

Role of terrestrial ecosystems in determining CO₂ stabilization and recovery behaviour

By CHRIS JONES^{1*}, SPENCER LIDDICOAT¹ and JASON LOWE², ¹*Met Office Hadley Centre, Exeter EX1 3PB, UK;* ²*Met Office Hadley Centre (Reading Unit), Department of Meteorology, University of Reading, Reading RG6 6BB, UK*

(Manuscript received 22 December 2009; in final form 29 June 2010)

ABSTRACT

Terrestrial ecosystems are sensitive to climate and can also influence it through both biophysical and biogeochemical feedbacks. Natural carbon uptake by ecosystems will control future evolution of CO₂ and climate, but the ecosystems themselves may be committed to long-term changes. Here we use a coupled climate-carbon cycle GCM with dynamic vegetation to investigate the policy-relevance of these feedbacks in several idealized scenarios. Our results show that the natural carbon cycle in the ocean and on land controls the recovery of atmospheric CO₂ following emissions reductions at three action points during the 21st century. Initial rates of recovery are similar but for different reasons. Ocean carbon uptake exceeds terrestrial uptake, with higher CO₂ levels leading to increased ocean uptake whereas on land greater climate change at higher CO₂ leads to decreased carbon storage. There are long-term committed changes to terrestrial ecosystems which vary in sign regionally and create a complex dynamic response of terrestrial carbon storage as it slowly approaches a new steady state. Neither stabilization nor CO₂ recovery allows ecosystems to recover back to their initial state and the ecosystems continue to respond for decades or even centuries following emissions reductions. These long-term committed changes, in addition to realized, transient changes, must be considered when defining dangerous climate change and identifying emission-pathways to avoid it.

1. Introduction

Future climate change and the carbon cycle are tightly coupled, with many studies having shown positive feedbacks in which ecosystems can amplify climate change (Cox et al., 2000; Friedlingstein et al., 2006; Denman et al., 2007) and influence global emissions pathways to stabilization (Matthews 2005; Jones et al. 2006; House et al., 2008). Changes in climate may also lead to significant changes in the ecosystems themselves, especially tropical (Jones et al., 2009; Phillips et al., 2009) and boreal forests (Sitch et al., 2008). In the absence of man made atmospheric carbon removal mechanisms natural carbon fluxes will determine the rate of recovery of atmospheric CO₂ if we overshoot a CO₂ concentration or temperature target and subsequently reduce anthropogenic emissions (Lowe et al., 2009).

With increasing interest in policy relevant research into mitigation scenarios, we have performed simulations with the coupled climate-carbon cycle GCM, HadCM3LC to assess the behaviour of the climate and ecosystems following complete reduction of anthropogenic carbon emissions at different action

points during the 21st Century. These simulations first presented by Lowe et al. (2009) showed the limit of recovery rate placed on the climate system by the natural carbon cycle. Here we examine in more detail the interactions between climate and ecosystems in these scenarios. We explore both the mechanisms and regions which determine the role of ecosystems in recovery of atmospheric CO₂ and also look at the subsequent impacts of these scenarios on the ecosystems themselves. We assess carbon storage and ecosystem changes both in terms of short-term transient response and long-term committed changes, and describe to what extent recovery of atmospheric CO₂ contributes to any possible recovery of climate and ecosystem health. The role of the ocean will be analysed in future work.

Our experiments comprised a set of idealized emission reduction scenarios, where CO₂ emissions followed SRES A2 values until being set to zero at years 2012, 2050 or 2100. Although highly idealized, the purpose of these experiments is to show the overall constraints on concentration and temperature reduction inherent in the Earth system and its subsequent impact on ecosystems. For simplicity, non-CO₂ greenhouse gases and aerosol forcings were omitted from these scenarios.

We explore how the mechanisms and regions of carbon uptake differ following the action points and also the short and long-term dynamics of terrestrial ecosystem carbon storage. Whilst

*Corresponding author.

e-mail: chris.d.jones@metoffice.gov.uk

DOI: 10.1111/j.1600-0889.2010.00490.x

on short timescales climate effects on the component carbon fluxes (productivity and respiration) may drive changes in terrestrial carbon stores, on longer timescales changes in biome composition will also become important. It has been shown that terrestrial ecosystems may see large impacts of climate change which continue even after climate stabilization (Jones et al., 2009). We have extended the simulations of Lowe et al. (2009) to look at the multicentury response of ecosystems and explore the complex interplay of different timescales across different regions.

Section 2 describes, in brief, the model we use and summarizes the recovery and commitment simulations. Section 3 describes results showing the role of both the terrestrial and ocean carbon cycle in determining the rate and magnitude of this recovery and the response of ecosystems themselves under our extended scenarios with a focus on the long-term implications of ecosystem commitments on terrestrial carbon storage. Section 4 presents a discussion and our conclusions.

2. Methods

2.1. Model description

For our experiments we used the coupled climate-carbon cycle GCM, HadCM3LC, as described by Cox et al. (2000). It comprises the Met Office Hadley Centre climate model HadCM3 (Gordon et al., 2000) with $2.5^\circ \times 3.75^\circ$ horizontal resolution in the atmosphere and 19 vertical levels. It has a reduced ocean horizontal resolution also of $2.5^\circ \times 3.75^\circ$ for computational efficiency and flux corrections of heat and freshwater are applied to prevent climate drift. The GCM is coupled to terrestrial and ocean carbon cycle models TRIFFID (Cox, 2001) and HadOCC (Palmer and Totterdell, 2001) which represent storage of carbon and exchange of CO₂ with the atmosphere.

TRIFFID defines the state of the terrestrial biosphere in terms of the soil carbon, and the structure and coverage of five plant functional types (PFTs: Broadleaf tree, Needleleaf tree, C3 grass, C4 grass and shrub). The areal coverage, leaf area index and canopy height of each PFT are updated using a carbon balance approach, in which vegetation change is driven by net carbon fluxes calculated within the MOSES-2 land surface scheme (Essery et al., 2003) in which a separate surface flux and temperature is calculated for each of the land cover types present in a GCM gridbox. Carbon fluxes for each of the vegetation types are derived using the coupled photosynthesis-stomatal conductance model developed by Cox et al. (1998). The resulting rates of photosynthesis and plant respiration are dependent on both climate and atmospheric CO₂ concentration and thus the response of vegetation cover to climate occurs via climate-induced changes in the vegetation-atmosphere carbon balance. A fraction of net primary productivity (NPP) is utilized in increasing the fractional coverage and the remainder increases the carbon content of the existing vegetated area. The Lotka-Volterra equations for

intraspecies and interspecies competition determine the evolution of PFT fractions based on a tree-shrub-grass dominance hierarchy.

Soil carbon storage is increased by the total litterfall and reduced by microbial soil respiration which returns CO₂ to the atmosphere. The rate of soil respiration is dependent on the soil temperature according to a 'Q10' exponential function (with a globally uniform value of $q_{10} = 2$, see Jones and Cox, 2001) and on volumetric soil moisture such that respiration is limited in very dry or wet soils and is maximal at intermediate moisture contents.

There is no explicit representation of disturbance of vegetation by either natural fire or pest or disease. A time-invariant mask of present day agriculture is used to prescribe regions where trees and shrubs do not grow, but there is no disturbance due to changing anthropogenic land-use.

2.2. Experimental design

Coupled climate-carbon cycle experiments were performed with HadCM3LC to assess the recovery of atmospheric CO₂ following a sudden cessation of anthropogenic carbon emissions. Taking the SRES-A2 scenario as a baseline as used in the C4MIP study (Friedlingstein et al., 2006), three GCM simulations were performed following a sudden cut of emissions to zero in the years 2012, 2050 and 2100. We will refer to these 'peak and decline' simulations as our recovery experiments as they are used to assess the extent and implications of subsequent recovery of atmospheric CO₂ below some peak level. Three further simulations were performed where atmospheric CO₂ was held fixed at 2012, 2050 and 2100 levels of 404, 558 and 1024 ppm, respectively. These are our stabilization experiments, referring to stabilization of CO₂ rather than of climate itself. In the recovery experiments the model simulates the evolution of atmospheric CO₂ in response to natural marine and terrestrial carbon fluxes. In the stabilization experiments the simulated carbon fluxes are diagnostic but do not affect the atmospheric CO₂ concentration which is prescribed to the model as an input. It is the stabilization and recovery periods which are the focus of our study the business-as-usual SRES A2 scenario is simply used to provide the initial conditions for these experiments. The subsequent model states after stabilization will be largely independent of the pathway to the initial conditions.

The experimental design and results are discussed in more detail elsewhere (Lowe et al., 2009) but Fig. 1 summarizes the emissions prescribed to the model following historical and SRES A2 (Nakicenovic et al., 2000) scenario up to 2100, with cuts to zero emissions at the three action points. In Section 3.1, we analyse the mechanisms of CO₂ recovery in the first 100 yr following emissions reductions. We are also interested in the longer term impacts of stabilization or CO₂ recovery on ecosystems and so the experiments were extended to 200 yr beyond 2012 and 2100 and to 400 yr beyond 2050 and results are shown in Section 3.2.

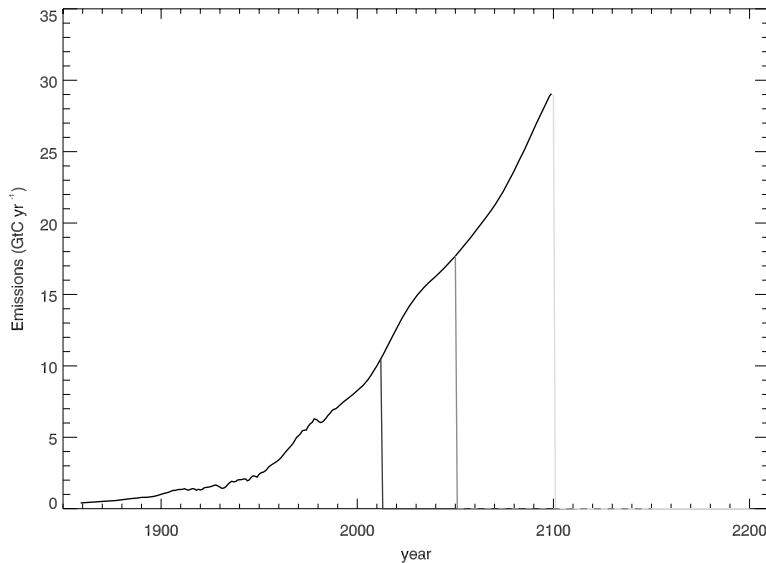


Fig. 1. Anthropogenic emissions of CO₂ prescribed to HadCM3LC following historical and SRES A2 emissions up to 2100 (black line), with complete emissions cuts to zero at three action points: 2012 (dark grey line), 2050 (mid-grey line) and 2100 (light grey line).

The climate at 2050 in our baseline SRES-A2 scenario is at a stage where the Amazon forest is especially vulnerable to even small climate perturbations (Jones and Lowe, 2010) which are why a longer extension of these simulations from 2050 is of interest.

