

Uncertainty in climate–carbon-cycle projections associated with the sensitivity of soil respiration to temperature

By CHRIS D. JONES^{1*}, PETER COX¹ and CHRIS HUNTINGFORD², ¹*Hadley Centre, Met. Office, Bracknell, Berkshire RG12 2SY, UK;* ²*Centre for Ecology and Hydrology, Wallingford OX10 8BB, UK*

(Manuscript received 14 January 2002; in final form 12 June 2002)

ABSTRACT

Carbon-cycle feedbacks have been shown to be very important in predicting climate change over the next century, with a potentially large positive feedback coming from the release of carbon from soils as global temperatures increase. The magnitude of this feedback and whether or not it drives the terrestrial carbon cycle to become a net source of carbon dioxide during the next century depends particularly on the response of soil respiration to temperature. Observed global atmospheric CO₂ concentration, and its response to naturally occurring climate anomalies, is used to constrain the behaviour of soil respiration in our coupled climate–carbon-cycle GCM. This constraint is used to quantify some of the uncertainties in predictions of future CO₂ levels. The uncertainty is large, emphasizing the importance of carbon-cycle research with respect to future climate change predictions.

1. Introduction

Modelling studies have demonstrated that climate–carbon-cycle feedbacks over the next century may have a large impact on future CO₂ levels and climate (Cox et al., 2000; Friedlingstein et al., 2001). Whilst ocean and land ecosystems currently absorb slightly more than half of human CO₂ emissions (Prentice et al., 2001), atmosphere–ocean and atmosphere–land exchanges of carbon are sensitive to climate as well as to atmospheric levels of carbon dioxide. Cox et al. (2000) describe how a coupled climate–carbon-cycle GCM (HadCM3LC) simulates a significant acceleration of climate change in the next century due to a positive feedback from the global carbon cycle. Figure 1 shows that the model's atmospheric CO₂ concentration rises to 980 ppmv when IS92a anthropogenic CO₂ emissions are specified, compared to 710 ppmv in the standard IS92a concentration scenario (i.e. the

concentration scenario derived by using IS92a emissions to drive an off-line carbon-cycle model without any climate–carbon-cycle feedbacks). Rapid carbon release from the soil as temperatures increase dominates over increased vegetation uptake due to elevated CO₂ levels, and the terrestrial biosphere becomes a net source of carbon from about 2050. However, this competition between CO₂ fertilization and enhanced respiration means that the magnitude of the modelled response, and even its sign, are highly dependent on the sensitivity of plant growth and soil respiration to climate change. It is therefore important to quantify the uncertainties associated with the sensitivity of soil respiration to temperature.

Atmospheric CO₂ levels are sensitive to natural climate anomalies such as El Niño – Southern Oscillation (ENSO) or cooling following a volcanic eruption (Jones et al., 2001; Jones and Cox, 2001b). Figure 2 shows how interannual changes in CO₂ [with the anthropogenic rise removed as described in Jones et al. (2001)] correlate very closely with ENSO, rising in El Niño years and falling in La Niña years. It is also clear that CO₂ decreases following the major

*Corresponding author.
e-mail: chris.d.jones@metoffice.com

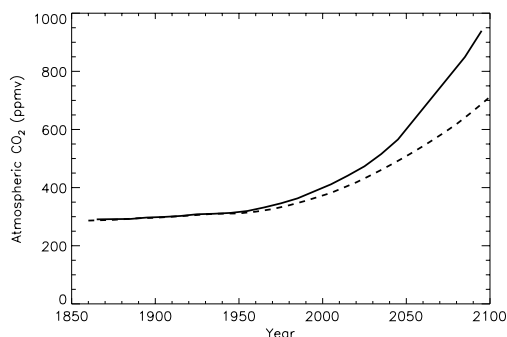


Fig. 1. Impact of climate–carbon-cycle feedbacks on global mean atmospheric CO₂. Coupled model results (with IS92a emissions; solid line); IS92a concentration scenario (without climate–carbon-cycle feedbacks; dashed line).

