

Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model

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Abstract

The future of the land carbon sink is a significant uncertainty in global change projections. Here, key controls on global terrestrial carbon storage are examined using a simple model of vegetation and soil. Equilibrium solutions are derived as a function of atmospheric CO₂ and global temperature, these environmental variables are then linked in an idealized global change trajectory, and the lag between the dynamic and equilibrium solutions is derived for different linear rates of increase in atmospheric CO₂. Terrestrial carbon storage is departing significantly from equilibrium because CO₂ and temperature are increasing on a similar timescale to ecosystem change, and the lag is found to be proportional to the rate of forcing. Thus peak sizes of the land carbon sink, and any future land carbon source, are proportional to the rate of increase of CO₂. A switch from a land carbon sink to a source occurs at a higher CO₂ and temperature under more rapid forcing. The effects of parameter uncertainty in temperature sensitivities of photosynthesis, plant respiration and soil respiration, and structural uncertainty through the effect of fixing the ratio of plant respiration to photosynthesis are explored. In each case, the CO₂ fertilization effect on photosynthesis is constrained to reproduce the 1990 atmospheric CO₂ concentration within a closed global model. New literature compilations are presented for the temperature sensitivities of plant and soil respiration. A lower limit, $Q_{10} = 1.29$, for soil respiration significantly increases future land carbon storage. An upper limit, $Q_{10} = 3.63$, for soil respiration underpredicts the increase in carbon storage since the Last Glacial Maximum. Fixing the ratio of plant respiration to photosynthesis (R/P) at 0.5 generates the largest and most persistent land carbon sink, followed by the weakest land carbon source.

Keywords: carbon dioxide, carbon sink, carbon source, carbon storage, Last Glacial Maximum, temperature

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Introduction

Human-induced coupled increases in atmospheric CO₂ and surface temperature are driving changes in land carbon storage. At present, they contribute to a land carbon sink of the order of 2 Gt C yr⁻¹ (Prentice, 2001). Some models (White *et al.*, 1999; Cox *et al.*, 2000; Lenton, 2000) predict that, in future, climate change will cause the land carbon sink to cease and then become a land carbon source, while others predict a persistent land carbon sink (Cramer *et al.*, 2001). The dynamic global vegetation models (DGVMs) differ considerably

in their predictions of future terrestrial carbon storage (Cramer *et al.*, 2001) for reasons that are not completely understood, and are often obscured by model complexity. When one of these DGVMs is embedded in a general circulation model (GCM), its predictions of future land carbon storage are altered as a consequence of their feedback on atmospheric CO₂ and temperature projections (Cox *et al.*, 2000). Among the potentially important causes of uncertainty in future projections of land carbon storage are uncertainty in CO₂ fertilization effect on photosynthesis and uncertainty in the temperature sensitivities of photosynthesis, plant respiration and soil respiration.

Here, we study controls on terrestrial carbon storage using a simple model of vegetation and soil, which was

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introduced as the land carbon cycle component of an Earth system model (Lenton, 2000). We focus on the response of terrestrial carbon storage to changes in global mean surface temperature (T) and atmospheric CO_2 concentration (c_a). The simplicity of the model allows for some degree of analytical treatment and hence a clearer understanding of system behaviour. A simple model is also a logical place to start exploring the implications of different hypotheses for controls on the processes represented. In particular, we consider (i) a range of temperature sensitivities of terrestrial carbon fluxes, derived from the literature, and (ii) the possibility that the ratio of plant respiration/gross photosynthesis is insensitive to temperature (Waring *et al.*, 1998; Dewar *et al.*, 1999).

Equations are derived for equilibrium terrestrial carbon storage as a function of T and c_a , and transient terrestrial carbon sink/source created by different idealized, linear rates of increase in c_a . In all cases, the parameter determining the CO_2 fertilization effect on photosynthesis was adjusted so that the closed global model (Lenton, 2000) reproduced the 1990 level of the atmospheric CO_2 of 353 ppmv. The ocean component of the global model was kept constant; hence, this meant that the choice of parameters was constrained to predict a current land carbon sink of $\sim 2 \text{ GtC yr}^{-1}$. There is still considerable uncertainty in the size of the current land carbon sink, with the IPCC giving an estimate of 1.9 GtC yr^{-1} for the 1980s but a range of -0.3 to 3.8 GtC yr^{-1} (Prentice, 2001). Processes of nitrogen enrichment and re-growth, which are not included in this study, are thought to be contributing to the current land carbon sink. This means that the actual range of combinations of terrestrial responses to CO_2 and temperature change that is consistent with the current land carbon sink is wider than we consider here.

Present-day global vegetation is estimated to contain about 450 GtC (Bolin *et al.*, 2000), to have lost about 150 GtC as a result of land-use change activities

(Houghton, 1999), and to have gained $>0 \text{ GtC}$ due to CO_2 and N fertilization. This suggests an equilibrium value in the preindustrial and preagricultural conditions of $<600 \text{ GtC}$. Other estimates range from 420 to 830 GtC , with a mid-value of 625 GtC (Post *et al.*, 1990). Estimates of present-day soil carbon are much more variable, ranging from 1200 – 1600 GtC for surface soils (Post *et al.*, 1990) to about 2000 GtC for soils to 1 m depth (Bolin *et al.*, 2000). Here, we adopt the estimates of preindustrial carbon reservoirs of 550 GtC in vegetation and 1500 GtC in soil (Houghton *et al.*, 1990), for consistency with earlier use of the model (Lenton, 2000). The estimates of preindustrial global gross primary productivity (GPP) of 100 GtC yr^{-1} and net primary productivity (NPP) of 50 GtC yr^{-1} (Houghton *et al.*, 1990) give a default NPP/GPP ratio of 0.5 . Vegetation carbon has a turnover time of 5.5 years with respect to GPP. The soil respiration of 50 GtC yr^{-1} gives soil carbon an average turnover time of 30 years.

One method of constraining uncertainty in the functional responses of the model is to compare its predictions of equilibrium terrestrial carbon storage with independent estimates for times in the past for which T and c_a are reasonably well known. We attempt this approach for the Last Glacial Maximum (LGM) ($c_a = 180 \text{ ppm}$ and $T \sim 10^\circ \text{C}$). The various estimates of change in global terrestrial carbon stocks since the LGM are given in Table 1. Unfortunately, they vary considerably, depending on the method used. The most straightforward estimates have been made using global carbon isotope mass balance, which suggests $500 \pm 200 \text{ GtC}$. Estimates in this range are also emerging from the application of complex vegetation and soil models. However, estimates based on the ecosystem reconstructions produce much larger values, of around 1000 – 1500 GtC . This is a rather unsatisfactory situation unless we can confidently favour one approach over the others.

Table 1 Estimates of change in land carbon storage since the Last Glacial Maximum (LGM)

Technique	From LGM to	Change in carbon storage (GtC)	Reference
Global carbon isotope mass balance	Mid-Holocene	+ 550–680	Beerling (1999)
	Preindustrial	+ 610	Crowley (1995)
	Preindustrial	+ 310–550	Bird <i>et al.</i> (1994)
Ecosystem reconstruction	Early/mid-Holocene	+ 1500 (900–1900)	Adams and Faure (1998)
	Preindustrial	+ 750–1050	Crowley (1995)
	Preindustrial	+ 1350	Adams <i>et al.</i> (1990)
Modelling	Mid-Holocene	+ 668	Beerling (1999)
	Preindustrial	+ 606	Francois <i>et al.</i> (1998)
	Preindustrial	+ 300–700	Prentic <i>et al.</i> (1993)
Reconstruction and modelling	Preindustrial	+ 715 (430–930)	Van Campo <i>et al.</i> (1993)

Terrestrial carbon cycle model

The terrestrial carbon cycle component of the Earth system model of Lenton (2000) has two carbon reservoirs (vegetation and soil) and four fluxes (photosynthesis, plant respiration, litter-fall turnover and soil respiration). This structure is equivalent to Model 1 of Harvey (1989), who studied the effects of the number of vegetation and soil carbon reservoirs on the equilibrium and dynamic responses to the discontinuous (step-function) changes in CO₂ and temperature.

Governing equations

Vegetation carbon is supplied by photosynthetic uptake and lost through plant respiration and turnover (litter fall):

$$\frac{dC_v}{dt} = k_p C_{v,0} f_1(c_a) f_2(T) - k_r f_3(T) C_v - k_t C_v, \quad (1)$$

where C_v (GtC) is vegetation carbon reservoir, t is time (year), k_p (year⁻¹) is a rate constant for photosynthesis, $C_{v,0}$ is preindustrial vegetation carbon reservoir (GtC), f_1 is a normalized photosynthetic response to atmospheric CO₂ concentration, c_a (ppmv), f_2 is a normalized photosynthetic response to surface temperature, T (K), k_r (year⁻¹) is a rate constant for plant respiration, f_3 is a normalized plant respiration response to temperature and k_t (year⁻¹) is a rate constant for turnover (litter fall).

Soil carbon is a balance between the incoming litter and soil respiration loss:

$$\frac{dC_s}{dt} = k_t C_v - k_s f_4(T) C_s, \quad (2)$$

where C_s (GtC) is the soil carbon content, k_s (year⁻¹) is a soil respiration rate constant and f_4 is a normalized soil respiration response to temperature.

The environmental response functions f_1 , f_2 , f_3 and f_4 are normalized (i.e. set to unity) at the preindustrial CO₂ concentration of $c_{a,0} = 280$ ppmv and global mean surface temperature of $T_0 = 288.15$ K (15 °C). The

functional forms are those adopted previously in a simple Earth system model (Lenton, 2000), which were best estimates from the literature:

$$f_1 = \mu_1 \frac{c_a - k_c}{k_m + c_a - k_c}, \quad (3)$$

$$f_2 = \mu_2 (T - T_{\min})^2 (T_{\max} - T), \quad (4)$$

$$f_3 = \mu_3 e^{-E_a/RT}, \quad (5)$$

$$f_4 = \mu_4 e^{-308.56/(T-227.13)}. \quad (6)$$

The 'standard' parameter values used are given in Table 2. $R = 8.314$ J mol⁻¹ K⁻¹ is the molar gas constant. We used a version of the closed global model with land and ocean warming and updated ocean chemistry (Lenton & Cannell, 2002), within which a CO₂ fertilization half-saturation value of $k_m = 145$ ppmv was found to reproduce the 1990 level of atmospheric CO₂ (= 353 ppmv), as before (Lenton, 2000). Where a parameter or function was altered (examples later in the paper), the model was re-calibrated each time by adjusting k_m within the closed global model in order to reproduce the 1990 level of atmospheric CO₂.