3. Results

We focus our analysis on two aspects of the simulations. Section 3.1 presents analysis of the mechanisms of CO₂ recovery in the first 100 yr following emissions reductions and Section 3.2 the results of the experiments extended to 200 or 400 yr beyond the action points.

3.1. Mechanisms of atmospheric CO₂ recovery

Subsequent behaviour of global average atmospheric CO₂ concentration following the emissions cuts at the three action points is shown in Fig. 2a as reported in Lowe et al. (2009). Figure 2b shows the three recovery rates superimposed. It is remarkable how closely the three curves match, especially during the first 50 yr, given the very different levels of CO₂ and climate change associated with each action point. This raises the question of whether there is a fundamental mechanism controlling CO₂ recovery which limits the recovery to the same rate regardless of action point.

As shown in Fig. 2b the initial recovery of atmospheric CO₂ following emissions cuts is remarkably constant (at an initial rate of around 0.5–1 ppm yr⁻¹ for the first few decades) after each of three different action points, although recovery from lower levels tends to saturate sooner, leading to reduced cumulative recovery over the subsequent centuries. Here we explore the reasons, mechanisms and implications of the rate of recovery during the first 100 yr following emissions cuts. We find that

there is not a single mechanism of recovery nor any fundamental reason why the recovery rate should be so similar across action points. The recovery for our three simulations shown here is for very different mechanisms and regions of carbon storage.

The total carbon uptake implied by Fig. 2b masks the mechanisms behind it. Figure 3 shows the geographical distribution of terrestrial carbon uptake and changes in both vegetation and soil carbon storage following the 2012 action point. Figures 4 and 5 show likewise carbon changes following the 2050 and 2100 action points, respectively. The magnitude of changes in carbon storage are summarized by region in Table 1 and by biome in Table 2.

In terms of the ocean carbon cycle, at each action point the global average atmospheric CO₂ is higher than the surface ocean *p*CO₂. This drives chemical dissolution of CO₂ in the ocean and results in a net ocean sink during the 100 yr following each action point. As the atmospheric CO₂ rises much faster than the ocean *p*CO₂ in the business-as-usual scenario leading up to the emissions cuts, each subsequent action point has a greater disequilibrium between atmosphere and ocean and so the ocean sink increases for 2050 and 2100. Unlike in the terrestrial biosphere, the ocean carbon uptake is not primarily due to biological activity. Hence the increased sink after the 2100 action point may mask any impact of the CO₂ levels and large carbon uptake on marine ecosystems. The impact of the three scenarios on ocean acidification will be analysed in subsequent work.

The terrestrial biosphere on average takes up carbon during the 100 yr following emissions cuts in 2012 (Fig. 3) whereas it loses carbon following the 2050 and 2100 action points (Figs 4 and 5, respectively). At 2012 enhanced plant productivity as a result of elevated CO₂ exceeds enhanced decomposition of soil organic carbon and the land is a net sink. By 2050 and more so by 2100, higher global temperatures result in increased soil decomposition which outweighs the CO₂ fertilization effect

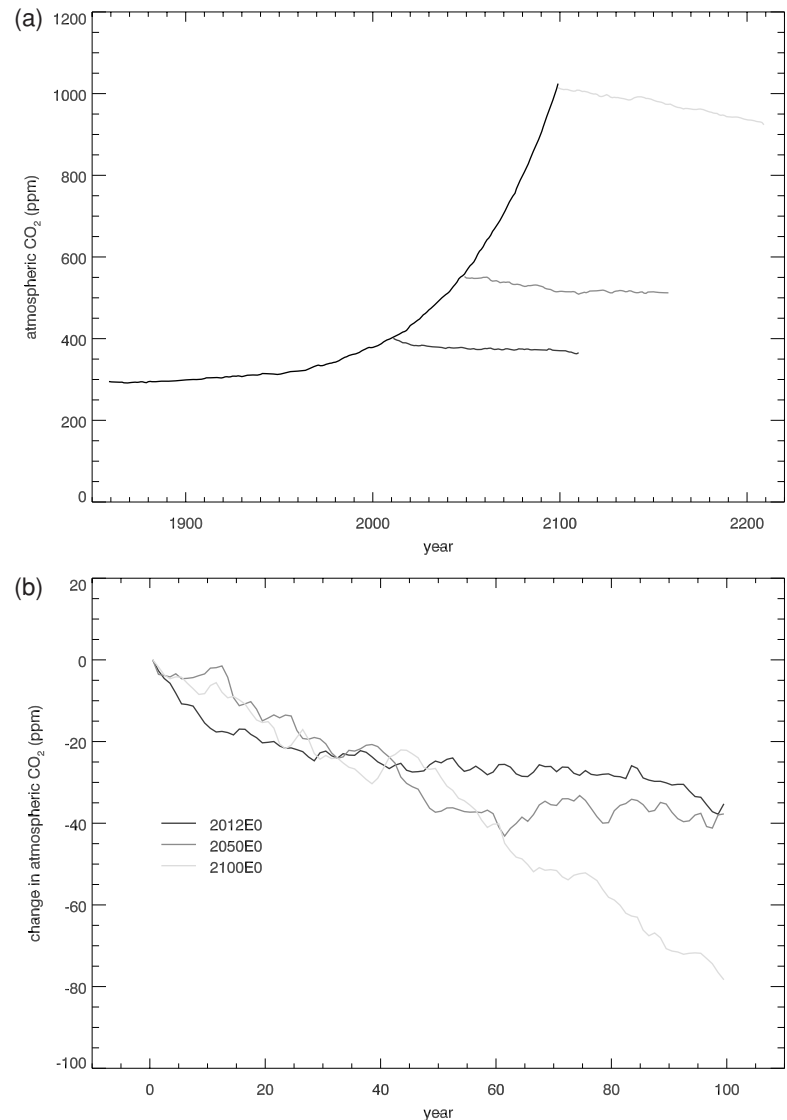


Fig. 2. (a) Evolution of atmospheric CO₂ concentration simulated by HadCM3LC following SRES A2 emissions up to 2100 (black line), and subsequent recovery of atmospheric CO₂ following emissions cuts to zero at three action points: 2012 (dark grey line), 2050 (mid-grey line) and 2100 (light grey line). (b) Comparison of the rate of recovery by superimposing the lines from panel (a).

on productivity and the terrestrial biosphere is a net source of carbon.

The different behaviour of tropical and extra-tropical regions is quite marked. Following the 2012 action point, both tropics and extra-tropics act as a small net sink of similar magnitude (of the order of 10–15 GtC over 100 yr). However, following 2050 and 2100 the tropics act as large sources of carbon and the extra-tropics act as a moderate sink after 2050 and are near carbon-neutral after 2100. The reasons for this differing behaviour can be seen if we consider the regional breakdown in carbon uptake between biomass and soil carbon stores.

After the 2012 action point the changes in extra-tropical carbon are mainly in the biomass (Fig. 3), caused by both CO₂ fertilization of plant growth and also some enhancement of boreal forest growth due to slightly warmer conditions (in particular a longer snow-free growing season (Harrison et al., 2008; Piao

et al. 2008). Changes in soil carbon storage are very small with extra input of organic matter from plant litterfall countered by enhanced microbial decomposition in the warmer temperatures, although regionally extra-tropical soil shows net accumulation in North America and loss over Eurasia.

After the 2012 action point the changes in tropical carbon are similar to those in the extra-tropics with small net uptake in both the biomass, caused mainly by CO₂ fertilization, and also small net uptake by the soils with the extra input of organic matter from plant litterfall exceeding any enhanced decomposition in the warmer temperatures. This is consistent with observations of prolonged present day carbon sinks in intact tropical forests (Amazon: Phillips et al., 2009; Africa: Lewis et al., 2009). In the 100 yr following this action point there is a small loss of biomass in the Amazonian forest region implying the region may already be very close to a climate threshold of maximal carbon uptake

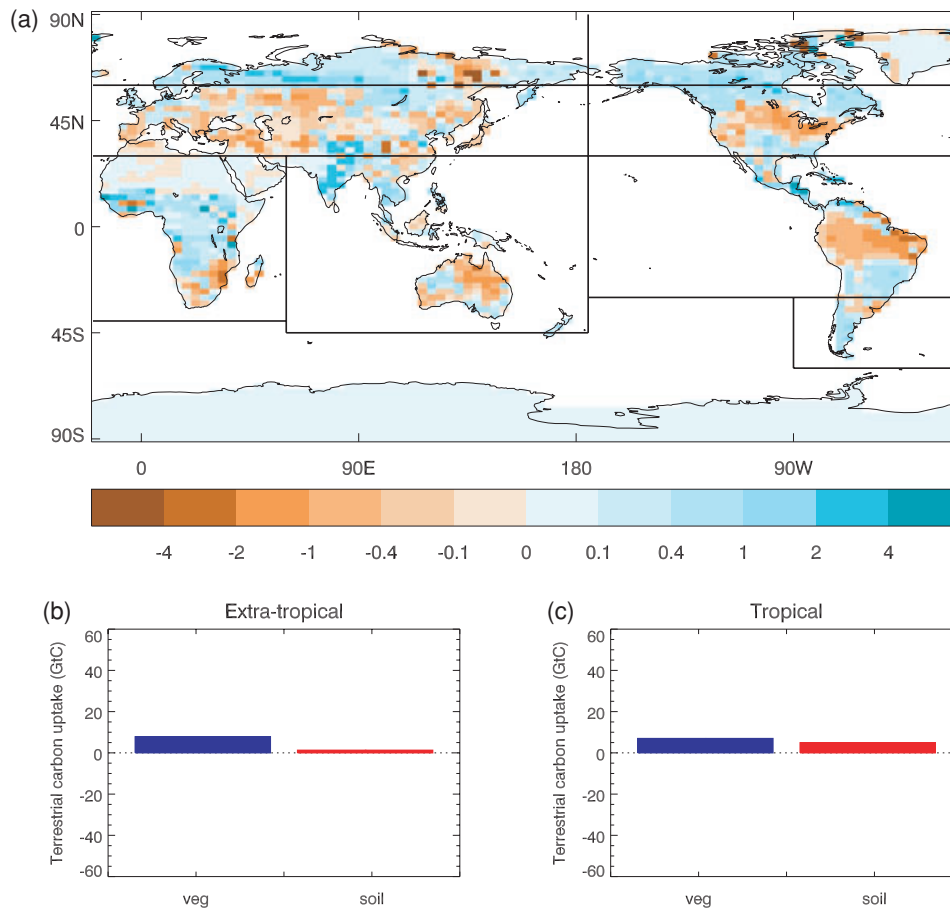


Fig. 3. Terrestrial carbon uptake in 100 yr following emissions reductions in 2012. (a) distribution of net soil and vegetation carbon changes (KgC m^{-2}), where positive values indicate net uptake by the land surface. (b) and (c) breakdown into vegetation (blue bars) and soil carbon changes (red bars) for extra-tropical and tropical regions respectively.

such that even small additional warming (or more likely, drying) could lead to release of stored carbon (Cox et al., 2008; Phillips et al., 2009).

