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A modelling study of the effects of changes in atmospheric CO_2 concentration, temperature and atmospheric nitrogen input on soil organic carbon storage

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ABSTRACT

There has been recent debate as to whether the world's soils are currently a net source or sink for carbon. This question was investigated with a model of soil organic matter coupled to a simple biochemically-based productivity model. In line with our plant physiological understanding, plant productivity was predicted to increase strongly with atmospheric CO_2 concentration at higher temperatures, but to respond less to CO_2 concentration at lower temperatures. The model showed equilibrium soil organic carbon contents to increase with increasing atmospheric CO_2 concentration, but to decrease with increasing temperature. Equilibrium soil organic carbon contents also increased with increasing rates of nitrogen input from atmospheric deposition or biological fixation. Time course analyses of changes in stored organic carbon suggest that approaches to new equilibria take many centuries, especially at lower temperatures. As a consequence, in response to a step increase in atmospheric CO_2 concentration, carbon storage in warm soils would continue to increase for more than 500 years, and the change would be even slower in cooler soils. The model was then used to estimate changes in soil organic carbon storage over the past 130 years in response to recorded changes in CO_2 concentration and temperature. The model suggests that there may have been an increase in soil organic carbon storage in warmer regions, whereas in cooler regions, soil organic carbon contents are likely to have decreased. Nitrogen deposition rates, which have increased due to atmospheric pollution, are likely to have caused increased soil carbon storage in heavily polluted areas but this is not likely to have had more than a small impact in a global context.

1. Introduction

The global atmosphere currently contains about 700 Gt C ($700 \cdot 10^{12}$ kg C), which is increasing by about 3.4 Gt C per year. Fossil fuel burning annually adds about 5.4 Gt C to the atmosphere, and a further 1.6 Gt C come from deforestation and land clearing (Watson et al., 1990). At the same time, Tans et al. (1990) have estimated that oceans can take up no more than 1.0 Gt C, which means that emission rates from known sources exceed accumulation in known sinks by 2–3 Gt C per year.

The world's standing biomass contains about 800 Gt C and the world's soils contain another 1500 Gt C (Melillo et al., 1990). Small increases in these could therefore easily account for the remaining difference, yet such changes would be difficult to measure. Increasing CO_2 concentration and increasing atmospheric deposition of nitrogen and other plant nutrients (i.e., sulfur) are seen as the factors that could have stimulated plant growth and increased carbon storage (Melillo et al., 1990).

It has been reported that between the end of World War II and the mid 1970s the standing biomass of forests in northern mid-latitude increased at a rate of 1.6–1.9 Gt C per year (Armentano and Ralston, 1980; Johnson and Sharpe, 1983). This trend has apparently continued up until the present (Kauppi et al., 1992) despite the more recent forest decline in parts of Central Europe and North America.

It is an as yet unresolved issue whether the world's soils are acting as a source or sink for carbon. The experimental work was recently reviewed by Van Veen et al. (1991) who could not resolve the issue unequivocally from the available evidence. There have also been several recent attempts to test theoretically what effect global changes might have had on the amount of carbon stored in the world's soils. Schimel et al. (1990) and Jenkinson et al. (1991) ran soils models for different temperature conditions and showed how a future temperature increase could lead to the release of large quantities of carbon from the world's soils.

Schimel et al. (1990) included soil nitrogen cycling in the analysis and showed how increased nitrogen availability due to faster decomposition could transiently increase plant productivity before reaching a new equilibrium many centuries later. However, neither of these studies included effects of increasing CO_2 or increasing atmospheric nitrogen deposition on plant performance and carbon storage.

Thornley et al. (1991) in a similar analysis included a direct effect of CO_2 on plant performance as well as the effect of additional nitrogen input due to atmospheric pollution. In their study, carbon storage increased for increases in CO_2 and nitrogen input, and decreased for increasing temperature. Kohlmaier et al. (1991) included the CO_2 fertilising effect and the effect of increasing temperature on enhancing the rate of soil respiration. They tested their model for a range of sensitivities of plant and soil processes to temperature and CO_2, and concluded that the biosphere (apart from deforestation) is likely to currently be a net sink for carbon. Other studies with similar aims have been undertaken by Goudriaan (1990) and Rastetter et al. (1991).

None of these studies included a realistic representation of the effect of CO_2 on plant productivity. The atmospheric CO_2 concentration affects plant growth and ultimately carbon storage through the process of photosynthesis. The mechanistic basis of photosynthesis in C_3 plants is now reasonably well understood (Farquhar and von Caemmerer, 1982), and it is clear that the response and sensitivity of plants to CO_2 is strongly modified by temperature (Kirschbaum and Farquhar, 1984; McMurtrie and Wang, 1992). It is therefore important to take the knowledge of the biochemical basis of the response of plants to CO_2 into account in any analysis.

In addition, all these studies, except those by Schimel et al. (1990) and Kohlmaier et al. (1991), used models of soil organic carbon that did not explicitly provide for the dynamics of the recalcitrant pool of organic carbon which may account for as much as half of total soil organic carbon and has turn-over times of hundreds to thousands of years (Parton et al., 1987). To be able to assess how soil carbon responds to changed conditions, it is necessary to include the time course of change into any realistic analysis.

I therefore combined a simple biochemically-based model of plant response to CO_2 and temperature with a soil organic carbon model (Parton et al., 1987) to assess the effect of changing environmental conditions on current trends in soil carbon storage.