Equilibrium solutions

To calculate the amounts of carbon in the global terrestrial vegetation and soil at equilibrium, $C_{v,eq}$ and $C_{s,eq}$, respectively, Eqn (1) may be rearranged as

$$C_{v,eq} = \frac{k_p C_{v,0} f_1 f_2}{k_r (f_3 + k_t/k_r)}. \quad (7)$$

An estimate of preindustrial vegetation carbon reservoir (assumed to be in equilibrium) of $C_{v,0} = 550$ GtC was adopted (Houghton *et al.*, 1990), corresponding to an average of 4.135 kg C m⁻² over the terrestrial surface of 1.33×10^{14} m².

By its definition and at time $t = t_0$ (when $f_1 = f_2 = f_3 = 1$) from Eqn (7),

$$\frac{k_p}{k_r} = 1 + \frac{k_t}{k_r}. \quad (8)$$

Table 2 Model parameters and standard values

Parameter and value	Description
$k_c = 29$ ppmv	CO ₂ compensation point for photosynthesis
$k_m = 145$ ppmv	CO ₂ half-saturation point for photosynthesis
$T_{\min} = 0$ °C	Minimum temperature for photosynthesis
$T_{\max} = 40$ °C	Maximum temperature for photosynthesis
$E_a = 5.483 \times 10^4$ J mol ⁻¹	Activation energy for plant respiration
$\mu_1 = 1.478$	Normalizing constant for photosynthesis CO ₂ response (f_1)
$\mu_2 = (5625)^{-1}$	Normalizing constant for photosynthesis T response (f_2)
$\mu_3 = 8.7039 \times 10^9$	Normalizing constant for plant respiration T response (f_3)
$\mu_4 = 157.072$	Normalizing constant for soil respiration T response (f_4)

That is, the initial condition has already placed a constraint upon the parameters. For this work, we assume that rate constants for photosynthesis and plant respiration, k_p and k_r are prescribed, which implies a value of turnover rate constant, k_t . If f_1 , f_2 and f_3 are assumed to be well understood, then the equilibrium solution is characterized by just one non-dimensional parameter, k_p/k_r , and prescribed values of c_a and T .

The equilibrium soil carbon content is given by

$$C_{s,eq} = \frac{k_t C_{v,eq}}{k_s f_4}. \quad (9)$$

$C_{s,eq}$ becomes a function of k_t/k_s , and through $C_{v,eq}$, also k_p/k_r . An estimate of preindustrial soil carbon content (when vegetation is assumed to be in equilibrium) of 1500 GtC is adopted (Houghton *et al.*, 1990), corresponding to an average $11.278 \text{ kg C m}^{-2}$ over $1.33 \times 10^{14} \text{ m}^2$. This initial condition provides another constraint upon the system. It implies that k_s/k_t is fixed (effectively the initial condition gives a value to $k_s/k_t = C_{v,0}/C_{s,0}$) and, as such, the problem collapses to variation in k_p/k_r alone.

Adding Eqns (7) and (9), total equilibrium carbon storage $C_{t,eq}$ (vegetation plus soil) is given by

$$C_{t,eq} = \frac{k_p C_{v,0} f_1 f_2}{k_r (f_3 + k_p/k_r - 1)} \left(1 + \frac{C_{s,0}}{C_{v,0} f_4} \right). \quad (10)$$

We adopt the estimates of $k_p = 100 \text{ GtC yr}^{-1}$ and $k_r = 50 \text{ GtC yr}^{-1}$ (Houghton *et al.*, 1990); hence $k_p/k_r = 2$ as our standard case (Lenton, 2000), with f_1 – f_4 as in Eqns (3)–(6).

The trajectories of equilibrium carbon storage are constrained by the fact that changes in atmospheric CO_2 cause changes in global surface temperature. In the case of human-induced global change, atmospheric CO_2 concentration and surface temperature can be related by

$$\Delta T = (T - T_0) = \frac{5.4}{\lambda} \ln \left(\frac{c_a}{c_{a,0}} \right). \quad (11)$$

$\lambda = 0.82 \text{ W m}^{-2} \text{ K}^{-1}$ based upon GCM simulations, giving a relatively high climate sensitivity (compared to other GCMs) of 4.56 K for a doubling of CO_2 from the preindustrial level.

Carbon storage results

Figure 1 shows the vegetation, soil and total equilibrium carbon storage for $0 < \text{CO}_2 < 1000 \text{ ppmv}$ and $0 < T < 30^\circ \text{C}$. The approximate conditions at LGM are marked with a cross ($c_a = 180 \text{ ppm}$ and $T = 10^\circ \text{C}$), and the dashed line indicates the idealized trajectory for a coupled increase in CO_2 and temperature from preindustrial conditions ($c_a = 280 \text{ ppm}$ and $T = 15^\circ \text{C}$).

Optimum mean global temperature for carbon storage in soils was cooler than the optimum for vegetation ($\sim 12^\circ \text{C}$ compared with $\sim 21^\circ \text{C}$), because of greater temperature sensitivity of the soil respiration compared with the temperature sensitivity of the net primary production (gross photosynthesis minus plant respiration), which supplies carbon to the soil. The preindustrial global mean temperature of 15°C emerges as close to optimal for the total carbon storage. Increasing the CO_2 concentration increases the land carbon storage, but the hyperbolic response (Eqn (3)) means that the effect saturates. The land carbon storage becomes more sensitive to changes in temperature as CO_2 concentration increases. Conversely, at temperatures further from optimal, land carbon storage is less sensitive to changes in the CO_2 concentration.

The predicted global land carbon storage at the LGM was about 1500 GtC, approximately 550 GtC less than the preindustrial equilibrium (Table 3). This difference is in the middle of the range of independent estimates made from the global carbon isotope mass balance and from more complex models, but below the estimates made by the ecosystem reconstruction (Table 1). The total global carbon storage was predicted to exceed 2700 GtC for $\text{CO}_2 > 1000 \text{ ppmv}$ at $T \sim 15^\circ \text{C}$, driving conditions that may have occurred $\sim 400 \text{ M years}$ ago after plants first colonized the land surface (Berner, 1994) (the solar luminosity was $\sim 5\%$ lower at the time).

Figure 2 shows the vegetation, soil and total equilibrium carbon storage following the idealized global change trajectory for different values of k_p/k_r (the fraction of photosynthesis respired by plants in the preindustrial equilibrium state). The solution for $k_p/k_r = 2$ corresponds to the trajectory marked in Fig. 1. All solutions show an initial increase in the land carbon storage followed by a decline. Thus, if CO_2 and temperature continue to increase, an initial land carbon sink is expected to become a land carbon source. This pattern is consistent with the predictions of some DGVMs (Cramer *et al.*, 2001). It derives largely from greater temperature dependence of soil respiration compared with net primary production (Kirschbaum, 2000; Rustad *et al.*, 2000). Increasing k_p/k_r was found to increase peak total carbon storage and shift the peak to a slightly higher CO_2 and temperature. However, the results are not particularly sensitive to k_p/k_r .

Dynamic solutions

To obtain simple dynamic solutions, an idealized forcing is used with atmospheric CO_2 concentration assumed to increase linearly with time:

$$c_a = c_{a,0} + \alpha(t - t_0), \quad (12)$$

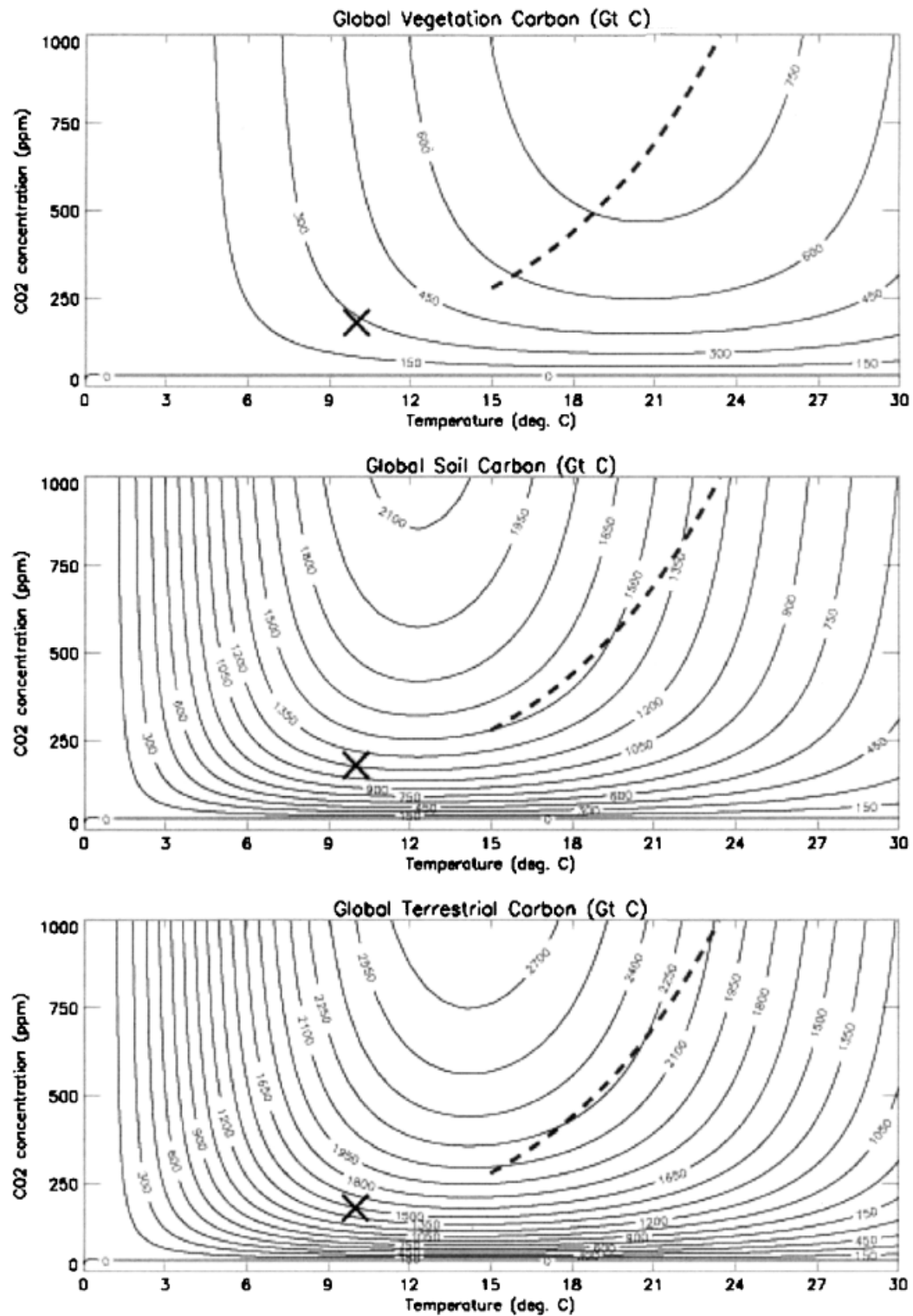


Fig. 1 Predicted terrestrial carbon storage at equilibrium as a function of CO₂ (0–1000 ppmv) and temperature (0–30 °C) in (a) global vegetation, (b) global soil and (c) their sum (total global terrestrial carbon). The cross marks the Last Glacial Maximum conditions. The dashed line marks the idealized trajectory for a coupled increase in CO₂ and temperature from the preindustrial state, related by Eqn (11). The standard model parameterization is used (Table 2), with the ratio of the rate constants for photosynthesis and respiration $k_p/k_r = 2.0$.