Following 2050 the extra-tropical biomass increases by more than after 2012 (about 25 GtC; Fig. 4). The reasons are the same as before but both the atmospheric concentration of CO_2 and the warming are greater at 2050 than at 2012. Similarly the soil carbon shows only a weak response, but now it is evident that the enhanced soil decomposition is starting to dominate over the increase litter input and the net effect is negative (i.e. a net loss of soil carbon in the extra-tropics following the 2050 action point), although again with small net accumulation in North America.

Unlike in the extra-tropics, the tropical terrestrial carbon balance comprises similar losses of carbon from both biomass and soil and is dominated by the response of the Amazon forest. The reasons for this are that the degree of climate change by 2050 is enough to reduce tropical vegetation productivity—whereas warming is generally beneficial in the extra-tropics (especially in the boreal forest region) warming and drying in Amazonia leads to reduced vegetation growth (Cox et al., 2004; Scholze

et al., 2006) and storage of carbon in biomass (Phillips et al., 2009) and also long term reductions in forest cover (Betts et al., 2004; Jones et al., 2009). As before, warmer temperatures also lead to reduction of soil carbon storage as decomposition rates increase. Across Africa, southern Asia and Australia there is net loss of carbon, mainly from soils, countered by slight biomass increases.

Following the 2100 action point extra-tropical vegetation now stores yet more additional carbon (about 40 GtC), showing a steady rate of increase in biomass from the other action points (Fig. 5). Not only does the higher CO_2 and warmer climate lead to greater productivity of the existing vegetation but it also changes the vegetation cover itself, with increasing fractions of boreal forest further north than they could hitherto survive. However, unlike tropical reductions in Amazon forest cover, the timescale for transition to new forest is slow, and 100-yr increases in boreal forest fractional coverage are modest. But now the soil carbon also shows a strong signal. The greater warming by and following 2100 leads to significantly increased loss of soil carbon from decomposition due to the non-linear

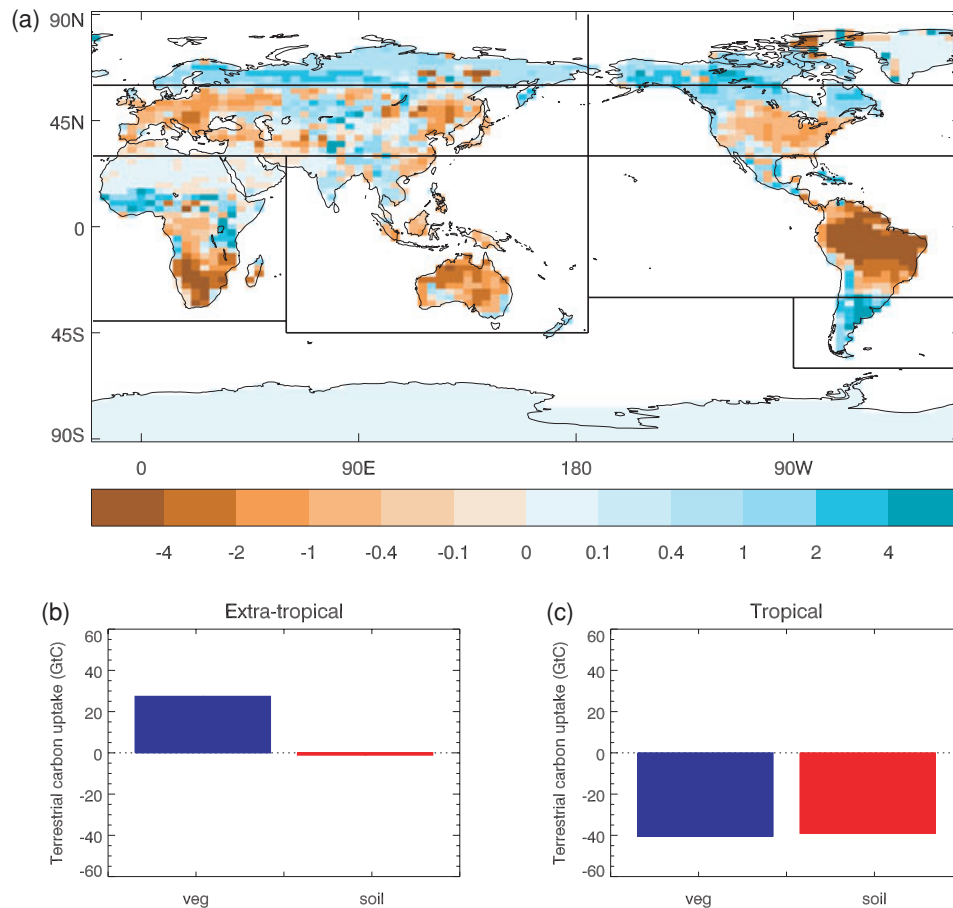


Fig. 4. As Fig. 3 but for 100 yr following 2050.

relationship between decomposition and temperature. This now dominates over the enhanced vegetation growth and the net response of the terrestrial biosphere in the extra-tropics is a small loss of carbon.

Following 2100 tropical carbon storage responds similarly to after 2050, with vegetation now storing even less carbon and soil carbon also showing losses. It might have been assumed that by 2100 the tropics would have been losing even more carbon than this, so it is at first sight surprising that the losses are not significantly greater than those following the 2050 action point (in fact for soil carbon the losses are smaller). The reason for this is the difference in the state of the biosphere at the action point. By 2100 the tropical biosphere has already lost a lot of carbon relative to 2050, so any loss following 2100 is limited by this. Both losses in tropical forest cover and soil carbon to 2100 limit the amount of carbon which may be lost subsequently.

The conclusion from this analysis is that although the initial global recovery rate of atmospheric CO₂ following emissions cuts at the three action points is similar, the underlying mechanisms and regional behaviour of the land and ocean carbon cycle is very different. Increasing ocean uptake for the higher CO₂ concentration at later action points is driven by the increas-

ing difference in atmospheric and oceanic CO₂ concentration but this is countered by a decreasing ability of the terrestrial biosphere to absorb carbon. In particular the tropics act as a significant carbon source following the 2050 and 2100 action points. We find there is no single mechanism or region which is most important for determining atmospheric CO₂ recovery following peaking of CO₂ concentration. There is a complex interplay of sink and source behaviour which depends on the initial climate state and CO₂ concentration and the duration of the interval considered following peaking.

3.2. Response of ecosystems to CO₂ recovery and stabilization

We have looked at how ecosystems and the natural carbon cycle control recovery of atmospheric CO₂ following emissions cuts, and now we ask how such recovery of CO₂ affects the ecosystems themselves especially on longer timescales. To what extent are ecosystems committed to changes and how do such commitments change under either stabilization or overshoot scenarios. Does CO₂ recovery lead to ecosystem recovery?

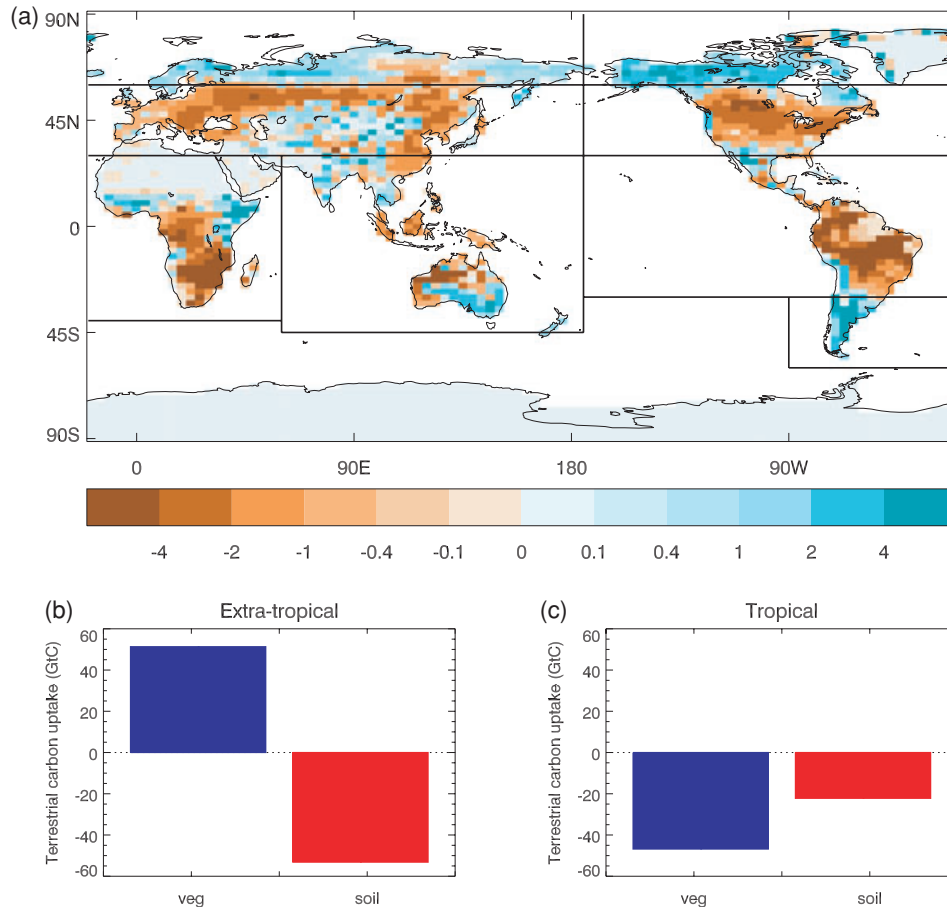


Fig. 5. As Fig. 3 but for 100 yr following 2100.

Even though atmospheric CO_2 showed similar rates of recovery for the first few decades following each of the 3 action points this does not persist over multicentury timescales (Fig. 6). Even after 100 yr we see the high CO_2 (2100) case has sustained reductions in atmospheric CO_2 , due to continued ocean uptake. After 200 yr this is even more pronounced and the 2012 case stabilizes and we see little further recovery. CO_2 recovers by 78 and 86 ppm in the first and second centuries respectively following emissions cuts in 2100; by 37 and 32 ppm following 2050, and by 35 and 10 ppm following 2012. The 2050 peak and decline simulation has been extended to 400 yr and shows recovery by a further 38 ppm after that time. The CO_2 level at the 2050 action point is very close to 550 ppm (558 ppm) and the recovery by 2450 is to very close to 450 ppm (446 ppm). Thus this experiment compared with the stabilization experiment from 2050 provides an opportunity to quantify the differences and possible benefits of CO_2 recovery from 550 to 450 ppm compared with simply stabilizing CO_2 at 550 ppm. Here we look at climate and ecosystem response to both stabilization at 550 ppm and peak at 550 followed by eventual recovery to 450 ppm after 400 yr.