2. The Model

2.1. Plant productivity

Plant productivity is modelled for a generalised non species-specific stand of non-woody vegetation. Net primary productivity, P_n, is calculated as:

$$P_n = P_m \cdot f_1(N) \cdot f_2(L) \cdot f_3(T) \cdot f_4(C), \qquad (1)$$

where P_m is maximum productivity without any limitation and $f_1(N)$, $f_2(L)$, $f_3(T)$ and $f_4(C)$ are limitation functions for plant internal nitrogen concentration, light interception by leaves, temperature and CO_2 concentration, respectively. Water availability is not included as a limitation in the model in its present form other than for a series of exploratory runs.

Nitrogen limitation is expressed as a linear function of the ratio of plant internal nitrogen to carbon for ratios less than a maximum value, and a constant for ratios greater than that maximum (Ingestad, 1982; Ågren, 1985; Ingestad and Lund, 1986):

$$f_1(N) = (N/C)/R_{\max} \quad \text{if} \quad N/C < R_{\max}, \qquad (2a)$$

$$f_1(N) = 1 \quad \text{if} \quad N/C \geq R_{\max}, \qquad (2b)$$

where N and C are the amounts of nitrogen and carbon in the plant, and $R_{\max}$ is the ratio of

nitrogen and carbon at which the response to nitrogen is saturated. The ratios of nitrogen to carbon in roots and shoots are assumed to be equal.

The effect of light interception on productivity is modelled, using a Beer's law formulation (McMurtrie, 1991), as:

$$f_2(L) = 1 - e^{-kL}, \tag{3}$$

where L is leaf area index and k the light extinction coefficient.

Leaf area index is calculated as:

$$L = S_l C_l, \tag{4}$$

where S_l is leaf area per unit carbon and C_l is the amount of carbon in leaves. No effect of nutritional status on specific leaf area is included in the present study.

The temperature dependence of productivity is calculated as (Lieth, 1973):

$$f_3(T) = \frac{1}{1 + e^{1.693 - 0.1047T}}, \tag{5}$$

where T is leaf temperature. Leaf temperature is assumed to be equal to soil temperature. The constants in eq. (5) differ from those given by Lieth (1973) because the response described by the equation is relevant for non-limiting CO_2. These constants were chosen so that in normal air, the combined model responds to temperature almost exactly like the relationship given by Lieth (1973).

The effect of CO_2 on productivity is described by (Kirschbaum and Farquhar, 1987; McMurtrie et al., 1992):

$$f_4(C) = \frac{(c_i - \Gamma_*)}{(c_i + 2\Gamma_*)}, \tag{6}$$

where c_i is the intercellular CO_2 concentration and Γ_* is the CO_2 compensation point in the absence of non-photorespiratory respiration. This term is determined by the biochemical constants of Rubisco that together predominantly determine the plant response to CO_2. The intercellular CO_2 concentration is taken as a constant fraction of the ambient CO_2 concentration (Wong et al., 1979; Bell, 1982; Ball et al., 1987; McMurtrie et al., 1992).

The value of Γ_* (ppmv) at different temperatures is calculated with a normalised Arrhenius function with activation energies based on the work of Badger and Collatz (1977) as:

$$\Gamma_* = 40.6e^{\{9.46(T-25)/(T+273.2)\}}. \tag{7}$$

Newly grown carbon is divided between leaves and roots in the ratio of 2:1. Stem growth is not included in the model. Nitrogen is assumed to be the only element limiting plant growth. Plants are assumed to take up all the nitrogen made available from decomposition and external nitrogen input. Nitrogen input into the system comes from biological nitrogen fixation and natural atmospheric deposition. For one modelling run, atmospheric pollution was included as an additional nitrogen source. Natural atmospheric deposition is set constant at $0.5\ g\ m^{-2}\ yr^{-1}$. Atmospheric pollution input was calculated on the basis of recorded emissions and the known land surface area of the Earth, with the assumption that deposition is evenly distributed across the land area. This is an extreme assumption that sets the upper bound on any potential impact of increasing nitrogen deposition.

Biological nitrogen fixation, N_f, is calculated as:

$$N_f = F_m \cdot F_2(L) \cdot f_3(T) \cdot f_4(C), \tag{8}$$

where F_m is the maximum rate of nitrogen fixation and the other terms are the same limitation functions as defined above.

Constant fractions of leaves and roots are assumed to senesce at each weekly time step. Senescing tissue is assumed to have the same nitrogen concentration as living tissue. Constants used for the modelling runs are given in Appendix A.

2.2. *Soil organic matter*

The soil organic carbon model is basically that described by Parton et al. (1987) as diagramatically shown in Fig. 1. Soil organic carbon is divided into 7 different pools, surface structural litter, surface metabolic litter, soil structural litter, soil metabolic litter, active (microbial) organic matter, slow organic matter and recalcitrant organic matter.

Each pool has first order decay kinetics with rate constants taken from Parton et al. (1987).

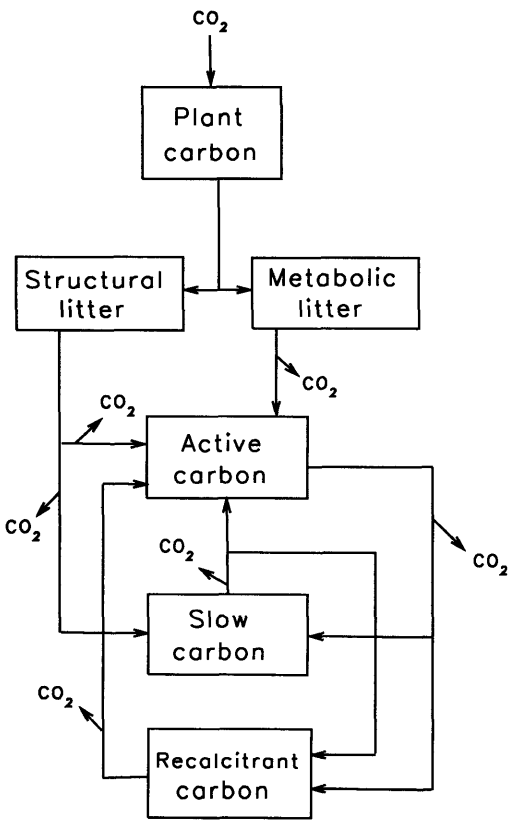

Fig. 1. Flow diagram of the carbon fluxes in the model (after Parton et al., 1987).

