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Vegetation–climate feedbacks in a greenhouse world

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The potential for feedbacks between terrestrial vegetation, climate, and the atmospheric CO_2 partial pressure have been addressed by modelling. Previous research has established that under global warming and CO_2 enrichment, the stomatal conductance of vegetation tends to decrease, causing a warming effect on top of the driving change in greenhouse warming. At the global scale, this positive feedback is ultimately changed to a negative feedback through changes in vegetation structure. In spatial terms this structural feedback has a variable geographical pattern in terms of magnitude and sign. At high latitudes, increases in vegetation leaf area index (LAI) and vegetation height cause a positive feedback, and warming through reductions in the winter snow-cover albedo. At lower latitudes when vegetation becomes more sparse with warming, the higher albedo of the underlying soil leads to cooling. However, the largest area effects are of negative feedbacks caused by increased evaporative cooling with increasing LAI. These effects do not include feedbacks on the atmospheric CO_2 concentration, through changes in the carbon cycle of the vegetation. Modelling experiments, with biogeochemical, physiological and structural feedbacks on atmospheric CO_2, but with no changes in precipitation, ocean activity or sea ice formation, have shown that a consequence of the CO_2 fertilization effect on vegetation will be a reduction of atmospheric CO_2 concentration, in the order of 12% by the year 2100 and a reduced global warming by 0.7 °C, in a total greenhouse warming of 3.9 °C.

Keywords: climate, climate change, vegetation, carbon cycle, soil

1. INTRODUCTION

A map of the world's terrestrial vegetation (e.g. Olson *et al.* 1983) indicates complex geographical patterns of vegetation. However, large-scale patterns exist that are strongly correlated with variations in climate, in particular temperature, radiation and precipitation (Woodward 1987; Peixoto & Oort 1992). Temperature has been shown to be a critical controller of vegetation distribution (Woodward 1987), and the range of mean temperatures between northern and southern limits of different vegetation types can be quite small. For example, the difference in mean temperature between the northern and southern limit of the boreal forest can be as little as 3 °C (Box 1981). A similar temperature range is also seen for the temperate mixed forest of China. Similarly small temperature changes are also predicted for the end of the next century (Houghton *et al.* 1996), indicating the potential for large changes in vegetation distribution. The mechanisms that control the distribution of different vegetation types, when temperature is the major controller, do not operate directly through the annual mean temperature but through some correlates, such as the lowest temperature and the temperature of the growing season (Woodward 1987).

Small changes in temperature are therefore expected to cause significant changes in the distribution of different vegetation types. Not only will these changes in climate influence vegetation, the changes in vegetation functioning (e.g. evapotranspiration, net primary productivity (NPP), nutrient cycling, and net ecosystem productivity) and structure (e.g. vegetation height, albedo, distribution) will also exert a feedback on climate itself (Shukla *et al.* 1990; Bonan *et al.* 1992; Lean & Rowntree 1993; Foley *et al.* 1994). The degree, the sign (negative or positive), and the geographical distribution of the vegetation feedback on climate will all play a role in determining the final distribution and functioning of vegetation.

The importance and uncertainty about the feedbacks of vegetation on climate therefore indicate a need for further investigation. This paper addresses the subject using two modelling approaches that aim to tease out the likely nature and magnitude of the feedbacks from vegetation to climate in a future greenhouse world. The first approach expands on a recent publication (Betts *et al.* 1997) which has investigated vegetation feedbacks on climate using a vegetation model (Woodward *et al.* 1995) coupled to a UK Meteorological Office general circulation model (GCM) of future climate (Mitchell *et al.* 1995) and also including a coupled slab-ocean model. The approach here has been to build on this research and to investigate the geographical nature and sign of the vegetation feedbacks on climate. The second approach was to model the impacts of future transient changes in climate and atmospheric CO_2 on the capacity of vegetation and soils to sequester atmospheric CO_2 through changes in productivity (Woodward *et al.* 1995). The impacts of these changes in productivity on atmospheric CO_2 concentration critical as they may change the radiative forcing and ds of a future climate (Mitchell *et al.* 1995).

OUPLED VEGETATION–CLIMATE IMULATIONS

llers *et al.* (1996) demonstrated, with a coupled tation GCM, that a doubling in the atmospheric concentration should lead to a reduction in atal conductance of vegetation, in keeping with y experimental observations (Field *et al.* 1995), with ttendant reduction in vegetation transpiration and possibility of warming through the resultant reduc- in latent heat transfer. However, at the global this effect was very small, about a 0.1 °C warming op of a 1.9 °C warming due to the radiative effects of oubling in the CO_2 concentration. Although the al effect was small, the terrestrial regional effect ned about +0.9 °C in tropical regions, a significant ion of the 1.7 °C radiative warming in such areas. simulations demonstrated rather small climatic backs from mid- and high-latitude vegetation.

tts *et al.* (1997), using a different vegetation model odward *et al.* 1995), and GCM produced comparable geographically rather different results. With only a iological feedback through impacts on stomatal uctance, local air temperatures in some regions were n to increase by about +1 °C, with a global mean ease of 0.2 °C on top of a 4.3 °C warming due to radia- forcing. This extra warming was most widespread over hern Hemisphere land, in contrast with the results of rs *et al.* (1996) which showed little further warming at latitudes and a slightly reduced warming at high lati- s, despite a 30% reduction in conductance in these s. These model differences are difficult to reconcile as GCMs appear to include coupled ocean and sea-ice els. Model experiments with the Potsdam climate m model (M. Claussen, personal communication), investigating the impacts of vegetation on climate, indicated that at high northern latitudes rather t impacts of vegetation structure on climate are lified by impacts on the melting of sea-ice, a feature h is also seen in the model runs of Betts *et al.* (1997). Sellers *et al.* (1996), Betts *et al.* (1997) showed marked ctions in transpiration in the tropics, but in the latter the resulting temperature increases were smaller and localized as a result of a warmer, highly evaporating l climate. The global mean effects of this physiology- response are shown in table 1.

ne vegetation model used by Betts *et al.* (1997) can predict a structural response by the vegetation, ugh changes in leaf area index (LAI), the net uctance at the canopy scale, and NPP, in response creases in atmospheric CO_2 and changes in climate. osynthesis and NPP generally increase with CO_2 nderson & Wullschleger 1994; McGuire *et al.* 1995), this response plus the increased water use efficiency es vegetation leafiness (LAI) to increase (Jarvis ; Woodward 1992). In general, the structural onse by the vegetation diminishes the physiological cts (table 1), primarily by increasing the vegetation otranspiration with a greater LAI and net conduc- e at the canopy scale.