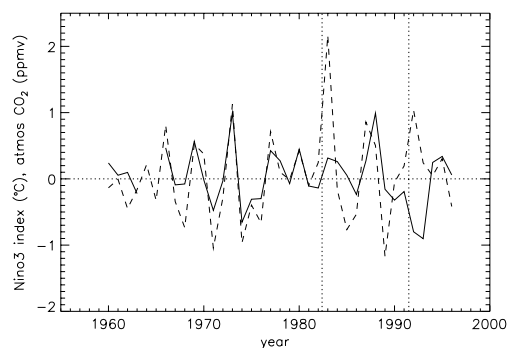


Fig. 2. Time series of the observed Nino3 index (°C, dashed line) and the natural changes in atmospheric CO₂ (ppmv, solid line). Scale for both quantities is the same. The eruptions of El Chichon and Mt. Pinatubo are indicated by the vertical dotted lines.

volcanic eruptions of El Chichon in 1982 and Mt. Pinatubo in 1991. Jones and Cox (2001a) use this data to infer the sensitivity of global soil respiration to changes in temperature. By varying the model's parametrization of soil respiration within these observed constraints it is possible to estimate the associated uncertainty in future levels of CO₂ and climate change.

Section 2 describes how observed CO₂ concentrations can be used to constrain the sensitivity of soil respiration to temperature. Section 3 introduces a simple zero-dimensional model for recreating the GCMs behaviour, and section 4 discusses the results of this model using a range of soil respiration sensitivities. Some conclusions are drawn in section 5.

2. Constraining soil respiration sensitivity to temperature

In the GCM the soil respiration rate (R_s) is assumed to increase exponentially with temperature following a so-called “Q10” formulation (Raich and Schlesinger, 1992):

$$R_s = r C_s f(M) q_{10}^{(T-10)/10} \quad (1)$$

where C_s is soil carbon, r is specific respiration rate at 10 °C, $f(M)$ is a function of soil moisture (McGuire et al., 1992), and q_{10} is the factor by which the specific soil respiration rate increases for each 10 °C warming. The model does not allow for spatially or temporally varying values of q_{10} : the value used represents a global mean bulk soil respiration parameter. A value of $q_{10} = 2.0$ was used in the original HadCM3LC runs (Cox et al., 2000). Temperature, T , refers to soil temperature rather than air temperature. The use of air temperature in the formula would lead to significantly lower q_{10} values (Kicklighter et al., 1994).

The sink-to-source transition described by Cox et al. (2000) is inevitable at some critical CO₂ concentration providing that (i) CO₂ fertilization of photosynthesis saturates at high CO₂ and (ii) $q_{10} > 1$ (Cox et al., 2001). The first condition is widely believed to be true (McGuire et al., 1992; Collatz et al., 1991; Collatz et al., 1992; Sellers et al., 1996). However, the temperature response of R_s is a key uncertainty, with some studies suggesting that in the long term R_s will not be sensitive to temperature once the fast turnover carbon store is exhausted: i.e. $q_{10} = 1$ (Giardina and Ryan, 2000).

On a global scale though, Jones and Cox (2001a) found $q_{10} \approx 2$ to be consistent with observed CO₂ variability due to ENSO and the Pinatubo volcanic eruption. By reconstructing the model results for different values of q_{10} it is possible to determine what range of this parameter is allowed to keep the model consistent with observations. Jones and Cox (2001a) found that values of $q_{10} = 1.9 \pm 0.4$ are required for the model to capture the observed CO₂ anomaly associated with the Pinatubo eruption, and $q_{10} = 2.1 \pm 0.7$ for consistency with the observed magnitude of the ENSO correlation. This uncertainty in q_{10} implies an uncertainty in climate–carbon-cycle projections, which we estimate in the next two sections.