Carbon flows between specified pools, with constant fractions of carbon lost as respiration. Rate constants are modified by temperature, with a response function given by Parton et al. (1987). The effect of soil moisture is not included in the present model other than for a series of exploratory runs (shown in Table 1).

Each pool is associated with nitrogen with either fixed C/N ratios that are different for various pools or, in the case of the two metabolic litter pools, with a C/N ratio that varies between 10 and 25. Organic matter entering the soil has a C/N ratio that is determined by the relative rates of nitrogen uptake and carbon fixation by the plant. Nitrogen transfers between pools are calculated as the flows of carbon between the pools multiplied by the N/C ratio of the source pool. If, after the transfer of carbon and nitrogen between pools, any pools have nitrogen in excess of their critical C/N ratios, then nitrogen is mineralised. If pools are deficient in nitrogen then they can take up nitrogen from the mineral nitrogen pool.

As a departure from the formulation of Parton et al. (1987), mineral nitrogen is assumed to consist of two pools, an ammonium pool that is available only for recycling between organic matter pools, and a second pool, consisting of both ammonium and nitrate, that is accessible to plants. No loss of nitrogen to the atmosphere is assumed in the recycling of nitrogen between pools in the soil. A part of the ammonium not taken up by other soil pools can then be oxidised to nitrate. As part of the overall processes of converting nitrogen into forms available for uptake by plants, it is assumed that 5% of the nitrogen becoming available is lost to the atmosphere.

No seasonal or diurnal cycle was incorporated into the model for the present purpose, although a number of exploratory runs with seasonal and diurnal cycles and a more realistic parameterisation of nutrient levels in senescing tissue were done. Additionally, a simulation was run for water-limited conditions. The results of these are given in Table 1 below.

The conclusions of the present work are strongly dependent on the assumption about the dependence of soil and above-ground processes on temperature and CO_2 concentration. In the following, I have discussed the appropriateness of some of these assumption.

2.3. *Plant response to CO_2*

Despite much work on plant responses to CO_2 concentration, our understanding of ecosystem responses to CO_2 concentration is still surprisingly poor (Melillo et al., 1990). This may be due to experimental difficulties (Arp, 1991), large species-to-species differences in responses, interactions with other factors, such as water or nutrient limitations, and the absence of a good theoretical framework within which to analyse observations. I have therefore based plant responses to CO_2 on the well-understood physiological basis of the photosynthetic response to CO_2.

The biochemical basis for leaf responses of C_3 plants to CO_2 concentration is now well understood, and mathematical descriptions for this response are available (Farquhar and von Caem-

merer, 1982). In these equations, it is necessary to distinguish between plants being limited by ribulose-1,5-bisphosphate (RuBP) regeneration or by the activity of RuBP carboxylase-oxygenase (Rubisco). It was assumed here that plant responses could be described by reference to limitation by RuBP regeneration.

This is clearly appropriate in low-light conditions (Kirschbaum and Farquhar, 1987). In high-light conditions, it is dependent on the relative activities of Rubisco and RuBP regeneration capacity. An increase in CO_2 concentration by itself would move plants towards more pronounced limitation by RuBP regeneration capacity, whereas increasing temperature would impose greater limitation by Rubisco activity (Kirschbaum and Farquhar, 1984). In addition, plants can further optimise photosynthesis by a change in the ratio of Rubisco to RuBP-regeneration capacity (Farquhar and von Caemmerer, 1982). As plant responses to CO_2 are stronger if photosynthesis is limited by Rubisco rather than RuBP regeneration (Kirschbaum and Farquhar, 1984), these considerations suggest that plant responses to CO_2 concentration could possibly be somewhat stronger than used in the present model.

For C_4 plants growing without water limitation, on the other hand, only a very small response to CO_2 would be expected as the primary carboxylation enzyme, PEP carboxylase, has no oxygenase activity and is saturated at low CO_2 concentrations. As about 95% of land plants are C_3 plants (Melillo et al., 1990), it seemed justified to concentrate on the response that is appropriate for C_3 plants. Ecosystems with both C_3 and C_4 plants should, however, respond slightly less to CO_2 than calculated for C_3 plants alone.

Important in these consideration is the value of the intercellular CO_2 concentration. It was assumed here that some stomatal closure would accompany increases in the atmospheric CO_2 concentration in such a way that the ratio of intercellular to ambient CO_2 concentration remained constant (Bell, 1982). This is a contention that is well supported by a number of short-term studies of leaf responses to changing the CO_2 concentration in the surrounding air (Ball et al., 1987), and from longer-term studies of plants growing in air with different CO_2 concentrations (Morison, 1987). Had stomatal conductance been kept constant then there would have been a stronger response to CO_2 concentration. On the other hand, had a larger intercellular CO_2 concentration been assumed then the response to increasing CO_2 concentration would have been weaker.

For plants growing under water-limited conditions, a relatively stronger response to CO_2 could be expected because productivity would then be limited by the diffusion of CO_2 into the leaf, which in turn is limited by the availability of water for diffusion out of the leaf. At higher CO_2 concentrations more CO_2 can be gained per unit water lost. This is equally applicable for C_3 and C_4 plants. Under such conditions, growth can scale linearly with the ambient CO_2 concentration.

