of deserts on total terrestrial carbon storage is, however, greatly affected by the inclusion or omission of carbonates (Schlesinger 1982; Kern & Schlesinger 1992). In deserts, a large fraction of total carbon is contained in inorganic form, primarily as $CaCO_3$, which can greatly exceed the amount stored in organic carbon (Schlesinger 1982). Studies of past carbon storage have not generally included inorganic carbon,

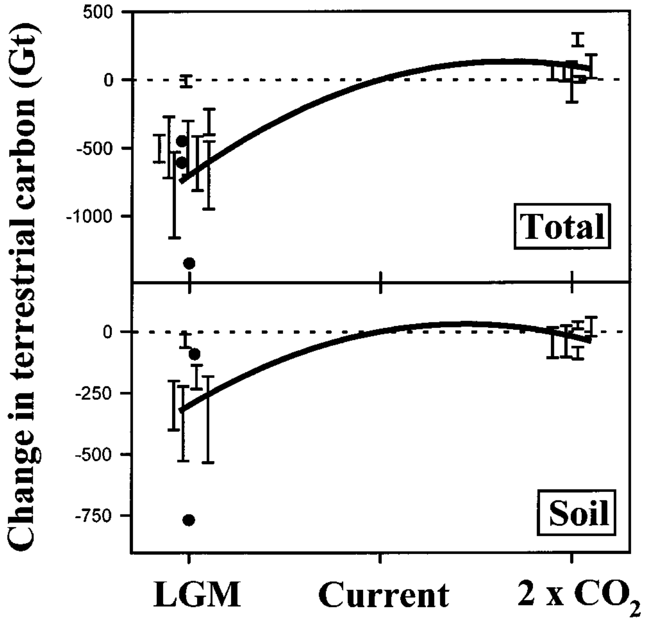

Figure 2. Estimates of changes in global carbon storage from the Last Glacial Maximum and under $2\times CO_2$ relative to carbon stored at present. The top panel shows total biospheric carbon and the bottom panel shows estimates for soil carbon only. The curves are only indicative to approximate the trends implied by the various estimates. Different estimates have been placed next to each other to allow identification of individual estimates even though they all refer to the same times. Some workers only presented individual estimates, indicated by solid symbols, whereas others presented a range of values, with the bars in the graph covering the reported range. Data are from Prentice & Fung 1990; Adams et al. 1990; Crowley 1991, 1995; King & Neilson 1992; Friedlingstein et al. 1992; Prentice et al. 1993; van Campo et al. 1993; Cramer & Solomon 1993; Solomon et al. 1993; Neilson 1993; Bird et al. 1994, 1996b; Prentice & Sykes 1995; King et al. 1997.

and this may provide part of the reason for differences between isotope-based analyses and studies based on modelling the distribution of biomes.

For a $2\times CO_2$ future, most modelling studies indicated little change (Prentice & Fung 1990; King & Neilson 1992; Cramer & Solomon 1993; Neilson 1993; Prentice & Sykes 1995), with a slight increase in total carbon storage but a slight loss of soil carbon (Figure 2). The convergence of estimates was to a large extent due to similar modelling exercises having been used that are based on simulating altered biome distributions. Only King et al. (1997) based their analysis on a simple, yet physiological-based, ecosystem model that was responsive to climatic factors, but they did not include vegetation shifts in their analysis.

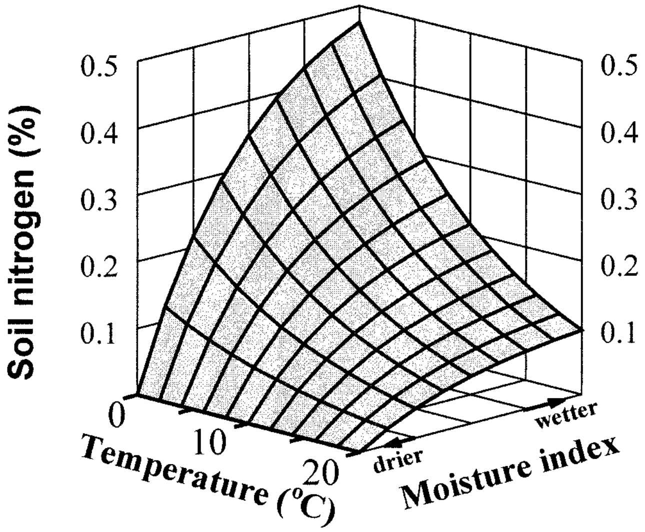

Figure 3. Soil organic nitrogen for the Great Plains of North America plotted as a function of mean annual temperature and a soil moisture index. Redrawn from the equation of Jenny (1980).

Additional factors also need to be considered. When King et al. (1997) included the direct effect of CO_2 concentration they estimated higher carbon storage (not included in Figure 2). On the other hand, Cramer and Solomon (1993) assessed the effect of agriculture on carbon storage, and concluded that agriculture would make the future carbon balance significantly more negative.

Soil organic matter across contemporary temperature gradients

A number of studies have reported amounts of soil organic carbon across climatic gradients (e.g. Harradine & Jenny 1958; Jenny 1980; Burke et al. 1989; Carter et al. 1997). Each of these studies reported a strong effect of temperature on soil organic carbon or nitrogen, with decreasing amounts with increasing temperature. The study reported by Jenny (1980), for example, covered the Great Plains area of North America.

Jenny's (1980) data have been redrawn in Figure 3. For constant moisture indices, they implied an almost 5-fold increase in soil organic nitrogen for mean annual temperatures from 20 °C down to 0 °C. These findings were consistent with the more recent study of Burke et al. (1989) for the same area.

Jenny (1980) also reported that hay yields in the U.S.A., as a measure of NPP, showed no discernible trend with temperature, but that presumably included a trend towards increasing moisture limitation with increasing temperature so that for constant moisture limitation, NPP might have increased with increasing temperature. Work by Epstein et al. (1997) gave a more complex picture, with productivity of C_3 plants decreasing and that of C_4 plants increasing with increasing temperature. They also observed complex interactions with rainfall and soil texture.

The equation used by Jenny (1980) translates into a decrease in organic nitrogen with temperature with a constant Q_{10} of 2.2, which implies that over the area studied, the temperature sensitivity of soil organic carbon decomposition greatly exceeds that of NPP.

Global patterns in soil organic carbon and nitrogen have been compiled and analysed by Post et al. (1982, 1985). They represented their findings through Holdridge diagrams, in which amounts of soil organic carbon were expressed as functions of mean annual temperature and the ratio of potential evapotranspiration to precipitation (PET/P). For constant PET/P, their data also indicated a trend of decreasing soil organic carbon with increasing temperature (Figure 4).

However, the trend was only weak, with relative soil organic carbon decreasing by one third between 0 °C and 30 °C and being inconsistent across different PET/P. While the driest biomes (ratio = 8) and the wettest biomes (ratio = 0.125) showed a clear and consistent trend of decreasing organic carbon with increasing temperature, the trend was inconsistent for biomes with intermediate moisture levels: biomes with ratios of 0.25 and 0.5, for example, had highest soil organic carbon levels at low, but not the lowest, temperatures before decreasing at higher temperatures.

In contrast to studies of a more restricted area, like that of Jenny (1980), these global compilations therefore implied organic carbon decomposition to have only marginally greater temperature sensitivity than net primary production. However, it is difficult to draw firm conclusions from these global compilations as solar radiation and vegetation types would have generally co-varied with temperature as well. It is, therefore unclear which part of the observed trend was due to temperature alone and which part due to co-varying factors.