Table 1. *Climate (land surface) and vegetation responses to vegetation feedbacks on climate*

(The no-feedback column indicates the absolute values after the imposition of radiative climatic change. The physiological feedback allows vegetation stomatal conductance (conductance in this table) to respond to the changes in climate and CO_2, while the vegetation feedback allows both a physiological response and a response of leaf area index (LAI) (from Betts *et al.* 1997).)

variable	no feedback	physiological feedback	vegetation feedback
temperature	11.4 °C	+0.2 °C	−0.1 °C
precipitation	2.5 mm d^{-1}	−0.7%	−0.2%
evaporation	1.5 mm d^{-1}	−1.8%	−0.3%
LAI	3.4	0%	+7.2%
conductance	6.1 mm s^{-1}	−19.6%	−12.1%

The research by Sellers *et al.* (1996) and Betts *et al.* (1997) clearly shows that vegetation responses to changes in climate and CO_2 can feedback and influence climate. Generally, when only physiological responses are considered, the feedbacks on climate are positive, leading to increases in temperature. When structural changes are included, the feedbacks can be either positive or negative. The geographical distributions and signs of these feedbacks are of considerable ecological interest, and are shown (figure 1) as the temperature change due to the vegetation feedback alone divided by the change in vegetation structure, in this case LAI. It should be noted that the vegetation responses are equilibrium responses, indicating that any change in vegetation structure will have continued to completion. The map of this response is complex, but it is possible to recognize large regions of similar sign and magnitude of feedback. In eastern Russia and Siberia and north-east Canada, the model projection was for increases in LAI and temperature. This positive feedback of vegetation on climate was due to an increase in vegetation height and a masking of the high albedo of winter snows. A positive correlation between LAI and temperature response is also seen in arid regions of North Africa and the Middle East. In these areas the already low LAI is decreased further in the warmer climate, causing an increase in albedo from the more reflective soil, which leads to a cooling.

Very large areas, e.g. USA, Canada, Europe, West Russia, India, China, the southern regions of South America and Africa, and areas of Australia all show a negative feedback of vegetation change on temperature. In these areas LAI is predicted to increase with an attendant negative feedback or cooling effect on temperature, as a consequence of increased rates of evapotranspiration.

3. COUPLING THE VEGETATION CARBON CYCLE TO THE ATMOSPHERE

(a) *Introduction*

The feedback experiment of Betts *et al.* (1997) does not consider the impacts of any changes in the terrestrial carbon cycle on the atmospheric CO_2 concentration. Smith & Shugart (1993) and Xiao *et al.* (1997) have

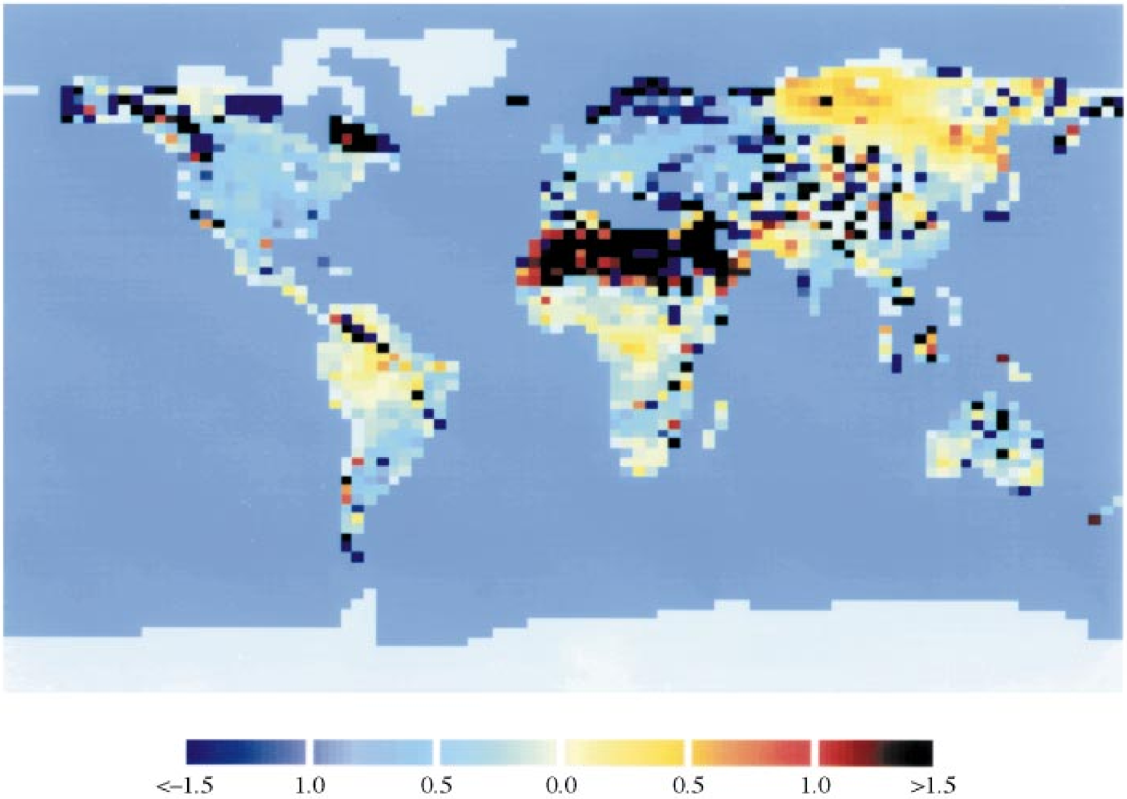


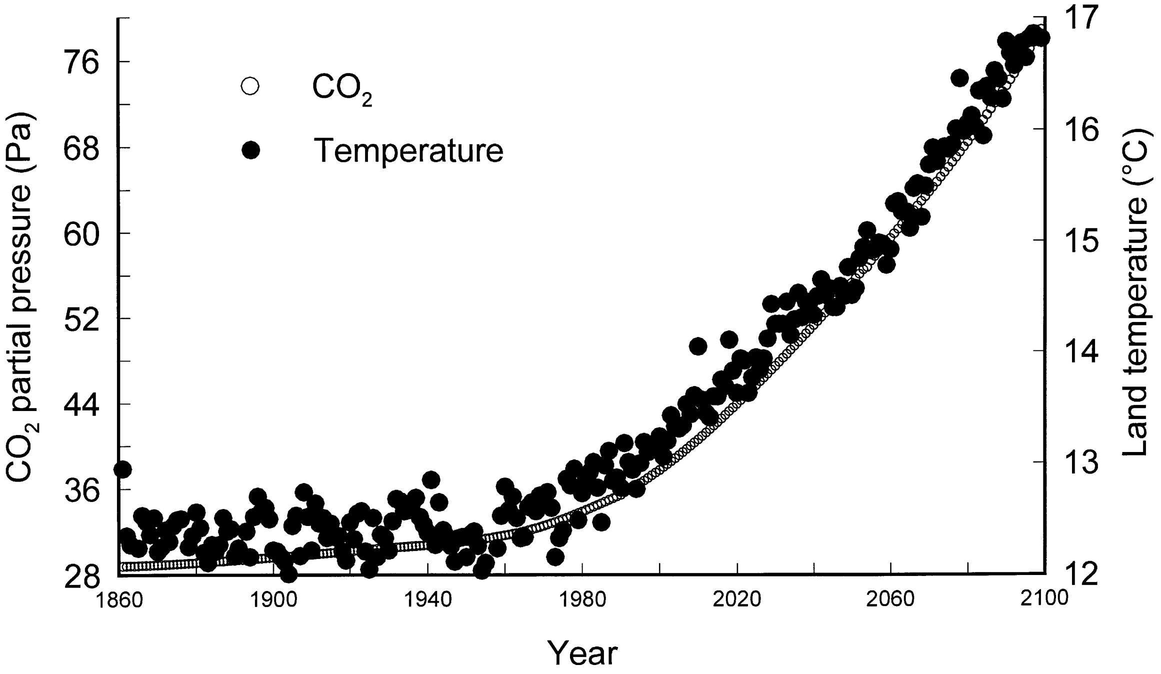
Figure 1. The impact of changes in vegetation LAI on temperature, mapped as temperature change per unit change in LAI (°C LAI^{-1}).