The response of vegetation to CO_2 is critical in the present analysis, yet different lines of reasoning suggest either a stronger or a weaker response than the one assumed here. In the absence of clear information pointing to a different type of response, it seemed appropriate to use the response based on the well-known biochemical reactions, which is broadly consistent with experimental evidence (e.g., Kimball, 1983; Gifford, 1992), especially if the frequently observed downward adjustment of photosynthetic capacity is entirely an experimental artefact (Arp, 1991).

2.4. Temperature response of plant and soil

Plant responses to temperature were based on the work of Lieth (1973). He expressed the productivity of different ecosystems as a function of their mean annual temperature. This analysis thereby implicitly takes account of species shifts towards species optimally adapted to different climatic regions. This was seen as the appropriate function for the present purpose as the response of ecosystems to temperature was investigated rather than the response of a particular species. This function also discounts for the higher respiration rate at higher temperature and describes net primary productivity. Again, this was seen as appropriate for the present work as the carbon input into the soil system is determined by the net primary productivity of the ecosystem.

The temperature response function of decomposition rate was taken from Parton et al. (1987). This function gives a good representation of the responses observed experimentally with different soils (e.g., Nyhan, 1976; Ross and Cairns, 1978; O'Connell, 1990).

3. Results

Parameter values for the model runs are given in Appendix A. The first part of the paper presents equilibrium plant and soil responses. Subsequent sections of the paper deal with time courses of change from a starting point at which plants and soil had come to an equilibrium under an initial set of conditions.

3.1. Equilibrium responses

Fig. 2 shows the response of productivity to CO_2 concentration at three different temperatures. The important features are the increase of productivity with temperature at higher CO_2 concentrations and the increase in CO_2 sensitivity with increasing temperature. This is particularly strong at the current ambient CO_2 concentration.

The effect of temperature on the CO_2 sensitivity at the current ambient CO_2 concentration is further illustrated in Fig. 3, which gives the calculated β-values as a function of temperature. The parameter β is the sensitivity of growth to increasing CO_2 concentration, calculated as:

$$\beta = \frac{(P_{n,C} - P_{n,350})/P_{n,350}}{(C - 350)/350}, \qquad (9)$$

where $P_{n,C}$ is net primary productivity at some future CO_2 concentration, C, and $P_{n,350}$ is net primary productivity at a CO_2 concentration of 350 ppmv. Because of the strong non-linearity of the response of plant productivity to CO_2 concentration (see eq. (6), Fig. 2), eq. 9 is only valid for CO_2 concentrations close to 350 ppmv.

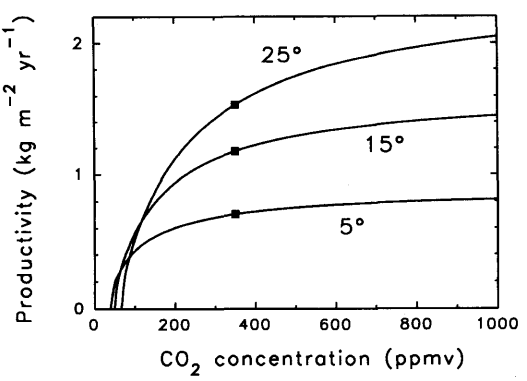

Fig. 2. Productivity as a function of CO_2 concentration and temperature. Data at the current atmospheric CO_2 concentration are indicated as squares.

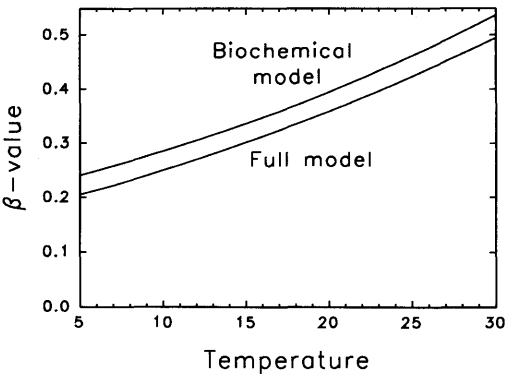

Fig. 3. Temperature dependence of β with only the biochemical model or the full model that includes interactions with nitrogen nutrition.

In the model, the CO_2 sensitivity increased considerably with temperature (Fig. 3). For the biochemical model alone, β increased from about 0.25 to 0.55 as temperature increased from 5° to 30°C. Interactions with nitrogen in the full model reduced the sensitivity to CO_2 to some extent. At higher CO_2 concentration, plants could initially fix more carbon. However, as the nitrogen uptake rate was limited by the amount becoming available from decomposition of soil organic matter, the plant internal nitrogen concentration was lowered, which introduced a greater subsequent nitrogen

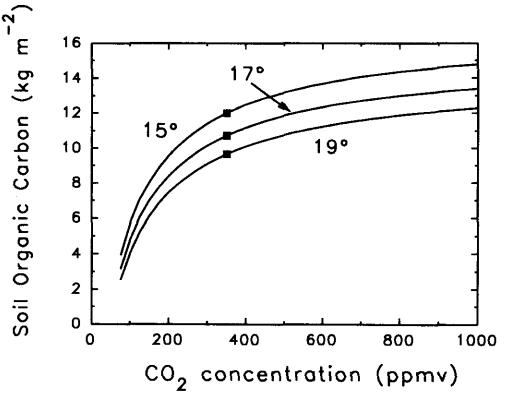

Fig. 4. Equilibrium soil organic carbon contents as a function of atmospheric CO_2 concentration at three different temperatures. Data at the current CO_2 concentration are indicated as square symbols.

limitation. With this negative feed-back in the model, the CO_2 sensitivity was reduced at all temperatures (Fig. 3).