Turn-over times inferred from carbon isotope ratios

The relative abundance of the stable carbon isotopes, ^{12}C and ^{13}C, and the radioactive isotope ^{14}C can be used to infer turn-over rates of carbon in the soil (O’Brien & Stout 1978; Anderson & Paul 1984; Jenkinson et al. 1992),

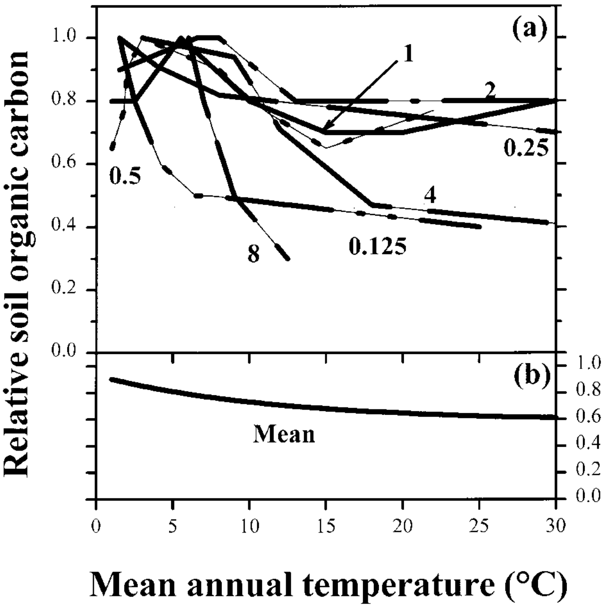

Figure 4. The temperature dependence of soil organic carbon observed in different biomes. Data are based on Post et al. (1985), and have been redrawn by plotting the relative amounts of soil organic carbon as a function of mean annual temperature for constant PET/P as indicated in (a). Data are expressed relative to the highest amounts observed at each PET/P. The curve denoted 'Mean' in (b) is the mean of all curves.

or to follow the change in organic carbon upon transitions between C_3 and C_4 vegetation (Balesdent et al. 1987; Vitorello et al. 1989; Martin et al. 1990).

The atmospheric abundance of ^{13}C is decreasing due to the dilution with ^{12}C from the burning of fossil fuels. Bird et al. (1996a) used that trend to infer the turn-over times of soil organic carbon components, and found a latitudinal gradient in the abundance of the stable carbon isotopes, which implies a faster turn-over time in warmer regions. However, the observed trend was only weak and confounded by other factors so that it could not be used to quantitatively relate temperature and soil organic carbon turn-over times.

A stronger signal can be obtained by using ^{14}C. Its natural abundance increased sharply during atmospheric bomb tests up to the early 1960s, and has been decreasing since then. Organic carbon that turns over very slowly would be only slightly enriched, whereas organic carbon that turns over faster must show greater enrichment by ^{14}C, and fractions that turn over very fast are already depleted again. Hence, the ^{14}C concentration in total organic carbon, or in specific fractions of organic carbon, can be used to infer its turn-over time.

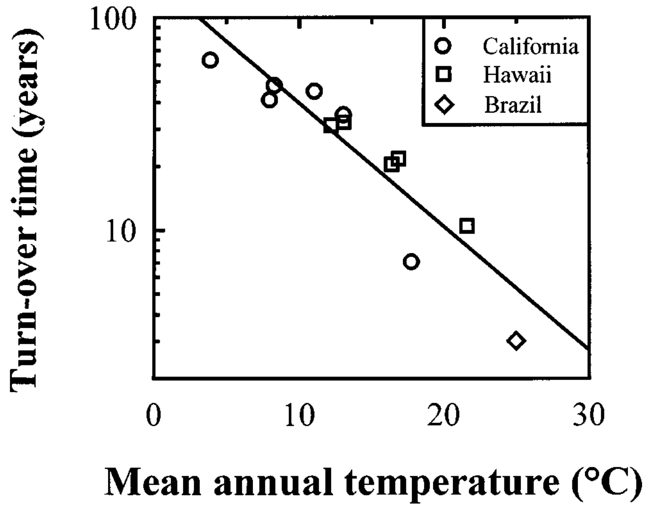

Figure 5. Soil organic carbon turn-over times of the light fraction of organic carbon inferred from the relative abundance of ^{14}C in samples from California, Hawaii and Brazil (redrawn from Trumbore et al. 1996). The line fitted to the data is given by

$$t = 151 \exp(-0.134T) \qquad (4)$$

where t = turn-over time and T = mean annual temperature.

Trumbore et al. (1995, 1996) and Townsend et al. (1995) used this technique to infer the turn-over times of isolated organic carbon fractions and expressed that as a function of temperature. Their data have been redrawn in Figure 5, together with a relationship fitted to the data. It implied that turn-over time increased exponentially with temperature with a Q_{10} of 3.8.

The strength of this technique is that it can measure turn-over times under field conditions, but it does rely on several critical assumptions. For example, when different isolated fractions of organic carbon are compared at different sites, it must be assumed that these fractions do correspond to equivalent pools, which may not be valid.

Also, and maybe most importantly, different temperatures at different sites can be confounded by different moisture levels, with warmer sites generally having lower moisture levels (Townsend et al. 1995). Hence, the enhancing effect of warmer temperatures might have been partly negated by the inhibiting effect of reduced soil moisture, although at the Hawaiian sites, even the observed lower moisture levels at higher temperature were considered to have been non-limiting by the authors (Townsend et al. 1995). Nonetheless, it is possible that the effect of temperature on turn-over times *per se* could have been greater than inferred by these studies.

Soil respiration measured *in situ*

Raich and Schlesinger (1992) estimated the temperature dependence of decomposition rate from measurements of CO_2 efflux from different soils. They compiled data from a comprehensive range of ecosystems and expressed observed fluxes as a function of mean annual temperature. However, for any system in steady state, soil respiration over a year or more must equal the rate of carbon input. Soil respiration under steady-state conditions must therefore be proportional to NPP. Consistent with that consideration, Raich and Schlesinger (1992) found a good linear correlation between annual soil respiration rate and NPP. Their data can therefore not be used to infer the temperature dependence of organic carbon decomposition.

Another way of obtaining the temperature dependence of decomposition is by measuring soil respiration throughout the year with seasonally varying temperatures. For example, Keith et al. (1997), working in a cool *Eucalyptus pauciflora* forest near Canberra, Australia, measured soil respiration over one year and expressed measured fluxes as a function of temperature and moisture contents. Their data are re-expressed in Figure 6, shown as a function of temperature both at the observed field moisture levels (Figure 6(a)) and as rates corrected for moisture (Figure 6(b)).

The data of Keith et al. (1997) illustrate an important point. Measurements at higher temperatures are typically associated with lower moisture which tends to reduce respiration rates. Data corrected for the effect of moisture (Figure 6(b)), consequently showed stronger temperature dependence (Figure 6(c)) by up to $1^1/_2$ units on the Q_{10} scale. This leads to the important conclusion that the temperature dependence of soil respiration cannot be adequately described unless the interaction with moisture is either explicitly included, or by ensuring that only samples are analysed that are not limited by moisture.

A comprehensive data set of observed seasonal soil respiration rates was compiled and analysed by Lloyd and Taylor (1994) who developed an equation that best described the observed temperature dependence (eqn. A7). That relationship is almost indistinguishable from that shown in Figure 6(b). Lloyd and Taylor (1994) restricted their review to systems thought not to be limited by moisture stress. However, it is not clear whether this confounding effect can ever be fully excluded in field studies unless respiration rates are simultaneously described as functions of temperature and moisture.

In deciduous forest systems, or grasslands that die off in autumn, the estimation of temperature dependence is also confounded with changes in litter quantity and quality, as large amounts of readily decomposable litter become available at a cool time of the year. This input of high-quality substrate can support higher respiration rates than would be expected based on temperature alone.

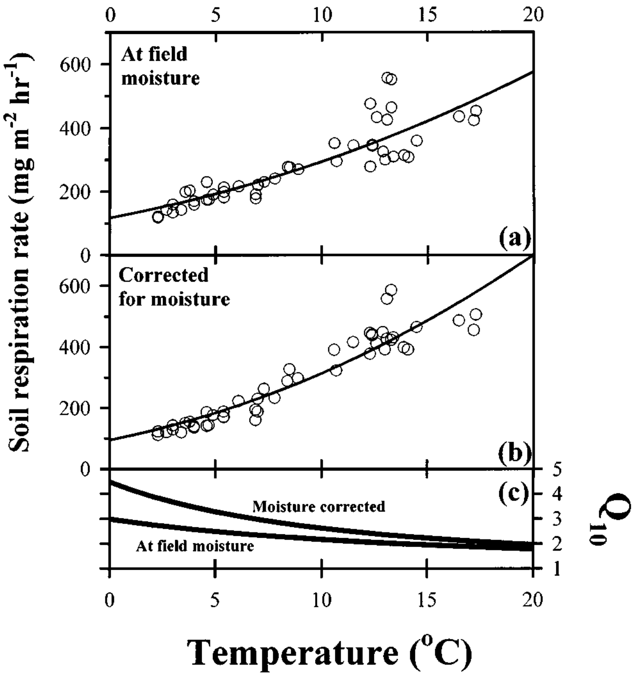

Figure 6. Soil respiration as a function of temperature (after Keith et al. 1997; Control plots only). Figure 6(a) shows data at temperatures and moisture levels observed in the field and with eqn. A.8 fitted to the data. Each observation was then corrected for moisture by calculating a notional rate at constant moisture. Those modified data are shown in Figure 6(b), and eqn. A.8 was again fitted to the modified data. Both fitted relationships are shown on a Q_{10} plot in Figure 6(c).