3. Simple zero-dimensional climate–carbon-cycle model

It is too computationally expensive to run a range of fully coupled GCM experiments with different parameter values, so a method was devised which could be used to estimate the GCM sensitivity to q_{10} . Results from transient experiments with $q_{10} = 2$ were used to calibrate and check a simple zero-dimensional (0-D) model which could then be used to predict the full model behaviour for a range of q_{10} values.

We consider the total carbon stored in vegetation, C_v , which is increased by photosynthesis, Π , and reduced by plant respiration, R_p , and litterfall, Λ :

$$\frac{dC_v}{dt} = \Pi - R_p - \Lambda \quad (2)$$

where Π is sometimes called gross primary productivity (GPP). In common with many others (McGuire et al., 1992; Collatz et al., 1991; Collatz et al., 1992; Sellers et al., 1996; Cox et al., 1998), we assume that GPP depends directly on the atmospheric CO_2 concentration, C_a , and the climate:

$$\Pi = \Pi_{\max} \left(\frac{C_a}{C_a + C_{0.5}} \right) f(T) \quad (3)$$

where $\Pi_{\max}$ is the value which GPP asymptotes towards as $C_a \rightarrow \infty$ and $C_{0.5}$ is the “half-saturation” constant (i.e. the value of C_a for which Π is half this maximum value). The climate dependence of GPP is represented by f , which can be considered as an arbitrary function of mean temperature, T , because regional climate change patterns (including those in precipitation) have been found to scale almost linearly with temperature (Huntingford et al., 2000). Plant respiration is taken as the sum of a maintenance component, which depends on vegetation carbon and temperature, and a growth component, which is 25% of the remaining assimilate (once the maintenance respiration has been removed). This part of the model is identical to that used in the full TRIFFID dynamic global vegetation model (Cox, 2001). Annual litterfall is a fixed fraction of the vegetation carbon, $\Lambda = C_v/\tau_v$. A similar balance equation applies for the soil carbon, C_s :

$$\frac{dC_s}{dt} = \Lambda - R_s \quad (4)$$

where R_s is the soil or heterotrophic respiration. In line with the full TRIFFID model we assume that R_s is proportional to the soil carbon, C_s , and that the spe-

cific respiration rate (i.e. the respiration per unit carbon) follows a “Q10” dependence. As for TRIFFID, R_s is therefore given by eq. (1), but the simple model neglects the soil moisture dependence [i.e. it uses eq. (1) with $f(M) = 1$], since this was found to be relatively weak in the full GCM results. Near the surface, temperatures are assumed to increase approximately logarithmically with the atmospheric CO_2 concentration, C_a (Huntingford and Cox, 2000):

$$\Delta T = \frac{\Delta T_{2 \times \text{CO}_2}}{\log 2} \log \left(\frac{C_a}{C_a(0)} \right) \quad (5)$$

where ΔT is the surface warming, $\Delta T_{2 \times \text{CO}_2}$ is the climate sensitivity to doubling atmospheric CO_2 , and $C_a(0)$ is the initial CO_2 concentration. The ocean carbon cycle response was captured using the impulse–response approach as described by Joos et al. (1996).

This simple 0-D climate–carbon model was calibrated against full HadCM3LC results with and without climate feedbacks on the carbon cycle (Cox et al., 2000). The use of both of these GCM runs allowed the direct CO_2 effects to be separated from climate effects on the carbon cycle. Many of the simple model parameters were taken directly from the GCM without calibration. These included the q_{10} values for both plant maintenance and soil respiration, which were both set to 2.0 at this stage. Fitted parameters included the half-saturation constant for CO_2 ($C_{0.5} = 469$ ppmv) and the climate sensitivity ($\Delta T_{2 \times \text{CO}_2} = 3.18$ K). The function $f(T)$ was fitted to a quadratic: $f(T) = 1 - 0.06 \Delta T^2$. Initial values of the terrestrial fluxes and stores were used to fix the turnover times and specific respiration rates for soil and vegetation carbon. However, it was found that the specific soil respiration also needed to increase slightly with temperature to capture the impact of the GCM warming pattern, which enhances temperatures most in the high-latitude regions that contain the greatest soil carbon densities. The impulse–response ocean uptake model was as given by Joos et al. (1996) for a 3-D ocean model, but with a reduced “mixed layer depth” of 40 m to capture lower ocean uptake rates in HadCM3LC. The ocean was also assumed to experience a lower rate of warming than the land (by a factor of 1.87) in line with the full GCM results (Huntingford et al., 2000). This warming influences the uptake of carbon through the impact of the mean ocean temperature on the solubility of CO_2 in seawater (Joos et al., 1996). Other climatic impacts on ocean uptake, such as possible changes in