Table 3 Predicted land carbon storage under the Last Glacial Maximum conditions ($c_a = 180$ ppmv, $T = 10^\circ\text{C}$) for the lower and upper limits on the temperature responses of photosynthesis (P), plant respiration (R_P) and soil respiration (R_S), and for a fixed ratio of plant respiration to photosynthesis ($R_P/P = 0.5$)

Model variant	Altered parameter	k_m (ppmv)	Vegetation (Gt C)	Soil (Gt C)	Total (Gt C)	Change from present (Gt C)
Baseline	None	145	283	1213	1496	− 554
P (low)	$T_{\max} = 35^\circ\text{C}$	169	289	1239	1529	− 521
P (high)	$T_{\max} = 45^\circ\text{C}$	137	277	1187	1465	− 585
R_P (low)	$Q_{10} = 1.68$	127	271	1144	1415	− 635
R_P (high)	$Q_{10} = 2.8$	175	288	1220	1508	− 542
R_S (low)	$Q_{10} = 1.29$	84	299	927	1226	− 824
R_S (high)	$Q_{10} = 3.63$	206	268	1396	1664	− 386
R_P/P fixed	$\mu = 0.5$	110	244	1044	1288	− 762

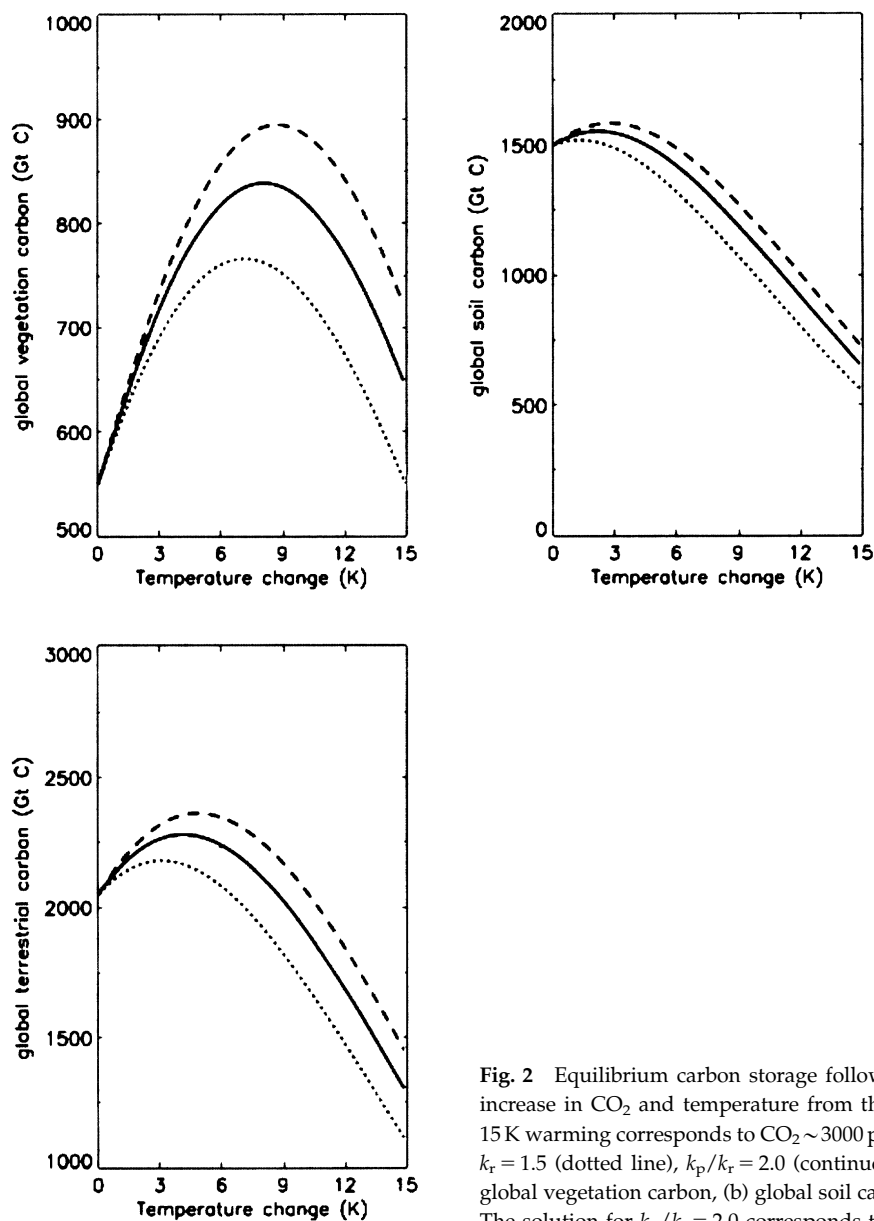


Fig. 2 Equilibrium carbon storage following an idealized trajectory for a coupled increase in CO_2 and temperature from the preindustrial state, related by Eqn (11). 15 K warming corresponds to $\text{CO}_2 \sim 3000$ ppmv. Sets of solutions are for values of $k_p/k_r = 1.5$ (dotted line), $k_p/k_r = 2.0$ (continuous line) and $k_p/k_r = 2.5$ (dashed line): (a) global vegetation carbon, (b) global soil carbon and (c) total global terrestrial carbon. The solution for $k_p/k_r = 2.0$ corresponds to the dashed line in Fig. 1.

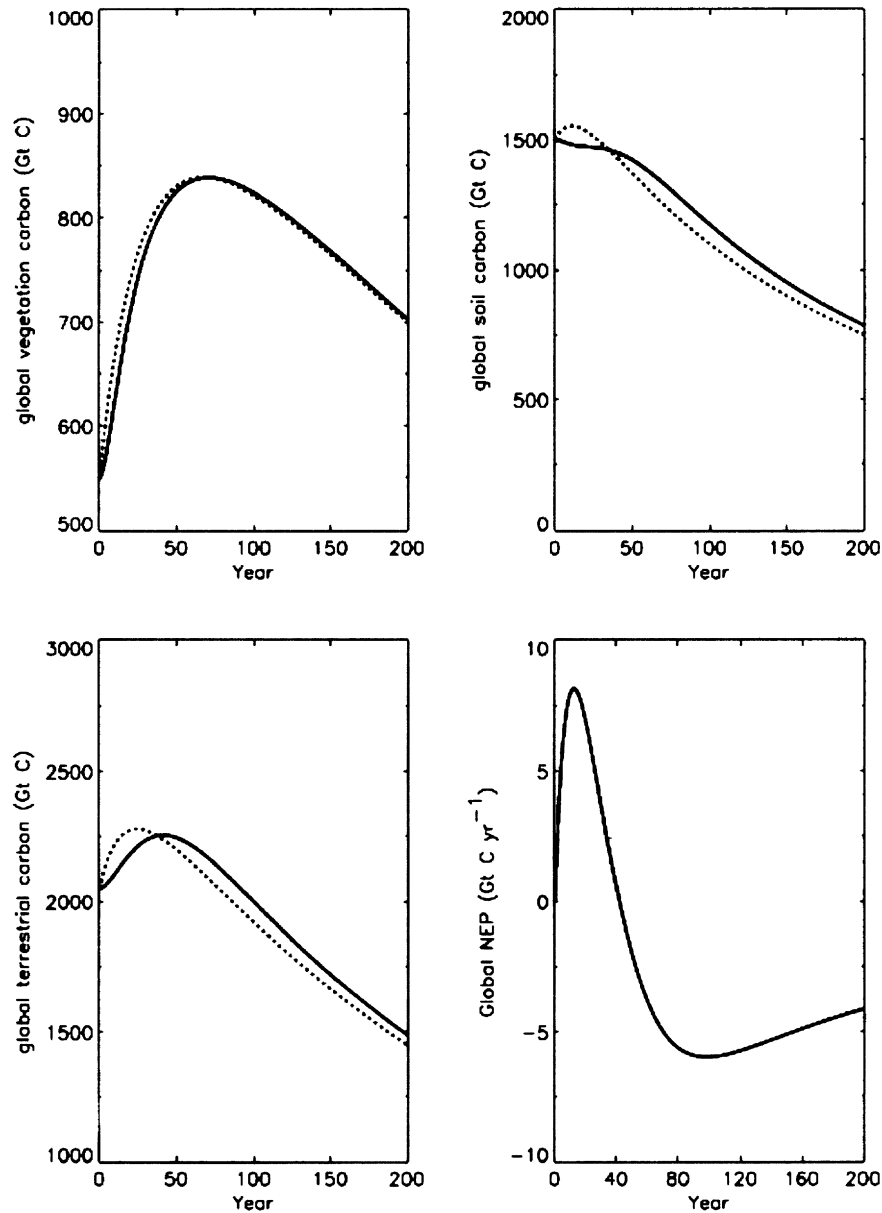


Fig. 3 Predicted equilibrium (dotted line) and dynamic (solid line) terrestrial carbon storage over 200 years of an idealized, linear increase in atmospheric CO_2 of 10 ppmv yr^{-1} , starting from the preindustrial conditions for (a) global vegetation, (b) global soil and (c) their sum (total global terrestrial carbon). Also shown in (d) is the net ecosystem productivity in the dynamic case. The standard model parameterization is used (Table 2), with the ratio of the rate constants for photosynthesis and respiration $k_p/k_r = 2.0$.