Finally, measured soil CO_2 efflux originates from the decomposition of soil organic carbon and root respiration, and it seems unlikely that both should have the same temperature or moisture sensitivity. Boone et al. (1998) experimentally separated the effects of temperature on the litter layer, humus and root components in a deciduous forest in Massachusetts, U.S.A., and concluded that the different components had distinctly different temperature sensitivities. The root component had the strongest temperature sensitivity and CO_2 efflux from humus the weakest. It is important to know whether similar relative temperature sensitivities also apply to other ecosystems.

Soil warming experiments

The most direct way to measure the effect of warming on soil processes is by experimentally heating patches of soil under otherwise normal field

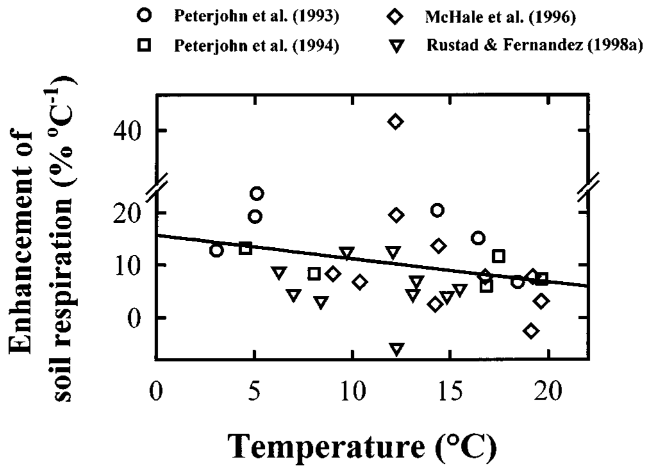

Figure 7. Enhancement of soil respiration in experimental soil warming experiments at different natural temperatures. Each point refers to the average of one month's data. For McHale et al. (1996), the mean of the enhancements at three different temperatures was used. The curve is given by the relationship

$$d(T) = \exp[\alpha + 0.15T(1 - 0.5T/36.9)]. \quad (5)$$

conditions. A number of such experiments have been conducted or have been initiated over recent years (e.g. Lükewille & Wright 1997; L.E. Rustad, pers. comm.). Several studies are still in their early stages, with published information not yet being available.

The studies published to date have highlighted the effects on a variety of important ecological processes in the treated ecosystems. For example, van Cleve et al. (1990), Peterjohn et al. (1993, 1994), McHale et al. (1996) and Rustad and Fernandez (1998a) showed that soil warming could increased litter decomposition and nitrogen and phosphorus mineralisation rates. On the other hand, Pajari (1995) found no significant effect of warming on soil respiration, and Robinson et al. (1995) found that litter decomposition could even be reduced by soil warming. This inhibitory effect was probably due to higher temperature causing considerable drying of the litter layer which had a stronger inhibitory effect than the stimulation from warming itself.

Only a few of these studies have reported their findings in sufficient detail that they can be quantitatively compared (Peterjohn et al. 1993, 1994; McHale et al. 1996; Rustad & Fernandez 1998a). Figure 7 shows the relative stimulation of soil respiration per degree warming at different background temperatures, with a generalised relationship fitted to the data.

There are, however, a number of systematic problems with trying to deduce the temperature sensitivity of organic carbon decomposition from soil warming experiments. If the decomposition of organic carbon and litter is stimulated by warming, it thereby exhausts its own supply of readily decomposable material (e.g. van Cleve et al. 1990; McHale et al. 1996; Rustad & Fernandez 1998b). One would therefore have to expect that the relative stimulation of soil respiration diminishes over time as the supply of substrate is exhausted. This leaves it uncertain how findings from these studies can be interpreted and generalised.

Laboratory incubations

The methods discussed above cannot directly assess the effect of temperature on organic carbon decomposition without the confounding effects of changing soil moisture, litter quantity and quality, or root respiration. Such confounding effects can be minimised by studying organic carbon decomposition under controlled laboratory incubations, provided moisture levels are adequately controlled and contribution from autotrophic respiration from any fine roots can be prevented (e.g. Koepf 1953; Nyhan 1976; Ross & Cairns 1978; Schleser 1982). Laboratory incubations are, however, conducted under highly artificial conditions and generally exclude important interacting factors, such as soil macro-fauna or wetting/drying cycles, although it is not clear how omission of those factors would systematically alter the inferred temperature sensitivity of organic carbon decomposition.

Kirschbaum (1995) summarised the temperature sensitivity of organic carbon decomposition obtained in various laboratory incubation studies (Figure 8). Very high temperature sensitivities have been reported at low temperatures, and moderately high values were maintained at higher temperatures. Q_{10} values were generally around 2 for temperatures above 20 °C, and increased to values greater than 8 at a temperature of 0 °C.

Q_{10} values of around 2 at moderately high temperatures are typical for many biological reactions. The high Q_{10} values at lower temperature are probably indicative of low-temperature thresholds being reached that inhibit some enzymatic reactions. The graph also shows that the use of relationships that assume a constant Q_{10} is not justified and should be avoided over any wider temperature range.

Laboratory incubations can also be used to study nitrogen mineralisation rates (e.g. Stanford et al. 1973; Kladivko & Keeney 1987; Nadelhoffer et al. 1991; Goncalves & Carlyle 1994). In a comparison of studies of decomposition and net nitrogen mineralisation rates, Kirschbaum (1995) found that organic carbon decomposition studies reported greater temperature sensitivity than mineralisation studies, especially at lower temperature. It is not

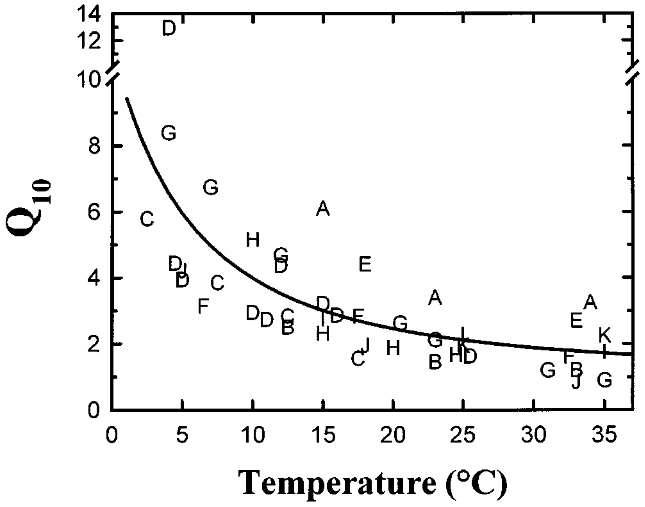

Figure 8. The temperature sensitivity of CO_2 efflux from soil or litter observed in different studies. Different studies are designated by different letters (for details, see Kirschbaum 1995). The fitted curve is described by eqn. A.10 with E_0 = 241.5 and C_0 = 31.79. This fitted curve is different from that used by Kirschbaum (1995) as eqn. A.10 gives a marginally better fit and, consistent with the data, maintains a higher temperature sensitivity above 25 °C.

obvious why there was such a difference between the apparent temperature sensitivities of decomposition and mineralisation rates.

Net nitrogen mineralisation is a more complex process than organic carbon decomposition and involves numerous processes that may include both mineralisation and immobilisation with only the net difference being observed. Long-term mineralisation rates, however, are ultimately dependent on organic carbon decomposition so that the temperature sensitivity of decomposition is the most relevant in determining long-term effects on both decomposition and mineralisation.