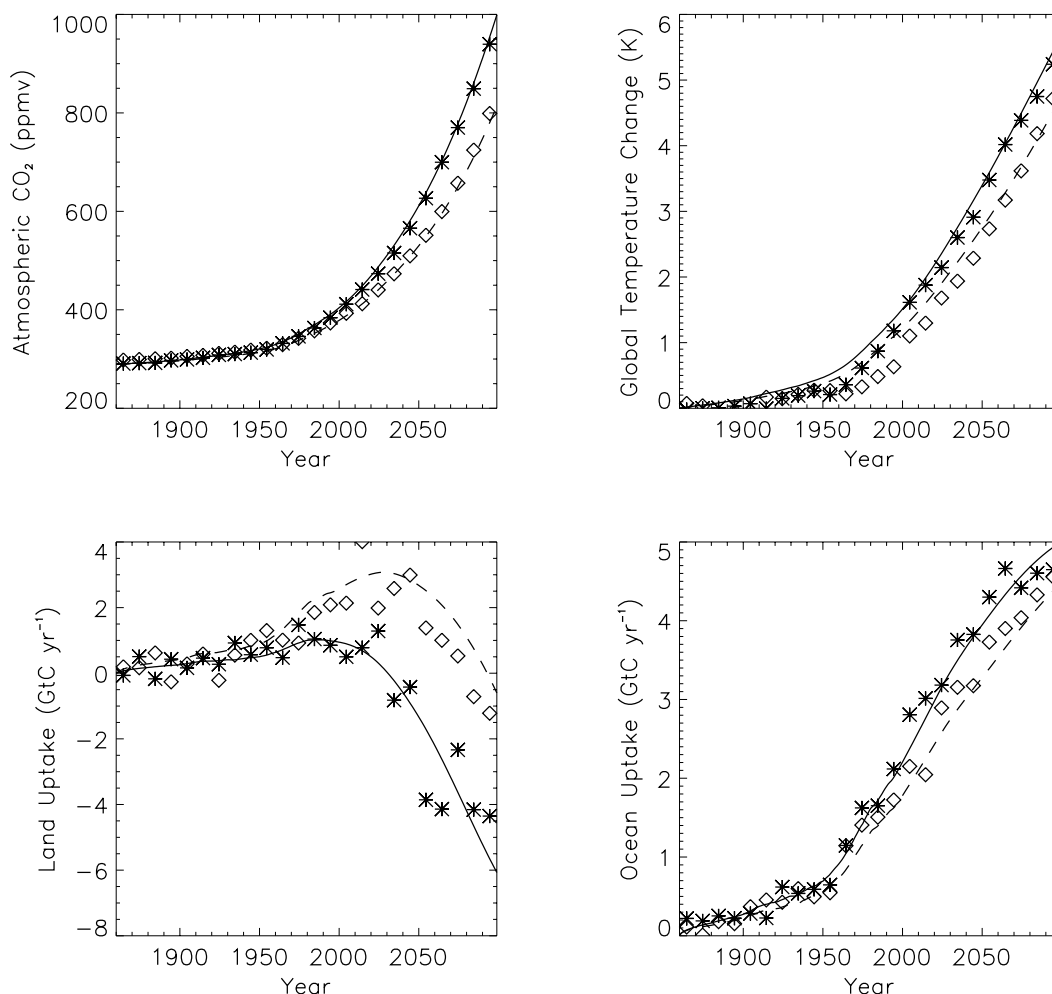


Fig. 3. Comparison of the simple model against results from the GCM for two values of the soil respiration sensitivity to temperature, $q_{10} = 2$ and $q_{10} = 1$. The GCM outputs are shown by the symbols (stars for $q_{10} = 2$, diamonds for $q_{10} = 1$), and the simple model is shown by the lines (continuous for $q_{10} = 2$, dashed for $q_{10} = 1$).

ocean thermohaline circulation, are not explicitly included in this simple model.

Figure 3 compares the fitted 0-D model against the full GCM results for two different soil respiration sensitivities, $q_{10} = 2$ (Cox et al., 2000), and $q_{10} = 1$ (unpublished). The 0-D model was calibrated directly against the $q_{10} = 2$ GCM results (with and without climate effects on the carbon cycle). The $q_{10} = 1$ comparison is a “blind test” of the robustness of this 0-D model. The agreement between the simple model and the GCM in this case suggests that the former provides a good estimate of the sensitivity of the GCM results to changes in q_{10} . A range of experiments was performed

with the simple model to convert the error bars in soil q_{10} into error bars in future CO_2 and climate change.

4. Results and discussion