demonstrated, by modelling experiments, that changes in the distribution, structure, and function of vegetation can influence the CO_2 concentration of the atmosphere. In addition, increases in atmospheric CO_2 concentrations should also stimulate the rate of photosynthesis, at least in plants with C_3 photosynthetic metabolism (Gunderson & Wullschleger 1994), in addition to the well-established radiative forcing by changes in atmospheric CO_2 concentrations on climate. Therefore, complete models of climate, atmosphere and vegetation (earth system models) must incorporate all of these processes. This section will consider the future interactions between vegetation, atmospheric CO_2 concentration and climate in three steps. The first step will investigate the impact on the carbon cycle of vegetation and soils by changes in atmospheric CO_2, which also forces transient GCM projections of climate (Mitchell *et al.* 1995) from 1860 to 2100. Any changes in the vegetation carbon cycle will have some impact on the atmospheric CO_2 concentration, and vice versa, and so the second stage will investigate these feedbacks. The vegetation-derived changes in atmospheric CO_2 concentration will also have some impact on global temperatures, and this feedback is considered finally. The work presented here concentrates on terrestrial feedbacks on atmospheric CO_2 concentration and climate, so for simplicity, further oceanic effects on the carbon cycle and climate are neglected.

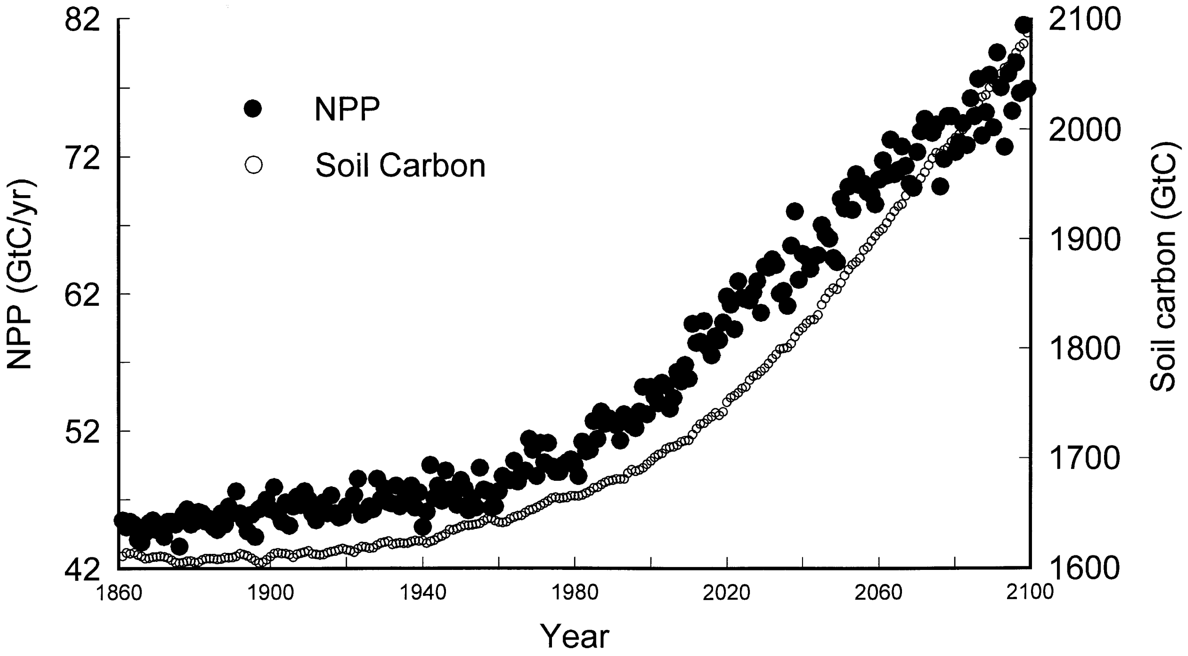
The vegetation model used in these simulations (Woodward *et al.* 1995), including details of model testing, has been modified for these simulations through one major change. The change is for a dynamic coupling with the Century model of soil carbon and nitrogen cycling (Parton *et al.* 1993). Therefore, the vegetation model now only requires climate, CO_2 and soil texture data as inputs. The coupling of the Century model with the vegetation model now allows litter formation and decomposition, and so the vegetation and soil carbon cycle is complete. The vegetation model predicts a number of vegetation characteristics, in particular LAI, gross primary productivity (GPP) and NPP, net ecosystem productivity (NEP) and evapotranspiration, at the global scale. NEP, which is calculated as NPP less heterotrophic respiration, is the necessary vegetation characteristic for interacting with atmospheric CO_2, as it accounts for any changes in the carbon cycle of the vegetation and the soil.

(b) *The impact of changes in atmospheric CO_2 on vegetation and soils*

The mean atmospheric CO_2 concentration used in Mitchell *et al.*'s (1995) transient climate simulation shows (figure 2) a doubling of the current CO_2 partial pressure of 37 Pa by 2091 and a final CO_2 partial pressure of 79 Pa by the year 2100. This trend in atmospheric CO_2 concentration is taken to represent the IS92a CO_2 emissions scenario (Wigley & Raper 1992) which only includes an ocean uptake of CO_2 (1.95 Gt C yr^{-1} in the 1980s) and a simple view of no uptake by the terrestrial biosphere. This trend in atmospheric CO_2 is about midway between the high (IS92e) and low (IS92c) CO_2 emission trends (Wigley & Raper 1992). The global land surface temperature is predicted to increase from 13.1 °C at the present day to 16.9 °C by 2100. There is no obvious trend in land precipitation over this period.



re 2. Trends in annual land surface temperature and atmospheric CO$_2$ partial pressure, as predicted in Mitchell *et al.*'s (1995) ient climate projection. Control: no vegetation feedback.



re 3. Predicted trends in vegetation net primary productivity and soil carbon, using the climate and CO$_2$ data from Mitchell *et* 995) as input drivers of a vegetation model (Woodward *et al.* 1995). Control: no vegetation feedback.

he vegetation model (Woodward *et al.* 1995) predicts
both vegetation NPP and soil carbon (figure 3)
w closely the trends in temperature and CO$_2$ (figure
Iowever, the rate of increase in NPP slows from the
s. Soil carbon is the major terrestrial store of carbon,
iderably exceeding that in vegetation by about 2.5-
(Siegenthaler & Sarmiento 1993). Over the period of
model run, with no feedback of vegetation and soils on
ate, or atmospheric CO$_2$ concentration, the soil
carbon content increases by 78 Gt of C from 1860 to 1997, and by 375 Gt of C from 1997 to 2100. Over the same periods, NPP, which is the sole immediate source of carbon for sequestration in the vegetation and soil, increased by 8 Gt C yr^{-1} from 1860 to 1997 and by 42 Gt C yr^{-1} from 1997 to 2100.