Summarising the evidence

The various lines of evidence discussed above give somewhat different estimates of the temperature sensitivity of soil organic carbon decomposition (Figure 9(a)). The analysis of carbon isotope ratios resulted in a relationship with constant Q_{10} and a fairly high temperature sensitivity. However, this relationship was based on a very limited number of studies and gives an integrated assessment of turn-over times affected by both temperature and moisture relationships. Hence, this relationship may underestimate the effect of temperature alone.

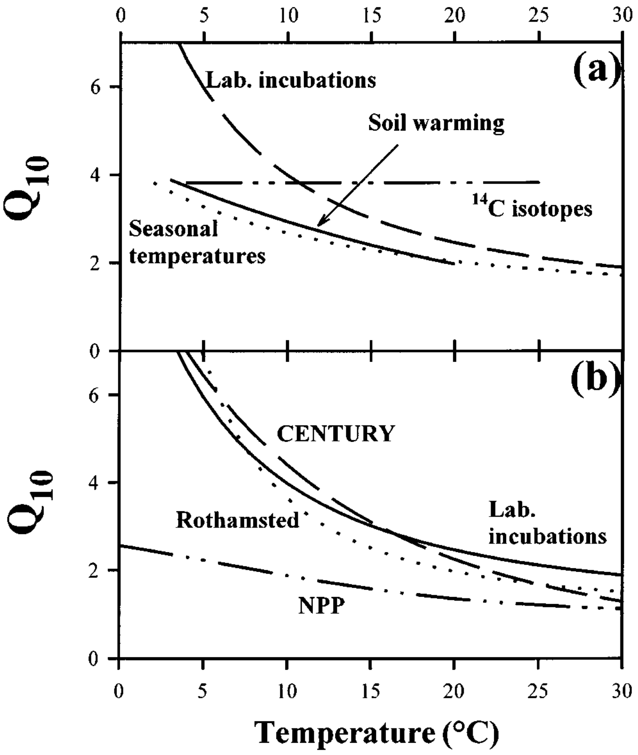

Figure 9. Estimates of the temperature sensitivity of organic carbon decomposition based on different lines of evidence in (a), and comparison of estimated temperature dependence based on laboratory incubations with the relationships used in the CENTURY (eqn. A.11; Parton et al. 1987) and Rothamsted (eqn. A.12; Jenkinson et al. 1991) models and a relationship describing the temperature sensitivity of net primary production (eqn. A.1; Lieth 1973) in (b).

The evidence from soil warming experiments was also based on only a very small number of studies and was affected not only by the direct effect of warming, but also by the confounding inhibitory effect of drying and exhaustion of readily decomposable material. Therefore, it, too, is likely to underestimate the temperature sensitivity of organic carbon decomposition.

The evidence from measuring soil respiration with seasonally varying temperatures suffers from fewer of these problems, especially when attempts are made to avoid confounding of temperature with moisture limitations (Lloyd & Taylor 1994). However, in most environments, these measurements were still confounded with seasonal changes in litter quality and quantity and the uncertain role of root respiration. This method, too, is therefore likely to underestimate the temperature sensitivity of organic carbon decomposition.

Obtaining the temperature dependence of organic carbon decomposition under laboratory conditions suffers from the fewest of these confounding effects. However, incubations over extended periods may lead to exhaustion of readily decomposable material, which would be most pronounced under the most favourable conditions (Koepf 1953). This could reduce decomposition rates and also lead to underestimation of its temperature sensitivity. Confounding of temperature with moisture can still be a problem if moisture is not adequately controlled, and root respiration may contribute to carbon flux if intact soil cores are used for analysis. Apart from that, laboratory incubations are conducted under highly artificial conditions, lacking, for example, wetting-drying cycles that occur under field conditions. It is unclear, however, whether that might systematically bias any derived temperature sensitivity.

Hence, the temperature sensitivity obtained under laboratory conditions is considered to give the least-biased estimation of the true temperature dependence of organic carbon decomposition, and this estimate is used for the simulation runs below. Figure 9(b) compares the temperature dependence of NPP (Equation A.1) according to the relationship of Lieth (1973) with the temperature dependence of soil organic carbon decomposition obtained from laboratory incubations and the relationships used in the CENTURY (Parton et al. 1987) and Rothamsted models (Jenkinson et al. 1991). The functions used in the Rothamsted and CENTURY models are fairly consistent with the relationship derived from analysis of laboratory incubations, but the equation used in the Rothamsted model increases to very high Q_{10} values at temperatures below 5 °C.

NPP has a much weaker temperature dependence than decomposition rates at all temperatures, with the largest difference at lowest temperatures. This suggests that with increasing temperature, soil organic carbon decomposition should be stimulated much more than NPP. This is consistent with the observation that total amounts of soil organic carbon generally decrease with increasing temperature (Figures 3, 4).

Interactions with moisture limitations

In assessing the temperature sensitivity of organic carbon decomposition, the interaction with moisture limitations must be considered (e.g. Keith et al. 1997; Davidson et al. 1999). As moisture limitations tend to increase with increasing temperature, the interaction with moisture confounds responses to temperature, and acts to lower apparent temperature sensitivities in the field.

But the situation is too complex to be corrected in a simple manner. Firstly, the extent and nature of the confounding effect will differ between sites. In some environments with pronounced dry spells, the effect of warming may lead to significantly enhanced moisture limitation, but in other environments that are very moist at present, there may still be no moisture limitations even under warmer conditions. In some regions, increased water loss at higher temperature might also be balanced by increased rainfall so that soil water balances will not be altered. Furthermore, if warming were to lead to general drying, it is likely to also reduce carbon inputs into the system by reduced NPP. It is therefore not possible to apply a general correction factor to all temperature response data as the net effect may be different for different environments. For the modelling runs below, it is simply assumed that the extent of moisture limitation remains the same.

Modelling approaches

The effects of temperature changes on soil organic carbon amounts have been modelled by Schimel et al. (1990), Jenkinson et al. (1991), Thornley et al. (1991), Kirschbaum (1993, 1995), Wang and Polglase (1995) and others, who used soil organic carbon models to show how a future temperature increase could lead to the release of large quantities of carbon from the world's soils. These studies differed in the details of simulating soil carbon dynamics, in the sophistication of the plant modules and in the interactions with other factors that were investigated. However, for assessing the effects of warming on soil carbon dynamics, the most critical component in these models are the relative temperature sensitivities for organic carbon decomposition and NPP. As most models have used similar equations that all resulted in greater temperature sensitivity for decomposition than net primary production, they all concluded that warming would lead to considerable losses of soil carbon.

In the following, a number of simulations are shown that are based on the model described in detail by Kirschbaum (1993). That model used a simple yet physiologically-based plant production module that includes the dependence of photosynthesis on CO_2 concentration and temperature, but without water limitations. It used a version of the CENTURY model for soil organic carbon dynamics and includes the full range of feed-back effects between plant productivity and soil organic matter. That model is updated here by using the temperature dependence of organic carbon decomposition following Equation 6, based on data from the laboratory incubations (Figure 8).

Figure 10 shows the percent carbon loss per degree warming for soils at different initial temperatures. The Figure indicates the potential for large losses of organic carbon with warming. The losses are likely to be most pronounced for soils at lowest temperature, especially for regions with small seasonal temperature variation. As soils in cool regions tend to have higher

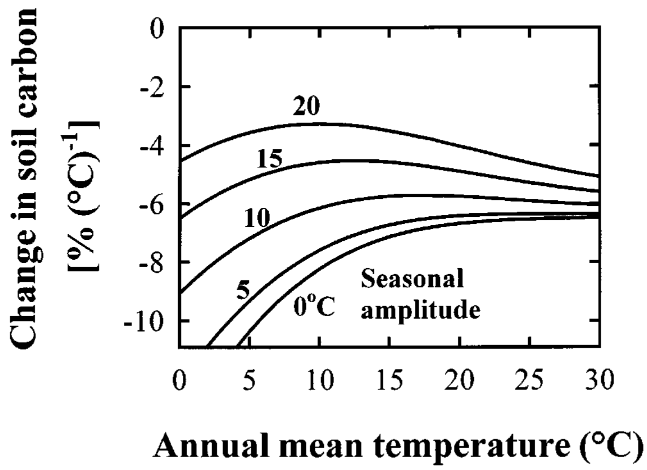

Figure 10. Modelled equilibrium change in soil organic carbon with warming for soils at different initial temperatures. Based on data from laboratory incubations (Figure 8), the temperature sensitivity of organic carbon decomposition was calculated as

$$d(T) = \exp[3.36(T - 40)/(T + 31.79)]. \qquad (6)$$

The runs assumed different extents of the seasonal temperature amplitude as shown in the Figure.

soil carbon contents, a given percentage of carbon loss corresponds to a higher absolute loss in cooler regions. A carbon loss of 6% °C^{-1} would translate into a total soil carbon loss of over 140 Gt C from all the world's soils. Hence, soil carbon losses alone could provide a powerful positive feed-back on global warming.