In terms of global temperature, the stabilization scenarios see a continued increase in temperature as expected due to thermal

inertia (Wigley, 1995; Meehl et al., 2005; Hare and Meinshausen, 2006). Just as the high CO_2 simulations saw greater and more prolonged uptake of CO_2 they also see greater and more prolonged committed warming under stabilization (Fig. 7). The zero-emission simulations show an approximately stable global temperature—in other words the decreasing radiative forcing as CO_2 recovers approximately compensates for the committed warming at the action point. This is in agreement with other studies (e.g. Matthews and Caldeira, 2008) which show the need for declining GHG concentrations in order to stabilize climate. After 200 yr the 2012, 2050 and 2100 simulations see about 0.53, 0.69 and 0.73 K of difference, respectively, with the recovery simulations cooler. For the 2050 simulations, this difference increases to 0.78 K as CO_2 recovers to 450 ppm after 400 yr.

3.2.1. Carbon storage. Ocean uptake continues strongly after 2050 in both stabilization and recovery simulations (Fig. 8a). Following stabilization there is some degree of decrease in the rate of uptake, but carbon is still being absorbed by the ocean after 400 yr at about half the initial rate at 2050. After 2050 in the zero-emissions simulation, the reductions in atmospheric CO_2 rapidly reduce the air–sea difference in $p\text{CO}_2$ and hence reduce

Table 1. Cumulative carbon uptake (GtC) during the 50 and 100 yr following each action point by carbon pool (vegetation biomass, soil carbon or ocean) and region

| Action point | Duration (yr) | Carbon pool | Carbon uptake by region (GtC) | | | | | | | |
|--------------|---------------|-------------|-------------------------------|-------------------|-------------------|----------------|-------------------------|--------|-----------|-------|
| | | | Temperate N. America | Boreal N. America | temperate Eurasia | Boreal Eurasia | S. and tropical America | Africa | Australia | Globe |
| 2012 | 50 | Biomass | 1.41 | 0.36 | 1.48 | 1.04 | −0.09 | 6.55 | 2.11 | 12.9 |
| | | Soil carbon | 0.55 | 2.86 | 0.43 | 1.56 | −0.96 | 4.04 | 0.28 | 8.8 |
| | | ocean | | | | | | | | 32.1 |
| | 100 | Biomass | 2.26 | 1.00 | 2.41 | 2.14 | −1.93 | 6.14 | 2.77 | 14.8 |
| | | Soil carbon | −0.37 | 3.67 | −2.70 | 0.68 | 1.75 | 2.43 | 0.77 | 6.2 |
| | | Ocean | | | | | | | | 54.4 |
| 2050 | 50 | Biomass | 7.35 | 2.16 | 4.24 | 3.69 | −25.6 | 4.33 | 2.30 | −1.5 |
| | | Soil carbon | 4.17 | 5.19 | −2.56 | 3.68 | −10.2 | 3.70 | −4.77 | −0.8 |
| | | Ocean | | | | | | | | 80.8 |
| | 100 | Biomass | 9.57 | 4.01 | 7.61 | 6.20 | −45.2 | 1.69 | 3.08 | −13.0 |
| | | Soil carbon | 0.86 | 6.31 | −10.9 | 2.68 | −22.4 | −4.28 | −12.26 | −40.0 |
| | | Ocean | | | | | | | | 133.8 |
| 2100 | 50 | Biomass | 6.99 | 4.80 | 6.37 | 5.94 | −33.3 | −6.65 | 2.91 | −12.9 |
| | | Soil carbon | −15.0 | 3.94 | −29.4 | −5.12 | −6.13 | −9.52 | −8.68 | −69.8 |
| | | Ocean | | | | | | | | 145.1 |
| | 100 | Biomass | 13.5 | 10.4 | 14.4 | 13.1 | −40.4 | −11.2 | 4.69 | 4.5 |
| | | Soil carbon | −16.6 | 4.4 | −33.0 | −8.01 | −6.43 | −8.75 | −7.03 | −75.4 |
| | | Ocean | | | | | | | | 234.8 |

Notes: The regions are as shown in black boxes in Figs 3–5. ‘temperate N. America’ denotes North America north of 30°N and south of 60°N and includes the portion of South America south of 30°S which is too small here to be treated as a separate region, ‘boreal N. America’ denotes North America north of 60°N and includes Greenland, ‘S. America’ denotes tropical and South America between 30°S and 30°N, ‘temperate’ and ‘boreal’ Eurasia denote Eurasia between 30°N and 60°N and north of 60°N, ‘Africa’ denotes Africa and Saudi Arabia and ‘Australia’ denotes Australia and southern Asia.

the oceanic CO₂ uptake relative to the stabilization case. The uptake rate is reduced to a third of its initial rate after 400 yr.

As before, global total terrestrial carbon uptake (Fig. 8b) hides competing regional behaviour. Patterns of terrestrial carbon uptake are very heterogeneous in both space and time, with the global sign of uptake changing during the 400 yr after stabilization or peaking. This behaviour is driven by different regional behaviour having both opposite signs and very different timescales (Fig. 9). Vegetation carbon decreases rapidly in the tropics and remains approximately constant after 100 yr as the climate change both reduces productivity (especially over Amazonia) and also leads to loss of forest area in Amazonia, although other tropical areas do not see large changes in biome composition. However, temperate and boreal regions see increased productivity due to climate change and this leads to increased fractional coverage of trees and large increase in vegetation carbon. This extra-tropical increase in vegetation carbon, though, is slower but continuous throughout (and beyond) the 400 yr of simulation. Soil carbon in the tropics decreases rapidly due to both increased decomposition in warmer conditions and also reduced vegetation productivity. Again, this remains approximately constant after the first 100 yr, implying that tropical

carbon balance reaches a new steady state on much quicker timescales than the extra-tropics, where soil carbon increases slightly initially due to increased carbon input from vegetation, but then increased rates of soil respiration in the warmer conditions lead to eventual soil carbon losses, albeit at a slower rate than in the tropics as they are offset by increased litter input to the soils.

Thus the long-term global picture of terrestrial carbon uptake is a balance between rapid carbon loss in the tropics and slower carbon gain in the northern latitudes. The net result is an initial carbon loss following 2050 followed by a slower, but more prolonged carbon sink starting around 120–130 yr after 2050. By 2450 the global terrestrial carbon store has almost recovered to the 2050 level in the stabilization simulation, although the regional composition of this is markedly different and high-latitude carbon storage is still increasing. A simulation run on to full steady state (the equilibrium simulations of Jones et al. (2009) assuming constant climate following 2050) showed an increase in extra-tropical vegetation carbon a further 60 GtC higher than that achieved here at 2450.

This behaviour of changing sign is not unexpected and was postulated by Smith and Shugart (1993) who estimated the likely

Table 2. Fractional coverage (%) and vegetation carbon storage (GtC) for biomes at each action point and the subsequent change after 100 yr of simulation

| Action point | | Biome | | | | |
|--------------|----------------------------|--------------------|----------------|----------------------------|----------------------------|------------------------|
| | | Tropical evergreen | Tropical grass | Temperate/boreal deciduous | Temperate/boreal evergreen | Temperate/boreal grass |
| 2012 | % cover | 39.9 | 28.6 | 2.3 | 39.7 | 38.2 |
| | change in cover | 0.5 | 1.4 | 0.4 | −0.1 | −0.3 |
| | Veg carbon (GtC) | 391 | 10.4 | 18.2 | 132.8 | 14.9 |
| | change in veg carbon (GtC) | 6.2 | 0.5 | 2.5 | 5.6 | 0.0 |
| 2050 | % cover | 41.6 | 29.1 | 2.7 | 42.5 | 36.6 |
| | change in cover | −2.1 | −0.5 | 1.0 | 1.5 | −1.4 |
| | Veg carbon (GtC) | 421 | 11.3 | 23.4 | 151.9 | 14.6 |
| | change in veg carbon (GtC) | −40 | −1.0 | 8.9 | 18.7 | −0.2 |
| 2100 | % cover | 39.8 | 24.5 | 3.5 | 46.8 | 33.1 |
| | change in cover | −6.7 | 1.2 | 4.0 | −0.6 | −2.1 |
| | Veg carbon (GtC) | 387.4 | 8.9 | 34.9 | 183.2 | 13.9 |
| | change in veg carbon (GtC) | −48.8 | 0.4 | 37.0 | 16.1 | −0.9 |

Notes: ‘Biomes’ in this case are not simulated directly by the model but have been recreated by assuming a simple mapping to PFTs and so can only approximately be compared with equivalent real-world biomes. Here we define ‘tropical forest’ to be all trees and shrubs between 30°S and 30°N; ‘temperate/boreal evergreen’ to be needleleaf trees and shrubs north of 30°N or south of 30°S; ‘temperate/boreal deciduous’ to be broadleaf trees north of 30°N or south of 30°S. ‘Grass’ is the sum of C3 and C4 grass PFTs in those same latitude bands.

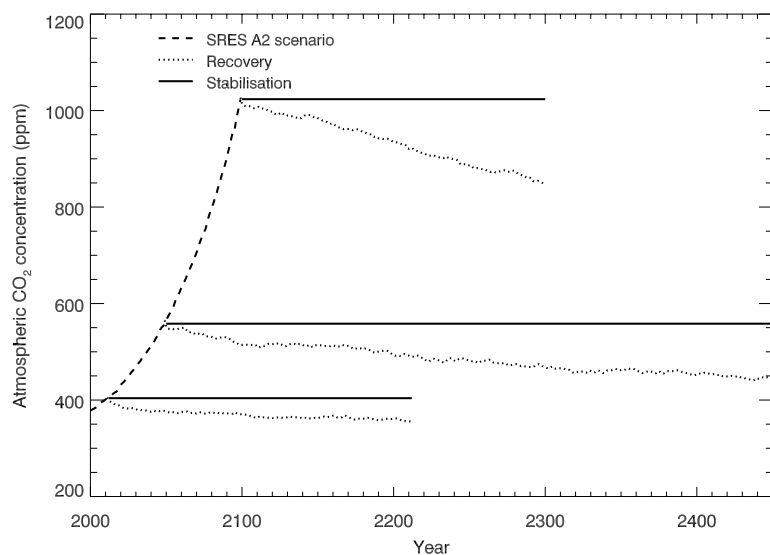


Fig. 6. Evolution of atmospheric CO₂ concentration simulated by HadCM3LC following cessation of emissions at 2012, 2050 and 2100 (‘recovery’: dotted lines). The stabilization simulations are included for comparison (solid lines). The SRES A2 scenario from which these simulations were initialized is also shown (dashed line).

biome and carbon storage response to climate change by deriving a fit of observed biomes to bioclimatic regions and applying this to climate model output with assumed timescales for loss and growth of forests. Their results showed very similar behaviour of a long term carbon sink due to climate change but an initial loss of carbon as the loss processes proceeded more quickly than the gains. By using a process based model which explicitly takes into account mechanisms of vegetation productivity, dynamics and feedbacks with climate we can more reliably quantify the timing and magnitude of this succession of source/sink behaviour.