Fig. 4 shows equilibrium soil organic carbon contents as a function of atmospheric CO_2 concentration at three different temperatures. A temperature of 15°C was used as base temperature as that is close to the current global average temperature. The other two temperatures correspond to two warming scenarios. This Figure shows the significant increase of equilibrium organic carbon contents with increasing CO_2 concentration. The sensitivity to CO_2 is especially pronounced at CO_2 concentrations less than the current concentration of 350 ppmv.

At the same time, Fig. 4 also shows the even larger effect of temperature. At 15°C, for example, an increase in CO_2 concentration from 300 to 400 ppmv would lead to an eventual increase in soil organic carbon from 11.4 to 12.5 kg m^{-2}, but if the temperature concurrently increased from 15° to 17°C then equilibrium soil organic carbon will decrease to 11.2 kg m^{-2} instead.

The interaction between temperature and CO_2 concentration on equilibrium soil organic carbon contents was further investigated by plotting equilibrium soil organic carbon contents as a function of temperature at two CO_2 concentrations (Fig. 5a). The difference between equilibrium carbon contents between the runs at 300 and 400 ppmv is shown in Fig. 5b.

Equilibrium soil organic carbon contents are much higher at lower temperature because decomposition has a more pronounced temperature dependence than primary productivity. These responses are consistent with the temperature dependence of soil organic nitrogen contents (which are closely linked to organic carbon) shown for Indian and American soils by Jenny (1980).

Warmer soils, however, showed a more pronounced relative response to increasing CO_2 concentration than did cooler soils. This was due to the greater sensitivity to CO_2 concentration at higher temperature. Consequently, while equilibrium soil organic carbon decreased to about one fifth for an increase in temperature from 5° to 30°C (Fig. 5a), there was only an approximate two-fold difference in the change in soil organic carbon as a result of increasing the atmospheric CO_2 concentration from 300 to 400 ppmv (Fig. 5b).

The slope of the curves in Fig. 5a gives an indication of the sensitivity of equilibrium soil organic carbon to temperature. It shows that cold

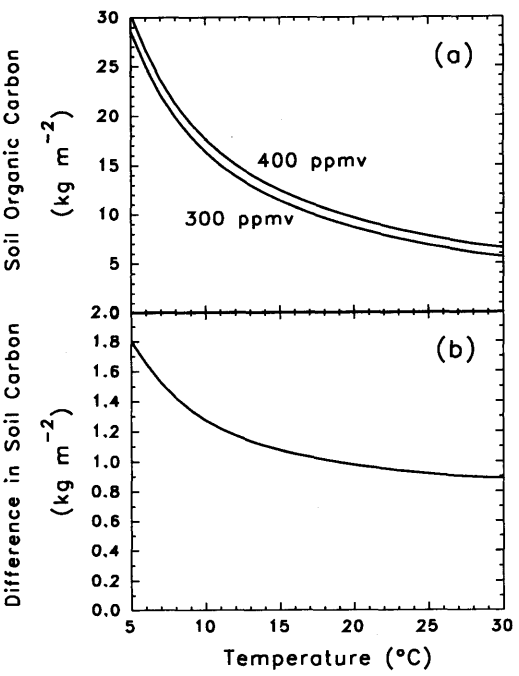

Fig. 5. Equilibrium soil organic carbon contents as a function of temperature at CO_2 concentrations of 300 and 400 ppmv (a), and the difference between the values at 300 and 400 ppmv (b).

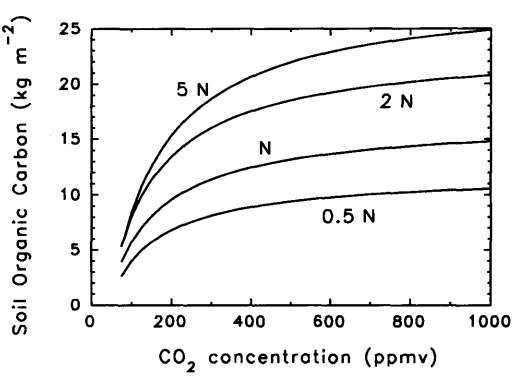

Fig. 6. Equilibrium soil carbon contents as a function of CO_2 concentration at 4 relative levels of nitrogen input. Nitrogen input was changed by scaling base parameters by the multipliers given in the Figure.

soils are much more sensitive to temperature than warm soils. For the same absolute increase in temperature, cold soils would lose much more carbon than warmer soils.

In the model, productivity and soil carbon storage responded to nitrogen input rates over a wide range (Fig. 6). Responses to CO_2 were observed at all nitrogen input rates, and response to nitrogen was observed at all but extremely low CO_2 concentrations.

Large increases in soil carbon in response to increasing CO_2 concentration are possible under nitrogen-limited conditions because the amount of nitrogen in the system can be increased through changes in nutrient dynamics and through increasing nitrogen fixation rates. In contrast, if productivity is limited by a nutrient of which soils contain only a fixed total amount, such as phosphorus or sulfur, then only a marginal response to CO_2 concentration could be expected.

3.2. *Time courses of change*

When the CO_2 concentration was changed in a single step from 300 to 400 ppmv, it took more than 500 years before a new equilibrium was reached at the higher temperature of 25°C (Fig. 7). At cooler temperatures, the soil was still far from any new equilibrium after even 500 years. A comparison of Figs. 5b and 7 shows that the soil at 25°C had reached about 80% of the equilibrium change of about 1 kg C m^{-2} after 500 years, whereas the soil at 5°C, had not reached more than one third of the eventual change of about 1.8 kg C m^{-2}. Consequently, soils at warmer temperatures show a greater response to increasing CO_2 concentration for many hundreds of years. These time courses are surprising, given that at equilibrium, soils at 5°C can store about 5 times as much carbon as soils at 25°C (Fig. 5a).