In runs with different assumptions about the temperature amplitude of the seasonal cycle, the projected carbon loss increased with reduction in the temperature amplitude of the seasonal cycle (Figure 10). When mean annual temperature is low, but there is a large seasonal cycle, the soil will still experience warm temperatures for part of the year that allows substantial rates of organic carbon decomposition. Such soils are therefore likely to lose less carbon with increasing temperature than regions with the same mean annual temperature but a lower seasonal temperature range.

The question of time

Schlesinger (1990) compiled information from a variety of sources to show that organic carbon accumulation in newly formed soils tends to be very slow, with maximal organic carbon accumulation rates of about 100 kg C ha^{-1} yr^{-1}.

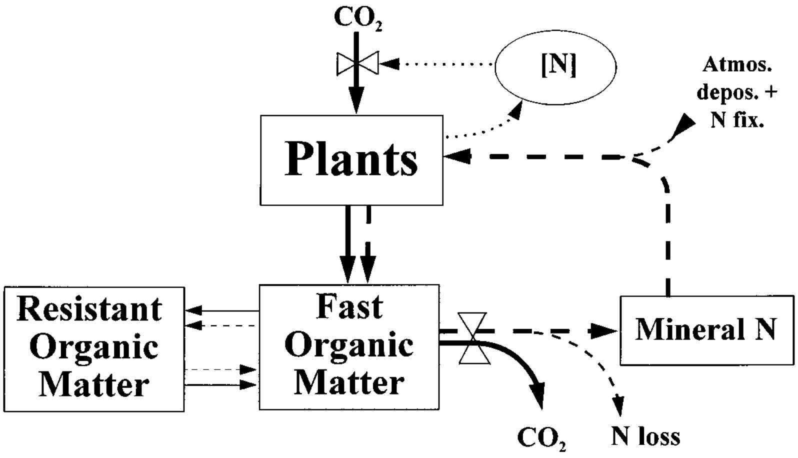

Figure 11. Diagrammatic representation of the soil organic carbon and nitrogen cycles, and the consequent interaction between organic matter decomposition, nitrogen cycling and net primary production. Carbon fluxes are shown with solid and nitrogen fluxes with dashed curves.

These were based on historical analyses of lands newly colonised after deglaciation, dune stabilisation or volcanic eruptions and covered periods from 1,000 to 10,000 years (Schlesinger 1990).

This slow change in soil organic carbon is due to the close linkage of the soil organic carbon and nutrient cycles, here illustrated through the carbon and nitrogen cycle (Figure 11). Death and senescence of plants transfers carbon and nitrogen to the soil where a fraction of it forms organic matter. Organic carbon is eventually lost through decomposition during which nitrogen is mineralised and becomes available for plant uptake. Biological nitrogen fixation and atmospheric deposition supply additional nitrogen. This total amount of nitrogen available to plants becomes an important constraint on carbon gain through net primary production.

Any build-up of soil organic carbon immobilises soil nitrogen and makes it unavailable for plant uptake. This inhibits subsequent carbon gain. Build-up of soil organic carbon in new soils is slow because each unit of extra soil carbon immobilises nitrogen and phosphorus in organic matter. These nutrients must be gained from external sources to allow further carbon fixation and organic matter formation. Organic matter also consists of fractions with different turn-over times that are in a dynamic equilibrium with each other. Any external perturbation initially affects the faster pools and sets up a long-term flux of carbon and nitrogen between the faster and more resistant pools to account for a long and slow further adjustment of soil organic carbon pools.

These considerations primarily act as constraints on the rate of organic carbon build-up. Carbon losses can be faster as can be observed in agriculture (e.g. Detwiler 1986) when crop removal reduces litter input and regular cultivation stimulates decomposition rates. Mineralised nitrogen may then be in excess of requirements to saturate NPP so that the system moves outside the control of the negative feed-back effects outlined here.

The same applies to any changes in soil organic carbon as a consequence of climate change. Any stimulation of the rate of organic carbon decomposition would also increase the rate of nitrogen mineralisation, thereby stimulating carbon uptake by plants. This provides a negative feed-back on the initially enhanced rate of carbon loss. Eventually, however, soil carbon will be lost from the system as with each turn-over of nitrogen, a fraction of mineralised nitrogen is lost from the system. With the faster rate of nitrogen turn over, more nitrogen is lost, and this ultimately reduces the amount of soil organic carbon.

This is further illustrated through simulations which show changes in soil organic carbon following an initial increase in temperature by 1 °C (Figure 12). Carbon loss in these simulations is very slow, requiring many centuries to be completed, especially in cool regions. While the ultimate carbon loss is much more pronounced in cool regions, there is virtually no difference with temperature over the first 50 years. At all temperatures, there is an initial loss of about 60 kg ha^{-1} over the first year which rapidly reduces to a lower subsequent loss rate of only about 2 to 3 kg ha^{-1} yr^{-1}. While potentially being able to transfer a large total amount of carbon to the atmosphere, changes in soil organic carbon due to climate change alone are likely to only add it at a small annual rate.

Interaction with CO_2 concentration

While the feed-back effect between temperature and soil organic carbon is specifically addressed here, it must be borne in mind that potential future temperature changes are part of a complex of global change phenomena, the most pervasive of which is the increasing CO_2 concentration. While increasing temperature may cause a net loss of soil organic carbon, increasing CO_2 concentration can stimulate NPP, thus adding extra carbon to the system and increasing total soil carbon storage (e.g. Kirschbaum 1993; King et al. 1997).

The combined effect of temperature and CO_2 concentration is illustrated in Figure 13, where changes in soil organic carbon are modelled since 1860. The model used here has been described in detail by Kirschbaum (1993) but

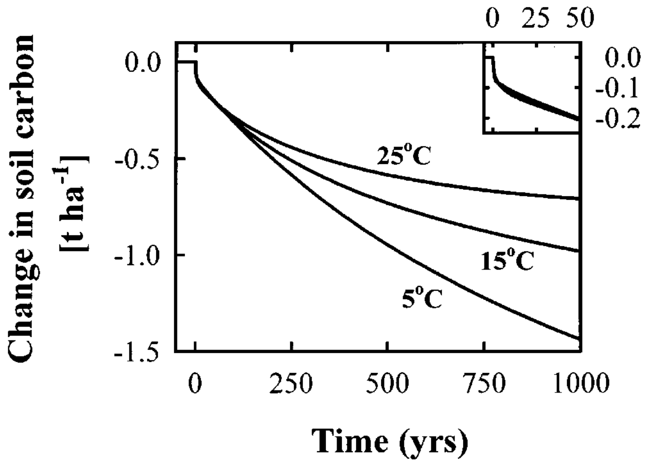

Figure 12. Modelled change in soil organic carbon, following a 1 °C increase in temperature for soils at three base temperatures as given in the Figure, using eqn. 6 and a seasonal temperature amplitude of 10 °C. The insert in the Figure enlarges the response over the first 50 years.

with the temperature dependence of organic carbon decomposition according to Equation 6.

Temperature and CO_2 effects may have effects on soil organic carbon of similar magnitude, but they act in opposite directions so that there may be little net effect. However, there are likely to be significant regional effects, with the temperature effect dominating in cool and the CO_2 effect dominating in warmer regions because of the greater CO_2 sensitivity of photosynthesis at higher temperature (Kirschbaum 1994). Consequently, soil organic carbon is likely to have increased in warm regions, with a slight loss in cool regions. These trends are likely to become more pronounced over the next century (Figure 13).