Because the long term behaviour is a balance between competing processes of opposite sign the net is very sensitive to changes in the driving climate conditions. Hence the long term carbon balance is quite different between the stabilization and recovery simulations, even though regional behaviour is qualitatively the same in each. When considering the tropical and extra-tropical soil and vegetation carbon evolution in the two simulations (Fig. 9), perhaps the biggest difference is the degree of increase of extra-tropical vegetation carbon, which can be seen to be quite pronounced in stabilization simulation, but less

Fig. 7. Change in global mean near-surface temperature following cessation of emissions in 2100 and 2100 ('recovery': dotted lines) and stabilization at the initial CO₂ level (solid lines). The SRES A2 scenario from which these simulations were initialized is also shown (dashed line).

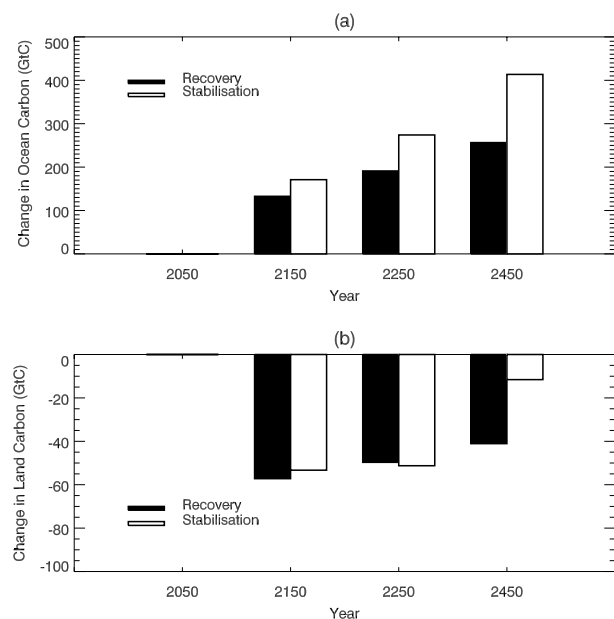
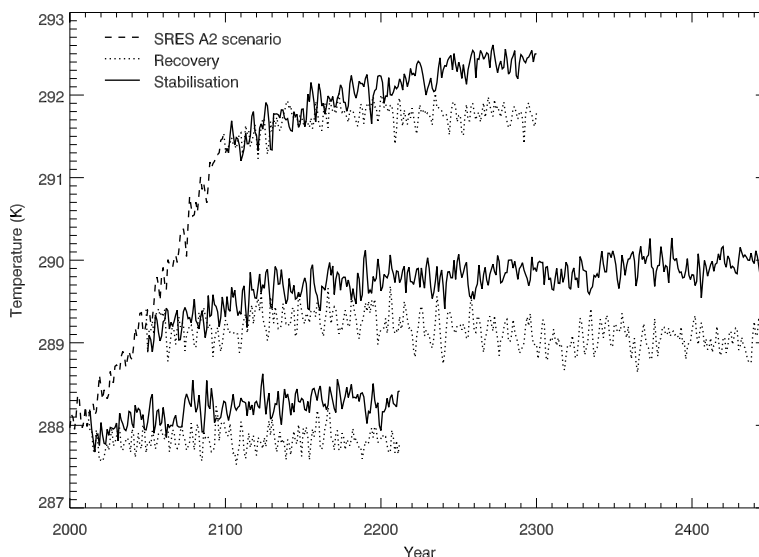


Fig. 8. Changes in carbon storage after 100, 200 and 400 yr in the 2050 recovery simulation (solid bars) and the 2050 stabilization simulation (open bars). (a) Change in ocean carbon inventory. (b) Change in land carbon store. Note the different vertical scales for the two panels as the ocean changes are much greater than the land.

so in the recovery simulation. This can be attributed to the rate of boreal forest expansion as discussed later.

Globally, as with the ocean, the terrestrial carbon uptake is greater following stabilization than recovery. So in this context the recovery of atmospheric CO₂ from 550 back to 450 ppm does not result in enhanced natural carbon uptake—the higher CO₂ fertilization effect under stabilization and positive climate impact on boreal forest extent outweigh the impact of the greater

extent of climate change on tropical ecosystems. However, this result is not globally uniform and we should consider the relative impacts of the two scenarios on individual biomes.

3.2.2. Amazon forest response. During the transient evolution of the model up to 2050 there is very little change in the forest cover of the Amazon region, as shown in Jones et al. (2009). However, our model predicts that there is a significant degree of dieback already committed by this stage even if climate is subsequently stabilized. Figure 10 shows the fractional vegetation cover in Amazonia 400 yr after 2050 with both stabilized CO₂ concentration and with zero emissions (which lead to declining CO₂ and approximately stabilized global temperature). There is significant loss of forest cover in both simulations. Despite the relatively slow rate of recovery of CO₂ after 2050, (110 ppm over 400 yr) and relatively small difference in global temperature (of about 0.78 K) there is a quite marked difference in the degree of subsequent Amazon dieback. Following stabilization the forest decreases by 77% of its former coverage whereas it reduces only by 56% in the peak and recovery case. Thus the surviving forest following peaking and recovery is almost twice that following CO₂ stabilization.

Further, not only does the extra degree of warming in the stabilization case result in substantially less forest cover, it also results in a greater degree of desertification in the Amazon region. As the forest cover recedes in the recovery scenario it is progressively replaced by grassland which still survives at 2450. However, in the CO₂ stabilization scenario the climate change is sufficient that even some of this grassland is not supported by the climate and gives way to bare soil (Fig. 10). Compared with a global temperature difference of 0.78 K between these two simulations, the difference over this region of South America is 0.66 K.

The reason for this large sensitivity of forest survival to relatively small changes in environmental drivers is discussed by

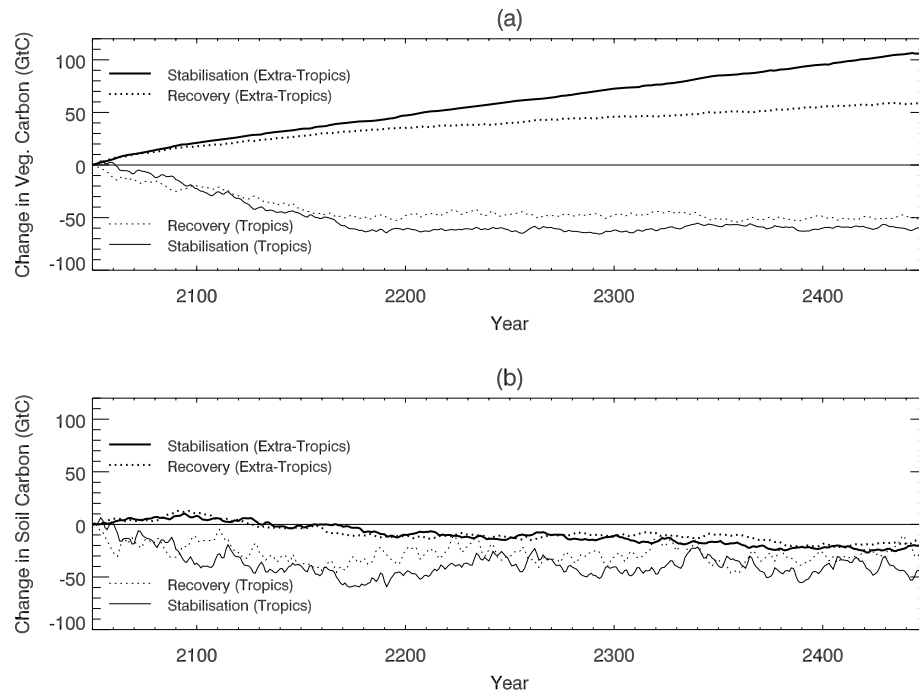


Fig. 9. (a) Vegetation carbon changes in the tropics (thin lines) and extra-tropics (thick lines) in the 2050 recovery simulation (dotted) and the 2050 stabilization simulation (solid). (b) as (a) but for soil carbon.

Jones and Lowe (2010). Jones et al. (2009) present the degree of committed Amazon forest cover as a function of global temperature and show that most of the dieback of the forest occurs in the temperature range from 1° to 3° of global warming above pre-industrial, with changes beyond 3° showing much less sensitivity to further warming. In the region of this tipping point even a small additional warming can be important, with 4% additional forest loss for each additional 0.1 K of global warming, although it is all aspects of local climate that determine forest resilience, not just temperature. Thus, following stabilization or peaking at 2050 where global temperatures rise is about 2° above pre-industrial, the extra warming in the stabilization simulation gives rise to substantial additional forest loss (Fig. 11). Much more detailed analysis is required into the mechanisms of this and how to diagnose the strength of such feedbacks.

Figure 11 also shows that the Amazon forest in our model is very close to a threshold for dieback at present day. Following the action points at 2012 the forest appears to be stable in the recovery simulation (which has approximately constant climate—see Fig. 7), but is committed to some degree of dieback in the stabilization simulation due to the small (0.53 K) committed warming following CO_2 stabilization. The evolution of Amazon forest cover following 2100 stabilization or recovery is much less sensitive to the extra warming in the stabilization case, and both simulations following 2100 show almost exactly the same degree of committed dieback.

The conclusion is therefore that even a seemingly modest degree of recovery of CO_2 and global temperature can lead to very

significant improvements in the sustainability of ecosystems at the regional scale—especially where local feedbacks between vegetation cover and climate are strong.

3.2.3. Boreal forest response. Jones et al. (2009) and Plattner (2009) highlighted that ecosystem commitments can be of either sign—that is, both committed loss or committed expansion of ecosystems, with the boreal forest as an example of committed expansion in our model. A warmer future climate allows northward expansion of the boreal forest into present day tundra regions due to both longer snow-free growing season and higher summer temperature. Such expansion has been reported in several vegetation models (Sitch et al., 2008) and for several GCMs (Scholze et al., 2006) and has also been seen in the palaeo-record during previous warm periods (Macdonald et al., 2008), although a longer growing season does not necessarily imply an enhanced carbon uptake as higher temperatures also allow enhanced soil respiration (Harrison et al., 2008; Piao et al., 2008).