The top panel of Fig. 4 shows how the atmospheric CO_2 concentration would increase over the next century for various q_{10} values. The central, solid line denotes the model values of Cox et al. (2000), while the shaded region shows the uncertainty in this assuming q_{10} is in the range 1.9 ± 0.4 , i.e. it is bounded by $q_{10} = 2.3$ (above) and $q_{10} = 1.5$ (below). This is the

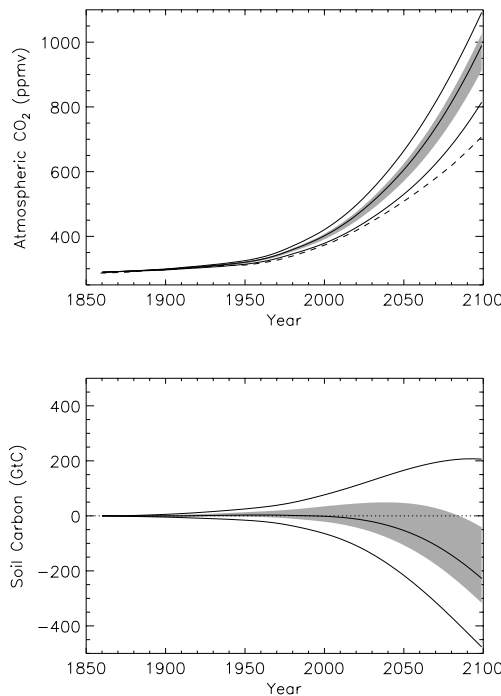


Fig. 4. Uncertainty bounds on future CO₂ levels (top panel) and soil carbon storage (bottom panel) for a range of q_{10} values. The central solid line shows the coupled GCM results with $q_{10} = 2$. The shaded region shows results for the range of q_{10} values consistent with observed CO₂ variability, and the outer solid lines show behaviour for $q_{10} = 1.0$ and $q_{10} = 3.0$. The IS92a CO₂ concentration scenario is shown by the dashed line.

range which is consistent with observed sensitivity to both ENSO and volcanic forcing. The outer lines show the behaviour for $q_{10} = 1$ (lower line) and $q_{10} = 3$ (upper line). The simple model predicts that the upper and lower bounds on CO₂ for the realistic range of q_{10} values are 1030 and 910 ppmv, respectively. For q_{10} values of 1 and 3, CO₂ levels reach 810 and 1090 ppmv, respectively. The dashed line shows the IS92a scenario for reference.