All the simulated changes are quite small, however, amounting to a change in soil carbon of only a few percent. This is because the effects of increasing CO_2 concentration and temperature partly cancel each other out, and because of the slowness of any changes in soil organic carbon. We should, therefore, not expect cataclysmic changes in soil carbon over short time intervals. However, these changes are globally pervasive and are likely to continue for a long time after an initial perturbation.

Summing up

The various ways of assessing the temperature dependence of soil organic carbon decomposition all agreed by indicating a strong temperature sensi-

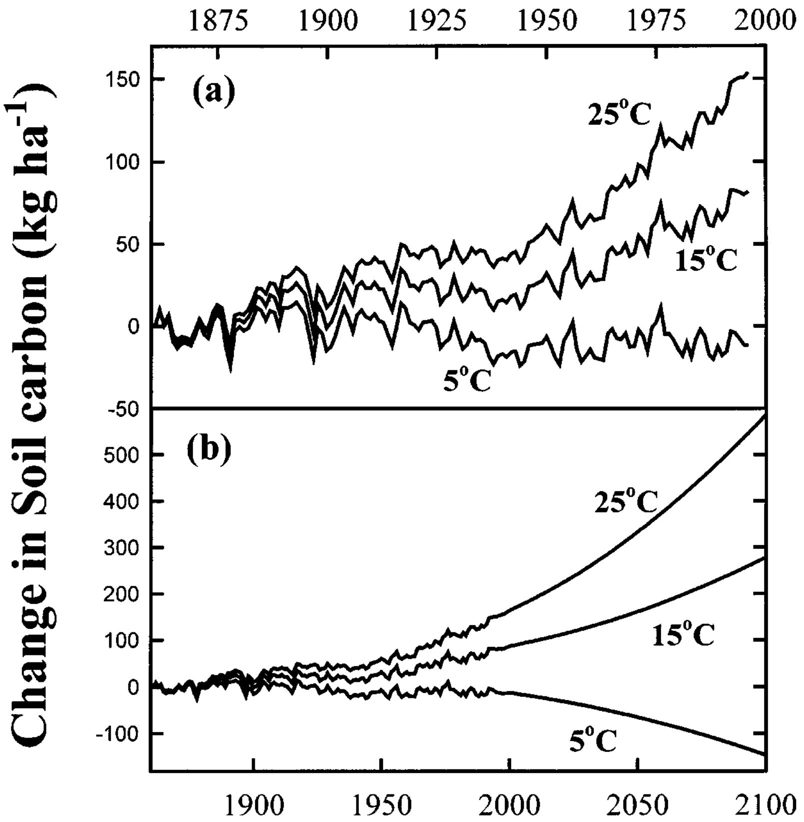

Figure 13. Modelled changes in soil organic carbon in response to observed anomalies in temperature and CO_2 concentration since 1860 (in a) and projected to 2100 based on the IPCC 92a scenario (in b). Simulations are shown for three base temperatures as shown in the Figure, with global temperature anomalies added to those base temperatures. Simulations were run with a seasonal temperature amplitude of 10 °C.

tivity that greatly exceeded that of NPP. The strongest evidence came from laboratory incubations in which most confounding factors could be excluded. Results from these studies also resulted in highest inferred temperature sensitivities.

Soil warming experiments, field measurements of soil respiration and inference of organic carbon turn-over times from carbon isotope ratios, gave similar results, although with somewhat lower temperature sensitivity. As these field studies suffered from a number of confounding factors that generally reduce the inferred temperature sensitivity, the conclusions from these studies were consistent with that based on laboratory based incubations.

Steady state soil organic carbon amounts have generally been observed to decrease with increasing temperature, and are, thus, also consistent with the inferred greater temperature sensitivity of organic carbon decomposition than NPP. However, there was also considerable variation, with different studies giving greater or lesser decreases in organic carbon with increasing temperature. Especially for a global compilation of soil organic carbon, the extent of change with temperature was less than that inferred from other lines of evidence.

Studies of the inferred organic carbon contents at the Last Glacial Maximum or a future with doubled CO_2 concentration, however, were inconsistent with those from other lines of evidence. The low inferred terrestrial carbon storage at the Last Glacial Maximum may be due to low CO_2 concentration or generally drier conditions at that time, which may have been more important than the effect of temperature. Studies which modelled the past distribution of biomes generally obtained higher carbon storage than inferences from carbon isotope ratios or those that derived biome distribution from palaeoecological evidence. The former analyses included drought but not CO_2 effects, whereas those based on observational data would have implicitly included all relevant factors.

Studies of future carbon storage can only use models. In these simulations, CO_2 effects have rarely been included (King et al. 1997). Radiation effects have also rarely been included. The assumption has generally been made that biomes that currently occupy a certain temperature niche will be able to occupy that same temperature niche in a future warmer world. However, in the future, those same temperature niches will occur in more polar regions where they will receive less radiation. It is questionable whether biomes will be able to store as much organic carbon with less radiation than they do currently at the same temperature but with more radiation. On the other hand, since these modelling studies tended to ignore both CO_2 and radiation effects, their combined errors may not have been too large.

Hence, with the temperature sensitivity of organic carbon decomposition being significantly greater than that of NPP, changes in soil carbon could constitute a significant positive feed back. However, because of negative feed back within the plant-soil system, these changes are likely to be slow, requiring many centuries before approaching new equilibria. Furthermore, because of the additional effect of CO_2 concentration on enhancing plant production and soil organic carbon storage, the overall feed-back from soil organic carbon on the atmosphere is likely to be small.

Within that broad global pattern, there are likely to be important regional differences, with the effects of increased CO_2 concentration dominating in warmer regions, leading to gains in soil carbon in tropical regions and the effects of increased temperature dominating in cooler regions, leading to possible losses in soil carbon in boreal and tundra regions. This general conclusion does not preclude simultaneous losses of soil carbon at greater rates due to land use changes, especially any conversions of grassland or forests for cropping that tends to reduce soil carbon amounts and can potentially lead to significant fluxes of carbon to the atmosphere.

Acknowledgements

This work was supported by the NGAC Dedicated Greenhouse Research Grants Scheme, and contributes to CSIRO's Climate Change Research Program. M.U.F. Kirschbaum's attendance at the Soil Science Society of America's symposium on "Controls on Soil Respiration: Implications for Climate Change" was supported by a grant from the U.S. National Science Foundation. I wish to thank R. Boone, H. Keith, P.J. McHale and L.E. Rustad for having made their original data available for inclusion in this review, and C. Carlyle, M. Howden and H. Keith for many helpful comments on the manuscript.

Appendix

The temperature dependence of net primary production, p(T), can be described following Lieth (1973) as

$$p(T) = 1/[1 + \exp(1.315 - 0.119T)], \tag{A1}$$

where T is temperature. It is expressed here as a relative modifier with a maximum of 1 at nonlimiting temperature. This equation is probably the one used most widely, although it was originally developed based on only a very small data set, and recent efforts have attempted to reassess whether this equation is indeed the most appropriate (Schloss et al. 1999; Cramer et al. 1999). However, this equation will continue to be used here until a clearly superior equation emerges for future use.

Different workers have used different equations to describe the temperature response of decomposition. Some of the most important of those are briefly described below. The Q_{10} function has been the most widely used.

$$Q_{10} = [\alpha(T_2)/\alpha(T_1)]^{[10/(T_2 - T_1)]}, \tag{A2}$$

where $\alpha(T_2)$ and $\alpha(T_1)$ are the rate constants of decomposition at two observed temperatures, T_2 and T_1. This can be re-expressed as

$$d(T) = \alpha(T_{ref})Q_{10}{}^{[(T - T_{ref})/10]}, \tag{A3}$$

where d(T) is a function to calculate decomposition rates at any temperature, based on the rate at a reference temperature T_{ref} and the Q_{10} constant. This relationship is easy to use and provides a ready indication of the temperature sensitivity of any system even though it lacks any theoretical justification. Importantly, this equation implies that there is a constant temperature sensitivity across any temperature range, which is often not observed (see below). Forcing observed data to a constant Q_{10} relationship can, therefore, give greatly misleading results. However, a Q_{10} at a particular temperature is a useful indicator of the temperature sensitivity of a process at that temperature (e.g. Kirschbaum 1995).