Comparison of the time courses of change in soil carbon between a step change in CO_2 concentration with the response to a gradual increase by 1 ppmv over one hundred years revealed a large difference apparent over the first 10 to 20 years, when the faster pools in the soil can respond quickly to changed conditions (Fig. 8). Subsequent changes are dominated by the responses of slower soil pools which have much longer turn-over times, and thus changes in soil carbon in response to step changes or gradual increase run much in parallel.

3.3. *Runs with historical data*

To address the question of how soil organic carbon contents may have changed over the past 130 years, and whether significant amounts of carbon may have been stored in organic matter of the world's soils, the model was run with recorded global temperature changes since 1860 (Jones et al., 1986; Folland et al., 1990), and with CO_2 concentrations deduced from ice core measurements and more recent direct measurements of atmospheric concentrations (Watson et al., 1990). The simulations were run for three base temperatures of 5, 15 and 25°C for the 1951–1980 reference period to assess to what extent soils

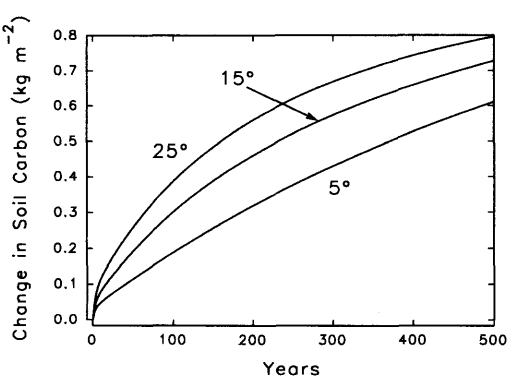

Fig. 7. Change in soil organic matter carbon for 500 years after a change in atmospheric CO_2 concentration from 300 to 400 ppmv at 3 different temperatures.

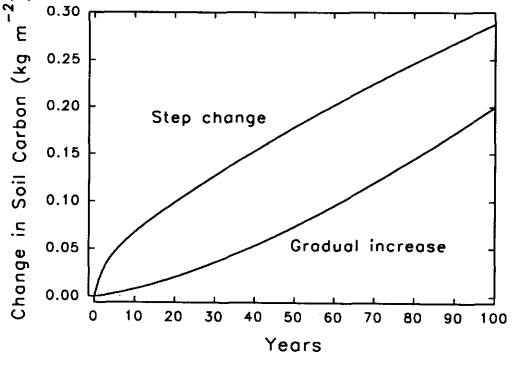

Fig. 8. Comparison of changes in soil organic carbon over 100 years in response to either a step increase in CO_2 concentration from 300 to 400 ppmv or a gradual increase from 300 ppmv by 1 ppmv per year.

in different thermal regions of the world might have been affected differently. For all temperature regimes, the runs were started after soils had been allowed to come to equilibrium at the conditions pertaining prior to 1860. All regions were assumed to have experienced the same absolute changes in temperature and CO_2 concentration. Temperature increased by about half a degree between the 1860s and the 1980s, and the CO_2 concentration increased from 290 to 354 ppmv from 1860 to 1990.

The simulation showed that warm soils are likely to have increased in carbon content over the last 130 years (Fig. 9) because of a strong plant response to increased CO_2 concentration (see Fig. 2) and only a relatively small decrease in soil carbon with increasing temperature (the slope of the curve in Fig. 5a).

Cool soils, on the other hand, are likely to have lost carbon over the last 130 years, as plant response to CO_2 in cool locations is limited, and there would be a strong effect of increasing temperature on speeding decomposition in these soils. At a temperature of 15°C, these two factors appear to be approximately equal in magnitude and opposite in sign so that there is only a slight trend towards increasing carbon gain (Fig. 9).

All these changes are relatively small compared to the total amount of organic carbon in each soil. For the period of 1860–1990, the changes correspond to −0.41%, +0.37% and +1.84% of initial soil carbon content for the soils at 5, 15 and 25°C, respectively. The small magnitude of changes is due to the compensating nature of increases in temperature and CO_2 concentration and due to the slow response times of soils to changes in external conditions.

The past 130 years have also seen an increase in nitrogen input into the world's ecosystems due to atmospheric pollution (Dignon and Hameed, 1989), with a value for 1980 of 22.1 Mt N yr^{-1}. For the present modelling, the trend of increasing emissions between 1860 and 1980 (Dignon and Hameed, 1989) was extrapolated through to 1990.

The effect of increasing nitrogen deposition was modelled for a soil at a base temperature of 15°C together with historical changes in CO_2 concentration and temperature. To model the global effect of nitrogen pollution, it was assumed that emitted nitrogen was evenly deposited over the wole land surface area of the Earth. This provides an overestimation of the effect of increasing nitrogen deposition and sets an upper limit for global ecosystem responses.

It is overestimating the response for two reasons.

(1) Sources of emission and consequently deposition are very unevenly distributed across the globe; any non-linearity in the response to nitrogen deposition would therefore overestimate the response.

(2) The assumption that nitrogen deposition is confined to land areas is clearly overestimating the deposition per unit land surface area. However, as virtually all nitrogen emissions originate from land areas and deposition occurs not too far from the sources of pollution the error may not be large.

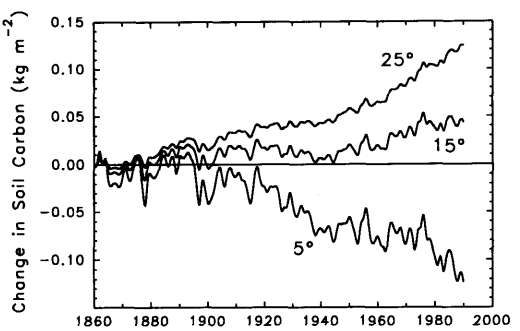

Fig. 9. Modelled change in soil organic carbon based on the observed records of CO_2 concentration and temperature. Simulations were run for three soils with different base temperatures in the 1951–1980 reference period.