where t_0 (year) is the initial year and α (ppmv yr^{-1}) is the rate of forcing. The dynamic solution is assumed to start from an equilibrium state. To understand the importance of lags, the problem is considered in a non-dimensional form. The vegetation carbon is scaled with initial vegetation carbon content, $C_{v,0}$, and time is scaled by a timescale implicit within forcing conditions, t_f (year). This is given an exact definition by setting t_f such that the final atmospheric CO_2 concentration is, for instance, five times the initial

condition. Hence, $t_f = 4(c_a/\alpha)$. For $c_a = 280 \text{ ppmv}$ and at a forcing rate of $\alpha = 10 \text{ ppmv yr}^{-1}$, this then gives $t_f = 112$ years. It is assumed that the actual model timescale and t_f are of the same order of magnitude (this is reflected within the choice of a factor of five in the increase in the atmospheric CO_2 concentration). Thus, setting

$$C_v^* = \frac{C_v}{C_{v,0}}, \quad t^* = \frac{t}{t_f}, \quad (13)$$

Equation (1) may be written in a non-dimensional form as

$$\frac{1}{k_r t_f} \frac{dC_v^*}{dt} = \frac{k_p}{k_r} f_1(t^*) f_2(t^*) - f_3(t^*) C_v^* - \left(\frac{k_p}{k_r} - 1 \right) C_v^*. \quad (14)$$

This implies that the problem is one of two parameters, namely $k_r t_f$ and k_p/k_r . The soil carbon content may be scaled as

$$C_s^* = \frac{C_s}{C_{s,0}}. \quad (15)$$

This gives the non-dimensional equation for soil carbon as

$$\frac{1}{k_t t_f} \frac{dC_s^*}{dt^*} = \left(\frac{C_{v,0}}{C_{s,0}} \right) C_v^* - \frac{k_s}{k_t} f_4 C_s^*. \quad (16)$$

As the solution is initialized at equilibrium, the argument presented above still holds such that the parameter k_s/k_t is effectively fixed. However, in addition, parameter $k_t t_f$ may be written as $k_t t_f = k_r t_f (k_t/k_r)$. Equation (8) confirms that this may be finally written as $k_t t_f = k_r t_f (k_p/k_r - 1)$. Hence, the entire problem for the dynamical solution depends upon k_p/k_r and $k_r t_f$ only. The critical parameter within Eqn (14) is $k_r t_f$. Provided that this parameter is large, then, to a very good first approximation, the dynamic solution may be written as

$$C_v = C_{v,eq} + (k_r t_f)^{-1} C_{v,1}^*, \quad (17)$$

where $C_{v,1}^*$ is of magnitude unity. That is, the difference between the equilibrium solution and dynamic

solution is a lag term of the order $(k_r t_f)^{-1}$. With $k_r = 0.092$ and $t_f = 112.0$, this then gives a value of $(k_r t_f)^{-1} = 0.1$. On converting back to dimensional coordinates, a typical lag will then be of the magnitude $0.1 C_{v,0} \sim 55 \text{ Gt C}$. The same analysis may be applied to the soil carbon content. A typical lag will now be of magnitude $(k_r t_f)^{-1} (k_p/k_r - 1)^{-1} C_{s,0} \sim 150 \text{ Gt C}$.

Transient carbon sink/source results

Figure 3 shows the equilibrium (dotted line) and dynamic (solid line) terrestrial carbon storage with a linear increase in CO_2 of 10 ppmv yr^{-1} from preindustrial conditions, and corresponding net ecosystem productivity (NEP) in dynamic solution. The equilibrium solution follows the trajectory in Fig. 1. Dynamic solution lags noticeably behind the equilibrium solution by an amount proportional to the rate of forcing, in agreement with the above analysis. The lag of dynamic solution means that the switch from the carbon sink to the source occurs at a higher CO_2 and temperature than would be expected from the equilibrium solution.

Figure 4 shows examples of magnitude of maximum and minimum NEP increasing (approximately linearly) with the rate of increase in CO_2 . Furthermore, the CO_2 and temperature at which NEP switched from a sink to a source was found to increase approximately linearly with the rate of increase in CO_2 . When the CO_2 levels increased at 2 ppmv yr^{-1} (close to current rate of

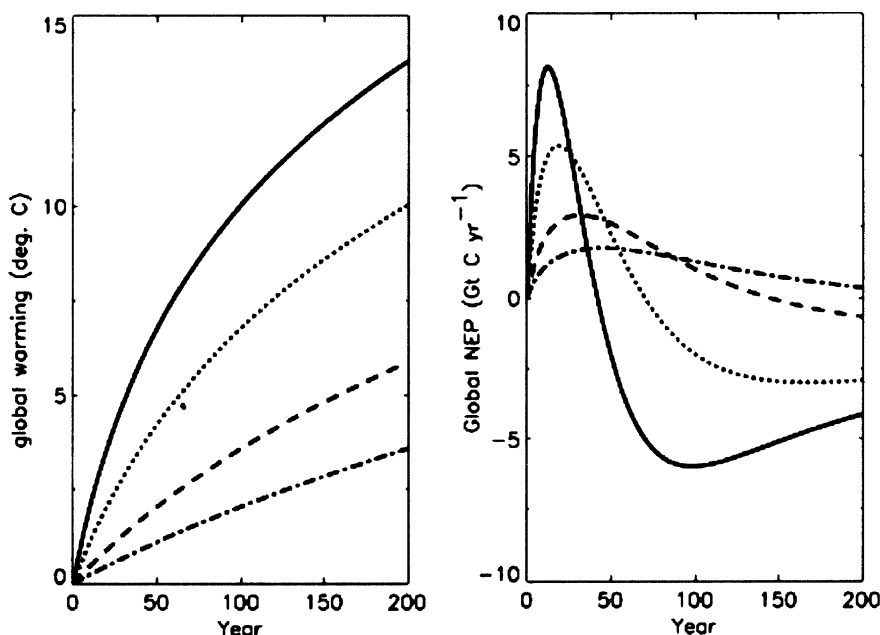


Fig. 4 Predicted changes in (a) the global mean temperature and (b) the net ecosystem productivity for different linear rates of increase in atmospheric CO_2 : 1 ppmv yr^{-1} (dot-dash), 2 ppmv yr^{-1} (dash), 5 ppmv yr^{-1} (dot) and 10 ppmv yr^{-1} (solid), using the standard model parameterization (Table 2).

forcing), a peak NEP of 2.9 GtC yr^{-1} was reached at 340 ppmv with 1.3°C warming, it switched to a source at 570 ppmv with 4.6°C warming, and a maximum source of 1.2 GtC yr^{-1} was generated at 1070 ppmv after 8.8°C warming. By contrast, when CO_2 levels increased at 10 ppmv yr^{-1} , a peak NEP of 8.2 GtC yr^{-1} was reached at 400 ppmv with 2.4°C warming, and it switched to a source at 700 ppmv with 6°C warming, which attained a maximum size of 6 GtC yr^{-1} at 1260 ppmv and 9.9°C warming. The rate of forcing determines the magnitude of NEP because it controls the timescale on which land carbon storage must adjust. A more rapid forcing increases the magnitude of NEP because land carbon storage must make the same adjustments in less time.

Range of temperature responses of terrestrial carbon fluxes

We now consider the possible range of temperature sensitivities of photosynthesis, plant respiration and soil respiration, treating each flux separately. For this purpose, temperature responses of plant and soil respiration (f_3 and f_4) were substituted with a simpler, generic ' Q_{10} ' function:

$$f_5(T) = Q_{10}^{\Delta T/10}, \quad (18)$$

where Q_{10} represents factorial increase in the rate of a process for a 10°C warming. The Q_{10} approach provides a good approximation to the original temperature responses of plant (f_3 substituted by f_5 with $Q_{10} = 2.15$) and soil respiration (f_4 substituted by f_5 with $Q_{10} = 2.4$).

Temperature sensitivity of photosynthesis

For photosynthesis, the original cubic temperature response function (f_2 , Eqn (4)) has a qualitatively different and more realistic shape than a Q_{10} response; hence it is retained. To capture the uncertainty in temperature response of photosynthesis, we vary the upper temperature limit parameter (T_{max}), which correspondingly alters the optimum temperature, T_{opt} (and the point of inflection). The upper and lower limits for temperature response of photosynthesis were based on a recent analysis (Medlyn *et al.*, 2002), which concluded that, for the majority of broadleaf and coniferous trees, the optimal temperature for photosynthesis varies between 23 and 30°C . The upper limit $T_{\text{max}} = 45^\circ\text{C}$ ($\mu_2 = (6750)^{-1}$) gives $T_{\text{opt}} = 30^\circ\text{C}$ and demands $k_m = 137 \text{ ppmv}$, whereas the lower limit $T_{\text{max}} = 35^\circ\text{C}$ ($\mu_2 = (4500)^{-1}$) gives $T_{\text{opt}} = 23.3^\circ\text{C}$ and demands $k_m = 169 \text{ ppmv}$. The corresponding ratios of photosynthesis rate at 30°C to the rate at 15°C are 2 and

1 (the original being 1.6), which is within the observed range of variation (Medlyn *et al.*, 2002).

Temperature sensitivity of plant respiration

Published studies of the temperature response of plant respiration can be subdivided into those that consider leaf/foliage dark respiration (the majority) and those that consider stem/branch (growth and maintenance)

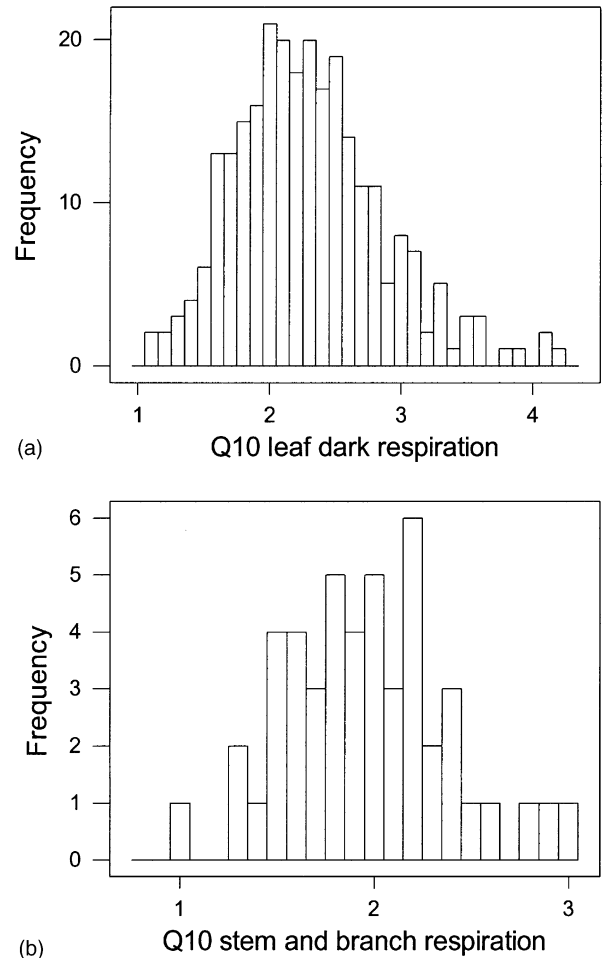


Fig. 5 Histograms of Q_{10} values for the temperature response of plant respiration: (a) leaf/foliage dark respiration and (b) stem/branch growth and maintenance respiration. (a) Q_{10} values for leaf/foliage dark respiration are from a recent literature compilation and accompanying measurements (Tjoelker *et al.*, 2001) plus more recent results (Hamilton *et al.*, 2001; Meir *et al.*, 2001; Turnbull *et al.*, 2001) and values from an earlier compilation (Ryan *et al.*, 1994) ($n = 264$, mean = 2.29, SD = 0.57). (b) Q_{10} values for the stem/branch growth and maintenance respiration are from a recent literature compilation (Damesin *et al.*, 2002) plus some additional results (Levy & Jarvis, 1998; Meir & Grace, 2002) ($n = 48$, mean = 1.96, SD = 0.42). A total data set combining (a) and (b) has $n = 312$, mean = 2.24, SD = 0.56.

respiration (the minority). (Root respiration is treated in the model, and in most field studies, as a component of soil respiration.)