The spatial distribution of the predicted changes in NPP from the 1990s (figure 4) to the 2090s (figure 5) indicates significant global-scale increases in NPP where

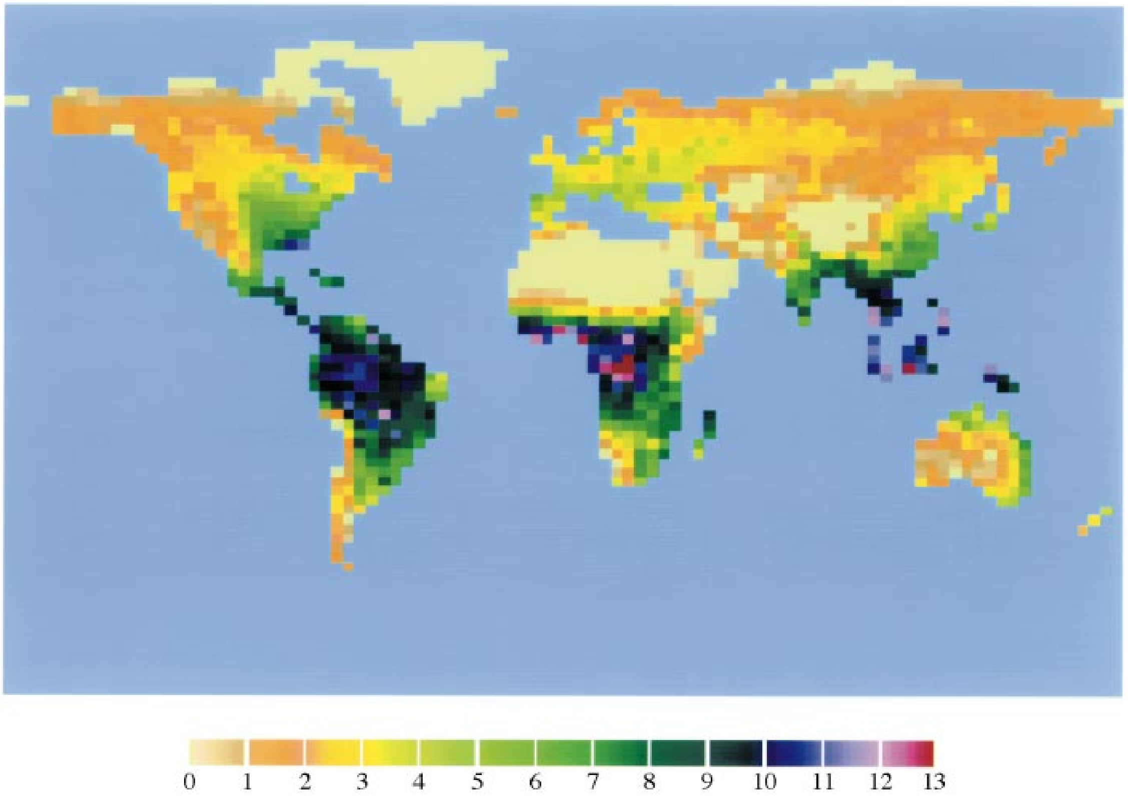


Figure 4. Predicted distribution of vegetation net primary productivity (tC ha^{-1} yr^{-1}) averaged for the 1990s.