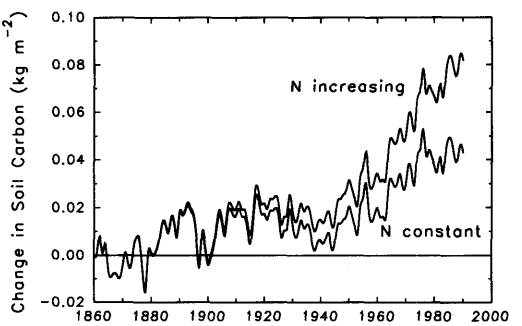

Fig. 10. Change in soil organic carbon since 1860. Nitrogen input was either kept constant or increased with increasing pollution, assuming that depositions were evenly distributed across the global land surface area. A base temperature of 15°C was assumed.

The resulting change in soil organic carbon is shown in Fig. 10. It shows that inclusion of atmospheric nitrogen deposition on the estimate of soil organic carbon is of only relatively small importance in a global context. Inclusion of nitrogen deposition with the upper bound assumptions used here enhanced the increase in carbon storage from 0.37% of background carbon storage to 0.72%, which still constitutes only a minor change. In heavily polluted areas, such as Central Europe or parts of the United States, increasing atmospheric inputs of nitrogen could well have greatly affected carbon storage, but in a global context the effect is only slight.

3.4. Test of key assumptions

In the interest of parsimony, the model used a very simple structure and formulation of plant responses to environmental conditions. To test whether this may have introduced any systematic errors in the estimation of trends in soil organic carbon, the model was tested with a change in some of the most critical assumptions. It was run with a seasonal cycle, a diurnal cycle, with the inclusion of nutrient retranslocation out of senescing tissue, and with the inclusion of all three changes together. The model was also run for water-limited conditions. Details of the conditions for the test runs are given in Appendix B. Results are shown in Table 1.

The response to historic changes in CO_2 concentration and temperature became more positive by the inclusion of both seasonal and diurnal cycles at all base temperatures. In the case of the diurnal cycle, this was due to photosynthesis operating at higher temperatures and therefore being more responsive to CO_2. In the case of the seasonal cycle, it was due to the non-linear response of the overall system to temperature. With the inclusion of a seasonal cycle, there was an effective shift to a higher operating temperature, and the response of a system with seasonal cycle was similar to that of a system at higher average temperature without seasonal cycle.

Table 1. *The effect of including diurnal cycles, seasonal cycles, retranslocation of nutrients and water limitations on soil carbon trends*

Modelled change in soil organic carbon from 1860 to 1990 ($g\ m^{-2}$).			
base temperature	5°	15°	25°
control	−123	+42	+124
diurnal cycle	−101	+62	+140
seasonal cycle	−47	+51	+130
retranslocation	−202	+40	+152
all	−62	+76	+181
water limited	+75	+150	+161

Inclusion of re-translocation of nutrients out of senescing tissue, amplified the response to environmental changes at both high and low temperatures. Without nutrient re-translocation, nitrogen feed-back in the system minimises changes due to changes in the environmental driving variables. This feed-back is reduced when nitrogen is recycled internally within the plant, and the response to external variables is more direct.

When all three factors were changed simultaneously, the overall effect gave a more positive carbon balance for all thermal regions. The effect was relatively small, however, and did not fundamentally alter the basic responses of the system. It also did not affect the different trends in the responses of soils in different thermal regions.

When plant productivity was assumed to be limited by water availability, the modelled change became more positive at all temperatures. The change was most pronounced at 5°C. For these simulations, I assumed productivity under water limited conditions to be limited by the diffusion of CO_2 into the leaf, which in turn was limited by the availability of water for diffusion out of the leaf. With this assumption, growth becomes linearly dependent on the concentration of CO_2. As growth at low temperature and without water limitation is not very responsive to increases in the CO_2 concentration (Fig. 2), a change to water-limited conditions had a marked effect on soil carbon storage.

Under warmer temperatures, the effect is less pronounced because the difference in the effects on productivity between water-limited and unlimited conditions are less marked. At the same time, since water-limited soils contain less carbon, the same percentage change leads to a smaller change in absolute terms. This meant that at 15°C, there was still a large effect of changing from water-unlimited to water-limited conditions, whereas at 25°C, there was only a small residual effect.

4. Discussion

The model runs suggest that soil organic carbon pools can respond significantly to changes in atmospheric conditions such as CO_2 concentration, temperature and nitrogen input (Figs. 4–6), but approach to a new equilibrium tends to be slow, requiring many hundreds of years, especially in cooler regions (Fig. 7). This is due to the very long turn-over times of the soil pools that contain the bulk of soil carbon (Martel and Paul, 1974; Parton et al., 1987).

Simulations with historic changes in temperature and CO_2 concentration over the past 130 years suggest that past changes should have had little overall effect on the global soil carbon storage, with some carbon gain in warmer regions and carbon loss in cooler regions (Fig. 9). Changes in either case would be small relative to the amount of carbon stored in soils. The inclusion of nitrogen input from atmospheric pollution gave a more positive carbon balance to soils (Fig. 10), but it, too, is likely to have had only a marginal effect in a global context.

The present work does not support the suggestion that soils at high northern latitudes may be a net sink for carbon (Tans et al., 1990). If there is any biospheric sink in northern high latitudes it is more likely to be the standing live biomass (Armentano and Ralston, 1980; Johnson and Sharpe, 1983; Kauppi et al., 1992). Soils in tropical regions, on the other hand, may well be a net sink for carbon (Enting and Mansbridge, 1991), albeit a small one because of the slow response time of soil pools. The present work is thus consistent with recent reassessment of the global carbon budget (Quay et al., 1992; Broecker and Peng, 1992; Sarmiento and Sundquist, 1992) which suggest only a small role for the global biosphere in sequestering carbon.