Figure 5 presents histograms of Q_{10} values for temperature responses of leaf/foliage dark respiration ($n = 264$) and stem/branch growth and maintenance respiration ($n = 48$) from a literature review (details of sources are given in the caption). The measurements of Q_{10} at different reference temperatures and at different

levels of CO_2 are all included to give the largest possible data set. Q_{10} values generally decline with increasing temperature (Tjoelker *et al.*, 2001). However, there is a wide range of reference temperatures across the vegetated land surface, which we would ideally like to take into account in our globally averaged response. Hence, we think it better to include all reference temperatures in the data set rather than restrict ourselves to studies at one reference temperature

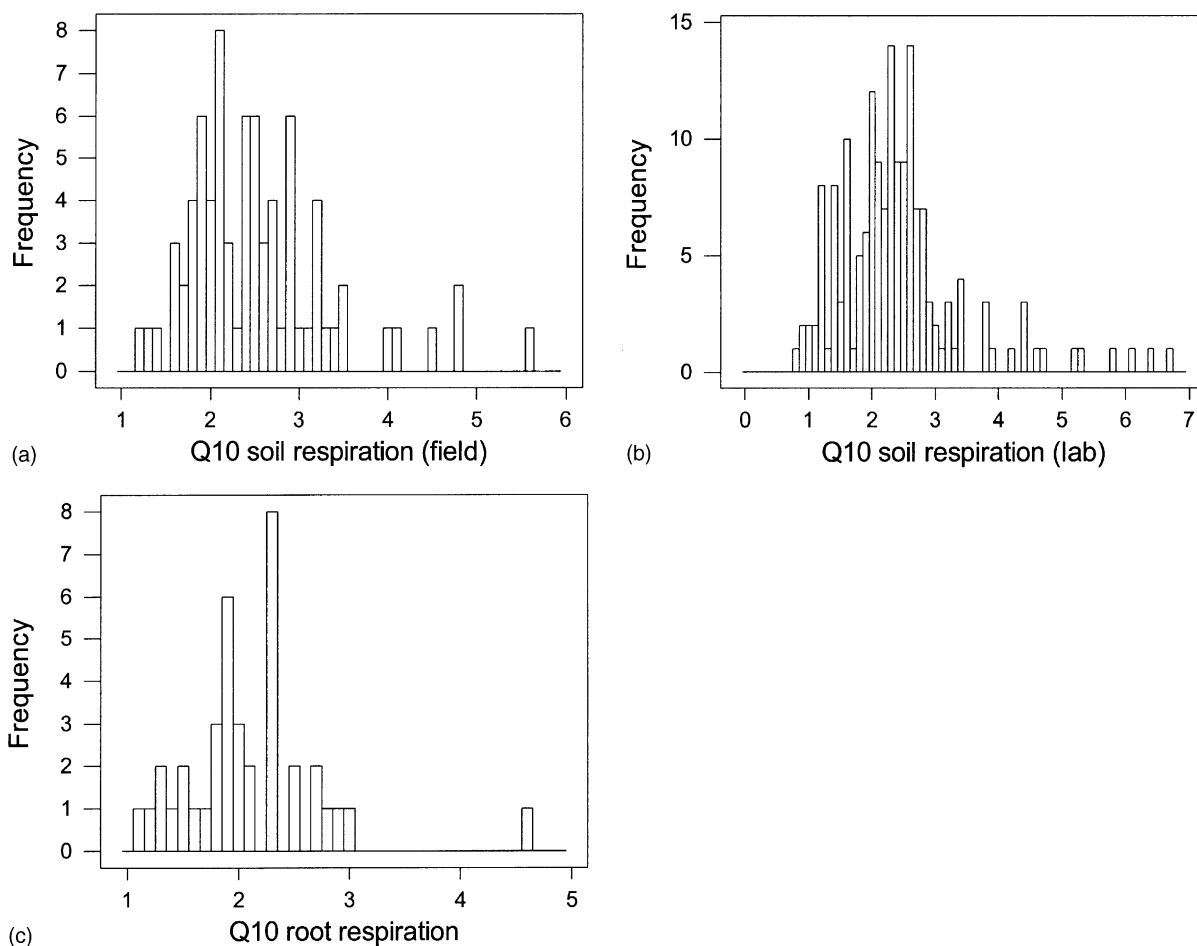


Fig. 6 Histograms of Q_{10} values for the temperature responses of (a) bulk soil respiration (including roots) from field studies, (b) soil respiration (excluding roots) from laboratory incubation studies and (c) root respiration from laboratory studies and one field study. (a) Q_{10} values for bulk soil respiration from field studies are an extension of the compilation of Raich & Schlesinger (1992) with values from Boone *et al.* (1998), Hersterberg & Seigenthaler (1991), Berg (1984), Cowling & MacLean (1981), Gordon *et al.* (1987), Schlentner & Van Cleve (1985), Ohashi *et al.* (1999), Londo *et al.* (1999), Hu *et al.* (2001), Buchmann (2000), Moren & Lindroth (2000), Davidson *et al.* (1998), and Xu & Qi (2001) ($n = 76$, mean = 2.54, SD = 0.82). (b) Q_{10} values for soil respiration from laboratory studies are based on the compilation of Kirschbaum (1995), with additional values from the compilation of Katterer *et al.* (1998) (avoiding duplication), Howard & Howard (1993), Townsend *et al.* (1997), Niklinska *et al.* (1999), and Chapman & Thurlow (1998) (taking only Q_{10} values based on CO_2 emission and at temperatures above 5°C because Q_{10} values below 5°C are meaninglessly large) ($n = 169$, mean = 2.51, SD = 1.37). Two outliers are not shown: $Q_{10} = 8.38, 12.92$. (c) Q_{10} values for root respiration are from the compilation of Atkin *et al.* (2000) (taking the average value when a small range is given and the lower end of the large range for *Festuca ovina*), with additional values from Boone *et al.* (1998), Ryan *et al.* (1994), Sprugel *et al.* (1995), (avoiding duplication) and values for *Pinus taeda* re-calculated from the original data (Boyer *et al.*, 1971) ($n = 39$, mean = 2.09, SD = 0.62). The outlier at $Q_{10} = 4.6$ is from a field study (Boone *et al.*, 1998). A total data set combining (a)–(c) has $n = 284$, mean = 2.46, SD = 1.17.

(e.g. 15 °C). Q_{10} values were not significantly affected by altering the reference CO_2 concentration (Hamilton *et al.*, 2001; Tjoelker *et al.*, 2001). Regardless of this, as atmospheric CO_2 is continuing to increase we think it reasonable to include all studies at different CO_2 levels.

The leaf/foliar dark respiration appears to be slightly more responsive to warming (Q_{10} mean = 2.29, SD = 0.57) than stem/branch respiration (Q_{10} mean = 1.96, SD = 0.42). The total data set has a mean Q_{10} = 2.24 (SD = 0.56), which may be an overestimate given that it is dominated by foliar values. The distributions of Q_{10} values are close to normal. Temperature response in our original model (approximate Q_{10} = 2.15), taken from the Hybrid model (Friend *et al.*, 1997), lies between the mean Q_{10} 's for leaf/foliar and stem/branch respiration and slightly below the mean of the total data set.

For the model, we take as upper and lower limit values for temperature sensitivity of soil respiration plus and minus one standard deviation from mean of the total data set: upper limit Q_{10} = 2.8 (k_m = 175 ppmv); lower limit Q_{10} = 1.68 (k_m = 127 ppmv). This is a pessimistic approach, because a better indicator of uncertainty in the global response is probably uncertainty in the mean, which is much smaller. However, Q_{10} range (1.68–2.8) is already smaller than that considered previously (1.4–3.0) (Lenton, 2000) from a more cursory inspection of the literature.

It should be noted that most of the Q_{10} measurements compiled here are based on short-term observations, and elevated rates of respiration measured may not be sustained on the much longer timescale of global change (see below).

Temperature sensitivity of soil respiration

Published studies of the temperature response of soil respiration can be subdivided into *in situ* field studies and laboratory incubation studies. Most field studies utilize seasonal (or sometimes diurnal) temperature variations. The field studies rarely separate the contribution of root respiration from that of free-living soil microorganisms and fauna, and in this regard they accord with our model. The laboratory incubation studies, in contrast, generally focus on sifted soil that excludes roots. There are a smaller number of separate laboratory incubation studies on roots only. One prominently published field study (Boone *et al.*, 1998) also attempts to separate the contribution of root respiration.

Figure 6 presents the histograms of Q_{10} values for the temperature response of bulk soil respiration (including

roots) from field studies (n = 76), heterotrophic soil respiration (excluding roots) from laboratory studies (n = 169) and autotrophic root respiration from laboratory studies and one field study (n = 39), all compiled from extensive literature reviews (details of sources are given in the caption). The field studies compiled deduce the temperature response from seasonal variations in the CO_2 efflux. The field studies compilation extends that of Raich & Schlesinger (1992). The compilations of Townsend *et al.* (1992) and Lloyd & Taylor (1994) helped in tracing older papers. Sites with strong soil moisture impacts on respiration rate (Carlyle & Than, 1988) are generally excluded, including all peat bog studies (Svensson, 1980; Stewart & Wheatley, 1990). The lab studies compilation is an extension of Kirschbaum (1995) and includes values from the compilation of Katterer *et al.* (1998) (which are at a common reference temperature). Q_{10} values from the laboratory incubation studies generally decline with increasing reference temperature (Kirschbaum, 1995), but in order to maximize the size of the data set and capture the range of reference temperatures existing in the real world, we include all different reference temperatures. The root respiration compilation is based on the studies of Atkin *et al.* (2000), Ryan *et al.* (1994), and Sprugel *et al.* (1995).