Figure 9 showed the long term changes in carbon storage in the extra-tropics, with a large increase in vegetation carbon storage but a decline in soil carbon. Figure 12 shows the evolution of tree cover in the same region in the 400 yr following 2050 and Fig. 13 shows the geographical extent of this expansion. The extra warming in the stabilization experiment compared with the recovery experiment leads to a more rapid expansion of boreal forest showing that the timescale of response is not entirely intrinsic to the ecosystem but also depends on the degree of forcing. As with the Amazon, biophysical feedbacks mean

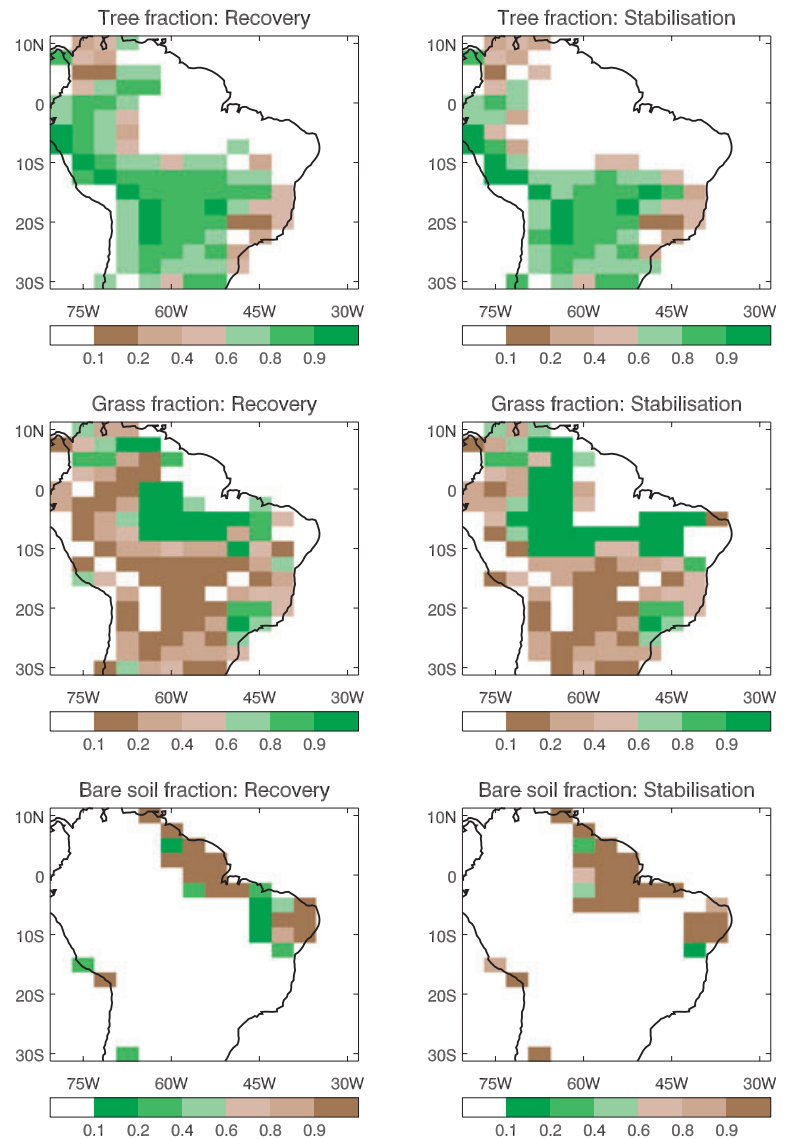


Fig. 10. Simulated fractional coverage of trees (upper row), grass (centre) and bare soil (bottom) in Amazonia in year 2450 following 400 yr of recovery (left-hand column) and stabilisation (right-hand column).

that boreal forest expansion will also affect the local climate, in this case through decreases in albedo. As forested surfaces are darker than the tundra they would replace, especially during periods of snow cover (Betts, 2000), expansion produces additional warming and hence a positive feedback on climate change (Foley et al., 1994). However, unlike in the Amazon forest we do not find that these feedbacks are strong enough in our model to cause any highly non-linear response of committed boreal forest cover to temperature (Jones et al., 2009).

Also unlike in Amazonia, the timescale to realize committed changes is much longer than our 400 yr simulation. Whilst the committed Amazon forest state took about 100 yr to establish following stabilisation, the boreal forest expansion is still proceeding after 400 yr. It is this difference in timescales of response which causes the complex temporal response of total terrestrial carbon storage which showed a rapid loss (of tropi-

cal vegetation) and a longer-term gain (of extra-tropical/boreal vegetation). Thus long-term committed changes must be considered in addition to transient, realized changes when assessing both climate impacts on ecosystems and climate-carbon cycle feedbacks.

4. Discussion and conclusions

We have performed simulations with a coupled climate-carbon cycle GCM to assess the behaviour of the climate and ecosystems under various stabilisation and recovery scenarios. The mechanisms and regions of carbon uptake differed following three action points to reduce emissions, with increased ocean uptake for progressively higher CO₂, but no similar pattern in the terrestrial carbon cycle response. Extra-tropical vegetation carbon increased strongly but soil carbon experienced competing

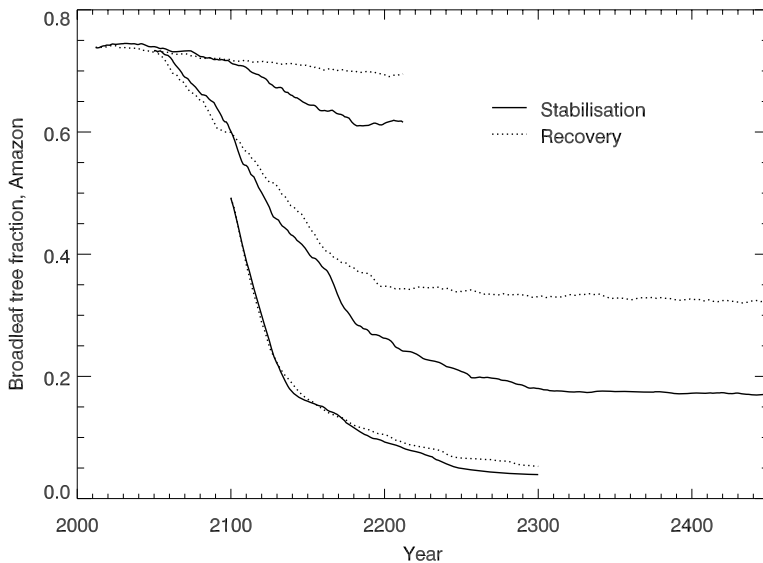


Fig. 11. Fractional tree cover (represented as fractional coverage of broadleaf trees in the region 40–70°W, 15°S–5°N) as it evolves following the action points at 2012, 2050 and 2100. Recovery simulations (dotted lines) and stabilization simulations (solid lines).

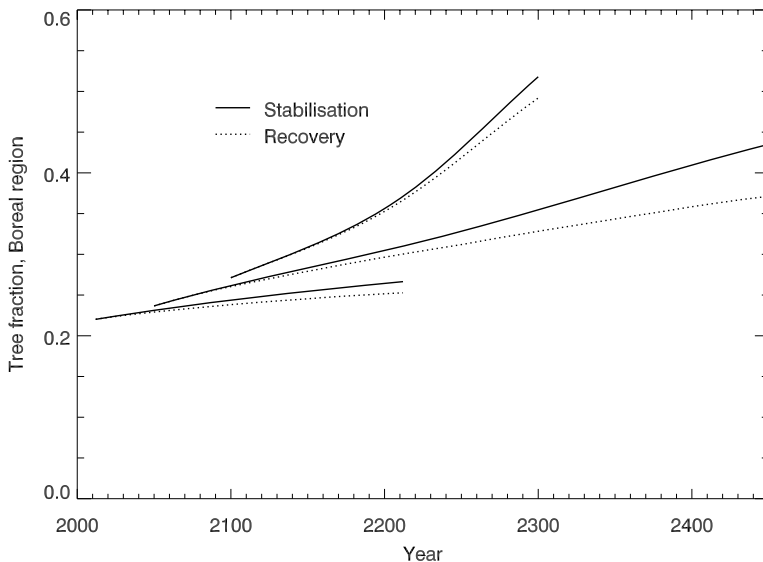


Fig. 12. Fractional tree cover (represented as fractional coverage of both broadleaf and needleleaf trees in the region 45–80°N) as it evolves following the action points at 2012, 2050 and 2100. Recovery simulations (dotted lines) and stabilization simulations (solid lines).

effects of increased input from vegetation and increased losses from decomposition. Tropical land areas experienced significant loss of carbon due to the higher levels of climate change after the 2050 and 2100 action points and this drove a net loss of terrestrial carbon.

On longer timescales changes in biome composition also become important in addition to climate impacts on vegetation productivity and soil decomposition. After the 2012 action point little future changes in vegetation cover occur, but after the 2050 action point there is large scale loss of the Amazon forest even though no loss was apparent at the time of the emissions cuts. After 2100, dieback continues rapidly. Not only does stabilization of greenhouse gas concentration not reverse or prevent dangerous climate change impacts on ecosystems, but progressively greater impacts continue to be seen for decades to centuries fol-

lowing stabilization. Our extended simulations show significant dieback of the Amazon forest and expansion of the boreal forest with global terrestrial carbon storage determined by a complex interplay of different timescales across different regions.

One result of note was the sensitivity of the degree of Amazon dieback following either stabilization or peak and decline from 2050. Peak and decline from close to 550 to 450 ppm over 400 yr resulted in significantly less Amazon dieback than CO₂ stabilized at 550 ppm, indicating that in this model at least there is a range of climate within which the Amazon forest cover is very sensitive to small changes in climate. This high degree of sensitivity is caused by strong regional feedbacks in the Amazonian forest-climate system which cause a sharp transition from wet climate with forest cover to dry climate with reduced cover. Loss of forest reduces the recirculation of precipitation to the

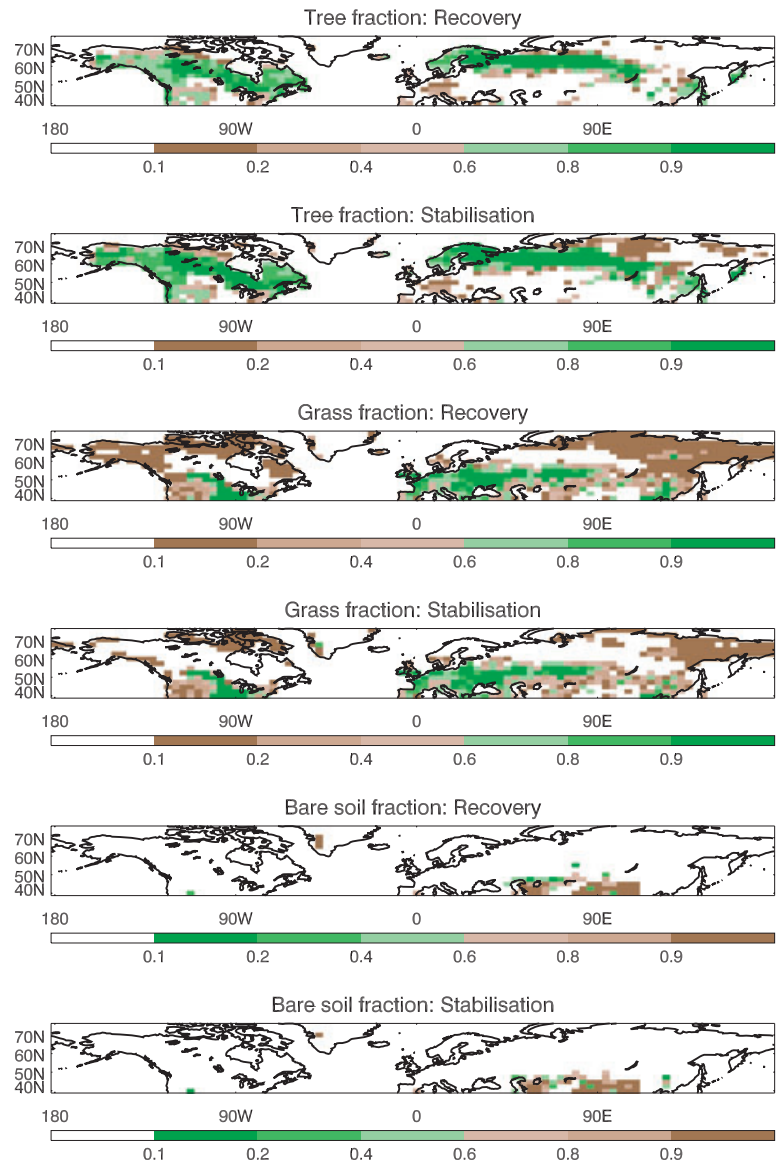


Fig. 13. Simulated fractional coverage of trees (first 2 rows), grass (centre 2 rows) and bare soil (bottom 2 rows) between 40°N and 80°N in year 2450 following 400 yr of recovery and stabilization.