The bottom panel of Fig. 4 shows how the global total soil carbon storage would change over the next century for the same q_{10} scenarios. The experiment with $q_{10} = 1.0$ sees a rise in soil carbon caused by an increase in vegetation carbon and hence litterfall. For all values of q_{10} consistent with the observed CO₂ variability (i.e. within the shaded region), the increase in soil respiration due to elevated temperatures is sufficient to dominate the increased litterfall, and the global

soils become a net source of carbon by 2100, although for q_{10} values towards the low end of the range soil carbon increases slightly until the middle of this century before decreasing again.

It can be seen that all values of q_{10} give a final CO₂ concentration well above IS92a. The reason for this is that the Amazonian die-back, and associated release of vegetation carbon, described in Cox et al. (2001) is unaffected by the q_{10} parametrization and still occurs in the model. No attempt is made here to quantify the uncertainty in CO₂ levels associated with this die-back, although this, too, will be significant.

It should be noted that the constraints placed on q_{10} values by observations rely on several assumptions: firstly, that the model's climate response to ENSO and volcanic forcing is realistic, and secondly that the other carbon fluxes in the model (e.g. GPP or ocean fluxes) respond accurately to these forcings. Jones et al. (2001) and Jones and Cox (2001b) demonstrate that the modelled responses to ENSO and volcanic forcings are indeed realistic. The model's behaviour also broadly agrees with other estimates of interannual variability in the land and ocean carbon cycle components (Le Quere et al., 2000; Bousquet et al., 2000). It remains possible that the coupled model contains balancing errors (e.g. an under-sensitive GPP compensated by an over-sensitive soil respiration), but it is unlikely that a common spurious q_{10} value could compensate for errors elsewhere in the model for the differing forcings associated with both ENSO and volcanoes. The assumption that q_{10} is the dominant uncertainty is supported by the fact that the optimum values derived for the ENSO and volcanic perturbations agree so well.

Other sources of uncertainty in the q_{10} reconstructions may also be important. For example, the model does not include a representation of natural fires. It is thought that the occurrence of fires is greater during El Niño years and that this contributes significantly to the observed rise in CO₂ levels (Keeling et al., 1995; Nicholls, 1991). If this is the case then it is possible that our reconstruction has overestimated q_{10} by assuming that soil respiration accounts for the missing contribution of fire activity. Conversely, it may be the case that the reconstruction is biased towards tropical q_{10} values. The majority of the modelled signal for both ENSO and volcanic perturbations occurs in the tropics, and so the observed sensitivity of the carbon cycle is largely the tropical sensitivity. However, it has been found that q_{10} values are likely to be higher in mid- and high-latitudes (Raich and Schlesinger, 1992). If this is the case then it may cause our reconstruction

to underestimate q_{10} . The extent to which these two effects may cancel is not known.

A further source of uncertainty in the projections of the simple model is whether or not the long-term behaviour of soil respiration is the same as the short-term behaviour: in other words, is it realistic to assume that the same q_{10} formulation persists into the future even when climate and soil carbon stores may have changed significantly? Holland et al. (2000) discuss the need to consider substrate limitation. In their study they found that tropical soil respiration did indeed follow a q_{10} formulation initially, but decomposition rates declined after long incubation periods as substrate became limiting. This is consistent with soil carbon pools declining owing to a period of negative carbon balance in which heterotrophic respiration exceeds litterfall. The situation projected for the future is rather different, since vegetation carbon densities, and thus litterfall rates, are predicted to increase almost as quickly as soil respiration. As a result it is possible that global soil carbon will not change markedly. This is broadly consistent with the GCM results presented by Cox et al. (2000), in which most of the positive feedback from soil carbon change comes not from reductions in soil carbon relative to the current day (about 150 GtC by 2100), but rather from reductions in soil carbon accumulation relative to scenarios in which climate–carbon-cycle feedbacks are neglected (about 400 GtC by 2100). In other words, it is not so much that soil carbon decreases in these GCM experiments, but that it fails to increase in the way implied by the standard IS92a CO₂ concentration scenario (without climate–carbon-cycle feedbacks), which implicitly assumes significant carbon accumulation on the land.