Field studies yield the temperature sensitivity for bulk soil respiration (Q_{10} mean = 2.54; SD = 0.82), which is in good agreement with that found for heterotrophic soil respiration from laboratory studies (Q_{10} mean = 2.51; SD = 1.37). The laboratory studies suggest that heterotrophic soil respiration is more responsive to warming than autotrophic root respiration (Q_{10} mean = 2.09; SD = 0.62). This contradicts one *in situ* field study (Boone *et al.*, 1998) that estimates a strong temperature sensitivity of root respiration (Q_{10} = 4.6). Our mean Q_{10} for root respiration is similar to mean Q_{10} values for the respiration of other parts of the plant (discussed above), which seems physiologically reasonable. Overall, soil respiration emerges as more temperature sensitive than plant respiration and less well constrained. The temperature response of bulk soil respiration in our original model (approximate Q_{10} = 2.4) from Lloyd & Taylor (1994) is close to the mean of the total data set (Q_{10} mean = 2.46; SD = 1.17).

For the model, we take as upper and lower limit values on temperature sensitivity of soil respiration plus and minus one standard deviation from the mean of the total data set: Q_{10} = 3.63 (k_m = 206 ppmv) and Q_{10} = 1.29 (k_m = 84 ppmv). Once again, a better indicator of uncertainty in the global response is probably the uncertainty in the mean, which is much smaller. The Q_{10} range is similar to that considered previously

(1.3–3.8) (Lenton, 2000) from a much narrower inspection of the literature.

Over the last decade, a number of ecosystem warming experiments have begun, and an attempt was made to estimate Q_{10} values from these using the contrast in the mean soil respiration rate between the control and heated plots, as detailed in Table 1 of Rustad *et al.* (2000). This yielded widely varying results: in two cases out of 17, warming leads to a decrease in the mean soil respiration; in one case, warming causes no change ($Q_{10} = 1$); and in the remainder, estimated Q_{10} ranges up to 14! A better method of estimating Q_{10} is to combine data covering the seasonal temperature variations from both the control and heated plots; using this approach, Peterjohn *et al.* (1994) found $Q_{10} = 2.5$, in close agreement with our compilations of field and laboratory studies.

It should be noted that Q_{10} measurements compiled here are based on relatively short-term observations and elevated rates of respiration measured may not be sustained on the much longer timescale of global change (see Discussion).

Effects on carbon storage and sink/source

The overall pattern of carbon storage for different combinations of c_a and T (as in Fig. 1) was not qualitatively altered by changing temperature sensitivities. The optimum global average temperature for land carbon storage at high CO_2 stayed within the range 13–17°C for the upper and lower limits in temperature responses of photosynthesis and plant respiration. It was more sensitive to extremes in temperature response of soil respiration, being <12°C for the upper limit and >18°C for the lower limit.

We considered whether some of the temperature parameter choices could be rejected on the basis of their predictions of change in terrestrial carbon storage since the LGM (Table 3). The predictions of LGM vegetation carbon storage are not sensitive to the temperature responses; in all cases, an approximate halving of the reservoir size is controlled by the 100 ppm reduction in atmospheric CO_2 . The predictions of the LGM soil carbon storage are more variable. Neither upper nor lower limit values for temperature responses of photosynthesis or plant respiration can be rejected as they all lead to similar predictions (520–640 GtC change). The high value for the temperature sensitivity of soil respiration ($Q_{10} = 3.63$) generates a 386 GtC decrease in LGM land carbon storage, which is smaller than the current estimates (Table 1). The low value for the temperature sensitivity of soil respiration ($Q_{10} = 1.29$) generated an 824 GtC decrease in the LGM land carbon storage,

which is out of the range of the isotope-derived estimates. However, if ecosystem reconstruction-based estimates are correct, it is the closest model variant to them.

Following the idealized global change trajectory, in all cases the land carbon storage exhibits an initial increase (land carbon sink) followed by a decline (land carbon source), but their sizes vary considerably. The most detrimental effects on future land carbon storage (largest net source) occur with lower-limit temperature sensitivity of photosynthesis (not shown) or upper-limit temperature sensitivity of plant respiration (Fig. 7). The upper-limit temperature sensitivity of soil respiration has a lesser effect, because for consistency with the recent atmospheric CO_2 record, it demanded the strongest CO_2 fertilization effect. The most beneficial effect on future land carbon storage (largest initial sink, smallest net source) occurs with the lower-limit temperature sensitivity of soil respiration (Fig. 8). This generates an increased lag of dynamic solution behind equilibrium solution. The upper-limit temperature sensitivity of photosynthesis and the lower-limit temperature sensitivity of plant respiration lead to similar predictions (not shown), which do not differ greatly from the baseline model (Fig. 3).

A constant ratio of plant respiration to photosynthesis

Almost all global vegetation models allow the ratio of plant respiration to photosynthesis (R/P) to vary with temperature (Dewar *et al.*, 1999). The model of Lenton (2000) is no exception. If global vegetation carbon is fixed (i.e. the instantaneous response), R/P decreases from plus infinity at 0°C to a minimum of 0.5 at 15°C, and then increases again to ~1 at 30°C and ~2 at 35°C. In the model, global vegetation carbon can vary with a consequent effect on R. Thus, at steady state (for changes in the temperature alone), R/P increases from 0.3 at 5°C through 0.5 at 15°C to 0.7 at 26°C and 0.8 at 34°C. However, an increasing amount of literature suggests that, in nature, time-averaged R/P varies within a much more restricted range.

Literature assessment

The coupling between photosynthesis and plant respiration was first noted in the finding that NPP per unit of carbon assimilated by photosynthesis varies within a restricted range over a wide range of environmental conditions (McCree, 1974). That is, NPP is a conservative fraction of GPP. More recently, many other experimental observations have shown that

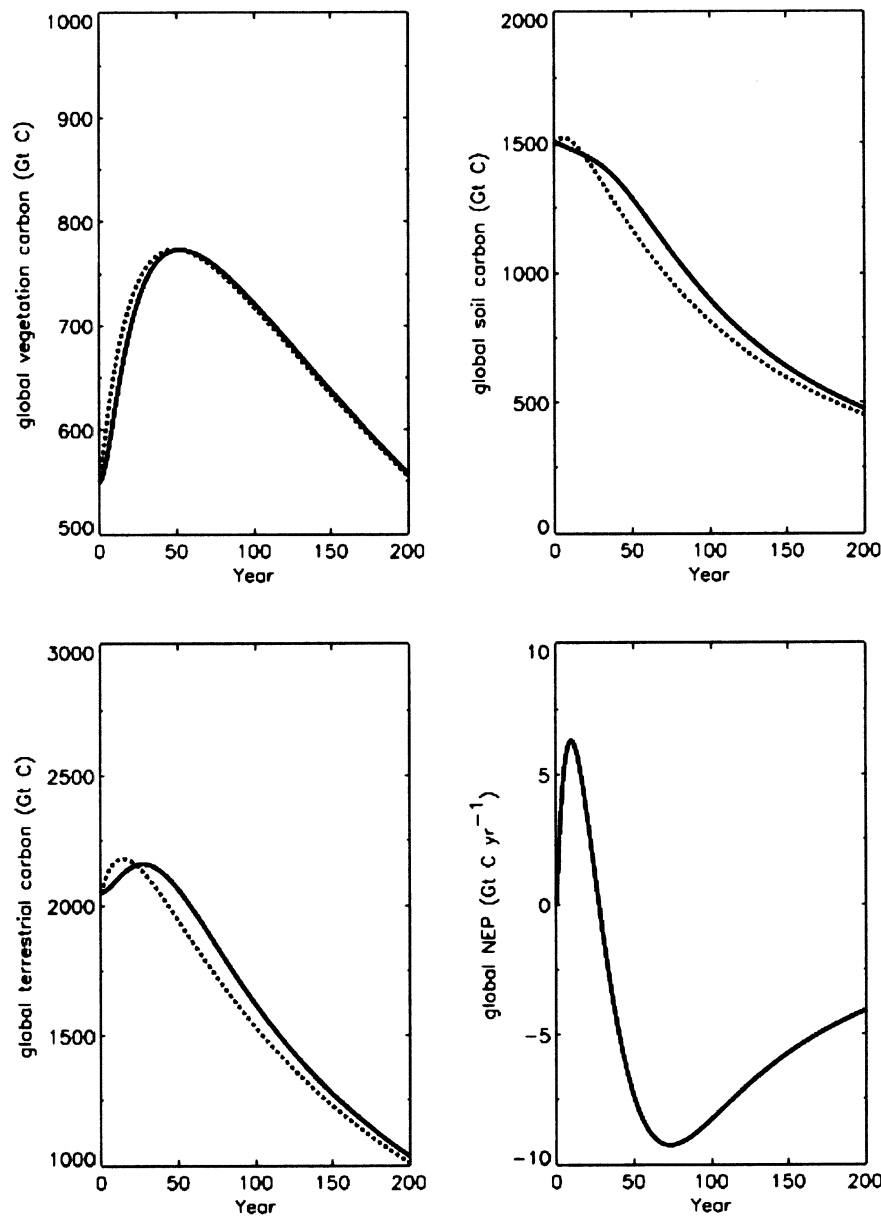


Fig. 7 Assume an upper limit for the temperature sensitivity of plant respiration ($Q_{10} = 2.8$). The predicted equilibrium (dotted line) and dynamic (solid line) terrestrial carbon storage over 200 years of an idealized, linear increase in the atmospheric CO₂ of 10 ppmv yr⁻¹, starting from preindustrial conditions for (a) global vegetation, (b) global soil and (c) their sum (total global terrestrial carbon). Also shown in (d) is the net ecosystem productivity in the dynamic case.

the ratio of plant respiration to gross photosynthesis in growing plants remains in the range 0.4–0.6 over an order of magnitude range of temperature and plant biomass (for wheat (Gifford, 1995), soybean (Ziska & Bunce, 1998), pine (Ryan *et al.*, 1996; Mäkelä & Valentine, 2001), and poplar and spruce (Goetz & Prince, 1998)).