atmosphere further drying the climate and leading to further forest loss (Betts et al., 2004). Lenton et al. (2008) discuss ‘tipping points’ in the climate system and define a tipping element as being able to undergo finite transitions for small changes in forcing, typically caused by local positive feedbacks. In our model, these feedbacks are not sufficiently strong to create a bistability (the forest does eventually recover to its initial state if the climate reverts to pre-industrial conditions; Jones et al. 2009), but they are strong enough to create a region of climate space where relatively small climate perturbations can lead to large changes in forest extent. Jones et al. (2009) found that under pre-industrial CO₂ concentrations but with 2100 committed loss of Amazon forest the regional climate could be as much as 0.9 K warmer and 23% drier than under pre-industrial forested conditions. In our experiments from 2050 the stabilization simulation which

showed significantly greater dieback than the recovery simulation (Fig. 11) also experienced 1.0 K warming and 39% drying after 200 yr whereas the recovery experiment cooled by 0.3 K and dried by just 10%. To what extent these local changes in climate *cause* or are *caused by* changes in vegetation is not known—the two are intricately linked. Further analysis is underway to explore these feedbacks and determine the relative importance of CO₂, temperature and dry-season length as environmental drivers of tropical forest resilience.

Quantifying the strength and implications of these biogeophysical feedbacks is therefore of crucial importance for determining the sensitivity of Amazon forest resilience to climate change—especially as this critical transition zone, or tipping point, occurs between 1° and 3° of warming of global temperature above pre-industrial.

Although our model simulates a significant northward expansion of boreal forest tree cover (in common with other modelling studies such as Scholze et al., 2006; Sitch et al., 2008) some have postulated loss of boreal forest as a possible dangerous tipping point in the climate system (Lenton et al., 2008). These results are not as contradictory as they might appear. The mechanism of possible boreal forest loss involves increased disturbance by both natural wildfire and pests or disease. Such impacts have been observed in some regions of forest already (Kurz et al., 2008a) but generally in well established regions of forest, whereas our model simulations of boreal expansion involve migration of the northern tree line into existing tundra regions (although increased fire frequency in tundra regions is also possible). Increased disturbance will compete with increased productivity to determine the boreal forest carbon balance (Kurz et al., 2008b). Some observed expansion of the tree-line has already been observed and attributed to 20th century climate change, especially in regions where the treeline is limited by growth (Harsch et al., 2009). Thus it is possible that instead of a large increase in total tree cover in boreal regions, the forest may experience simultaneous northward expansion of its northern treeline accompanied by retreat or forest thinning at the southern edges allowing a transition to more open woody ecosystems (Lenton et al., 2008). As with the loss of Amazon forest it is likely that any loss of boreal tree cover will occur at a different pace than expansion, and probably more rapidly if it happens through increased disturbance. Loss of existing species, perhaps due to increased summer heat stress may also occur more rapidly than succession by more temperate species. Hence this introduces further aspects to the transient behaviour of terrestrial carbon dynamics on the way to a longer-term steady state.

Our results are for just a single model and therefore carry quantitative uncertainty. However, there are some aspects which we expect to be robust in concept even if they vary in magnitude between models. The response of the terrestrial biosphere to increased levels of CO₂ is very likely to be increased productivity and carbon uptake. This response is robust across all land-surface models (Friedlingstein et al., 2006; Sitch et al., 2008), is seen in experimental results (Norby et al., 2005), and is thought to contribute significantly to the present day terrestrial carbon sink (Denman et al., 2007; Lewis et al., 2009; Phillips et al., 2009). The future response of soil carbon to a warming climate is also robust across models which simulate enhanced rates of decomposition and hence reduced carbon storage (Davidson and Janssens, 2006) although there is less confidence in future changes in soil moisture or the soil carbon response to them (Jones and Falloon, 2009). However, major uncertainty exists in two ways. First, in the balance between these two competing processes—especially as there is considerable uncertainty in the magnitude of the CO₂ fertilization effect (Gregory et al., 2009). Secondly, uncertainty exists in the response of vegetation productivity to changes in climate. In some models, increasing

temperature reduces tropical vegetation productivity (Matthews et al., 2005; Raddatz et al., 2007) and even tropical vegetation coverage (Cox et al., 2004; Jones et al., 2009), whilst in some models growth is enhanced across the world by higher temperatures (Miyama and Kawamiya, 2009). Changes in regional climate beyond simply temperature also play a role (Betts et al., 2004; Phillips et al., 2009), as some regions are predicted to become either drier or wetter in different climate models (Meehl et al., 2007). Hence, as has been shown before (Cramer et al., 2001; Sitch et al., 2008) there is considerable uncertainty over the magnitude of the terrestrial carbon cycle response to future changes in CO₂ and climate. The results presented here show that this fine balance of processes can change even during the course of a simulation of a single model.

As well as the uncertainty in carbon uptake and storage in response to changes in CO₂ and climate, there is also uncertainty in the transient dynamics of how and when these will be achieved. In our model changes in vegetation cover are simulated according to the relative carbon balance between PFTs and a Lotka-Volterra approach to competition between PFTs (Cox, 2001). However, it is very hard to evaluate the performance of the emergent timescales of large-scale land cover changes from the model due to lack of data. Palaeo proxy data exists to show that there were large scale changes in vegetation cover under different climate periods (e.g. Crucifix et al., 2005; Gajewski, 2008), but these data show the eventual state, rather than the rate of transition to it. However, to the extent that the loss of forest in our model is driven by the carbon balance of the trees then the rate of loss will be driven by the carbon balance processes. If increased disturbance frequency contributes to large scale biome changes then we would expect the rate of transition to be faster still—in this respect our model (without explicit representation of fire or pest disturbance) may be seen to underestimate the rate of loss of Amazonian forest. Better understanding and evaluation of the timescales of vegetation dynamics and competition is required and is being developed in next generation dynamic vegetation models, such as the Ecosystem Demography model of Moorcroft et al. (2001).

A final major area of uncertainty is in the future projections of climate, especially of precipitation and especially at regional scales. Climate projections across GCMs show consistent warming across the Amazonian region, but changes in precipitation are more varied although there is a consistent decrease in dry season rainfall in the South and East of the region (Meehl et al., 2007). It is likely that the presence or absence of Amazon dieback in any given simulation is more sensitive to the climate projection than the vegetation model response to it. For example, Sitch et al. (2008) found widespread loss of Amazonian forest in all 5 DGVMs studied when driven by climate change patterns from the HadCM3LC GCM. But the processes causing the regional warming and drying in this climate model are uncertain, with dry season changes in precipitation, thought to be the most significant for the forest, determined

by changes in tropical Atlantic sea-surface temperatures which cause a shift in the ITCZ (Good et al., 2008). Pacific SST anomalies may also cause a reduction in wet season rainfall enough to inhibit recharge of the enhanced dry-season soil moisture deficit (Harris et al., 2008). Reduced uncertainty in ecosystem projections also requires therefore improved understanding and projections of changes in atmospheric circulation, sea-surface temperatures and regional climate change.

In order to constrain this future uncertainty it is important that long term carbon storage and committed ecosystem changes are studied in multiple models. Previous studies have shown significant differences in the magnitude of response of coupled climate-carbon cycle models (Friedlingstein et al. 2006) and DGVMs (Sitch et al., 2008) to future climate. Applying a range of models to the issue of committed ecosystem changes will allow quantification of the uncertainty there. Reduction of this uncertainty though requires the use of observations to evaluate both process components of the models (e.g. through the metrics developed by Randerson et al., 2009) and top down evaluation of large-scale model behaviour (e.g. through the metrics developed by Cadule et al., 2010). Such evaluation is required to both improve existing model parametrizations such as the response of vegetation productivity or soil respiration to climate change, and also identify missing processes in models such as acclimation (Loveys et al., 2003; Atkin et al 2008) or limitations from nutrient cycles (Thornton et al., 2009; Wang and Houlton, 2009).

Our results show that the natural carbon cycle controls the recovery of atmospheric CO₂ following complete reduction of anthropogenic emissions. For three action points throughout the 21st century we simulated the evolution of climate and CO₂ and found initial rates of CO₂ recovery to be very similar but for different reasons. At progressively higher atmospheric CO₂ levels we found the ocean took up more CO₂, whereas on land greater climate change dominated the response and led to decreased carbon storage at higher temperatures. On longer timescales the lower action point at 2012 showed rapid saturation of uptake and hence CO₂ recovery was very slow after the first few decades. Following emissions cuts at 2100, recovery continued for much longer.

We then looked at the long-term implications of these scenarios on the ecosystems themselves and found long-term committed changes, which varied in sign regionally and created a complex dynamic response of terrestrial carbon storage as it slowly approached a new steady state. We found that neither stabilization nor peak and decline allowed ecosystems to recover back to their initial state and in fact ecosystems continued to respond to climate change for decades or even centuries following the action points.

Our experiments looked at both recovery of CO₂ and stabilization of CO₂ and allowed us to assess the relative impacts of higher CO₂ and climate change in the stabilization case against reducing CO₂ and the associated lesser degree of climate change, focussing on the case of the 2050 action point which corresponds

approximately to 550 ppm and 2° of global warming. The results varied regionally with extra-tropical ecosystems, and especially the boreal forest, benefitting from higher CO₂ and warmer climate and thus storing more carbon and expanding the northward extent of the treeline whilst in the tropics the detrimental impact of even this modest climate change resulted in reduced carbon storage and accelerated loss of Amazon forest in the stabilization case relative to the recovery case. Previous work (Jones and Lowe, 2010) has shown how sensitive the Amazon forest can be to even small changes in climate due to strong local biophysical feedbacks, and the result is that even modest rates of CO₂ recovery can lead to significant avoided dieback.

Overall, this work has shown the importance of climate-ecosystem feedbacks—both biophysical and biogeochemical—for evolution of both climate and the ecosystems themselves on both short and long timescales. The natural carbon cycle could be the key control of future climate recovery following any successful climate mitigation action and it is important to understand the quantitative details of the mechanisms controlling any such recovery and their associated uncertainties. Committed ecosystem changes, in addition to realized changes, must be considered when defining dangerous climate change and forming policy to avoid it.

5. Acknowledgments

This work was supported by the Joint DECC and Defra Integrated Climate Programme, DECC/Defra (GA01101).