A different equation is the Arrhenius equation (see Johnson & Thornley 1985):

$$d(T) = \alpha \exp[-E_a/(RT_K)], \tag{A4}$$

where α is a parameter that determines the absolute rate of the process, E_a the activation energy, R is the universal gas constant (8.314 J mol^{-1} K^{-1}) and T_K is temperature in Kelvins. This equation has a good theoretical basis for describing simple chemical reactions. However, it is doubtful whether that good theoretical basis remains meaningful when applied to systems as complex as a community of soil organisms.

A more flexible way of describing the temperature dependence of biological processes, like soil respiration rate, is given through

$$d(T) = \exp[\alpha + \beta T(1 - 0.5T/T_{opt})], \tag{A5}$$

where α and β are constants and T_{opt} is the optimum temperature for the process (O'Connell 1990; Kirschbaum 1995). In this equation, α determines the absolute rate of the process and β in conjunction with T_{opt} its temperature dependence.

From this equation, a Q_{10} can be calculated for any given temperature as

$$Q_{10} = \exp[10\beta(1 - T/T_{opt})]. \tag{A6}$$

Another flexible equation has been used by Lloyd and Taylor (1994):

$$d(T) = \alpha \exp[-E_0/(T_K - T_0)], \tag{A7}$$

where α is an overall rate term, E_0 is a parameter loosely related to the concept of an activation energy, T_K is temperature in Kelvins and T_0 is a parameter that must be less than any measurement temperature. Lloyd and Taylor (1994) used this equation with E_0 = 308.6 K and T_0 = 227.1 K.

This can be normalised to the rate at some reference temperature and expressed in degrees centigrade as

$$d(T) = \alpha(T_{ref}) \exp[\gamma(T - T_{ref})/(T + C_0)], \tag{A8}$$

where $\alpha(T_{ref})$ is the rate at some reference temperature T_{ref}, and C_0 is an off-set temperature that is equivalent to T_0, but expressed in units of °C so that $C_0 = 273.15 - T_0$. The constant γ is calculated as

$$\gamma = E_0/(T_{ref} + C_0). \tag{A9}$$

Equation A.8 can be transformed to calculate a Q_{10} as

$$Q_{10} = \exp[10E_0/(T + C_0)^2]. \tag{A10}$$

The principal difference between eqn. A.5 and A.7 is that eqn. A.5 assumes that there is an optimum temperature for decomposition, with rates decreasing at supra-optimal temperatures, whereas rates calculated by eqn. A.7 continue to increase with temperature increases. While all biological reactions clearly have optimum and maximum temperatures, those might well lie outside the temperature range normally experienced in soils. Hence, both equations can adequately describe observed responses over relevant temperatures.

Other empirical equations have been used by Parton et al. (1987) and Jenkinson et al. (1991) as modifiers in their respective models of soil organic carbon turn-over. The CENTURY model (Parton et al. 1987) used:

$$t_1 = (T_{max} - T)/(T_{max} - T_{opt}), \tag{A11a}$$

$$t_2 = \exp[0.076(1 - t_1^{2.63})], \tag{A11b}$$

$$d(T) = t_2 t_1^{0.2}, \tag{A11c}$$

where t_1 and t_2 are intermediate variables, T_{max} is the maximum and T_{opt} the optimum temperature for decomposition. The rate constant d(T) takes on values between 0 and 1, and was used by Parton et al. (1987) with T_{max} = 45 °C and T_{opt} = 35 °C.

The Rothamsted model (Jenkinson et al. 1991) used:

$$d(T) = \alpha/\{1 + \exp[106/(T + 18.3)]\}, \tag{A12}$$

where α is an overall rate constant and the rest are fitted parameters.

References

Adams JM, Faure H, Faure-Denard L, McGlade JM & Woodward FI (1990) Increases in terrestrial carbon storage from the Last Glacial Maximum to the present. Nature 348: 711–714

Anderson DW & Paul EA (1984) Organo-mineral complexes and their study by radiocarbon dating. Soil Sci. Soc. Am. J. 48: 298–301

Anderson JM (1992) Responses of soils to climate change. Adv. Ecol. Res. 22: 163–210

Balesdent J, Mariotti A & Guillet B (1987) Natural ^{13}C abundance as a tracer for studies of soil organic matter dynamics. Soil Biol. Bioch. 19: 25–30

Batjes NH (1996) Total carbon and nitrogen in the soils of the world. Eur. J. Soil Sci. 47: 151–163

Bird MI, Chivas AR & Head J (1996a) A latitudinal gradient in carbon turnover times in forest soils. Nature 381: 143–146

Bird MI, Lloyd J & Farquhar GD (1994) Terrestrial carbon storage at the LGM. Nature 371: 566

Bird MI, Lloyd J & Farquhar GD (1996b) Terrestrial carbon-storage from the Last Glacial Maximum to the present. Chemosph. 33: 1675–1685

Boone RD, Nadelhoffer KJ, Canary JD & Kaye, JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396: 570–572

Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K & Schimel DS (1989) Texture, climate, and cultivation effects on soil organic matter contents in U.S. grassland soils. Soil Sci. Soc. Am. J. 53: 800–805

Carter JO, Howden SM, Day KA & McKeon, GM (1998) Soil carbon, nitrogen, phosphorus and biodiversity in relation to climate change. In: Final Report for the Rural Industries Research and Development Corporation (pp 185–249). RIRDC, Canberra, Australia

Cramer WP & Solomon AM (1993) Climatic classification and future global redistribution of agricultural land. Clim. Res. 3: 97–110

Cramer WP, Kicklighter DW, Bondeau A, Moore III B, Churkina G, Nemry B, Ruimy A & Schloss AL (1999) Comparing global models of terrestrial net primary productivity (NPP): Overview and key results. Glob. Ch. Biol. 5: 1–15

Crowley TJ (1991) Ice age carbon. Nature 352: 575–576

Crowley TJ (1995) Ice age terrestrial carbon changes revisited. Glob. Biog. Cyc. 9: 377–389

Davidson, E, Belk, E & Boone, RD (1998) Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob. Ch. Biol. 4: 217–227

Detwiler, RP (1986) Land use change and the global carbon cycle: the role of tropical soils. Biogeochem. 2: 67–93

Epstein HE, Lauenroth WK, Burke IC & Coffin DP (1997) Productivity patterns of C_3 and C_4 functional types in the U.S. Great Plains. Ecol. 78: 722–731

Eswaran H, van den Berg E & Reich P (1993) Organic carbon in soils of the world. Soil Sci. Soc. Am. J. 57: 192–194

Friedlingstein P, Delire C, Müller JF & Gerard JC (1992) The climate induced variation of the continental biosphere: A model simulation of the Last Glacial Maximum. Geophys. Res. Lett. 19: 897–900

Goncalves JLM & Carlyle JC (1994) Modelling the influence of moisture and temperature on net nitrogen mineralisation in a forested sandy soil. Soil Biol. Bioch. 26: 1557–1564

Harradine F & Jenny H (1958) Influence of parent material and climate on texture and nitrogen and carbon contents of virgin California soils. I. Texture and nitrogen contents of soils. Soil Sci. 85: 235–243

Jenkinson DS, Adams DE & Wild A (1991) Model estimates of CO_2 emissions from soil in response to global warming. Nature 351: 304–306

Jenkinson DS, Harkness DD, Vance ED, Adams DE & Harrison AF (1992) Calculating net primary production and annual input of organic matter to soil from the amount and radiocarbon content of soil organic matter. Soil Biol. Biochem. 24: 295–308

Jenny H (1980) The Soil Resource: Origin and Behavior. Ecological Studies No. 37. Springer Verlag, New York

Johnson IR & Thornley JHM (1985) Temperature dependence of plant and crop processes. Ann. Bot. 55: 1–24

Keith H, Jacobsen KL & Raison RJ (1997) Effects of soil phosphorus availability, temperature and moisture on soil respiration in *Eucalyptus pauciflora* forest. Plant and Soil 190: 127–141