The effect of temperature on CO_2 sensitivity is firmly based on our physiological understanding of photosynthesis (Kirschbaum and Farquhar, 1984). Yet, most modelling studies of the effect of increased CO_2 concentration on plant productivity use a constant CO_2 sensitivity for all temperatures (e.g., Kohlmaier et al., 1989, 1991; Thornley et al., 1991), which is likely to overestimate effects under cool conditions and underestimate effects under warm conditions.

The present analysis uses a soils model that has been developed for grasslands, but similar responses to temperature, CO_2 and nitrogen input could be expected for forest systems. Similarly, the model takes no explicit account of water limitations. The comparison in Table 1 shows that in ecosystems limited by water the response to these environmental conditions should be similar, although generally more positive than for the simulation without water limitation. In this comparison, it was assumed that productivity increases linearly with increasing CO_2 concentration. This is an upper bound for likely responses, and realistic responses may be somewhat less. Moreover, the strongest effect of including water limitation was observed for the coolest ecosystems. These are ecosystems where water limitations would occur less frequently than in warmer ecosystems where water-limited and unlimited simulations showed less difference in the outcome. For these reasons, inclusion of water-limitation is not likely to fundamentally alter conclusions of the modelling runs.

These findings are only applicable for natural undisturbed ecosystems, yet vast areas are now used for agriculture, and even forest ecosystem are generally managed in various ways. Agricultural management affects soil organic carbon storage in many different ways: fertilisation, inclusion of legumes into crop rotations and irrigation generally enhance carbon storage, whereas soil cultivation, stubble burning and crop removal all lower carbon storage. Soil degradation, especially erosion and salinisation, can also greatly reduce soil carbon storage. For a global carbon budget, these positive and negative effects need to be quantified and included into any analysis, but this was not attempted in the present study.

4.1. Conclusions

When assessing the role of soil organic matter as a carbon store, it was found to be important to consider the effects of temperature on primary productivity as well as on soil organic matter decomposition. Further, the effect of increasing CO_2 concentration on plant productivity must be included, with the CO_2 sensitivity also being a function of temperature. Our understanding of all of these processes is still incomplete. While the present study attempted to make the most reasonable estimations of plant responses in natural non-woody ecosystems, it must be recognised that

prediction cannot yet be made with great confidence.

Predicted changes are also only very small fractions of background carbon contents. Because predicted changes are slight and slow, and because of the large natural variability in carbon contents in different soils, it is not possible to experimentally verify these predictions.

Despite these caveats, the present study showed that the observed changes in environmental conditions are not likely to have had much effect on global soil carbon storage. Increases in temperature and CO_2 concentration should have had effects that were similar in magnitude but opposite in sign, with the effect of temperature dominating in cooler regions, and the effect of CO_2 concentration dominating in warmer regions. Increasing nitrogen deposition would have led to some increase in carbon storage. While the effect may be significant in heavily industrialised and polluted regions, it is not likely to have been a large factor in a global context.

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6. Appendix

(A) Parameters used in the model

carbon content of plant dry matter	0.5 gC $(gDW)^{-1}$
fraction of leaves senescing weekly	0.015
fraction of roots senescing weekly	0.01
light extinction coefficient	0.5
lignin concentration in leaves	0.14 g $(gC)^{-1}$
lignin concentration in roots	0.11 g $(gC)^{-1}$
maximum productivity without limitation by light, CO_2, temperature or nitrogen	6 kgC m^{-2} yr^{-1}
maximum rate of nitrogen fixation	6 gN m^{-2} yr^{-1}
optimum foliar nitrogen concentration	0.0333 gN $(gDW)^{-1}$
proportion of sand in the soil	0.5
ratio of intercellular to ambient CO_2	0.667
root/shoot allocation ratio	0.5
specific leaf area	0.02 m^2 $(gDW)^{-1}$

Most of these parameters are based on values given in Parton et al. (1987). The light extinction coefficient of 0.5 is relevant for randomly oriented leaves. Maximum values of productivity and nitrogen fixation were chosen to obtain maximum production values similar to those listed by Lieth (1973), and the proportion of sand in the soil was taken as a representative value.

(B) Assumptions used in the testing of various hypotheses

Diurnal cycle: The temperature used for the calculation of the temperature dependence of CO_2 sensitivity taken as being 5°C above daily mean temperature.

Seasonal cycle: Sinusoidal change in temperature with an amplitude of ± 5°C around the annual mean temperature.

Senescence: Nitrogen concentration of senescing tissue assumed to be half that of living tissue.

Water limitation: Productivity is assumed to be proportional to the ambient CO_2 concentration and proportional to the ratio of rainfall and evaporation rate up to a maximum rate. Thereafter, the CO_2 limitation according to eq. (6) is assumed to operate. Decomposition rate constants are assumed to be modified by the equation:

$$r_w = 1.1252 - 0.9252e^{-2R/E} \quad \text{if} \quad R < E \qquad (10a)$$

$$r_w = 1 \quad \text{if} \quad R \geqslant E, \qquad (10b)$$

where r_w is the relative effect on decomposition rate constants, R is annual rainfall and E is the annual evaporation rate. This gives a minimal relative decomposition rate of 0.2 under very dry

conditions, a maximum of 1 when rainfall is equal to evaporation rate and a relative rate of 0.78 if annual rainfall is half of the annual evaporation rate. For the present simulation, annual rainfall was taken to be half of annual potential evaporation rate.

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