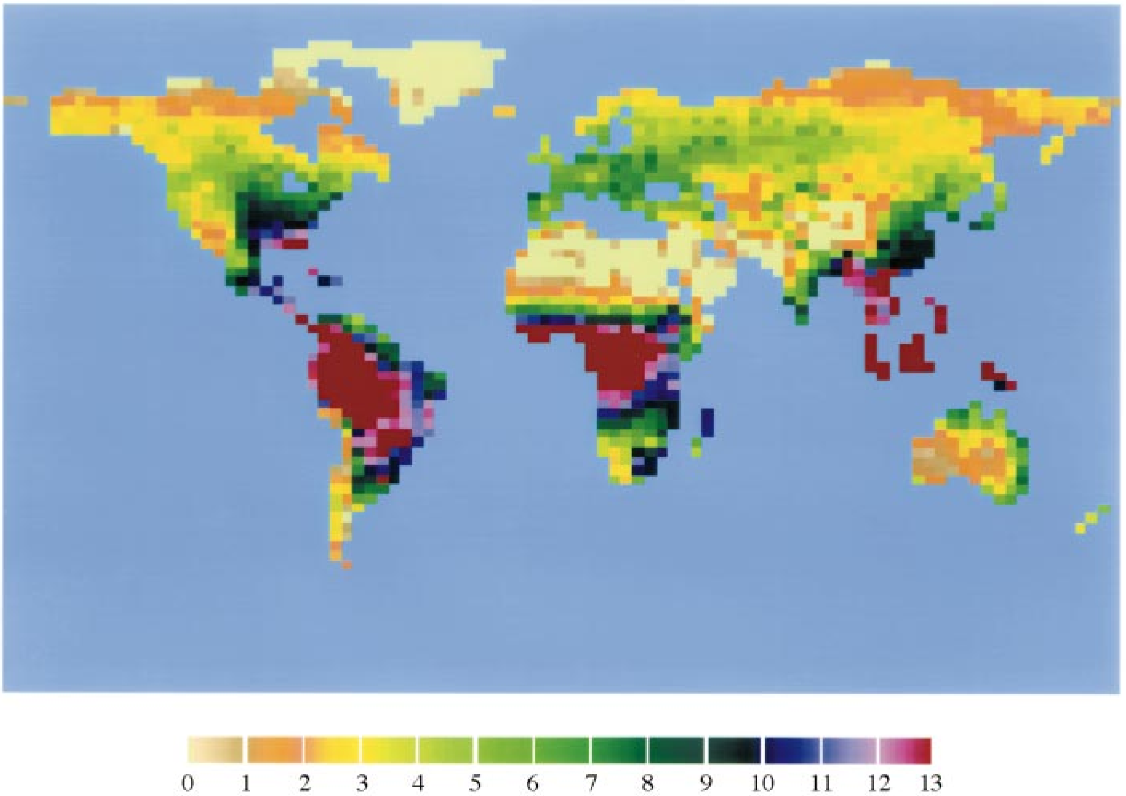
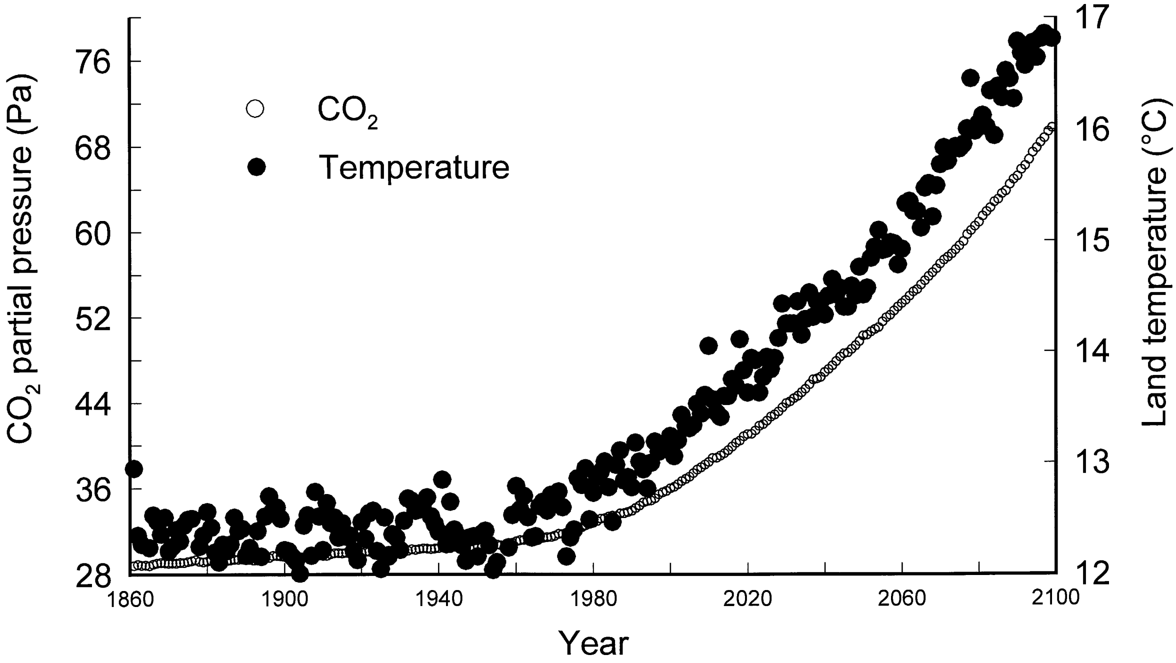


Figure 5. Predicted distribution of vegetation net primary productivity (tC ha^{-1} yr^{-1}) averaged for the 2090s.



:e 6. Trends in annual land surface temperature and atmospheric CO_2 partial pressure after feedback of vegetation on atmo-
ic CO_2 partial pressure.

ıpitation is relatively abundant. There is no evidence ignificant changes in very arid deserts, however, the -arid areas such as central Asia and southern Africa show increases in NPP, resulting from the dual ıcts of CO_2 enrichment on productivity and water efficiency (Woodward 1992).

'eedbacks between changes in atmospheric CO_2 and C-sequestration by vegetation and soils

om the 1860s to the 2090s, soil carbon is predicted to ease by 453 Gt (figure 3). Over the same period, the ospheric CO_2 concentration is predicted to increase)43 Gt of C, with no vegetation feedback; therefore, expected that changes in vegetation and soil activity ld exert some delay on the build-up of atmospheric concentration. This feature has been addressed by uting a new feedback between the vegetation model the atmospheric CO_2 emissions-based scenario of ges in atmospheric CO_2, which is used to force the 1. In this run there is no feedback on climate, but changes in vegetation and soil sequestration are imme- ly added to atmospheric CO_2 concentrations.

omparison between figures 2 and 6 indicates the ntial for the terrestrial biosphere to sequester carbon.)97, the atmospheric CO_2 concentration is 4.2% lower the no-feedback control, and 12% lower by 2100. The is a decline in both NPP and soil carbon accumulation out 3% by the year 2100 (figures 6 and 7).

ıe spatial impact on NPP due to the sequestering of on by vegetation is determined (figure 8) by calcu- g a global map of vegetation NPP, for the 2090s, then subtracting these values, pixel by pixel from NPP in the no-feedback simulation (figure 5). The rence map (figure 8) indicates little impact on rain- ts 'in the tropics', forests which are predicted to be ost CO_2-saturated by the 2090s, but with the greatest reductions in NPP in the seasonal (precipitation) forested and savannah areas of Central and South America, Africa, Australia and South-East Asia. Smaller reductions are seen in the higher latitude seasonal (temperature) forests.

(d) *Feedbacks between changes in carbon sequestration by vegetation and soils, atmospheric CO_2 and temperature*

The atmospheric CO_2 partial pressure, and the mean global land surface temperature, are very closely correlated through the radiative control of temperature. Therefore, in a simple feedback case, it will be possible to determine the impact on temperature due to the reductions in atmospheric CO_2 partial pressure arising from the sequestering capacity of the vegetation. This simulation therefore combines the impact of carbon sequestration on atmospheric concentration, followed by the impacts on land temperatures, and then a further set of feedbacks on vegetation sequestration and atmospheric CO_2 concentration. The impacts on temperature and atmospheric CO_2 partial pressure (figure 9) indicate a reduction of 0.7 °C below the total global warming of 3.9 °C by the year 2100. Therefore, vegetation feedbacks, through the carbon cycle alone and with no changes in precipitation or ocean uptake, exert a moderate cooling effect on future climates. The cooling has negligible (less than 1%) impact on CO_2 accumulation in the atmosphere.