Many of the estimates of Q_{10} for plant respiration given in the literature are based on short-term observations, over minutes to hours (including those

in Fig. 5). When plant respiration is considered over months to years, it is more strongly limited by the substrate supply (Reich *et al.*, 1998; Dewar *et al.*, 1999; Cannell & Thornley, 2000). Over these timescales, of interest here, the average R/P ratio normally remains around 0.5 ± 0.1 , regardless of the temperature, and the ecosystem models that operate on an annual time-step perform realistically when fixing the R/P ratio at 0.5 (Waring *et al.*, 1998). We therefore examined the effect of fixing the plant R/P ratio to 0.5 on the

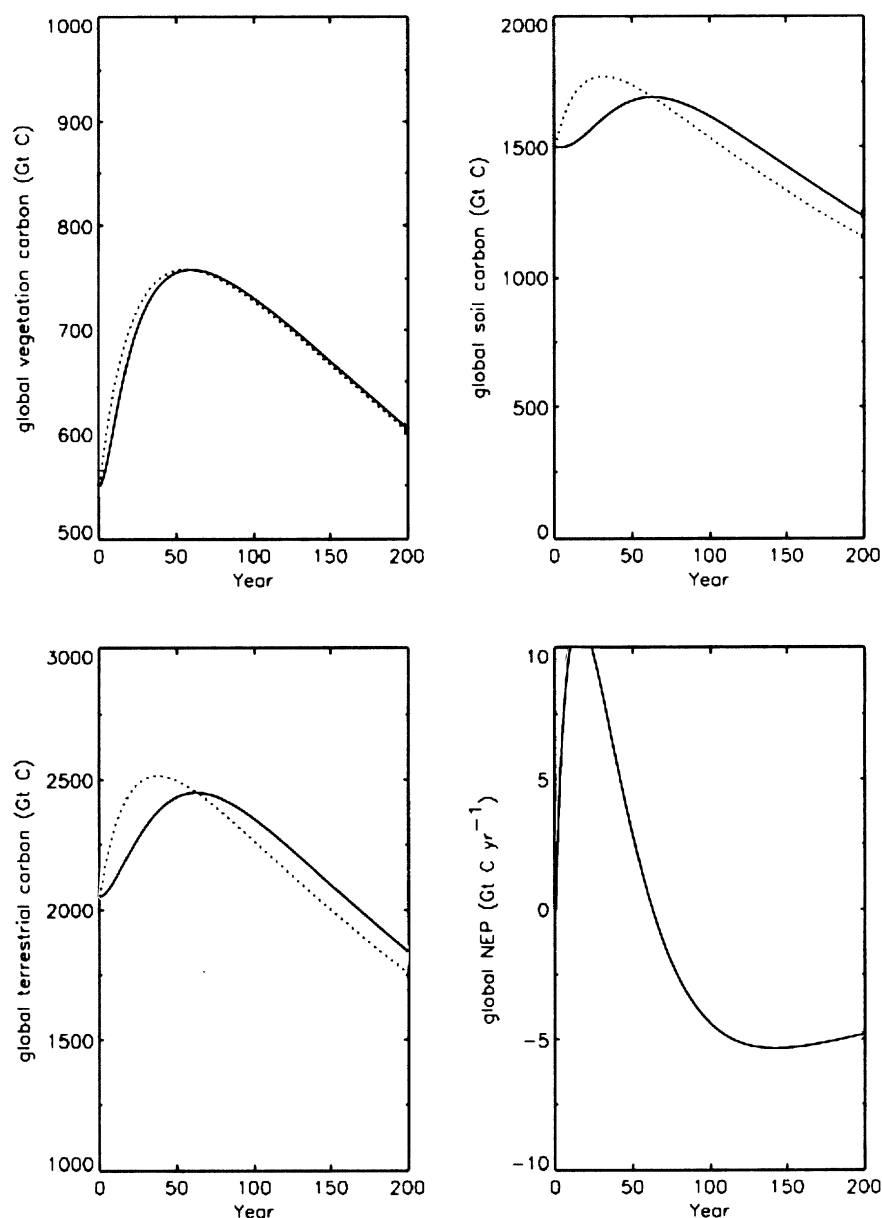


Fig. 8 Assuming a lower limit for the temperature sensitivity of soil respiration ($Q_{10} = 1.29$). The predicted equilibrium (dotted line) and dynamic (solid line) terrestrial carbon storage over 200 years of an idealized, linear increase in the atmospheric CO_2 of 10 ppmv yr^{-1} , starting from the preindustrial conditions for (a) global vegetation, (b) global soil and (c) their sum (total global terrestrial carbon). Also shown in (d) is the net ecosystem productivity in the dynamic case.

global terrestrial carbon storage and the terrestrial carbon sink.

Model reformulation

If we assume $R/P = r$, where $r < 1$ is a constant, and hence NPP is a constant fraction of GPP, then the following replaces Eqn (1):

$$\frac{dC_v}{dt} = k_p(1-r)C_{v,0}f_1(c_a)f_2(T) - k_t C_v. \quad (19)$$

If we know r at present and it is time independent, then from a steady state under preindustrial conditions ($f_1 = f_2 = 1$, $C_v = C_{v,0}$) the following is obtained:

$$\frac{k_p}{k_t} = \frac{1}{1-r}. \quad (20)$$

This removes the last degree of freedom from the problem. Knowing r gives k_p/k_t and k_t/k_s (from Eqn (9)) is fixed as before. Thus,

$$C_{v,\text{eq}} = C_{v,0}f_1f_2, \quad (21)$$

$$C_{t,eq} = C_{v,0} f_1 f_2 \left(1 + \frac{C_{s,0}}{C_{v,0} f_4} \right). \quad (22)$$

The temperature response of photosynthesis is now assumed to apply to NPP, and this amounts to a shift in optimum temperature for NPP, to a significantly higher value ($\sim 27^\circ\text{C}$ as opposed to $\sim 20^\circ\text{C}$). The CO_2 response of photosynthesis now operates on NPP as a whole, making R/P invariant to changes in CO_2 , which may not be accurate (Dewar *et al.*, 1999). Finally, there is no dependence of plant respiration and hence NPP on biomass, which was open to question in the original model given that the grasslands and forests can maintain similar NPP per unit area despite huge difference in biomass. With the assumption that $r = 0.5$ (i.e. $R/P = 0.5$, corresponding to $k_p/k_r = 2$), CO_2 fertilization effect had to be weakened to $k_m = 110 \text{ ppmv}$.

Effects on carbon storage and sink/source

The most striking effect of fixing the R/P ratio at 0.5 was that optimum temperature for land carbon storage increased from ~ 15 to $\sim 21^\circ\text{C}$ (comparing Figs 1 and 9), with the optimum for vegetation carbon increased to $\sim 27^\circ\text{C}$ and for soil carbon to 16°C (Fig. 9). These changes occurred because high-temperature optimum of photosynthesis now applies to NPP (gross photosynthesis minus plant respiration).

The fixed R/P formulation of the model leads to a larger predicted increase in total carbon storage since the LGM of $\sim 760 \text{ GtC}$ (Table 3). This value exceeds the estimates made using global carbon isotope balance and more complex models, but is at the lower end of the values estimated by ecosystem reconstruction (Table 1).

The higher optimum temperature for land carbon storage means that on following the idealized future trajectory of increasing temperature and CO_2 , there is a much greater initial increase in equilibrium carbon storage. Consequently, there is much greater scope for an increase in the predicted future land carbon sink. This is illustrated in Fig. 10 for a linear increase in CO_2 concentration of 10 ppmv yr^{-1} , which shows a sustained increase in vegetation carbon and a relatively small decrease in soil carbon compared with the standard model (Fig. 2). The equilibrium total carbon storage undergoes a greater increase, generating a larger net carbon sink, and the switch to a land carbon source occurs at a higher temperature. Having passed its peak, the total carbon storage declines more gradually, generating a smaller net carbon source. Furthermore, when R/P is fixed, the lag of the dynamic solution behind the equilibrium solution is increased.

This prolongs the terrestrial carbon sink and delays the switch to a land carbon source.

Discussion

Land carbon storage depends on a number of interacting processes, not all of which are captured in our simple model. Here, we discuss the limitations of the present study, lessons that have been learned from the previous work, and ways forward.

The temperature sensitivity of soil respiration emerges as a key control of land carbon storage and is the subject of much debate in the literature. Soil carbon occurs in different forms with very different lifetimes. A number of measurement techniques are probably biased towards fast-turnover litter and intermediate-turnover mobile soil, as in the litter mass-loss experiments (Berg *et al.*, 1996), measurements of surface soil ^{13}C depletion (Bird *et al.*, 1996), ^{14}C signature of the 'light' fraction (Trumbore *et al.*, 1996) and many laboratory incubation experiments (Kirschbaum, 2000). Thus our Q_{10} compilation (Fig. 6), based largely on short-term measurements, is probably biased towards the temperature response of shorter-lived soil carbon pools. On global change timescales, the community of organisms that respire soil organic matter may acclimate to warming, thus minimizing changes in the flux (Jarvis & Linder, 2000). Some measurements have been used to infer a surprisingly low temperature sensitivity of long-lived mineral soil organic matter (Liski *et al.*, 1999; Giardina & Ryan, 2000). However, the inferences drawn, especially between the turnover rates of soil at their native temperatures and their response to temperature perturbation, are potentially flawed (Ågren, 2000; Ågren & Bosatta, 2002). Thus, long-term response of soil carbon to warming remains uncertain.

To better model the response of the soil carbon reservoir, previous work (Lenton, 2000) has subdivided it into three components: fast-turnover detritus, mobile soil and resistant soil, with residence times of 1.8, 80 and 577 year, respectively. The future land carbon source becomes much more persistent, due to the slow response of the resistant soil reservoir, which shrinks over ~ 600 years. In mathematical terms, the lag of the dynamic solution behind the equilibrium solution is greatly increased. Even if the resistant soil is assumed to be independent of temperature, a transient land carbon source still occurs due to the loss of mobile soil organic carbon.