Kern RA & Schlesinger WH (1992) Carbon stores in vegetation. Nature 357: 447–448

King AW, Post WM & Wullschleger SD (1997) The potential response of terrestrial carbon storage to changes in climate and atmospheric CO_2. Clim. Change 35: 199–227

King GA & Neilson RP (1992) The transient response of vegetation to climate change: A potential source of CO_2 to the atmosphere. Water, Air, Soil Poll. 64: 365–383

Kirschbaum MUF (1993) A modelling study of the effects of changes in atmospheric CO_2 concentration, temperature and atmospheric nitrogen input on soil organic carbon storage. Tellus 45B: 321–334

Kirschbaum MUF (1994) The sensitivity of C_3 photosynthesis to increasing CO_2 concentration. A theoretical analysis of its dependence on temperature and background CO_2 concentration. Plant, Cell Environ. 17: 747–754

Kirschbaum MUF (1995). The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic carbon storage. Soil Biol. Biochem. 27: 753–760

Kladivko EJ & Keeney DR (1987) Soil nitrogen mineralization as affected by water and temperature interactions. Biol. Fertil. Soils 5: 248–252

Koepf, H. (1953) Die Temperatur/Zeit – Abhängigkeit der Bodenatmung. Z. f. Pflanz., Düng. Bodenk. 61: 29–48

Kuhlbusch TA & Crutzen PJ (1995) Toward a global estimate of black carbon in residues of vegetation fires representing a sink of atmospheric CO_2 and a source of O_2. Glob. Biog. Cyc. 9: 491–501

Lieth H (1973) Primary production: Terrestrial ecosystems. Human Ecol. 1: 303–332

Lloyd J & Taylor JA (1994) On the temperature dependence of soil respiration. Funct. Ecol. 8: 315–323

Lükewille A & Wright RF (1997) Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. Glob. Ch. Biol. 3: 13–21

Martin A, Mariotti A, Balesdent J, Lavelle P & Vuattoux R (1990) Estimate of organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. Soil Biol. Biochem. 22: 517–523

McHale PJ, Mitchell MJ, Raynal DJ & Bowles FP (1996) Increasing soil temperature in a northern hardwood forest: Effects on elemental dynamics and primary productivity. In: Hom J, Birdsey R & O'Brian K (Eds) Proceedings of 1995 Meeting of the Northern Global Change Program. General Technical Report NE-214 (pp 146–152). USDA Forest Service, Radnor PA, U.S.A.

Nadelhoffer KJ, Giblin AE, Shaver GR & Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six arctic soils. Ecology 72: 242–253

Neilson RP (1993) Vegetation redistribution: A possible biospheric source of CO_2 during climatic change. Water, Air, Soil Poll. 70: 659–673

Nyhan JW (1976) Influence of soil temperature and water tension on the decomposition rate of carbon-14 labelled herbage. Soil Sci. 121: 288–293

O'Brien BJ & Stout JD (1978) Movement and turnover of soil organic matter as indicated by carbon isotope measurements. Soil Biol. Biochem. 10: 309–317

O'Connell AM (1990) Microbial decomposition (respiration) of litter in eucalypt forests of south-western Australia: An empirical model based on laboratory incubations. Soil Biol. Biochem. 22: 153–160

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322–331

Pajari B (1995) Soil respiration in a poor upland site of Scots pine stand subjected to elevated temperature and atmospheric carbon concentration. Plant and Soil 168–169: 563–570

Parton WJ, Schimel DS, Cole CV & Ojima DS (1987) Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51: 1173–1179

Peterjohn WT, Melillo JM, Bowles FP & Steudler PA (1993) Soil warming and trace gas fluxes: Experimental design and preliminary flux results. Oecol. 93: 18–24

Peterjohn WT, Melillo JM, Steudler PA & Newkirk KM (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol. Appl. 4: 617–625

Post WM, Emanuael WR, Zinke PJ & Stangenberger AG (1982) Soil carbon pools and world life zones. Nature 298: 156–159

Post WM, Pastor J, Zinke PJ & Stangenberger AG (1985) Global patterns of soil nitrogen storage. Nature 317: 613–616

Prentice IC & Sykes MT (1995) Vegetation geography and global carbon storage changes. In: Woodwell GM & Mackenzie FT (Eds) Biospheric Feedbacks in the Global Climate System – Will the Warming Feed the Warming? (pp 304–312). Oxford University Press, Oxford, New York

Prentice IC, Sykes MT, Lautenschlager M, Harrison SP Denissenko O & Bartlein PJ (1993) Modelling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. Glob. Ecol. Biog. Lett. 3: 67–76

Prentice KC & Fung IY (1990) The sensitivity of terrestrial carbon storage to climate change. Nature 346: 48–51

Raich JW & Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B: 81–99

Robinson CH, Wookey PA, Parsons AN, Potter JA, Callaghan TV, Lee JA, Press MC & Welker JM (1995) Responses of plant litter decomposition and nitrogen mineralisation to stimulated environmental change in a high arctic polar semi-desert and a subarctic dwarf shrub heath. Oikos 74: 503–512

Ross DJ & Cairns A (1978) Influence of temperature on biochemical processes in some soils from tussock grasslands. N. Z. J. Sci. 21: 581–589

Rustad LE & Fernandez IJ (1998a) Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine, U.S.A. Glob. Ch. Biol. 4: 597–605

Rustad LE & Fernandez IJ (1998b) Soil warming: Consequences for foliar litter decay in a spruce-fir forest in Maine, USA. Soil Sci. Soc. Am. J. 62: 1072–1080

Schimel DS, Parton WJ, Kittel TGF, Ojima DS & Cole CV (1990) Grassland biogeochemistry: Links to atmospheric processes. Clim. Ch. 17: 13–25

Schleser GH (1982) The response of CO_2 evolution from soils to global temperature changes. Z. f. Naturf. 37a: 287–291

Schlesinger WH (1982) Carbon storage in the caliche of arid soils: a case study from Arizona. Soil Sci. 133: 247–255

Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature 348: 232–234

Schloss AL, Kicklighter DW, Kaduk J, Wittenberg U (1999) Comparing global models of terrestrial net primary productivity (NPP): Comparison of NPP to climate and the normalized difference vegetation index. Glob. Ch. Biol. 5: 25–34

Skjemstad JO, Clarke P, Taylor JA, Oades JM & McClure SG (1996) The chemistry and nature of protected carbon in soil. Aust. J. Soil Res. 34: 251–271

Smith TM, Leemans R & Shugart HH (1992) Sensitivity of terrestrial carbon storage to CO_2 induced climate change: Comparison of four scenarios based on general circulation models. Clim. Ch. 21: 367–384

Solomon AM, Prentice IC, Leemans R & Cramer WP (1993) The interaction of climate and land use in future terrestrial carbon storage and release. Wat. Air Soil Poll. 70: 595–614

Stanford G, Frere MH & Schwaninger DH (1973) Temperature coefficient of soil nitrogen mineralization. Soil Sci. 115: 321–323

Thornley JHM, Fowler D & Cannell MGR (1991) Terrestrial carbon storage resulting from CO_2 and nitrogen fertilization in temperate grasslands. Plant Cell Environ. 14: 1007–1011

Townsend AR, Vitousek PM & Trumbore SE (1995) Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecol. 76: 721–733

Trumbore SE, Chadwick OA & Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Sci. 272: 393–396

Trumbore SE, Davidson EA, de Camargo PB, Nepstad DC & Martinelli LA (1995) Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Glob. Biog. Cyc. 9: 515–528

van Campo E, Guiot J & Peng C (1993) A data-based re-appraisal of the terrestrial carbon budget at the last glacial maximum. Glob. Planet. Ch. 8: 189–201

van Cleve K, Oechel WC, Hom JL (1990) Response of black spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska. Can. J. For. Res. 20: 1530–1535

Vitorello VA, Cerri CC, Andreux F, Feller C & Victoria RL (1989) Organic matter and natural carbon-13 distribution in forested and cultivated oxisols. Soil Sci. Soc. Am. J. 53: 773–778

Wang YP & Polglase PJ (1995) Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: Scaling up from leaf physiology and soil carbon dynamics. Plant Cell Environ. 18: 1226–1244