Even if soil substrate does not become limiting, it remains possible that large-scale sink-to-source transitions will be avoided by a “down-regulation” of q_{10} . For example, Luo et al. (2001) recently published experimental results in which they detected a reduction of the q_{10} value for soils in tall grass prairie, when these soils were exposed to elevated temperatures for an extended period. The original temperature sensitivity of soil respiration at this site implied $q_{10} \approx 2.7$, but this reduced to $q_{10} \approx 2.5$ after about a year with a soil warming of 2 °C. Such down-regulation may be a result of microbial adaptation to the changing conditions or a consequence of the depletion of fast respiring carbon pools (i.e. a form of substrate limitation). Unfortunately, experiments of this type are not currently long enough to draw conclusions about the carbon cy-

cle in the 21st century. The final q_{10} value diagnosed by Luo et al. (2001) is still higher than that used by Cox et al. (2000), and would therefore lead to an even stronger positive climate–carbon-cycle feedback. To delay a sink-to-source transition in the land carbon sink requires that q_{10} drops significantly below 2 (Cox et al., 2001). Longer experiments and better process understanding are required to assess the likelihood of this occurring.

5. Conclusions

The response of soil respiration to temperature is critically important in determining the rate of future climate change. However, the exact nature of this response is uncertain. If increasing temperatures cause the soil to release more CO₂ then the terrestrial biospheric sink could saturate and even reverse, thus accelerating anthropogenic global warming.

Two independent sources of data have been used to constrain estimates of a global-mean model parameter of soil respiration. ENSO and volcanic induced perturbations to atmospheric CO₂ concentrations are in agreement with a “Q10” formulation, with a value of $q_{10} = 2.0$ as used in HadCM3LC. They also imply that an insensitivity of soil respiration to temperature (i.e. $q_{10} \approx 1$) is not consistent with the observed variability in atmospheric CO₂ on the 1–5 yr timescale.

These constraints on q_{10} allow us to estimate the uncertainty in the model’s predictions of future CO₂ levels associated with the temperature sensitivity of soil respiration. By 2100 positive feedbacks from the carbon cycle cause CO₂ levels to rise well above conventional scenario values. Using IS92a emissions, CO₂ levels in the fully coupled climate–carbon-cycle model reach 980 ppmv: 270 ppmv higher than without the feedbacks. Reconstructions with the simple model using q_{10} values within a range consistent with observed variability show a large uncertainty in the CO₂ level by the end of the century: values vary between 910 and 1030 ppmv. This represents an uncertainty of $\pm 25\%$ in the magnitude of the positive climate–carbon-cycle feedback.

6. Acknowledgements

This work was supported by the UK Department of the Environment, Food and Regional Affairs Climate Prediction Programme under contract PEC/D 7/12/37.