This highlights one limitation of aggregating the terrestrial biosphere into two carbon reservoirs (vegetation and soil): the range of timescales of response captured by the model is less than that of the real

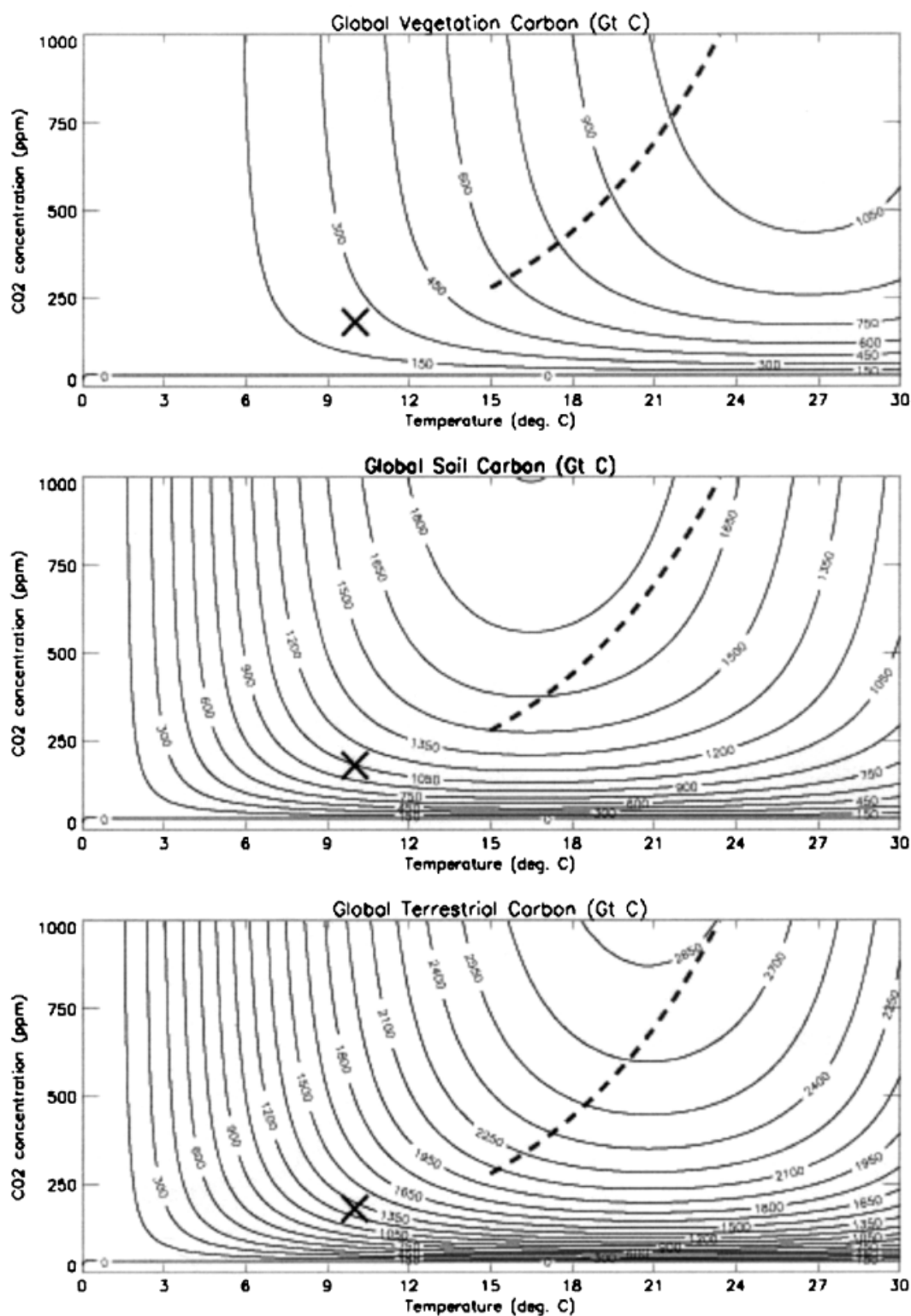


Fig. 9 Assume that the R/P ratio is fixed at 0.5. The predicted carbon storage at equilibrium as a function of CO₂ (0–1000 ppmv) and temperature (0–30°C) for (a) global vegetation, (b) global soil and (c) their sum (the total global terrestrial carbon). The cross marks the Last Glacial Maximum conditions. The dashed line marks the trajectory for a coupled increase in CO₂ and temperature from the preindustrial state, related by Eqn (10).

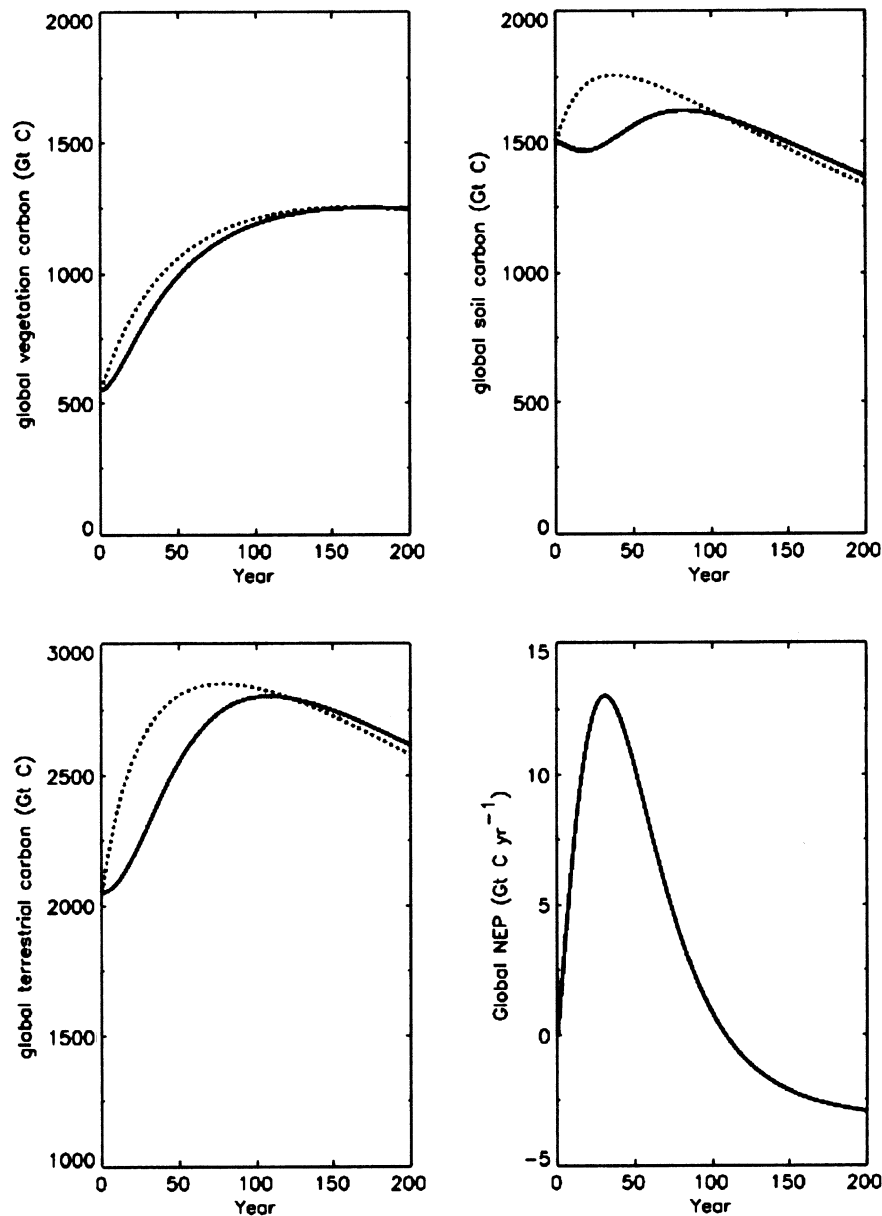


Fig. 10 Assume that the R/P ratio is fixed at 0.5. The predicted equilibrium (dotted line) and dynamic (solid line) carbon storage over 200 years of a linear increase in the atmospheric CO_2 of 10 ppmv yr^{-1} , starting from the preindustrial conditions for (a) global vegetation, (b) global soil and (c) their sum (the total global terrestrial carbon). Also shown in (d) is the net ecosystem productivity in the dynamic case.

system. The model also lacks any spatial distinction. Ecosystems at different latitudes are at different reference temperatures, have different temperature responses and rates of warming vary with the latitude. Colder ecosystems appear to be more temperature sensitive (Shibistova *et al.*, 2002), as reflected, for example, in the decline of soil respiration Q_{10} with the reference temperature. Furthermore, the assumption that soil temperature follows air temperature is flawed in high-latitude cases, where significant changes in

snow cover occur. Thus, we may have underestimated the contribution of the high-latitude soils to future global respiration flux.

Our model ignores an important interaction between the CO_2 concentration and temperature response of photosynthesis: as CO_2 increases, the optimum temperature for carbon assimilation increases (Farquhar *et al.*, 1980; Long, 1991). This should translate into an increase in the optimum temperature for carbon storage, and will tend to preserve a land carbon sink

and delay the switch to a land carbon source. A number of other factors influencing terrestrial carbon storage are missing from our model, including changes in vegetation distribution, precipitation, soil moisture, land use, nitrogen deposition, land ice cover and sea level. However, previous work (Lenton, 2000) has shown that if nitrogen deposition and/or re-growth contribute significantly to the current land carbon sink, then this demands a weaker CO₂ fertilization effect in order to balance the current carbon budget, thus generating an earlier land carbon sink to source transition and a larger future carbon source.

Conclusions

The transparency of simple models can aid understanding and suggest new insights, which can then be examined more thoroughly with complex models. In this case, a simple global vegetation and soil model reveals that a land carbon sink is to be expected at present because atmospheric CO₂ and surface temperature have thus far changed in a manner robustly predicted to increase land carbon storage. However, if CO₂ and temperature continue to increase, land carbon storage is predicted to peak and then decline, generating a land carbon source. Land carbon storage is departing significantly from equilibrium because human-induced changes in CO₂ and temperature are occurring on a similar timescale to ecosystem change. The resulting lag is proportional to the rate of forcing. Hence, peak sizes of the land carbon sink (positive NEP), and any future land carbon source (negative NEP), are predicted to be proportional to rate of increase of CO₂. If a switch from a land carbon sink to a source occurs, it does so at a higher CO₂ and temperature under more rapid forcing, because this generates a larger lag of the actual carbon storage behind the equilibrium solution.

Our conclusions regarding the effects of rate of forcing are not altered by uncertainties in the temperature responses of photosynthesis, plant respiration and soil respiration, nor do we expect them to be altered by other caveats raised in the discussion. Our prediction of a future land carbon sink to source transition is robust to all parameter and structural uncertainties simulated thus far, but there are more to be considered in future work. What is sensitive is the forcing threshold at which a sink–source transition occurs.

An attempt to use predicted changes in land carbon storage at the LGM to constrain the choice of model functions and parameters leads us to question high values for temperature sensitivity of soil respiration. For this method to be more successful demands better-constrained estimates of land carbon storage, ideally for

more historical combinations of CO₂ and temperature. At present, the LGM ecosystem reconstructions support the view that global temperature changes do not greatly affect soil carbon storage (instead both vegetation and soil carbon storage are suppressed by lower CO₂), while estimates from the global isotope mass balance support the view that global temperature change does affect soil carbon storage (in the LGM case of colder conditions, tending to increase it).

The constancy or otherwise of the ratio of plant respiration to photosynthesis (R/P) has a large effect on future size and persistence of the land carbon sink, and the degree of forcing required to generate a land carbon source. Hence, we suggest that more long-term field experiments be carried out to determine the degree of variability in R/P, and that its consequences be explored in more complex DGVMs. We also think it worth considering whether the ratio of soil respiration to net primary productivity (carbon supply to the soil) may be relatively invariant to temperature. If so, this would further tend to maximize the land carbon sink and minimize any future land carbon source.

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