References

- Atkin, O. K., Atkinson, L. J., Fisher, R. A., Campbell, C. D., Zaragoza-Castells, J. and co-authors. 2008. Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Glob. Change Biol.* **14**, 2709–2726. doi:10.1111/j.1365-2486.2008.01664.x.
- Betts, R. A. 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. *Nature* **408**, 187–190.
- Betts, R. A., Cox, P. M., Collins, M., Harris, P., Huntingford, C. and co-authors. 2004. The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest die-back under global climate warming. *Theor. Appl. Climatol.* **78**, 157–175.
- Cadule, P., Friedlingstein, P., Bopp, L., Sitch, S., Jones, C. D. and co-authors. 2010. Benchmarking coupled climate-carbon models against long-term atmospheric CO₂ measurements. *Global Biogeochem. Cycles* **24**, GB2016, doi:10.1029/2009GB003556.
- Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A. and co-authors. 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Glob. Change Biol.* **7**, 357–373.
- Cox, P. M. 2001. Description of the TRIFFID dynamic global vegetation model. Technical Note 24, Hadley Centre, Met Office.

- 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., Collins, M., Harris, P. P., Huntingford, C. and co-authors. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st Century. *Theor. Appl. Climatol.* **78** 137–156.
- Cox, P. M., Harris, P. P., Huntingford, C., Betts, R. A., Collins, M. and co-authors. 2008. Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature* **453**, 212–216.
- Crucifix, M., Betts, R. A. and Hewitt, C. D. 2005. Pre-industrial-potential and Last Glacial Maximum global vegetation simulated with a coupled climate-biosphere model: diagnosis of bioclimatic relationships. *Global Planet. Change* **45**, 295–312.
- Davidson, E. and Janssens, I. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173.
- Denman, K. L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P. M. and co-authors. 2007. Couplings Between Changes in the Climate System and Biogeochemistry. In: *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, USA.
- Essery, R. L. H., Best, M. J., Betts, R. A., Cox, P. M. and Taylor, C. M. 2003. Explicit representation of subgrid heterogeneity in a GCM land-surface scheme. *J. Hydrometeorol.* **43**, 530–543.
- Foley, J. A., Kutzbach, J. E., Coe, M. T. and Levis, S. 1994. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature* **371**, 52–54.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W. and co-authors. 2006. Climate-carbon cycle feedback analysis, results from the C4MIP model intercomparison. *J. Climate* **19**(14), 3337–3353, doi:10.1175/JCLI3800.1.
- Gajewski, K. 2008. The Global Pollen Database in biogeographical and palaeoclimatic studies. *Prog. Phys. Geogr.* **32**, 379–402, doi:10.1177/0309133308096029.
- Good, P., Lowe, J. A., Collins, M. and Moufouma-Okia, W. 2008. An objective tropical Atlantic sea surface temperature gradient index for studies of south Amazon dry-season climate variability and change. *Phil. Trans. R. Soc. B*, **363**, 1761–1766.
- Gordon, C., Cooper, C., Senior, C. A., Banks, H., Gregory, J. M. and co-authors. 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Clim. Dyn.* **16**, 147–168.
- Gregory J. M., Jones, C. D., Cadule, P. and Friedlingstein, P. 2009. Quantifying carbon-cycle feedbacks. *J. Climate* **22**, 5232–5250 doi:10.1175/2009JCLI2949.1.
- Hare B. and Meinshausen M. 2006. How much warming are we committed to and how much can be avoided? *Climatic Change* **75**, 111–149.
- Harris, P. P., Huntingford, C. and Cox, P. 2008. Amazon basin climate under global warming: the role of the sea surface temperature. *Phil. Trans. R. Soc. B* **363**, 1753–1759.
- Harsch, M. A., Hulme, P. E., McGlone, M. S. and Duncan, R. P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* **12**, 1040–1049, doi:10.1111/j.1461-0248.2009.01355.x.
- Harrison, R. G., Jones, C. D. and Hughes, J. K. 2008. Competing roles of rising CO₂ and climate change in the contemporary European carbon balance. *Biogeosciences* **5**, 1–10.
- House, J., Huntingford, C., Knorr, W., Cornell, S. E., Cox, P. M. and co-authors. 2008. What do recent advances in quantifying climate and carbon cycle uncertainties mean for climate policy? *Environ. Res. Lett.* **3**, 044002, doi:10.1088/1748-9326/3/4/044002.
- Jones, C. and Cox, P. 2001. Constraints on the temperature sensitivity of global soil respiration from the observed interannual variability in atmospheric CO₂. *Atmos. Sci. Lett.* **2**, 166–172, doi:10.1006/asle.2000.0041.
- Jones, C. D., Cox, P. M. and Huntingford, C. 2006. Impact of Climate-Carbon Cycle Feedbacks on Emission Scenarios to Achieve Stabilisation. In: *Avoiding Dangerous Climate Change*, Chapter 34 (eds H. J. Schellnhuber, W. Cramer, N. Nakicenovic, T. Wigley and G. Yohe). Cambridge University Press, Cambridge, UK.
- Jones, C. D. and Falloon, P. M. 2009. Sources of uncertainty in global modelling of future soil organic carbon storage. In: *Uncertainties in Environmental Modelling and Consequences for Policy Making* (eds P. Baveye, J. Mysiak and M. Laba). NATO Science for Peace and Security Series, Springer, Heidelberg, Germany, 34.
- Jones, C. D., Lowe, J. A., Liddicoat, S. K. and Betts, R. A. 2009. Committed terrestrial ecosystem changes due to climate change. *Nat. Geosci.* **2**, 484–487, doi:10.1038/NGEO555.
- Jones, C. D. and Lowe, J. A. 2010. Committed ecosystem changes. In: *Climate Change: Global Risks, Challenges and Decisions* (eds Katherine Richardson and Will Steffen). Cambridge University Press, in press.
- Kurz, W. A., Dymond, C. C., Stinson, G., Rampley, G. J., Neilson, E. T. and co-authors. 2008a. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987–990.
- Kurz, W. A., Stinson, G. and Rampley, G. 2008b. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? *Phil. Trans. R. Soc. B* **363**, 2259–2268.
- Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W. and co-authors. 2008. Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1786.
- Lewis, S. L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T. R. and co-authors. 2009. Increasing carbon storage in intact African tropical forests. *Nature* **457**, 1003–1006, doi:10.1038/nature07771.
- Loveys, B. R., Atkinson, L. J., Sherlock, D. J., Roverts, R. L., Fitter, A. H. and co-authors. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species. *Glob. Change Biol.* **9**, 895–910.
- Lowe, J. A., Huntingford, C., Raper, S. C. B., Jones, C. D., Liddicoat, S. K. and co-authors. 2009. How difficult is it to recover from dangerous levels of global warming? *Environ. Res. Lett.* **4**(014012), 9, doi:10.1088/1748-9326/4/1/014012.
- Macdonald, G. M., Kremenetski, K. V. and Beilman, D. W. 2008. Climate change and the northern Russian treeline zone. *Phil. Trans. R. Soc. B* **363**, 2283–2299.
- Matthews, H. D. 2005. Decrease of emissions required to stabilize atmospheric CO₂ due to positive carbon cycle-climate feedbacks. *Geophys. Res. Lett.* **32**, doi:10.1029/2005GL023435.

- Matthews, H. D., Eby, M., Weaver, A. J. and Hawkins, B. J. 2005. Primary productivity control of the simulated climate-carbon cycle feedback. *Geophys. Res. Lett.* **32**, doi:10.1029/2005GL022941.
- Matthews H. D. and Caldeira, K. 2008. Stabilizing climate requires near-zero emissions. *Geophys. Res. Lett.* **35**, L04705, doi:10.1029/2007GL032388.
- Meehl, G. A., Stocker, T. F., Collins, W. D., Friedlingstein, P., Gaye, A. T. and co-authors. 2007. Global climate projections Climate Change 2007: the physical science basis. In: *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis and co-authors.). Cambridge University Press, Cambridge, UK and New York, USA.
- Meehl, G. A., Washington, W. M., Collins, W. D., Arblaster, J. M., Hu, A. and co-authors. 2005. How much more global warming and sea level rise? *Science* **307**, 1769–1772.
- Miyama T. and Kawamiya, M. 2009. Estimating allowable carbon emission for CO₂ concentration stabilization using a GCM-based Earth system model. *Geophys. Res. Lett.* **36**, L19709, doi:10.1029/2009GL039678.
- Moorcroft, P. R., Hurtt, G. C. and Pacala, S. W. 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol. Monogr.* **71**, 557–586.
- Nakićenović, N., Alcamo, J., Davis, G., de Vries, B., Fenhann, J. and co-authors. 2000. *Special Report on Emissions Scenarios*. Cambridge University Press, Cambridge, UK, 599.
- Norby, R. J., DeLucia, E. H., Gielenm, B., Calfapietra, C., Giardina, C. P. and co-authors. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proc. Natl. Acad. Sci. U. S. A.* **102**, 18052–18056.
- Palmer, J. R. and Totterdell, I. J. 2001. Production and export in a global ocean ecosystem model. *Deep Sea Res.* **48**, 1169–1198.
- Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B. and Lloyd, J. 2009. Drought sensitivity of the Amazon rainforest. *Science* **323**, 1344–1347, doi:10.1126/science.1164033.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M. and co-authors. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* **451**, 49–52, doi:10.1038/nature06444.
- Plattner, G.-K. 2009. Terrestrial ecosystem inertia. *Nat. Geosci.* **2**, 467–468.
- Raddatz, T. J., Reick, C. H., Knorr, W., Kattge, J., Roeckner, E. and co-authors. 2007. Will the tropical land biosphere dominate the climate-carbon cycle feedback during the twenty first century? *Clim. Dyn.* **29**, 565–574, doi:10.1007/s00382-007-0247-8.
- Randerson, J. T., Hoffman, F. M., Thornton, P. E., Mahowald, N. M., Lindsay, K. and co-authors. 2009. Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Glob. Change Biol.* **15**, 2462–2484.
- Scholze, M., Knorr, W., Arnell, N. W. and Prentice, I. C. 2006. A climate-change risk analysis for world ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 13116–13120.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M. and co-authors. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using 5 Dynamic Global Vegetation Models (DGVMs). *Glob. Change Biol.* **14**, 2015–2039, doi: 10.1111/j.1365-2486.2008.01626.x.
- Smith, T. M. and Shugart, H. H. 1993. The transient response of terrestrial carbon storage to a perturbed climate. *Nature* **361**, 523–526.
- Thornton, P. E., Doney, S. C., Lindsay, K., Moore, J. K., Mahowald, N. and co-authors. 2009. Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences* **6**, 2099–2120.
- Wang, Y. -P. and Houlton, B. Z. 2009. Nitrogen constraints on terrestrial carbon uptake: implications for the global carbon-climate feedback. *Geophys. Res. Lett.* **36**, L24403, doi:10.1029/2009GL041009.
- Wigley, T. M. L. 1995. Global mean-temperature and sea level consequences of greenhouse gas concentration stabilisation. *Geophys. Res. Lett.* **22**, 45–48.