REFERENCES

- Bousquet, P., Peylin, P., Ciais, P., Le Quere, C., Friedlingstein, P. and Tans, P. 2000. Regional changes in CO₂ fluxes of land and ocean since 1980. *Science* **290**, 1342–1346.
- Collatz, G. J., Ball, J. T., Grivet, C. and Berry, J. A. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agric. Forest Meteorol.* **54**, 107–136.
- Collatz, G. J., Ribas-Carbo, M. and Berry, J. A. 1992. A coupled photosynthesis-stomatal conductance model for leaves of C₄ plants. *Aust. J. Plant Physiol.* **19**, 519–538.
- Cox, P. M. 2001. Description of the TRIFFID dynamic global vegetation model. Technical Note 24, Hadley Centre, Met. Office, UK.
- Cox, P. M., Huntingford, C. and Harding, R. J. 1998. A canopy conductance and photosynthesis model for use in a GCM land surface scheme. *J. Hydrol.* **212–213**, 79–94.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. and Totterdell, I. J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. and Totterdell, I. J. 2001. Modelling vegetation and the carbon cycle as interactive elements of the climate system. In: *Meteorology at the millennium*, (ed. R. Pearce), Academic Press, New York.
- Friedlingstein, P., Bopp, L., Ciais, P., Dufresne, J., Fairhead, L., LeTreut, H., Monfray, P. and Orr, J. 2001. Positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* **28**, 1543–1546.
- Giardina, C. and Ryan, M. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* **404**, 858–861.
- Holland, E., Neff, J., Townsend, A. and McKeown, B. 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models. *Global Biogeochem. Cycles* **14**, 1137–1151.
- Huntingford, C. and Cox, P. 2000. An analogue model to derive additional climate change scenarios from existing GCM simulations. *Clim. Dynam.* **16**, 575–586.
- Huntingford, C., Cox, P. and Lenton, T. 2000. Contrasting responses of a simple terrestrial ecosystem model to global change. *Ecol. Modelling* **134**, 41–58.
- Jones, C. and Cox, P. 2001a. Constraints on the temperature sensitivity of global soil respiration from the observed interannual variability in atmospheric CO₂. *Atmos. Sci. Lett.* doi:10.1006/asle.2000.0041.
- Jones, C. and Cox, P. 2001b. Modelling the volcanic signal in the atmospheric CO₂ record. *Global Biogeochem. Cycles* **15**, 453–466.
- Jones, C., Collins, M., Cox, P. and Spall, S. 2001. The carbon cycle response to ENSO: A coupled climate–Carbon cycle model study. *J. Clim.* **14**, 4113–4129.
- Joos, F., Bruno, M., Fink, R., Siegenthaler, U., Stocker, T., Le Quere, C. and Sarmiento, J. 1996. An efficient and accurate representation of complex oceanic and biospheric models of anthropogenic carbon uptake. *Tellus* **48B**, 397–417.
- Keeling, C. D., Whorf, T., Whalen, M. and der Plicht, J. V. 1995. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**, 666–670.
- Kicklighter, D., Melillo, J., Peterjohn, W., Rastetter, E., McGuire, A., Steudler, P. and Aber, J. 1994. Aspects of spatial and temporal aggregation in estimating regional carbon dioxide fluxes from temperate forest soils. *J. Geophys. Res.* **99**, 1303–1315.
- Le Quere, C., Orr, J., Monfray, P., Aumont, O. and Madec, G. 2000. Interannual variability of the oceanic sink of CO₂ from 1979 through 1997. *Global Biogeochem. Cycles* **14**, 1247–1265.
- Luo, Y., Wan, S., Hui, D. and Wallace, L. L. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* **413**, 622–625.
- McGuire, A., Melillo, J., Joyce, L., Kicklighter, D., Grace, A., Moore III, B. and Vorosmarty, C. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochem. Cycles* **6**, 101–124.
- Nicholls, N., 1991. The El Niño/Southern Oscillation and Australian vegetation. In: *Vegetation and climate interactions in semi-arid regions*, (eds A. Henderson-Sellers and A. J. Pitman), *Adv. Veg. Sci.* Vol. 12, Kluwer, Amsterdam, 23–36.
- Prentice, I., Farquhar, G., Fasham, M., Goulden, M., Heimann, M., Jaramillo, V., Kheshti, H., Le Quere, C., Scholes, R. and Wallace, D. 2001. The carbon cycle and atmospheric carbon dioxide. In: *Climate change 2001: The scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, (eds J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. van der Linden, X. Dai, K. Maskell and C. I. Johnson, chapter 3, Cambridge University Press, Cambridge, 183–237.
- Raich, J. and Schlesinger, W. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* **44B**, 81–99.
- Sellers, P., Randall, D., Collatz, C., Berry, J., Field, C., Dazlich, D., Zhang, C. and Collelo, G. 1996. A revised land surface parameterisation (SiB2) for atmospheric GCMs. Part I: Model formulation. *J. Climate* **9**, 676–705.