The impacts of the cooling on soil carbon accumulation (see figures 7 and 10 for the temperature effect) are small (less than 1%). However, NPP is reduced by 2% by the end of the run, and in comparison with the CO_2-only feedback case (figure 7). Overall, the combined effects of the carbon cycle on atmospheric CO_2 concentration and temperature are moderate when compared with the no-feedback case (figures 2 and 3). By the year 2100, the

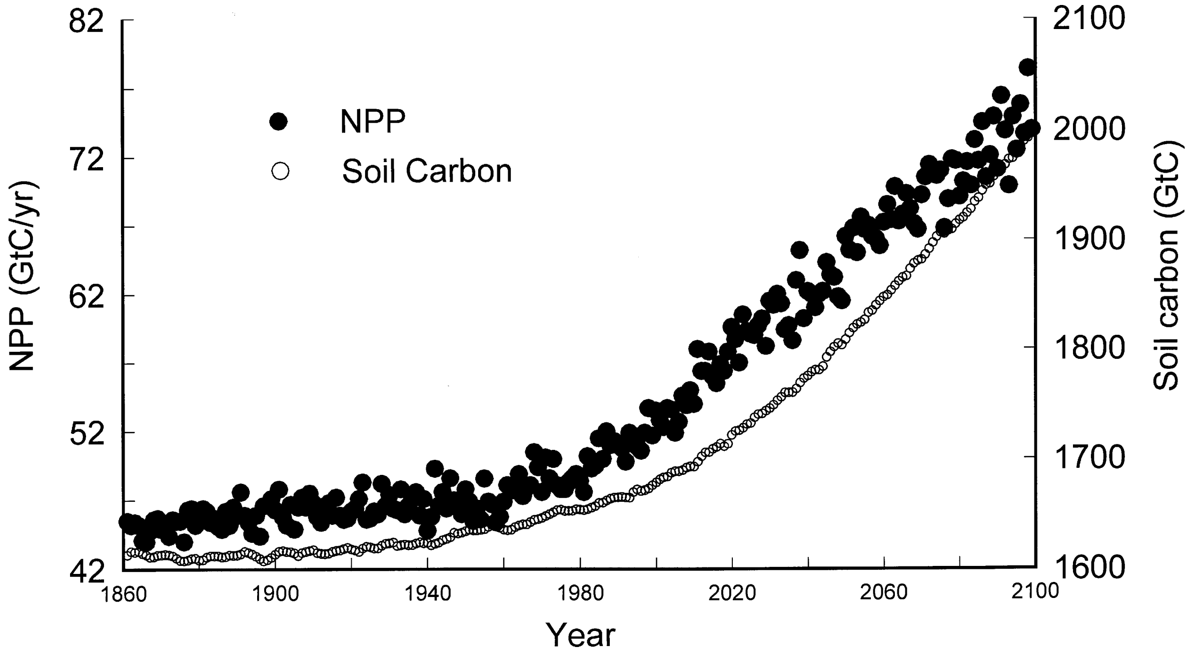


Figure 7. Predicted trends in vegetation net primary productivity and soil carbon after feedback of vegetation on atmospheric CO_2 partial pressure.

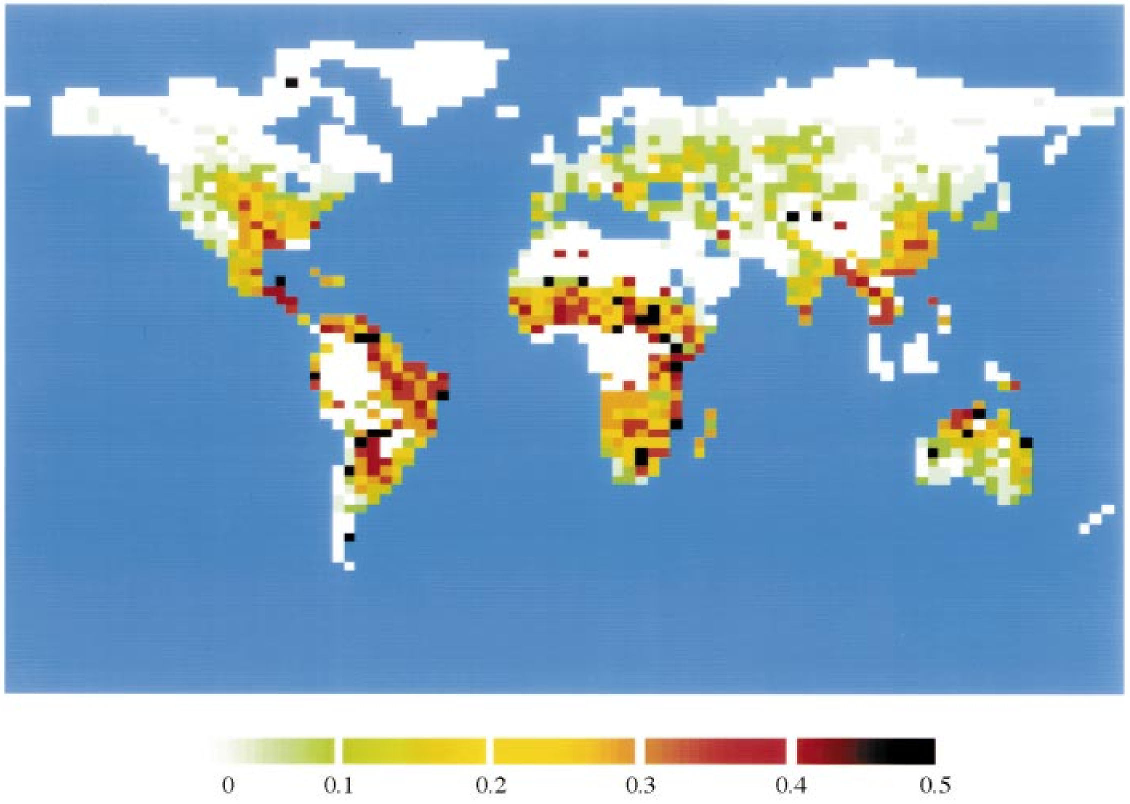
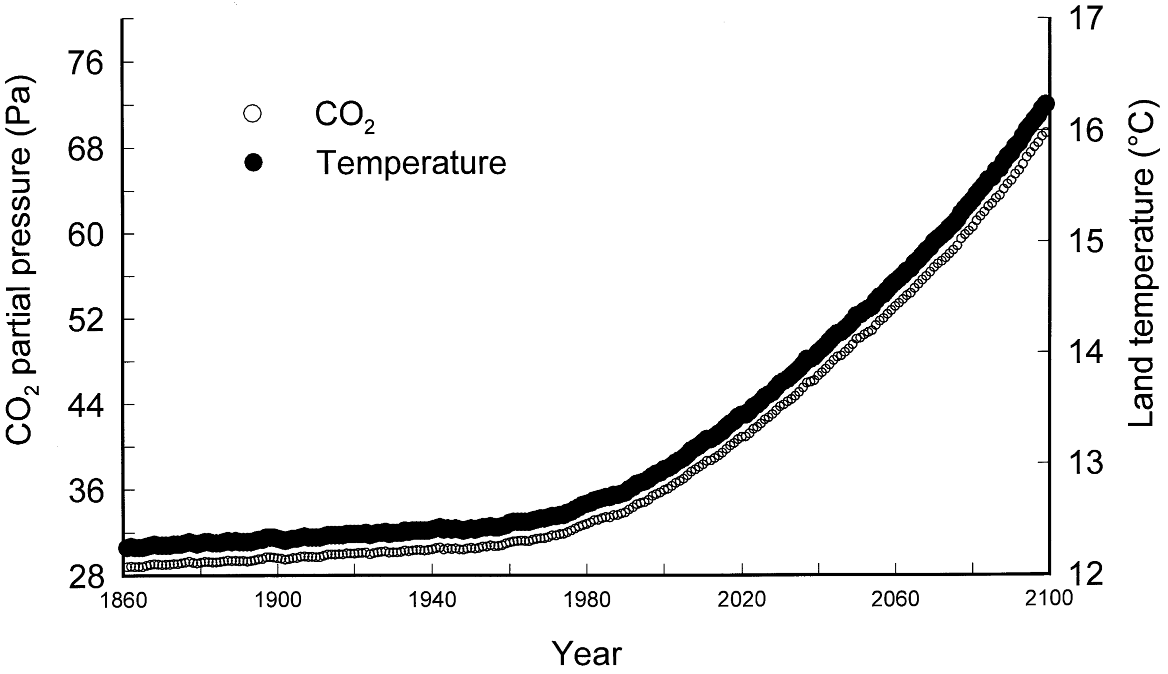


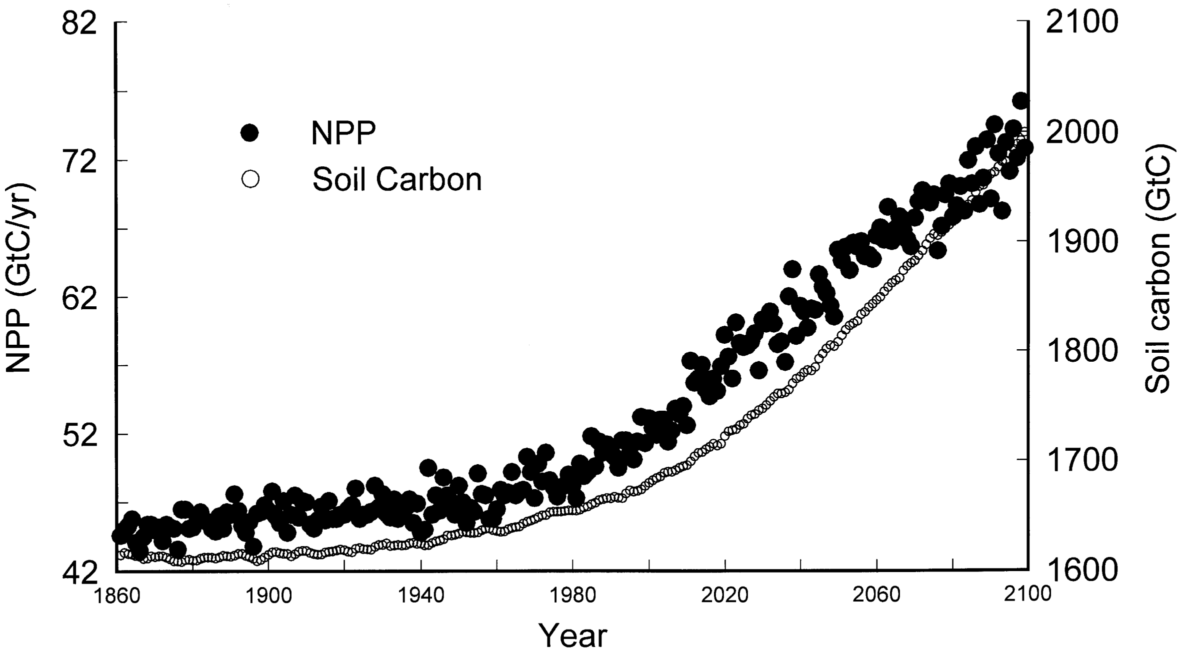
Figure 8. Difference map of global net primary productivities (NPPs) in the control run for the 2090s less the NPPs for vegetation feedbacks on atmospheric CO_2.

atmospheric CO_2 partial pressure is 12% lower, global land temperatures are 0.7 °C cooler, NPP is reduced by 6%, and soil carbon accumulation is reduced by 3%, all compared with the projected values with no vegetation feedbacks.

The NPP difference map, with and without the full suite of feedbacks (figure 11) indicates that the reduction in NPP is now more significant at higher latitudes, compared with the CO_2-only feedback (figure 8), as a consequence of the smaller increases in temperature. This indicates the



re 9. Trends in annual land surface temperature and atmospheric CO$_2$ partial pressure after feedback of vegetation on ospheric CO$_2$ partial pressure and temperature. The changes in temperature are calculated from the regression equation of surface temperature on CO$_2$ partial pressure (from figure 2): $T=(9.45\times 0.0973)C$, where T is temperature (°C) and C is CO$_2$ ial pressure (Pa).



re 10. Predicted trends in vegetation net primary productivity and soil carbon after feedback of vegetation on atmospheric partial pressure and temperature.

ter temperature sensitivity of NPP in these cold season ates.

ONCLUSION

e modelling experiments described here, in addition her modelling work by Betts *et al.* (1997), Sellers *et al.*), and Xiao *et al.* (1997) all indicate the potential for vegetation to exert a feedback on climate. When plant physiological responses alone are included the feedback is globally positive (table 1), but when physiological and structural feedbacks are included, the overall feedback is negative. The sign and magnitude of this more complete feedback has complex geographical patterns; however, in general, when there is winter snow and the vegetation increases in LAI, then the feedback is positive (Bonan *et*

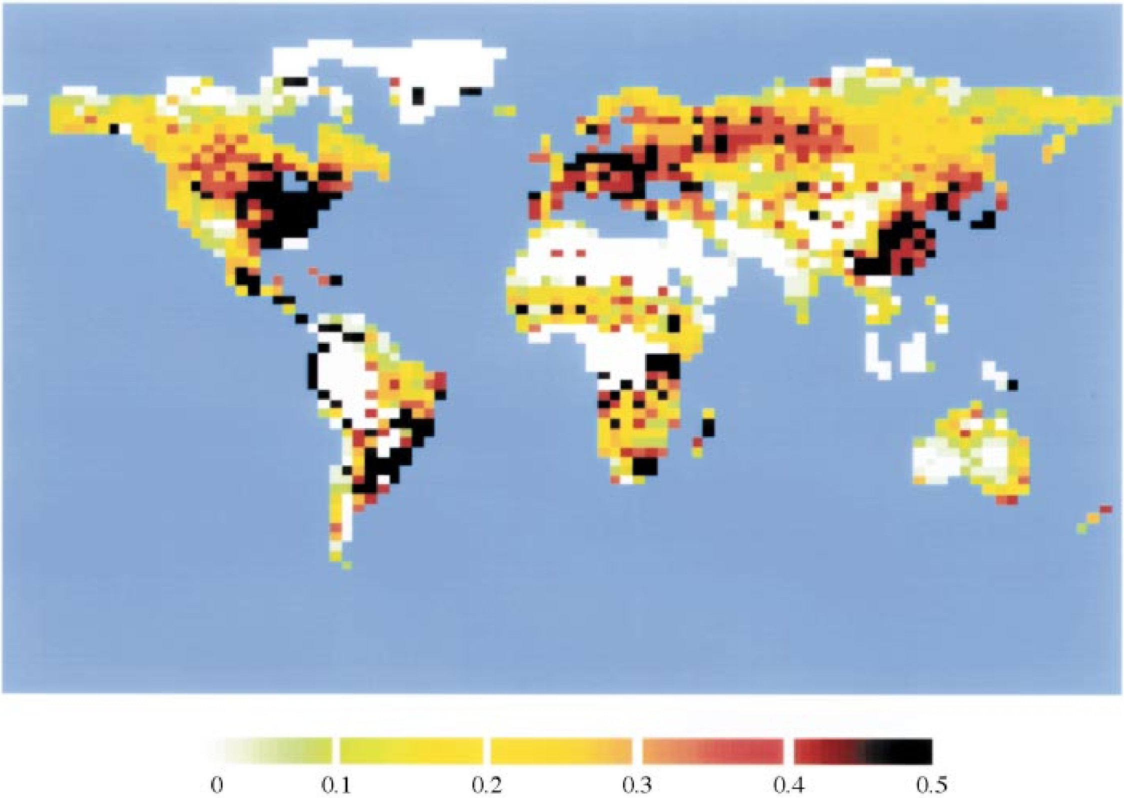


Figure 11. Difference map of global net primary productivities (NPPs) in the control run for the 2090s less the NPPs for vegetation feedbacks on atmospheric CO_2 and temperature.

al. 1992). For the majority of the other significantly vegetated areas of the world, the feedback is negative, a feature which counteracts the positive feedbacks due to physiological responses. Further experiments on these feedbacks will benefit from fuller analyses of synergistic feedbacks with other parts of the climate system, such as with the oceans and sea-ice formation.

These responses fail to include any feedbacks on the atmospheric CO_2 concentration, which exerts a radiative greenhouse effect. In addition, CO_2 concentrations have the capacity to enhance vegetation productivity (Gunderson & Wullschleger 1994). Simple model simulations, with no changes in global precipitation or ocean activity, have indicated that vegetation can exert a slowing effect on the increase in atmospheric CO_2 partial pressure, which can be as great as a 12% reduction in the atmospheric CO_2 concentration by 2100. In addition, the reduction in atmospheric CO_2 concentration, through increases in soil and vegetation biomass, also leads to a slight cooling effect of -0.7 °C on a total greenhouse warming of 3.9 °C. All of these negative feedbacks cause a reduction in NPP, which is greatest in the forested regions of the sub-tropics and mid-to-high latitudes. The small reductions in temperature caused by the feedbacks have the greatest effects in the mid-to-high latitude regions where temperatures limit NPP.

A major concern with these new developments which directly incorporates vegetation function in climatic feedback loops is how to test the model projections. One approach is to use the direct observations of feedbacks at the local and regional scale as described by Hayden (this volume), which provide clear evidence of a vegetative effect. Such responses as the impacts of vegetation greening on local to regional climatic trends, and the feedbacks of continental-scale vegetation on regional to continental-scale precipitation (Hayden, this volume) provide ideal tests of both the vegetation and the GCMs.

The impacts of changing atmospheric CO_2 and temperature on terrestrial NPP (e.g. figures 4, 5 and 11) offer potential for testing predictions against observations. However, NPP is difficult to measure, with significant error of measurement in addition to wide spatial variation, and so it will prove difficult to test these model projections. Nevertheless, the vegetation model also predicts NEP, and this can be tested against field observations of vegetation CO_2 fluxes, using the technique of eddy co-variance (e.g. special issue of *Global Change Biology*, June 1996, volume 2). Of course, these fluxes need to be run as long time-series, in order that the impacts of interannual variations in climate can be detected and used to test the model projections.

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Discussion

A. Wagner (*London, UK*). At the beginning of your talk you showed two graphs of CO_2 in recent years. I noticed there seemed to be no variation due to the oil shocks of the 1970s. Why is this? Is this just due to sampling inaccuracies?

F. I. Woodward. In fact, close analysis of the annually averaged CO_2 concentrations through the 1970s, as seen for example in Keeling *et al.* (1995), indicates quite marked changes in the rate of CO_2 accumulation in the atmosphere, which might be associated with the oil crises. However, it is important to note the last comment in the Keeling *et al.* (1995) paper, which is that *environmental factors appear to have imposed larger changes on the rate of rise of atmospheric* CO_2 than did changes in fossil fuel combustion rates, although this comment was not specifically referred to in the 1970s. (Keeling, C. D., Whorf, T. P., Wahlen, M. & van der Plicht, J. 1995 Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**, 666–670.)

M. Mulligan (*Department of Geography, King's College London, UK*). I have also carried out research into modelling the impact of climatic variability and change upon vegetation properties, but at a smaller scale (regionally) and using much more complex models. These models show that—in a given area and for a particular climate change—a population or distribution function of plant responses can be observed.

What plans do you have to incorporate this variability of response—which is due to variability in landscape factors such as soil type, aspect and other variables? The population of responses may not sum to the single response that your large-scale model produces for the same area.

F. I. Woodward. Operating vegetation models at the global scale, as a necessity, simplifies such features as topographic complexity and landscape characteristics. The major reason being that the global models are driven by global climatic data which are averaged to coarse grids. At their finest, these grids have a resolution of 0.5 × 0.5°, a feature which averages out landscape patterns. Finer-scale grids are neither available for current-day climates nor for outputs from GCMs, which are considerably coarser than 0.5 × 0.5°.

The possibility that operation of the vegetation models at landscape scales may lead to average characteristics which are different from the large grid averages is very real. However, the global models produce predictions of such features as NPP and LAI which are very similar to observations, all of which are made at the landscape scale, so there are grounds for optimism.

Finally, it should be noted that most vegetation models are in effect point models and so they can be used to operate at any scale and are only dependent on the availability of driving data.

C. N. Hewitt (*Institute of Environmental and Biological Sciences, Lancaster University, UK*). Have you carried out sensitivity analyses of your model calculations, and if so what do these tell you about the robustness of your conclusions?

F. I. Woodward. The robustness of our model calculations have been addressed in three ways. The first is by analysing the sensitivity of the model outputs to small changes in individual input variables, including temperature, relative humidity, solar radiation and precipitation. No single variable has such a large effect as to alter substantially our results from the model simulations.

The second approach has been to use very different versions of the GCM, particularly where we have been investigating feedbacks between vegetation and climate. In all cases, the global picture of the feedbacks does not change substantially.

The third approach has been applied to the impacts of vegetation on atmospheric CO_2. In this case, a different vegetation model (Cao & Woodward 1997) was used, and again the results obtained were very similar to those presented here. Therefore, I would consider that our model projections are quite robust.

Cao, M. & Woodward, F. I. 1997 Model estimates of carbon exchange between vegetation, soil and the atmosphere. *Global Clim. Biol.* (In the press.)